

Survival of Steller sea lions in Alaska: a comparison of increasing and decreasing populations

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Abstract: Steller sea lion (*Eumetopias jubatus* (Schreber, 1776)) populations have had differing dynamics in different regions of Alaska over the past 30 years. The western population (west of 144°W, near Cape Suckling) declined by approximately 85% between the 1970s and 2000, while the eastern population has increased at a rate of over 3%/year. Past research has indicated that the decline in the western population likely resulted from decreased juvenile survival and smaller declines in adult female survival and reproduction. Based on repeated observations (1987–2003) of sea lions branded as pups at Marmot Island (58.216°N, 151.840°W; western population; branded in 1987–1988) and at the Forrester Island rookery complex (54.859°N, 133.539°W; eastern population; branded in 1994–1995), we used mark–resight analyses to estimate age-specific survival probabilities. Juvenile sea lion survival probability at Marmot Island from 1988 to 1991 was lower than survival estimates at that location in the 1970s (assumed stable population) and lower than juvenile survival at Forrester Island from 1995 to 1998 (increasing population). Adult female survival at Marmot Island from 1992 to 2003 was only slightly reduced compared with that in the 1970s but was substantially lower than that at Forrester Island (1999–2003). In addition, and contrary to the typical pattern (e.g., Forrester Island), adult female survival probabilities at Marmot Island were indistinguishable from adult male survival probabilities. This suggests that regardless of which factors altered the dynamics of the western Steller sea lion population, they differentially affected females.

Résumé : Les dynamiques des populations de lions de mer de Steller (*Eumetopias jubatus* (Schreber, 1776)) ont divergé dans les diverses régions de l'Alaska au cours des 30 dernières années. La population occidentale (à l'ouest de 144°W, près du cap Suckling) a décliné d'environ 85 % entre les années 1970 et 2000, alors que la population orientale a augmenté de plus de 3 %/an. Des recherches antérieures ont indiqué que le déclin de la population occidentale est vraisemblablement dû à une diminution de la survie des jeunes et à une réduction moindre de la survie et de la reproduction des femelles adultes. D'après des observations répétées (1987–2003) de lions de mer marqués au fer dans leur jeunesse à l'île Marmot (58.216°N, 151.840°W; population occidentale; marquée en 1987–1988) et au complexe de roqueries de l'île Forrester (54.859°N, 133.539°W; population orientale; marquée en 1994–1995), nous avons pu estimer les probabilités de survie en fonction de l'âge à l'aide de techniques de marquage et de re-signalisation. La probabilité de survie des jeunes lions de mer à l'île Marmot de 1988–1991 est plus faible que les estimations de survie au même endroit dans les années 1970 (population stable présumée) et elle est inférieure à la survie des jeunes à l'île Forrester de 1995–1998 (population croissante). La survie des femelles adultes à l'île Marmot (1992–2003) est un peu plus faible que dans les années 1970, mais elle est nettement inférieure à celle des femelles adultes de l'île Forrester (1999–2003). De plus, les probabilités de survie des femelles adultes ne peuvent être distinguées de celles des mâles adultes, ce qui est différent du patron habituel (comme, par exemple, à l'île Forrester). Ces données indiquent que, quels que soient les facteurs qui aient modifié la dynamique démographique de la population occidentale des lions de mer de Steller, ils ont affecté les femelles de façon particulière.

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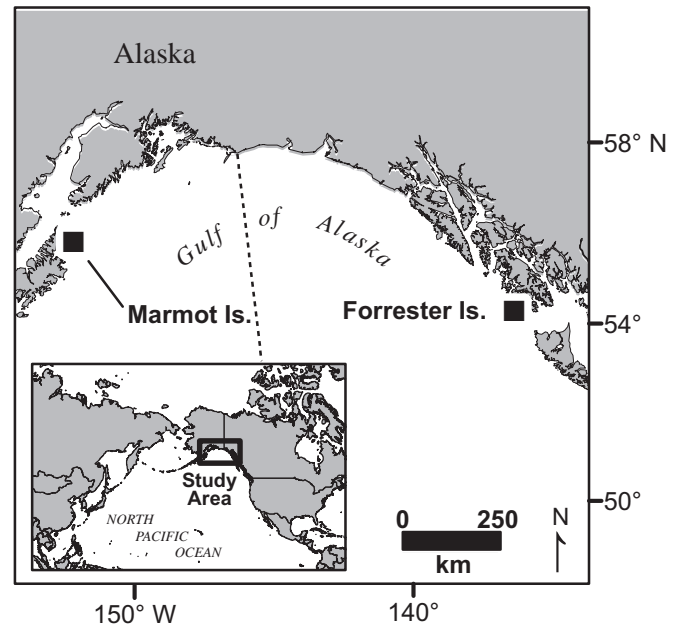
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Introduction

Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)), the largest members of the family Otariidae, inhabit the north Pacific Ocean rim from central California to northern Japan. Three populations have been identified through genetic analyses (Bickham et al. 1996; Loughlin 1997; Baker et al. 2005): the eastern, western, and Asian populations. Within Alaska, sea lions born at rookeries east of 144°W, near Cape Suckling, belong to the eastern population and those born to the west belong to the western population. Over the past 30+ years, the two populations in Alaska have exhibited notably different dynamics. The eastern population has increased at a rate of over 3%/year since the 1970s to historically high levels (Calkins et al. 1999; Sease et al. 2001). In contrast, the western population declined by approximately 85% between the early 1970s and 2000 (Sease et al. 2001), although the decline had stopped in most areas by 2004 (Fritz and Stinchcomb 2005). The decline in the western population was first detected in the eastern Aleutian Islands in the 1970s (Braham et al. 1980) and subsequently spread throughout the range of this population (Merrick et al. 1986; York et al. 1996). Food limitation is thought to have played a major role in the decline of the western population, at least in the early part of the decline (Merrick 1995; Calkins et al. 1998). Other factors that may have affected the population during the decline include predation by killer whales, incidental take in fisheries, and shooting (Loughlin and York 2000; Springer et al. 2003; Fritz and Hinckley 2005). Irrespective of the causative factor or factors, population change must occur through changes in vital rates (i.e., reproduction, survival, emigration, and immigration). Although some animals, especially juveniles, from each population visit the range of the other population (Raum-Suryan et al. 2002; Alaska Department of Fish and Game (ADFG), unpublished data), large-scale emigration and immigration are not thought to have occurred or to have been a component of the differing dynamics of the two populations (Bickham et al. 1996; Raum-Suryan et al. 2002); therefore, the trajectory of each population has been driven by birth and survival processes.

Estimates of birth rates and survival probabilities, vital parameters necessary for understanding the dynamics of populations, are completely lacking for the eastern population and are limited and dated for the western population. Based on life-table analyses using data from Calkins and Pitcher (1982) and changes in the mean age of adult females between the 1970s and the 1980s, York (1994) proposed that decreased survival, especially of juveniles, was the most likely vital rate change associated with the early decline in the western population, a view supported by further simulation analyses (Pascual and Adkison 1994; Holmes and York 2003). However, the rate of decline has not been consistent throughout the interval, and adult female survival and fecundity also have been implicated as factors during some periods and at some rookeries (Holmes and York 2003; Winship and Trites 2006). During the 1970s, >6500 Steller sea lion pups were born annually at Marmot Island in the western population, previously the largest Steller sea lion rookery; by 2002, this number had declined to ~500 pups (Merrick et al. 1986; Sease and Gudmundson 2002). In this region, the estimated birth rate for adult females was 63%

Fig. 1. Locations of Marmot Island (western population) and Forrester Island (eastern population) rookeries where Steller sea lion (*Eumetopias jubatus*) pups were branded. The dashed line is 144°W longitude, the dividing line between the eastern and western Alaska populations.



during the 1970s (Pitcher and Calkins 1981) and 53% in the mid-1980s (Calkins and Goodwin 1988), further suggesting that reduced reproduction also might have played a role in the decline of the western population.

In this paper, we use mark–resight analyses to estimate and compare age-specific survival rates for Steller sea lions from samples of branded animals from both the rapidly declining western population and the slowly increasing eastern population in Alaska. Although the two samples were not entirely contemporaneous, the estimates are associated with the periods of disparate population dynamics and should provide comparative survival probabilities and insight into the sex and age classes most affected.

Methods

Marking

At Marmot Island (MI) in the Gulf of Alaska (58.216°N, 151.840°W; western population; Fig. 1), we branded 751 sea lion pups (389 female (F), 362 male (M)) in 1987 ($n = 351$) and 1988 ($n = 400$). Pups were hot branded with a unique 2- or 3-digit number on either the left or the right shoulder (see Merrick et al. 1996 for details of the branding protocol, which was followed at both rookeries). At the Forrester Island rookery complex (FI) off of the southeastern Alaska coast (54.859°N, 133.539°W; eastern population; Fig. 1), we branded 799 (362 F, 437 M) sea lion pups in 1994 ($n = 399$) and 1995 ($n = 400$). They were hot branded with a unique 4- or 5-character brand (a leading 'F' followed by a unique 3- or 4-digit number) on the left shoulder. At both locations, all pups were weighed and measured and flipper tags were also attached to some pups; handling time for each pup was approximately 5 min except at FI in 1995, when gas anesthetic was used, requiring longer handling

times. Five pups identified as males when branded at FI were actually females, as determined from sightings as adults. We retained the original sex identification in our analyses. This results in slightly more similar survival estimates between sexes than actually occurs, but correcting these errors would bias the female survival estimates high because only those inaccurately sexed females that survived would be corrected, while those that died would not be corrected. Pups were about 3 weeks old at the time of branding and were assumed to have been born at the rookery where they were branded because pups do not begin dispersing from their natal rookery until about 2.5 months of age (Raum-Suryan et al. 2002). This research, including the methods of marking, was done under permit issued by the National Marine Fisheries Service after scientific review by the Marine Mammal Commission, Washington, D.C.

Resighting

Sighting effort was substantial but somewhat inconsistent for branded animals from both rookeries. For MI-branded sea lions, most dedicated resighting effort took place at MI during the winter (November 1987 through March 1988) following the 1987 branding and during the breeding seasons (June to July) of 1988–2003 (excluding 1989, 1990, and 1997). There also was intensive resighting effort at the Sugarloaf Island rookery (78 km north of MI) during the breeding seasons of 1994–1999 and at the Fish Island rookery (315 km northeast of MI) in 1995–1998. We conducted larger-scale resight surveys of the central Gulf of Alaska in May 2000–2003 and in August 2003. In addition, resights of sea lions branded at MI were made opportunistically by biologists and the public at many locations in Alaska and British Columbia.

For FI-branded sea lions, we conducted dedicated resighting effort at FI after branding in 1994 (July 1994 – February 1995). In subsequent years, we conducted increasingly intensive resighting effort at FI (May–July 1995, June–July 1996–1998 and 2000, June–October 2001, June–August 2002–2003), and we visited most rookeries and haul-outs in southeastern Alaska ($n = 21$) during June–July 1999 and in southeastern Alaska and northern British Columbia ($n = 42$) during June–July 2000–2003. Non-summer (mid-August through mid-May) observations were made opportunistically in conjunction with other Steller sea lion studies, but the intensity and the coverage of the range were less than for summer surveys. In addition, as for the sea lions branded at MI, resightings of sea lions branded at FI were reported by biologists and the public from many locations ranging from the Bering Sea to the state of Washington.

For resighting effort in 2000–2003 for sea lions branded at FI, we used only resights with photographs or those from multiple observers and assume that mistaken identification approached 0 for FI-branded animals during this period. Many of the earlier observations were made simultaneously by multiple observers, but photo-confirmation was not possible. Similarly, photo-confirmation was not available for resights of MI-branded sea lions prior to 2000. It is likely that earlier observations, including those from MI, those from less experienced observers, and those from the public, have somewhat higher misread probabilities, but we cannot estimate this; <2% of total observations were from the public.

We have made every effort to eliminate observations (approximately 1%) that we deemed unreliable based on observer experience and comments, when available.

In approximately 13% of the observations of sea lions branded at FI, one or more of the numbers could not, because of excessive scarring, be unequivocally determined, even under good viewing conditions. Assuming that sea lions with illegible brands have the same survival and resight probabilities as those with legible brands, about 13% of the branded animals have “unreadable” brands. If observations of these sea lions were dropped from the analyses, this would constitute tag loss, which would negatively bias estimates of survival probabilities. Based on repeated photographs of animals with unreadable brands, brands had largely stabilized by the time sea lions were 1–1.5 years old (ADFG, unpublished data). Consequently, bias caused by uncorrected tag loss will almost exclusively affect estimates of first-year survival. However, because brands do not change substantially over time, using photographs allowed us to match resights of animals with unreadable brands across years, even though we do not know their original identity. To include as many sea lions as possible in the analyses to reduce tag-loss bias, we assigned an identity to sea lions with unreadable brands based on two criteria: observations were based on photographs that could be matched across years (i.e., high-quality photographs), and the age and sex of the sea lion could be determined (i.e., the first number in the brand was readable, enabling us to determine the year of branding, and the animal was old enough to determine sex, at least in later years). The majority of the observations that we used are from 2000 or later, when digital cameras were initially used in the surveys. In a few instances, we “matched” non-photographic sightings from an earlier year with one of the unreadable brands based on sighting location, the observer’s description, and (or) brand sketches. For each sea lion with an unreadable brand that met the above criteria, we assigned a number from a branded sea lion that was never resighted after being branded as a pup, was of the same branding cohort and sex, and whose number was consistent with readable numbers in the unreadable brand. Observations of 21 sea lions were included in the analysis using this protocol (14 F, 7 M); 5 sea lions (2 F, 2 M, 1 unknown) with unreadable brands that did not meet the criteria were not used. We have no information about the presence or rate of unreadable brands in the MI-branded cohorts.

Analyses

We used Cormack–Jolly–Seber type (CJS) open-population mark–recapture models to estimate apparent annual survival (ϕ) and recapture probabilities (p) (Williams et al. 2001). CJS models estimate apparent annual survival because deaths cannot be separated from permanent emigration; estimation of true survival (i.e., deaths only) requires additional information. For brevity in the remainder of the paper, we use the term “survival” for apparent survival. Because of the extensive survey effort in southeastern Alaska, survival estimates for FI animals might be very close to true survival probabilities. Survival probabilities for MI animals are more likely to be underestimated because resighting effort prior to 2000 was more localized

and animals might have emigrated out of the limited survey area. For both data sets, we treated resightings between 15 May and 15 August as “recaptures”. To use additional sightings and potentially improve precision, we also evaluated models proposed by Barker (1997) and Barker and White (2001) (B models) that use between-capture resights (i.e., 16 August – 14 May) in addition to the annual “captures”. B models contain parameters for the probabilities of survival (S), capture (p), death between capture events with the death reported (r), resighting between capture events (R and R'), and risk of capture relative to previous risk status (F and F') (notation from Barker and White 2001).

All analyses were performed with MARK 4.1 (White and Burnham 1999). We initially fit a general model (i.e., most parameters) and, based on this general model, estimated an overdispersion factor (i.e., \hat{c} ; Burnham and Anderson 2002: 67–70) using a bootstrap approach (White et al. 2001). This factor adjusts estimated variances and goodness-of-fit statistics to account for lack of fit in the most general model; comparison of models is valid only when the most general model fits the data or is adjusted for overdispersion (Burnham and Anderson 2002). Subsequently, we fit simpler models with the same general structure but fewer parameters. For example, rather than estimating separate year-specific resight probabilities (i.e., $p(\text{year})$), we fit common parameters for groups of years (i.e., $p(1,2-4,5-9)$) or common resight probability for all years (i.e., $p(\cdot)$). We considered models with some age- or year-specific parameters constrained to be equal when the constrained ages or years were adjacent and when their separate estimates from previous models were similar; first-year survival estimates were always kept separate to “absorb” any bias due to unreadable brands into a single parameter estimate. For each model, we calculated the small-sample version of Akaike’s information criterion (AIC_c), which becomes $QAIC_c$ when adjusted for overdispersion (Burnham and Anderson 2002). Models with smaller $QAIC_c$ values were judged to have a better balance between an adequate description of the data, as measured by the likelihood contribution to $QAIC_c$, and parsimony, as measured by the number of parameters in the model.

For CJS models, we estimated age-specific survival probabilities and year-specific resight probabilities based on the assumptions that for sea lions marked in adjacent years, survival was more likely affected by the age of the animal and resight probability was more likely a function of resighting effort, which was year-dependent. In addition, the general model allowed survival and resight probabilities to vary by sex (i.e., $\phi(\text{sex} \times \text{age})$, $p(\text{sex} \times \text{year})$). To reduce the effect of potential heterogeneity in resight probabilities, we fit, in addition to the standard CJS models, another series of CJS models with resight parameters as functions of individual covariates (White 2002). In this series of models, resight probability was a function of whether an individual sea lion had been seen the previous year (beginning with the 3rd year of resighting) (Pradel 1993). Overdispersion factors cannot be estimated for models with covariates, so we used the \hat{c} estimate from the most general CJS model. This should give reasonable results because the covariate models should not fit worse than the standard CJS model. For B

models, our most general model allowed S , F , and F' to vary by age and p , R , and R' to vary by year. We had only one branded sea lion reported dead, which was not enough to justify additional parameters, so r was constrained to be 0. In the general model, all parameters varied by sex (e.g., $S(\text{sex} \times \text{age})$, $R(\text{sex} \times \text{year})$). Overdispersion estimation, reduced models, etc., for B models followed the same protocols used for CJS models.

Modeling

To evaluate whether the survival probabilities we generated were consistent with the observed population trends for the two populations, we used the formulation of the Euler–Lotka equation in Eberhardt and Siniff (1977) to estimate rates of population change that can be directly compared with the observed population trends. The estimated change (λ) is based on solution of the equation

$$[1] \quad 1 = \lambda^{-a} P_0 P_1 P_2 P^{a-3} F (1 - P/\lambda)^{-1}$$

where P_0 , P_1 , P_2 , and P are survival probabilities from 0 to 1, 1 to 2, 2 to 3, and annually for adults, respectively, a is the mean age at first reproduction, and F is the mean annual birth rate (number of female pups / female). Because estimated survival rates of females (i.e., P) at FI were not constant until age 5 (versus 4 at MI), the model for FI had an additional term, P_3 , and the exponent for P was $(a - 4)$. For model input for FI we used our estimates of female survival probabilities from FI and estimated birth rates of female pups ($0.63/2 = 0.315$) from a stable population in the Gulf of Alaska during 1975–1978 (Pitcher and Calkins 1981); for MI we used the estimated combined-sex survival probabilities from MI and an estimated birth rate ($0.53/2 = 0.265$) from the declining Gulf of Alaska population during 1985–1986 (Calkins and Goodwin 1988). For FI we used 5.9 years as the mean age at first parturition, estimated from a population thought to be stable ($5.9 = 1 + 4.9$, the age at first pregnancy; Pitcher and Calkins 1981), and for MI we used 6.5 years as the mean age at first parturition; the latter population was thought to have been nutritionally stressed to the extent that growth and reproductive performance were reduced (Calkins et al. 1998; Pitcher et al. 1998). We reduced first-year survival at both sites by 0.05 to account for neonatal mortality that occurred before the branding took place at about 3 weeks of age (Kaplan 2005). For each parameter in the model, we calculated elasticity, which is the proportional change in model output (i.e., population change) for a 1 SE change in an individual parameter.

Results

Of the 751 sea lions branded at MI, 276 were observed at least once after the summer they had been branded. One hundred and nineteen were observed in 1–10 additional summers (median 1) and 225 were seen during 1–5 non-summer periods (median 1), including 68 that were seen in both summer and non-summer. Sea lions branded at MI were observed at 28 locations other than MI, with the proportion observed at non-MI sites varying from 0% to 92% in individual years after the year of branding. More individuals were seen at non-MI sites than at MI during 1988–

Table 1. Model selection results (top 5 of 17 models and most general model) for Marmot Island data set.

Model* ($\hat{c} = 1.54$)	$\Delta\text{QAIC}_c^\dagger$	QAIC_c weight [‡]	No. of parameters
$\phi(a:1,2-3,4-16), p(s+t:1,2,3-4,5-6,7,8-9,10,11,12,13,14,15,16+r)$	0.000	0.588	18
$\phi(\cdot), p(s+t:1,2,3-4,5-6,7,8-9,10,11,12,13,14,15,16+r)$	0.927	0.185	15
$\phi(s+a:1,2-3,4-16), p(s+t:1,2,3-4,5-6,7,8-9,10,11,12,13,14,15,16+r)$	1.546	0.136	19
$\phi(s), p(s+t:1,2,3-4,5-6,7,8-9,10,11,12,13,14,15,16+r)$	2.352	0.091	16
$\phi(a), p(s+t:1,2,3-4,5-6,7,8-9,10,11,12,13,14,15,16+r)$	25.609	0.000	36
$\phi(s \times a), p(s \times t + rt)$ (most general model)	40.062	0.000	60

* ϕ is apparent survival probability with descriptors s (sex) and a (age); numbers following a indicate which age parameters were separate (e.g., $a:1,2$) or combined (e.g., $a:1-2$). p is resight probability with descriptors s (sex), t (time) (i.e., years), rt (year-specific previous-year capture covariates), and r (constant previous-year capture covariates); numbers following t indicate which year parameters were separate (e.g., $t:1,2$) or constrained to be equal (e.g., $t:1-2$). + indicates additive effects and \times indicates multiplicative effects.

[†] ΔQAIC_c is the change in QAIC_c from the best model.

[‡] QAIC_c weights indicate the support for each model relative to other models considered; weights sum to 1.

Table 2. Model selection results (top 5 of 10 models and most general model) for Forrester Island data set.

Model ($\hat{c} = 1.08$)	ΔQAIC_c	QAIC_c weight	No. of parameters
$\phi(s+a:1,2,3-4,5-9), p(s+t:1,2,3-4,5,6-9+rt)$	0.000	0.996	18
$\phi(s+a), p(s+t:1,2,3-4,5,6-9+rt)$	9.601	0.004	24
$\phi(s+a:1,2,3-4,5-9), p(s+t:1,2,3-4,5,6-9+r)$	16.083	0.000	13
$\phi(s \times a), p(s+t:1,2,3-4,5,6-9+rt)$	19.176	0.000	30
$\phi(s \times a), p(s+t+rt)$	24.240	0.000	33
$\phi(s \times a), p(s \times t + rt)$ (most general model)	33.207	0.000	41

Note: Refer to Table 1 for an explanation of the symbols and abbreviations.

1992, suggesting that bias in survival rates, caused by limited survey coverage missing permanently emigrating juveniles, might be low. Of the 799 sea lions branded at FI, 355 were observed at least once after the summer they had been branded. Two hundred and seventy-four were observed in 1–8 additional summers (median 3) and 246 were seen during 1–7 non-summer periods (median 1), including 165 that were seen in both summer and non-summer. Sea lions branded at FI were seen at 46 locations other than FI, with the proportion observed at non-FI sites varying from 12.5% to 100% in individual years after the year of branding. As would be expected because of juvenile dispersal prior to maturity, more individuals were seen at non-FI sites than at FI during 1995–1998.

For both data sets, models with resight probabilities adjusted for previous resighting were superior (i.e., smaller QAIC_c) to comparable models without resight covariates. Because B models included additional data (i.e., non-summer resights), they could not be compared with CJS models using QAIC_c . However, for both data sets, the best-fitting B model had survival estimates similar to those of comparable CJS models and the precision of the B model estimates was no better than the precision of those from the CJS model (see Table 4). Because of these results, we will discuss only estimates based on CJS models with previous-resight covariates.

The best models for each data set had many fewer parameters than the most general models (Tables 1 and 2). For the MI data, the best model was much more strongly supported than other models, but other models, including one with

constant survival across all ages and both sexes and another with an age effect and an additive sex effect on survival, also received some weight (Table 1). For the FI data, the best model was supported overwhelmingly and there was little support for alternatives (Table 2).

For both areas, estimated resight probabilities were substantially higher for sea lions that had been seen the previous year than for those that had not been resighted (Table 3). After the first 2 years of the study at MI, resight probabilities fluctuated among years with no evident pattern (i.e., increase or decrease) (Table 3). For FI sea lions, resight probabilities increased over the course of the study, most likely owing to increased effort and increasing philopatry and behavioral changes for sea lions >4 years old. For MI, the best model estimated common survival probabilities for males and females; survival varied with age, increasing to a constant rate for adults (\geq age 4) (Tables 1 and 4). For FI, the best model included increasing survival rates by age (constant after age 3) and an additive sex effect (Tables 2 and 4). After the first year, survival probabilities were higher for sea lions from FI than for those from MI, resulting in estimated cumulative survival at 9 years of 0.284 for FI females, 0.123 for FI males, and 0.094 for both males and females at MI (Fig. 2).

Estimated annual rates of population change from the Euler–Lotka model were -0.087 for the MI population and $+0.024$ for the FI population. Models for both populations were most sensitive to change (i.e., greatest elasticity) in adult survival probability, even though this was the most precisely estimated parameter, and least sensitive to change

Table 3. Annual resight probabilities for Steller sea lions (*Eumetopias jubatus*) from Marmot Island (1987–2003) and Forrester Island (1994–2003) study areas.

Year	Marmot Island				Forrester Island			
	F, 1	F, 0	M, 1	M, 0	F, 1	F, 0	M, 1	M, 0
1988	0.107	0.107	0.145	0.145				
1989	0.017	0.017	0.024	0.024				
1990	0.217	0.035	0.283	0.049				
1991	0.217	0.035	0.283	0.049				
1992	0.457	0.100	0.545	0.136				
1993	0.457	0.100	0.545	0.136				
1994	0.635	0.187	0.712	0.246				
1995	0.481	0.109	0.569	0.148	0.112	0.112	0.100	0.100
1996	0.481	0.109	0.569	0.148	0.166	0.166	0.149	0.149
1997	0.481	0.109	0.569	0.148	0.422	0.146	0.392	0.131
1998	0.559	0.143	0.643	0.192	0.275	0.146	0.250	0.131
1999	0.381	0.075	0.467	0.104	0.417	0.288	0.387	0.263
2000	0.375	0.073	0.461	0.101	0.572	0.603	0.541	0.572
2001	0.782	0.321	0.836	0.402	0.738	0.603	0.713	0.572
2002	0.488	0.111	0.576	0.152	0.649	0.603	0.620	0.572
2003	0.244	0.041	0.315	0.057	0.891	0.603	0.878	0.572

Note: F, female; M, male; 1, seen previous year; 0, not seen previous year.

Table 4. Estimated age-specific annual apparent survival probabilities (SE in parentheses) for Steller sea lions from Marmot Island (MI; 1987–2003) and Forrester Island (FI; 1994–2003) study areas.

Age	Cormack–Jolly–Seber model			York, F	Barker model		
	MI, F/M	FI, F	FI, M		MI, F/M	FI, F	FI, M
1	0.725 (0.210)	0.673 (0.062)	0.536 (0.071)	0.782	0.801 (0.077)	0.737 (0.032)	0.616 (0.034)
2	0.578 (0.095)	0.791 (0.075)	0.680 (0.098)	0.782	0.607 (0.039)	0.737 (0.032)	0.616 (0.034)
3	0.578 (0.095)	0.871 (0.033)	0.791 (0.048)	0.782	0.607 (0.039)	0.828 (0.071)	0.831 (0.093)
4	0.856 (0.030)	0.871 (0.033)	0.791 (0.048)	0.930	0.607 (0.039)	0.909 (0.014)	0.845 (0.021)
5	0.856 (0.030)	0.932 (0.014)	0.884 (0.023)	0.909	0.826 (0.026)	0.909 (0.014)	0.845 (0.021)
6	0.856 (0.030)	0.932 (0.014)	0.884 (0.023)	0.895	0.826 (0.026)	0.909 (0.014)	0.845 (0.021)
7	0.856 (0.030)	0.932 (0.014)	0.884 (0.023)	0.884	0.826 (0.026)	0.909 (0.014)	0.845 (0.021)
8	0.856 (0.030)	0.932 (0.014)	0.884 (0.023)	0.875	0.826 (0.026)	0.909 (0.014)	0.845 (0.021)
9	0.856 (0.030)	0.932 (0.014)	0.884 (0.023)	0.867	0.826 (0.026)	0.909 (0.014)	0.845 (0.021)
10	0.856 (0.030)			0.859	0.826 (0.026)		
11	0.856 (0.030)			0.853	0.826 (0.026)		
12	0.856 (0.030)			0.847	0.826 (0.026)		
13	0.856 (0.030)			0.841	0.826 (0.026)		
14	0.856 (0.030)				0.826 (0.026)		
15	0.856 (0.030)				0.826 (0.026)		
16	0.856 (0.030)				0.826 (0.026)		

Note: F, female; M, male; York, estimates for the Gulf of Alaska from York (1994) for the period 1975–1978.

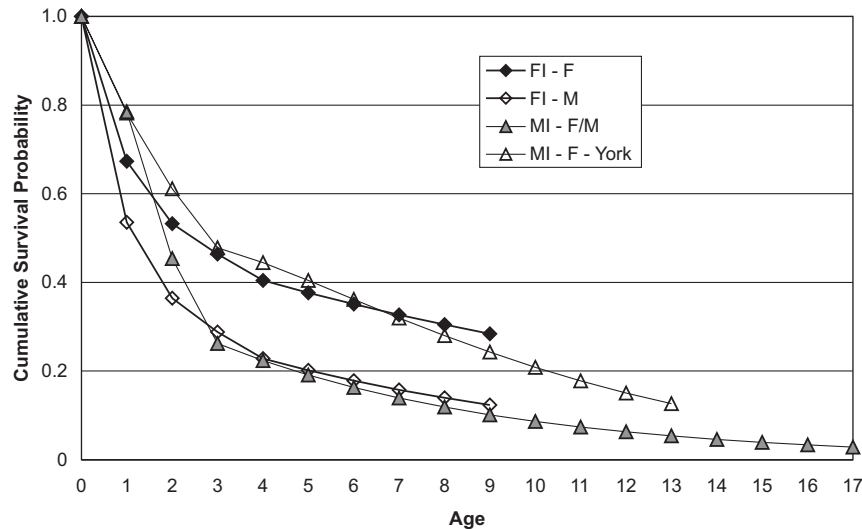
(i.e., smallest elasticity) in age at first reproduction. Reproductive rate had the second lowest elasticity for MI and was intermediate for FI, comparable to elasticities for P_0 and P_1 . Using survival estimates from the Barker model rather than the CJS model slightly reduced estimated population growth for both populations (–0.116 for MI and +0.011 for FI), but interpretations are the same.

Discussion

Based on life tables and age composition data from the 1970s and the 1980s, York (1994) suggested that the most likely cause of the decline in the sea lion population at MI was a decrease in juvenile survival. She found that the most

likely scenario for change between the 1970s (stable population) and the 1980s (declining population) was a decline in juvenile survival probability of 0.1–0.2, possibly coupled with a decline in adult (female) survival of 0.01–0.02. Holmes and York (2003), based on population count and composition data, suggested that though the western population declined continuously throughout the 1976–1998 interval, the rate of decline varied, as did the relative contributions to the population dynamics of changes in juvenile survival, adult survival, and reproduction. This pattern of changing factors affecting the population dynamics could have been caused by several “weak” cohorts that had low survival as juveniles, followed by low survival as adults, and finally reduced productivity (A. York, personal communication).

Fig. 2. Cumulative survival curves for male (M) and female (F) Steller sea lions branded at Marmot Island (MI; western population, 1987–1988) and Forrester Island (FI; eastern population, 1994–1995) and as estimated for 1975–1978 for the western population by York (1994). Observations of sea lions branded at Forrester Island were made from 1994 to 2003, and observations of sea lions branded at Marmot Island were made from 1987 to 2003.



The results of Holmes and York (2003) agree with those of York (1994) for the mid-1980s (1982–1987); they estimated that during this period juvenile survival was greatly reduced and that there were smaller reductions in adult survival and reproduction. For the interval 1988–1992, which most closely corresponds to the period for which we estimated juvenile survival probabilities at MI, Holmes and York (2003) reported juvenile survival at levels only slightly lower than those in the 1970s (stable population), with somewhat reduced reproduction and greatly reduced adult female survival. Our results are more consistent with those of York (1994), suggesting that if the driving force in the decline was a series of “weak” cohorts, the series might have continued into the late 1980s. Our estimated juvenile (age 1–3) sea lion survival probability for MI between 1988 and 1991 was 0.21 lower than York’s (1994) 1970s estimate. Our estimated adult female survival probability was 0.02 lower than her unweighted average adult female estimate for the 1970s. However, our adult survival estimate for MI is based on data from 1992 to 2003, which includes both the 1988–1992 period of reduced adult female survival and the 1993–1998 period of near-normal adult female survival (Holmes and York 2003); the composite of the estimates for these two periods might produce results similar to our slightly reduced estimate of adult female survival. For FI, our survival probability estimate for adult female sea lions was substantially higher than York’s (1994) estimates for MI in the 1970s, which is consistent with the increasing population in southeastern Alaska, although the two estimated cumulative survival curves (MI, 1970s and FI, 1994–2003) are quite similar (Fig. 2). Conversely, our survival curve for MI for 1987–2003 shows reduced cumulative survival consistent with a declining population (Fig. 2).

Somewhat surprisingly, estimated survival from time of branding (at 3 weeks old) to 1 year of age was higher at MI than at FI (Table 4), but this must be interpreted cautiously because the MI estimate is imprecise and estimates of sur-

vival to 1 year are the most likely to be affected by permanent emigration or by tag-loss bias because of unreadable brands. However, for all ages >1 year, estimated survival probabilities for FI sea lions, especially females 1–3 years old and older, were higher than corresponding estimates for MI sea lions.

Another surprising result was that the most parsimonious model for the MI data indicated no significant differences in survival probabilities for males and females. This contrasts with FI, where females had higher survival estimates than males for all ages, a pattern normally observed in large mammals. Other data from MI, including a high ratio of males to females in composition counts and similar longevity of males and females (National Marine Fisheries Service (NMFS) and ADFG, unpublished data), support the conclusion of similar survival for both sexes. These findings suggest that factors responsible for the population decline at MI disproportionately affected females, which would disproportionately affect the population; this also would seem to support the notion of food limitation. Because of their smaller body sizes and high energy demands during gestation and lactation, females have proportionately higher energy requirements and might be more greatly affected by reduced food availability. It is possible that differences (FI), or a lack of differences (MI), in apparent survival between sexes are functions of differing patterns of permanent emigration, although there are few empirical data to support this. Based on genetics data, Trujillo et al. (2004) suggested that dispersal, and hence permanent emigration, is greater for males and could be a factor in the sex difference in survival at FI but would not cause the lack of a difference at MI. A major hypothesis formulated to explain the decline proposes that young animals, pups and juveniles, had higher mortality (York 1994; Holmes and York 2003) because of difficulty in obtaining adequate prey (Merrick 1995). Most animals are not weaned until nearly 1 year of age or older (Pitcher and Calkins 1981; Trites and Porter 2002; ADFG, unpublished data) and therefore a shortage of prey might

not affect this age class as long as their mothers are able to transfer adequate energy through milk. However, pups weaned by 1 year of age might be particularly vulnerable to prey shortages because diving ability is still developing and they have limited foraging experience (Pitcher et al. 2005). The low survival estimates for 1–3-year-olds at MI relative to estimates for FI and from York (1994) are consistent with the hypothesis that juveniles might have been especially vulnerable to prey shortages. However, it appears that in addition to juvenile survival being low, adult (3–16 years of age) survival also was lower at MI than at FI and also contributed to the western-population decline. Our Euler–Lotka model results support this because estimates of population change were very sensitive to even small changes in adult female survival probability. Alternative hypotheses to explain reduced survival probabilities in the western population include increases in predation (Springer et al. 2003; Williams et al. 2004) and direct human-caused mortality (e.g., shooting, incidental catch in fisheries; Loughlin and York 2000), both of which might differentially affect unweaned juveniles.

Population trends of Steller sea lions in the MI area (central Gulf of Alaska) and the FI area (southeastern Alaska) differed substantially during the periods of the studies (MI, 1986–2003; FI, 1994–2002). The MI rookery population declined (as indexed by counts of pups) $-0.125/\text{year}$ ($P < 0.001$) between 1986 and 2003 (NMFS and ADFG, unpublished data), with a particularly severe decline between 1986 and 1993 ($-0.20/\text{year}$, $P < 0.001$), a period that included the two branded cohorts (1987 and 1988). In contrast, pup numbers at FI between 1994 and 2002 increased slightly ($+0.017/\text{year}$, $P = 0.031$) (NMFS and ADFG, unpublished data). The trend for the entire southeastern Alaska population during the same period was positive ($+0.036/\text{year}$, $P = 0.002$) (NMFS and ADFG, unpublished data), with growth in that population since about 1990 occurring at the smaller and newer rookeries (Calkins et al. 1999; NMFS and ADFG, unpublished data), in part because of emigration of females born at FI (Raum-Suryan et al. 2002). These trend estimates based on changes in pup counts are similar to our Euler–Lotka model estimates of population change of -0.087 for MI and $+0.024$ for FI. Because our survival data were for only two cohorts at each site and population change is affected by all cohorts present at a given time, we would not expect the Euler–Lotka model results to exactly match trend estimates based on pup counts.

For this study, we had samples from only one rookery in each population. However, these were the largest rookeries in each population (Sease et al. 2001; Sease and Gudmundson 2002) and likely reflect overall stock dynamics. For the western population, Winship and Trites (2006) found that most, but not all, rookeries had similar dynamics during the population decline, lending confidence that results from these two rookeries are representative of the larger populations.

Our survival estimates, when combined with estimates of reproductive performance, produce a population trajectory that closely resembles that observed in each population. However, we recognize weaknesses in the study that could affect our results. As previously mentioned, resighting effort

was sporadic early in the study. Also, rigorous protocols for both branding and resighting were not developed until recent years. Some FI brands were difficult or impossible to read. We included in the survival analyses as many animals with unreadable brands as possible by using photographs to match observations across years, which allowed us to obtain accurate capture histories for these animals in the later years of the study. But we could not use all observations of sea lions with unreadable brands (e.g., observations without photographs or where the birth year could not be determined); because of this, first-year, and hence cumulative, survival estimates could be biased low and should be regarded as minimums. We have no records of unreadable brands at MI. If such brands existed but were unrecorded, first-year survival for MI will be biased low; recall that the estimated first-year survival probability for MI is somewhat higher than the estimate for FI. In addition, some misreading of brands occurred prior to 2000, when we initiated use of photographic documentation in resighting; misread probabilities are extremely low after 2000. We made every attempt to edit misreads from the data set prior to analyses, but some undoubtedly remain; we believe that brand misread rates are similar for MI- and FI-branded animals. In a similar study, Schwarz and Stobo (1999) concluded that when the probability of a misread generating a valid brand number is high (1.0 in our study because no values were entered that were not within the range of brands deployed), the resulting bias will be positive early in the study and negative during the second half of the study. However, for long-lived species, such as Steller sea lions, they concluded that the bias was not severe. They based this on a tag misread rate of 0.10, which we suspect is not too different from that in the early years of our data. As a final cautionary note, the low juvenile (i.e., ages 1–3) survival probabilities we estimated for MI were for animals that were juveniles from 1988 to 1991. Sea lions of the same ages and in the same area in recent years might have quite different survival probabilities; ongoing studies will provide estimates to address this issue.

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