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Cohort effects and spatial variation in age-specific survival of Steller sea lions from southeastern Alaska

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Abstract. Information concerning mechanistic processes underlying changes in vital rates and ultimately population growth rate is required to monitor impacts of environmental change on wildlife. We estimated age-specific survival and examined factors influencing survival for a threatened population of Steller sea lions (*Eumetopias jubatus*) in southeastern Alaska. We used mark-recapture models and data from 1,995 individuals marked at approximately one month of age at four of five rookeries in southeastern Alaska, and resighted from Oregon to the Bering Sea. Average annual survival probability for females was 0.64 for pups and 0.77 for yearlings, and increased from 0.91 to 0.96 from age 3–7 yrs. Annual survival probability of males averaged 0.60 for pups and 0.88 by 7 yrs, resulting in probability of survival to age 7, 33% lower for males compared to females. Pups from northern southeastern Alaska (including an area of low summer population size but rapid growth) were twice as likely to survive to age 7 compared to pups from southern rookeries (including a large, historical, stable rookery). Effects of early conditions on future fitness were observed as (1) environmental conditions in the birth year equally affected first- and second-year survival, and (2) effects of body mass at approximately one month of age were still apparent at 7 yrs. Survival from 0–2 yrs varied among five cohorts by a maximum absolute difference of 0.12. We observed survival costs for long-distance dispersal for males, particularly as juveniles. However, survival was higher for non-pups that dispersed to northern southeastern Alaska, suggesting that moving to an area with greater productivity, greater safety, or lower population size may alleviate a poor start and provide a mechanism for spatial structure for sea lion populations.

Key words: age-specific survival; body mass; cohort effect; *Eumetopias jubatus*; life-history; marine mammal; natal rookery; otariid; population dynamics; sex differences; southeastern Alaska; Steller sea lion.

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INTRODUCTION

Current concerns about the loss of biological diversity and the ability of long-lived species to cope with rapid environmental change (Parmesan 2006, Schipper et al. 2008) underscore the need for predictive models to incorporate mechanistic processes describing how climate and environmental change influence the dynamics of wildlife populations (Stenseth and Mysterud 2002, Ozgul et al. 2010). Changes in environmental conditions often result in changes in demographic rates of wildlife populations that may in turn result in changes in population growth rates (Sibly et al. 2003). Monitoring demographic rates, in addition to abundance, is particularly useful to detect and understand changes in population status because (1) abundance results from multiple, possibly conflicting, demographic processes operating at different temporal and spatial scales (Croxall 2006) and (2) large or rapid shifts in vital rates may produce unstable age structure, with sudden, severe changes in abundance, particularly for species with long generation times (i.e., transient dynamics, Caswell and Neubert 2005, Koons et al. 2007).

Determining the life stages (e.g., neonate, juvenile, adult) and demographic processes contributing most to population change is critical for monitoring population status and for identifying conservation strategies needed for recovery of at-risk populations (Morris and Doak 2002). Unfortunately, large-scale and longitudinal data that allow direct estimation of age-specific probabilities of reproduction and survival are often not available for populations when population decline is detected. This is particularly true for long-lived, highly-mobile species with large geographic ranges, such as the Steller sea lion (*Eumetopias jubatus* Schreber 1776). The Steller sea lion population in Alaska declined by ~80% from ~250,000 sea lions in 1956 to 40,000 in 2004 (Trites and Larkin 1996, Demaster et al. 2006). Under the United States Endangered Species Act, the population west of longitude 144° W (Fig. 1) was listed as endangered in 1997 with the population to the east (California through southeastern Alaska) listed as threatened in 1990. A large-scale coordinated research effort that began in the 1990s has not led to a consensus about the cause of population collapse (National Research Council 2003).

Spatial and temporal variation in population trend, together with information on demographic processes and life-stages contributing to population declines, provided by modeling count and age-structure data, have critically influenced management actions and research priorities. Count data indicated the decline was widespread but shifted spatially and temporally between the late 1970s to 1990s, ranging from the central Aleutian Islands to the far eastern Gulf of Alaska (Merrick et al. 1987, Trites and Larkin 1996, York et al. 1996). Similarly, the role of different age-classes and demographic parameters in the decline likely shifted over time (York 1994, Holmes and York 2003, Pendleton et al. 2006, Winship and Trites 2006, Holmes et al. 2007). The current apparent stability of the western population in the Gulf of Alaska at a much reduced level (Eberhardt et al. 2005, Winship and Trites 2006, Holmes et al. 2007, Boyd 2010) may now depend upon maintaining high adult survival (Holmes et al. 2007) and may reflect a new carrying capacity (Trites and Donnelly 2003).

In contrast to declines in the west, the eastern population of Steller sea lions has grown at an average rate of 3.1%/yr since the 1970s, with growth in pup numbers slower at large established rookeries (<0.1–3.7%/yr) but ranging from 10–16%/yr in central and northern southeastern Alaska at the only newly established rookeries in the US range, and in northern California (Pitcher et al. 2007). Spatial heterogeneity in growth of non-pup numbers in the eastern population has also been documented; very high growth in non-pup numbers using the Glacier Bay and Icy Straits region in northern southeastern Alaska (boxed area in Fig. 2) in recent decades has ranged up to 16.6%/yr at some sites and averaged 8.2%/yr overall (Mathews et al. 2011).

Direct estimates of vital rates are available from Steller sea lions shot in the Gulf of Alaska from 1975–1978 ($n = 250$, Calkins and Pitcher 1982), and from mark-recapture studies of sea lions branded from 1987–1988 ($n = 751$) and from 1994–1995 ($n = 799$, Pendleton et al. 2006). In 2000–2001, the National Marine Fisheries Service (NMFS) and Alaska Department of Fish and Game (ADFG) initiated collaborative brand-resighting programs in the western (from the eastern Aleutian Islands to Prince William Sound; NMFS) and eastern (southeastern Alaska; ADFG) populations to concurrently estimate age-specific vital rates for recent years. Recent estimates are needed to re-examine life stages and demographic processes that may currently be limiting recovery in the west.

Beyond providing age and sex-specific esti-

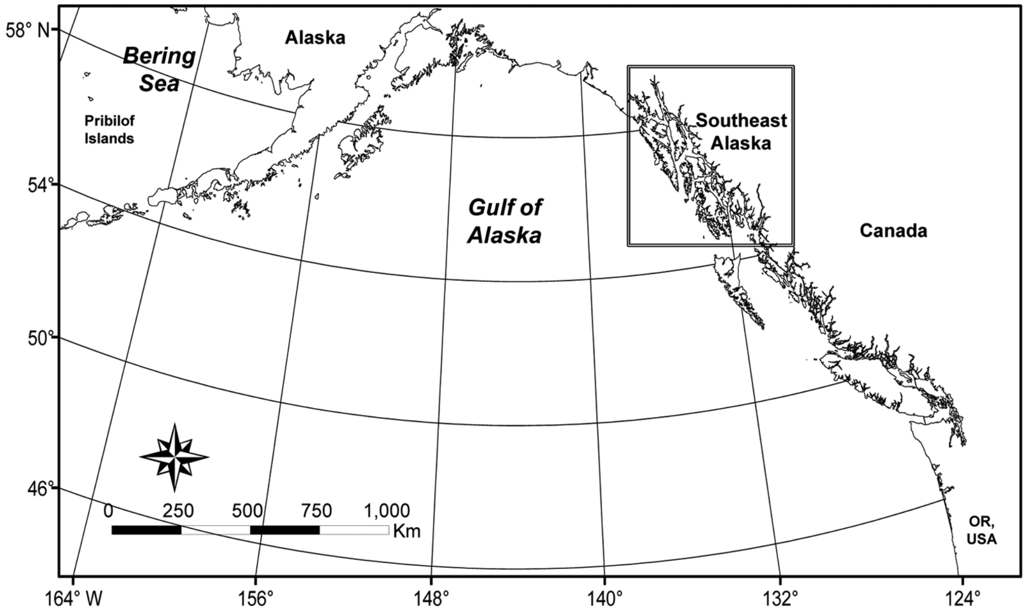

Fig. 1. Map of the area where Steller sea lions branded in southeastern Alaska were resighted from 2002 to 2009. The boxed area indicates southeastern Alaska, which together with northern British Columbia, Canada, constituted the main study area, shown in detail in Fig. 2.

mates for population models, large samples of marked sea lions over several years, coupled with high, consistent, geographically-broad resighting effort allow more detailed questions about what factors affect vital rates, such as effects of population density, phenotype, and environmental conditions. Evaluation of population viability will be improved by understanding the role of density dependence and the degree of environmental stochasticity in demographic processes for this species (Winship and Trites 2006). Here, we examine sex and age-specific survival patterns in the increasing eastern population in southeastern Alaska. We also examine spatial variation in survival among geographic areas in southeastern Alaska with differing population trends and sizes. Finally, we explored the role of temporal variation and effects of cohort and early body condition in shaping survival patterns, as possible indicators of population response to environmental variability.

METHODS

In late June–early July 2001–2005, the ADFG hot-branded 1,995 pups at four of five rookeries in southeastern Alaska (Figs. 1 and 2, Table 1). Pups were marked at Forrester Islands in four years, at Hazy Islands and White Sisters in three years, and at Graves Rock in two years (Table 1). Fewer than 50 pups were marked at Graves Rock per year due to the small size of this new rookery (~98 pups in 2002, Pitcher et al. 2007). Each individual received a unique alpha-numeric brand containing a single character for natal rookery and 1–4 numbers. Pups were captured by hand, anesthetized with isofluorane gas (Heath et al. 1996), weighed to the nearest 0.5 kg, branded, sexed, and measured (dorsal standard length and axillary girth). Pups < 20 kg (4% of pups) were released with dye marks or flipper tags only. Sea lions released with tags only were excluded from the study due to high tag loss rates and low tag resighting probabilities (ADFG, *unpublished data*). Branded pups were likely 2–4 wks of age at the time of branding, as the mean birth date was 4 June at Lowrie Island, Forrester Islands from 1992–1998 (Pitcher et al. 2001). Capture and branding procedures were reviewed and approved under U.S. Marine Mammal Permit Number 358-1564 issued to the ADFG.

Photograph-documented resightings of branded sea lions were collected during boat-based surveys covering all major rookeries and haul-

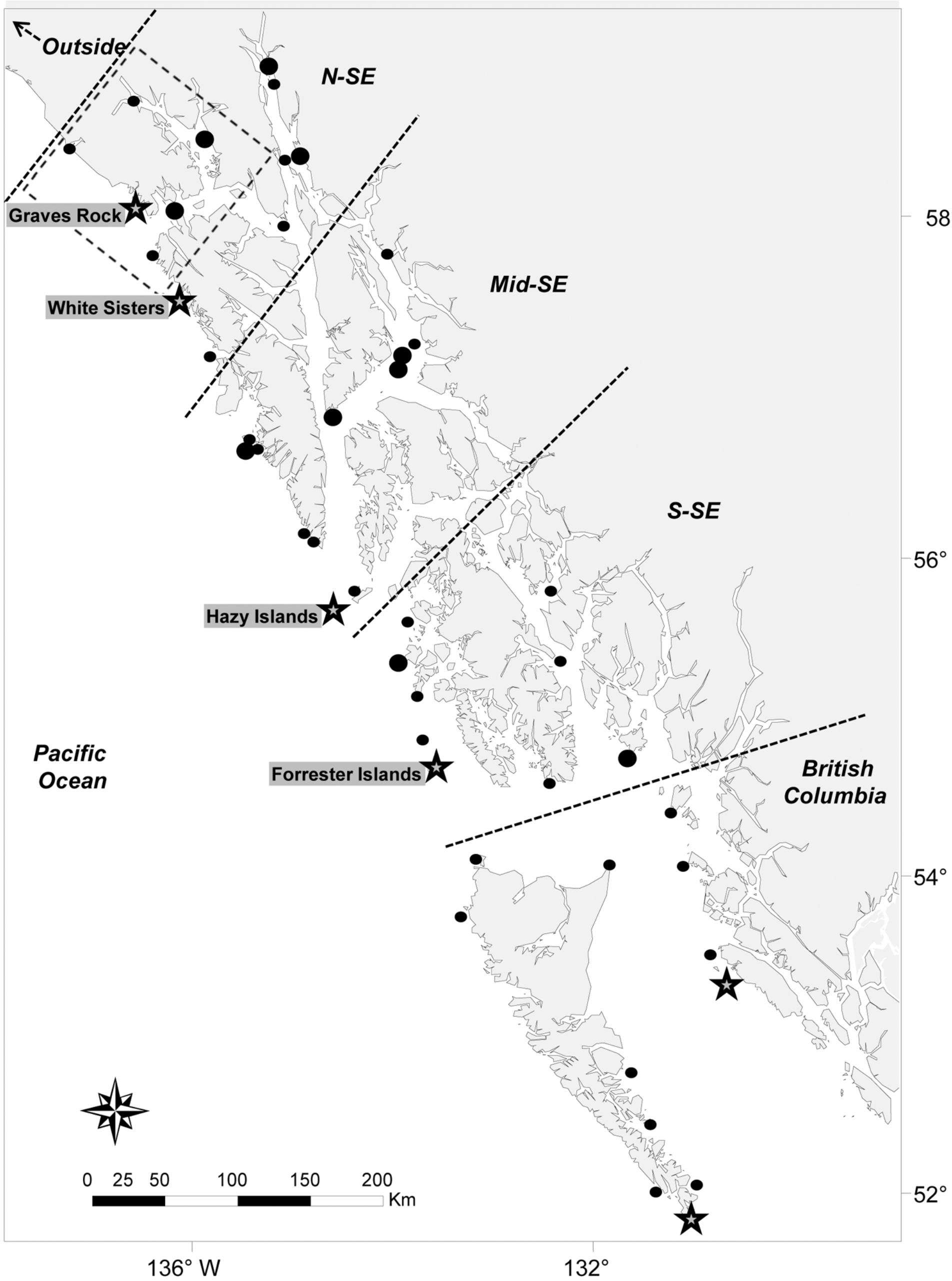

Fig. 2. Areas in southeastern Alaska (SE) and northern British Columbia (BC), Canada, where Steller sea lions were branded from 2001 to 2005 and resighted from 2002 to 2009. Rookeries are indicated by black stars. The four rookeries where pups were branded are shaded: Graves Rock, White Sisters, Hazy Islands and Forrester Islands. The North Danger and Cape St. James rookeries in BC are also shown. Haul-outs in SE and northern BC where <100 (small black circles) and ≥100 (large black circles) resightings of these animals were recorded in summer (May–August) are shown. Intensive annual summer surveys were conducted in SE and BC, and incidental resightings of these animals ranged from Oregon, USA to the Pribilof Islands in the Bering Sea. For multi-state mark-recapture models, the study area was divided into 5 geographic areas: BC, South-SE (S-SE), Mid-SE, North-SE (N-SE) and Outside (including sightings in Washington and Oregon, USA, southern BC, and all areas north and west of Cape Fairweather, Alaska). The area of high population growth in Glacier Bay/Icy Straits and west (Mathews et al. 2011) is indicated by the dashed box in region N-SE.

Table 1. Number of Steller sea lion pups marked per rookery, 2001–2005.

Year	F	H	W	G	Total
2001	286	213			499
2002	141		127	50	318
2003	291	101			392
2004	277		94		371
2005		225	147	43	415
Total	995	539	368	93	1995

Note: Rookeries were: F = Forrester Islands, H = Hazy Islands, W = White Sisters, G = Graves Rock.

outs in southeastern Alaska and northern British Columbia during May–August 2002–2009 (Fig. 2). Branded sea lions were photographed by observers from small boats 10–100 m from shore, during 2–3-week-long excursions June–July or from a field camp at Lowrie Island, 2002–2009 (May–July and occasionally through August). Critical to our study were additional photograph-documented resights from both inside and outside the study area (ranging from Oregon to the Bering Sea) contributed by other agencies and individuals. To prevent potential bias from misreading of brands and misshapen ("unreadable") brands, we used only resightings accompanied by a photograph confirmed against a master photograph library of all branded sea lions. The master photograph library allowed reclamation of unreadable brands and an assessment of problematic digits.

Explanatory variables and the Cormack-Jolly-Seber model

We examined variation in body condition index at capture ([axillary girth/dorsal standard length] × 100), body mass at capture, and pup sex-ratio among rookeries and years to assess relationships among explanatory variables. Effects of sex, year, rookery and all 2-way interactions on body condition at capture were assessed using general linear models and Akaike's Information Criterion (AIC, Akaike 1973). We created capture histories of nine annual occasions (2001–2009) for all branded individuals by treating multiple observations of an individual per summer (May–August) as a single annual observation. We excluded data from 17 individuals in which sex or body measurements were not recorded. We first assessed goodness-of-fit of the most complex model using Program RELEASE (Burnham et al. 1987) and the bootstrap and median $\hat{c}$ procedures in program MARK (Cooch and White 2010), to assess whether the model fit the data.

We used a 4-step approach and the Cormack-Jolly-Seber model (Cormack 1964, Seber 2002) to model effects of age, sex and natal rookery (group covariates), time (as year or cohort), and body mass or body condition at capture (individual covariates) on survival and resighting probabilities, based on a set of resighting and survival models chosen a priori (Burnham and Anderson 2002). We used this step-wise approach to reduce the number of models fit to focus on the most relevant explanatory variables, and to ease computation time, especially for models including effects of individual covariates.

In Step 1, we fit 49 resighting models including all possible combinations of age, year, sex, and natal rookery and all two-, three- and four-way interactions, using the most complex survival model. We first modeled the nuisance parameter, resighting probability, to provide more power for fitting survival probabilities, the parameters of interest (Lebreton et al. 1992). In Step 2 we fit 41 survival models, which included all possible combinations of covariates: natal rookery, sex, and age, using the best resighting model from Step 1. We also included two interaction terms: age × sex and age × natal rookery because we expected groups with potentially compromised survival to be particularly vulnerable as juveniles. For survival probabilities, age was modeled in six ways: (1) separate for all ages ("age"), (2) quadratic trend in survival over ages ("Age^2"), (3) grouped as two age-classes (0–1, 1+; "age2"), (4) three age-classes, (0–1, 1–2, 2+; "age3"), (5) four age-classes (0–1, 1–2, 2–3, 3+; "age4"), and (6) five age-classes (0–1, 1–2, 2–3, 3–4, 4+; "age5").

In Step 3, we fit models allowing temporal variation in survival by including either calendar year or cohort (birth year) in the top survival models from Step 2 (28 models fit). We fit effects of other factors before temporal effects (Step 2) because our main goal was to estimate age-specific survival. We suspected that any temporal effects would be harder to detect than age effects, due to our relatively short-time series of five cohorts and eight calendar years. Interactions between cohort and year were not estimable, and between cohort or year and age were complicated because pups from different natal rookeries were marked in different years.

To fit effects of time, we included models with temporal effects (1) additive across age, (2) only from 0–1 yr, (3) only from 0–1 and 1–2 yrs with effects differing between the two ages, and (4) only from 0–1 and 1–2 yrs with effects the same for the two ages. We fit models (2)–(4) because we expected that only juveniles may suffer from poor environmental conditions. We also included models with one interaction term, natal rookery × year or cohort, because we expected sea lions from the large southern rookeries may be most affected by poor environmental conditions. Cohort effects, in contrast to strictly year effects, were also fit because "poor" cohorts, with low survival and reproductive output throughout their lives, due to poor conditions in the birth year have been suggested as a potential contributor to population decline (Pendleton et al. 2006).

In Step 4 we conducted two separate modeling exercises to include either body condition index or body mass as individual covariates in the best survival model from Step 3 (23 models fit each). Individual covariates were included in the same manner as temporal effects. We also included models with these covariates interacting with sex and natal rookery, to allow survival of males and sea lions from southern rookeries to have a stronger body condition effect than females and sea lions from northern rookeries.

Multi-state model

We expected the large geographic coverage of our survey to prevent bias in estimates of survival from the Cormack-Jolly-Seber model due to emigration. However, we were concerned that potential heterogeneity in resighting probabilities in the Cormack-Jolly-Seber model due to lower resighting effort in areas outside southeastern Alaska may have produced underestimates of survival for sea lions that moved to these areas. We were also interested in spatial variation in survival patterns based on areas used by sea lions rather than only on their place of birth. To address these concerns, we fit multistate models (Nichols et al. 1992) based on the best model from Step 3, in which the states were five geographic areas: British Columbia, South-southeastern Alaska, Mid-southeastern Alaska, North-southeastern Alaska, and "Outside" (outside southeastern Alaska and British Columbia; Figs. 1 and 2). The multi-state model provided estimates of survival and resighting probabilities for each area, and movement probabilities between areas (ψ; Nichols et al. 1992).

Before modeling, we fixed parameters based on sampling zeros in the data. We first modeled nuisance parameters (movement and resighting probabilities) and lastly survival. We included the effects of natal rookery, age and sex on ψ. Age effects in ψ were fit as (1) no age effects, (2) first-year differing from 1+ yrs (two age-classes, "yr1"), (3) juvenile yrs (0–3) differing from adult yrs (3+ yrs; two age-classes, "age2"), and (4) first-year, juvenile (1–3) and adult (3+) yrs differing (three age-classes, "age3"). We also included an additive effect of geographic area on resighting probabilities due to lower survey effort in British Columbia and Outside, and highest effort in South-southeastern Alaska, due to an annual summer field camp at Forrester Islands. We included models with the area × natal rookery × sex interaction in resighting probability because we suspected sex differences in resighting probabilities (higher probability of resighting females than males) were more pronounced for animals born at southern versus northern rookeries (ADFG, *unpublished data*).

After determining the best model for movement and resighting probabilities, we examined whether sex and natal rookery effects on survival in our best Cormack-Jolly-Seber model were due primarily to emigration by comparing point estimates from the Cormack-Jolly-Seber versus the multi-state model that accounted for area effects in movement and resighting probabilities. We then examined whether survival was higher for sea lions using North-southeastern Alaska (an area of high population growth), while controlling for natal rookery effects. We included models with this effect occurring only for females or females from southern rookeries (female dispersers from a stable population), because we suspected females, that generally have smaller body sizes and high energy demands, may benefit most from using or dispersing to, a productive environment. Finally, we fit models in which males that dispersed outside the study area had different survival compared to males seen within the study area.

We used program MARK (White and Burnham 1999) to estimate parameters, and program RMark (Laake and Rexstad 2010, R Development Core Team 2010) to build MARK input and batch run models through MARK. The best model was determined by model weight based on Akaike's Information Criterion corrected for small sample size (AICc weight; Burnham and Anderson 2002). We calculated cumulative and average survival probabilities as the product and arithmetic mean, respectively, of age- or time-specific estimates from the best Cormack-Jolly-Seber model. Variances of transformed estimates were calculated using the delta method (Seber 2002, Powell 2007, Cooch and White 2010). Transformed estimates and their variances were then converted to the logit scale and then back-transformed to produce asymmetrical, unbiased 95% confidence intervals (Cooch and White 2010).

RESULTS

Explanatory variables and the Cormack-Jolly-Seber model

Inclusion of only photograph-confirmed resightings resulted in 9,555 summer resightings of 1,046 branded sea lions at 1+ years of age. Of sea lions seen after their birth year, 8.8% had unreadable digits in their brands such that a photograph library was required for accurate identification. In terms of explanatory variables, mass-at-capture was best explained by the model sex + yr + natal rookery. For condition index the best model was natal rookery*yr (* indicates main effects + interaction). As expected, males were 5 kg heavier on average than females, but the condition index did not differ between the sexes (Fig. 3). Northern pups averaged 1.5–2.0 kg heavier than southern pups, and average mass was reduced by ~1 kg in 2004–2005 compared to 2001–2003 (Fig. 3). Condition index was highest for Graves Rock pups, and was higher in 2004–2005 compared to 2001–2002 (Fig. 3). Our sample of marked pups was composed of 55.2% males (95% CI: 53.0%, 57.3%), and all but one of 12 rookery × year groups had >50% male pups. We captured pups without regard to sex, so the preponderance of males in our sample suggests that pup sex-ratios were skewed towards males at 2–4 wks of age, or behavioral differences between sexes resulted in a greater probability of capture for male pups than for female pups.

Model selection.—Correcting for overdispersion ($\hat{c}$) was unnecessary for our models because the goodness-of-fit tests in program RELEASE for each cohort fit separately (natal rookery*sex*age for each cohort to allow inclusion of age effects) indicated adequate fit of the most complex model, not including individual covariates, to our data ($X^2_{194} = 211.75$, $P = 0.82$, $\hat{c} = 1.09$). The bootstrap and median $\hat{c}$ procedures in program MARK also indicated adequate fit with maximum $\hat{c}$ of 1.15.

A single model for resighting probability including sex*age + time had an AICc weight that was two times that of the next best model (Table 2A). A single best model for survival was natal rookery + sex*Age^2 + cohort_yr1&2, which included a cohort effect from 0–1 and 1–2 yrs only, with the effect the same for both ages, was also strongly supported (AICc weight > 3.5 times that of the next best model; Table 2B–C). The model with age as four age-classes (age4) had greater weight than the Age^2 model, before year and cohort effects were fit (Table 2B). Point estimates from the final models with age as Age^2 (averaging estimates from 3+ yrs) and age4 were nearly identical, differing by a maximum of ±0.02. In Step 4, mass effects were best modeled as additive across all ages (Table 2D) but condition index affected only survival from 0–2 yrs and equally for these two ages (Table 2E). Model selection results indicated the three effects: cohort, sex and natal rookery, should be retained in models containing the individual covariates, suggesting effects of these group covariates were not confounded with effects of body size or condition (Table 2D–E).

Parameter estimates.—Annual survival probability of females averaged 0.64 for pups and 0.77 for yearlings, and increased from age 3–7 yrs from 0.91 to 0.96 (Table 3). Average annual survival of males was lower than females averaging 0.60 for pups, to 0.88 by age 7. The increasing sex difference with age was pronounced for Forrester and Hazy males (Table 3). Survival from marking (2–4 wks) to age 7 averaged 0.39 for females and 0.26 for males, such that females were 1.5 times more likely as males to be alive at 7 yrs (Table 3). Resighting probabilities increased with age, ranging from 0.61 to 0.92 among sex- age groups, and averaged

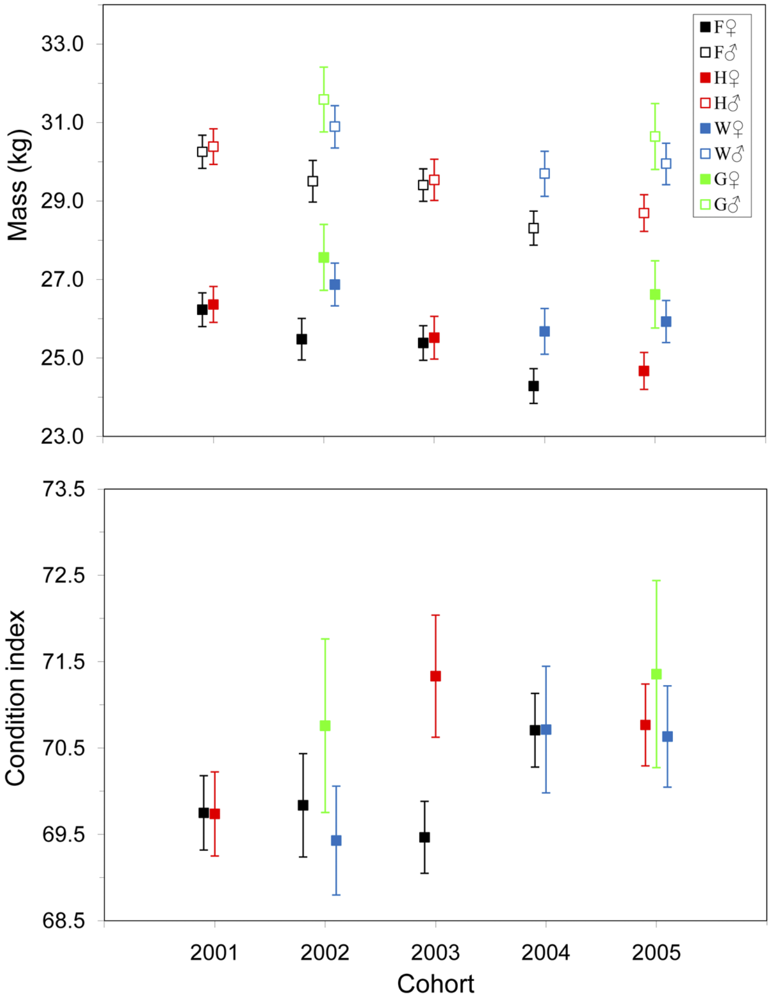

Fig. 3. Variation in body condition indices among sexes, rookeries and years for Steller sea lion pups branded in Southeast Alaska, 2001–2005. Natal rookeries were F (Forrester), H (Hazy), W (White Sisters) and G (Graves Rock). Fitted values (±95% CI) from the best regression models are plotted.

0.78 (Fig. 4). Estimates for males were lower than those for females from 2–6 yrs, but were similar to females at age 1 and 7–8 yrs (Fig. 4).

An additive natal rookery effect on survival was due to higher survival of animals born at Graves Rock than at White Sisters, or, particularly, at Forrester or Hazy Islands (Table 3). Rookery differences in survival were pronounced for juveniles. Individuals born at Graves Rock were 2.8 times as likely to survive to age 7 as Forrester- or Hazy-born sea lions (Table 3). Similarly, individuals from White Sisters were 1.8 times more likely to survive to age 7 than those born at Forrester (Table 3). Survival to age 2 was highest for the 2001 cohort and lowest for 2002 and 2005 cohorts (Fig. 5). For Forrester and Hazy sea lions, cumulative survival of juveniles from the worst (2005) and best (2001) cohorts differed by an absolute difference of 0.12. First- and second-year survival probabilities increased similarly with both mass and condition index at capture (Fig. 6). Mass continued to affect annual survival probability to 8 yrs, although this effect decreased with age until it was only subtle by 8 yrs (Fig. 6).

Multi-state model

Model selection.—While creating capture histo-

Table 2. Model selection results from the Cormack-Jolly-Seber model and program MARK used to estimate survival (S) and resighting (p) probabilities of Steller sea lions marked in southeastern Alaska.

Model	nPar	AICc	Weight
(A) Step 1: p (S = nr*age + sex*age + nr*time)—49 models			
sex*age + time	105	9242.34	0.41
sex*age + time + nr	108	9243.69	0.21
sex*age	98	9244.50	0.14
sex*time + age	105	9244.79	0.12
sex*time + age + nr	108	9245.51	0.08
(B) Step 2: S (p = sex*age + time)—41 models			
nr + sex*age4	34	9154.18	0.25
nr + sex*Age^2	31	9155.14	0.16
nr*Age^2 + sex*Age^2	34	9155.53	0.13
nr + sex + age4	31	9156.26	0.09
nr + sex*age5	36	9157.25	0.06
nr + sex + age5	32	9158.00	0.04
nr + sex*age3	32	9158.20	0.03
(C) Step 3: S (p = sex*age + time)—28 additional models			
nr + sex*Age^2 + cohort_yr1&2 (*BEST*)	36	9148.91	0.37
nr + sex*Age^2 + time_yr1&2	37	9151.52	0.10
nr + sex*age4 + cohort	38	9151.92	0.08
nr + sex*Age^2 + time	38	9152.11	0.08
nr + sex*Age^2 + time_yr1	36	9152.14	0.07
nr + sex*age4 + cohort_yr1&2	39	9152.45	0.06
nr + sex*Age^2 + cohort	35	9152.90	0.05
nr + sex*age4	34	9154.18	0.03
nr + sex*age4 + time	41	9154.38	0.02
(D) Step 4: Mass: S—23 models			
BEST + mass	37	9137.29	0.25
BEST + sex*mass	38	9137.36	0.24
BEST + sex*mass_yr1&2	38	9138.24	0.15
BEST + mass_yr1&2	37	9138.71	0.12
BEST + mass_yr1 + mass_yr2	38	9140.42	0.05
BEST + nr*mass_yr1&2 + sex*mass_yr1&2	41	9140.90	0.04
BEST + nr*mass_yr1&2	40	9141.58	0.03
(E) Step 4: Condition Index: S—23 models			
BEST + ci_yr1&2	37	9146.20	0.18
BEST + nr*ci_yr1	40	9147.16	0.11
BEST + sex*ci_yr1&2	38	9147.26	0.11
BEST + ci	37	9147.60	0.09
BEST + nr*ci_yr1&2	40	9147.62	0.09
BEST + ci_yr1 + ci_yr2	38	9148.07	0.07
BEST without cohort + nr*ci_yr1	35	9148.43	0.06
BEST + nr*ci_yr1&2 + sex*ci_yr1&2	41	9148.51	0.06
BEST	36	9148.91	0.05

Notes: Top models for survival and resighting probabilities are shown. nPar = number of parameters in model; AICc = Akaike's Information Criterion corrected for small sample size; Weight = relative strength of the model compared to other models; * = main effects + the interaction; nr = natal rookery; Age^2 = quadratic trend in survival with age; age4 = 4 age-classes: 0–1 yr, 1–2 yrs, 2–3 yrs, and annual survival 3+ yrs; age3 = 3 age-classes: 0–1 yr, 1–2 yrs, and annual survival 2+ yrs; age5 = 5 age-classes: 0–1 yr, 1–2 yrs, 2–3 yrs, 3–4 yrs, and annual survival 4+ yrs, time or cohort_yr1&2 = time or cohort effect at ages 1 and 2 yrs only, effect the same at both ages; time or cohort_yr1 = time or cohort effect at age 1 yr only; ci = condition index; individuals covariates (mass, ci): _yr1&2 = effect only fit at age 1 and 2 yrs, effect the same at both ages; _yr1 + _yr2 = effect only fit at age 1 and 2 yrs, effect different at each age; _yr1 = effect only fit at age 1 yr; *BEST* in (D)–(E) taken from best model in (C).

ries based on geographic areas for the multi-state model we noticed that within single summers, 94% of non-pups were seen in one geographic area, 6% in two areas and <1% in three areas. We randomly selected a single area from those observed in two or three areas to include in multistate capture histories. While this procedure may underestimate the variance of movement probability estimates, we believe the effect was small as this was observed for only 7% of observations and movement probabilities were nuisance parameters in our study. We used the

Table 3. Age-specific survival estimates for Steller sea lions born in southeastern Alaska, 2001–2005, with comparison to historical estimates.

Age (yrs)	Forrester Islands	Hazy Islands	White Sisters	Graves Rock	Forrester Islands 1994–1995†	Marmot Island 1987–1988†	Gulf of Alaska 1975–1978‡
Females							
0–1§	0.567	0.583	0.665	0.762	0.673	0.725	0.782
	(0.528, 0.604)	(0.540, 0.625)	(0.618, 0.709)	(0.689, 0.823)	(0.543, 0.781)	(0.167, 0.972)	
1–2§	0.718	0.731	0.795	0.862	0.791	0.578	0.782
	(0.676, 0.756)	(0.687, 0.771)	(0.753, 0.831)	(0.809, 0.902)	(0.609, 0.902)	(0.346, 0.780)	
2–3	0.878	0.887	0.927	0.955	0.871	0.578	0.782
	(0.848, 0.903)	(0.856, 0.912)	(0.903, 0.945)	(0.933, 0.971)	(0.791, 0.924)	(0.346, 0.780)	
3–4	0.915	0.922	0.950	0.970	0.871	0.856	0.930
	(0.895, 0.932)	(0.900, 0.939)	(0.934, 0.962)	(0.954, 0.980)	(0.791, 0.924)	(0.765, 0.913)	
4–5	0.934	0.939	0.962	0.977	0.932	0.856	0.909
	(0.913, 0.950)	(0.918, 0.955)	(0.947, 0.972)	(0.964, 0.985)	(0.898, 0.955)	(0.765, 0.913)	
5–6	0.942	0.947	0.967	0.980	0.932	0.856	0.895
	(0.914, 0.962)	(0.919, 0.965)	(0.947, 0.979)	(0.965, 0.988)	(0.898, 0.955)	(0.765, 0.913)	
6–7	0.943	0.947	0.967	0.980	0.932	0.856	0.884
	(0.896, 0.970)	(0.903, 0.972)	(0.937, 0.983)	(0.959, 0.990)	(0.898, 0.955)	(0.765, 0.913)	
7–8	0.936	0.941			0.932	0.856	0.875
	(0.850, 0.974)	(0.859, 0.977)			(0.898, 0.955)	(0.765, 0.913)	
0–7¶	0.277	0.292	0.410	0.569	0.327	0.130	0.320
	(0.240, 0.318)	(0.247, 0.343)	(0.352, 0.472)	(0.462, 0.671)			
Males							
0–1§	0.523	0.540	0.624	0.729	0.536	0.725	
	(0.485, 0.560)	(0.497, 0.582)	(0.578, 0.669)	(0.651, 0.794)	(0.397, 0.670)	(0.167, 0.972)	
1–2§	0.647	0.662	0.736	0.818	0.680	0.578	
	(0.601, 0.690)	(0.613, 0.707)	(0.688, 0.778)	(0.754, 0.869)	(0.469, 0.837)	(0.346, 0.780)	
2–3	0.816	0.829	0.887	0.930	0.791	0.578	
	(0.775, 0.850)	(0.787, 0.863)	(0.853, 0.913)	(0.896, 0.953)	(0.682, 0.870)	(0.346, 0.780)	
3–4	0.851	0.861	0.910	0.945	0.791	0.856	
	(0.822, 0.876)	(0.831, 0.887)	(0.885, 0.929)	(0.919, 0.963)	(0.682, 0.870)	(0.765, 0.913)	
4–5	0.866	0.875	0.919	0.951	0.884	0.856	
	(0.834, 0.892)	(0.843, 0.902)	(0.894, 0.939)	(0.926, 0.967)	(0.832, 0.922)	(0.765, 0.913)	
5–6	0.864	0.874	0.918	0.950	0.884	0.856	
	(0.814, 0.903)	(0.825, 0.911)	(0.881, 0.944)	(0.919, 0.970)	(0.832, 0.922)	(0.765, 0.913)	
6–7	0.847	0.858	0.907	0.943	0.884	0.856	
	(0.754, 0.908)	(0.768, 0.916)	(0.840, 0.947)	(0.892, 0.970)	(0.832, 0.922)	(0.765, 0.913)	
7–8	0.808	0.821			0.884	0.856	
	(0.635, 0.910)	(0.653, 0.917)			(0.832, 0.922)	(0.765, 0.913)	
0–7¶	0.156	0.168	0.274	0.439	0.158	0.130	
	(0.124, 0.193)	(0.130, 0.214)	(0.218, 0.337)	(0.326, 0.559)			

Note: Estimates were taken from the best model in Table 2C, with 95% CI in parentheses.

† Estimates from Pendleton et al. 2006.

‡ Estimates from York 1994.

§ Average among cohorts: confidence intervals of averages were calculated via the delta method using estimates from the best model (Table 2C: model 1 in the list). Cohort-specific estimates are shown in Fig. 5.

¶ Cumulative survival from 0–7 yrs: confidence intervals of cumulative estimates were calculated via the delta method using estimates from the best model without cohort effects (Table 2C, model 9 in the list). A reduced model was used to ease calculation by avoiding an unreasonable number of covariance terms due to cohort variation for the first 2 ages.

best Cormack-Jolly-Seber model without cohort effects in survival (S: natal rookery + sex*age4, p: sex*age + time; Table 2B) for multi-state modeling. A simpler model was required to prevent unreasonably long computation time when fitting these complicated, highly-parameterized models.

Due to the additive nature of the movement parameter, movement probabilities were complex, including areas of origin and destination, sex, and natal rookery. Of these six models, the most complex model was much preferred, with an AICc weight at nearly 1.0 (Table 4). The best model for resighting rates included four area effects (Outside-males only, British Columbia, South-southeastern Alaska and pooled North and mid-southeastern Alaska) with sex × area effects only in British Columbia and South-southeastern Alaska (weighted three times higher than the next model; Table 4). The best survival model included survival differing for males in Outside versus males in other areas, and a subtler effect of survival differing for both sexes in North-southeastern Alaska versus sea lions

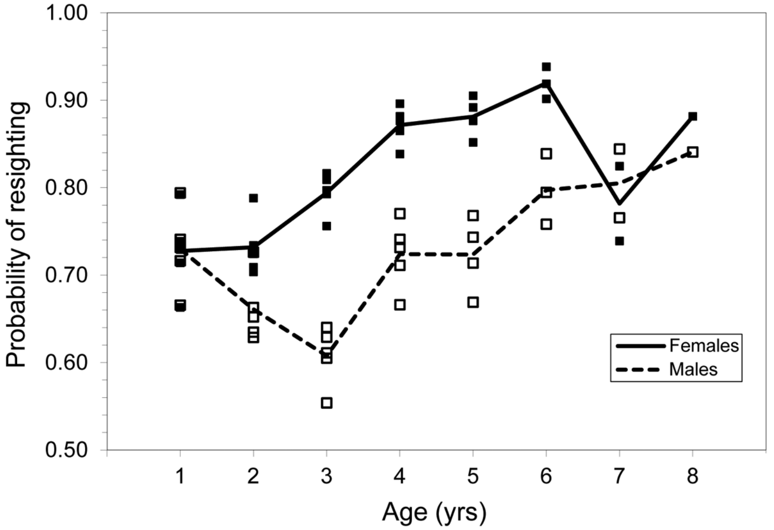

Fig. 4. Resighting probabilities of branded Steller sea lions by age, sex and year. Year-specific estimates are individual data points; lines indicate averages per age per sex. Because only the 2001–2005 cohorts were marked: 5 yrs were possibly for ages 1–4, 4 yrs for age 5, 3 yrs for age 6, 2 yrs for age 7 and 1 yr for age 8. For year specific estimates: 2003 > 2009 > 2006 > 2005 > 2007 > 2004 > 2008 > 2002, based on an additive effect of year. Estimates were taken from the best model in Table 2C: p (sex*age + time).

that used Mid-southeastern Alaska, South-southeastern Alaska or British Columbia (Table 4).

Parameter estimates.—Survival probabilities were essentially identical (differing by a maximum of ±0.012) between the Cormack-Jolly-Seber model and the best multi-state model that included area effects in resighting and movement probabilities. This suggested the natal rookery and sex effects in survival in the Cormack-Jolly-Seber model did not result from emigration of males to Outside, or of Forrester/Hazy sea lions to British Columbia, or from reduced survey effort in these areas. The wide geographic coverage seems to have been sufficient to account for emigration, even when area-specific heterogeneity in resighting probability was not accounted for.

Variation in resighting probability among geographic areas was as expected based on survey effort: resighting probability was highest in South-southeastern Alaska, lowest in Outside, next lowest in British Columbia and intermediate in Mid/North-southeastern Alaska. For females, resighting probability averaged 0.37 in British Columbia, 0.81 in Mid/North-southeastern Alaska, and 0.94 in South-southeastern Alaska. For males, differences in resighting rate among areas were not as pronounced, with averages of 0.49 in Outside, 0.57 in British Columbia, 0.74 in Mid/North-southeastern Alaska and 0.83 in South-southeastern Alaska.

A survival cost for males dispersing long distances was suggested by an absolute reduction in annual survival probability of 0.07–0.10 from 0–1 yr and 0.03–0.06 after 3 yrs for males outside the study area versus males in the study area (Table 5). Annual survival was improved for both sexes by use of the North-southeastern Alaska area by an absolute average of 0.03–0.05 for 1–2 yrs, and from 0.01–0.02 after 2 yrs (Table 5).

DISCUSSION

Spatial variation in demographic parameters

We observed positive correlations between survival probabilities, pup body size, and regional population growth rates, and negative correlations between these factors and regional summer rookery size. Compared to sea lions born at larger and more stable rookeries (2,050 non-pups at Hazy and 3,699 non-pups at Forrester in 2002; Pitcher et al. 2007), sea lions born at smaller rookeries in northern southeast-

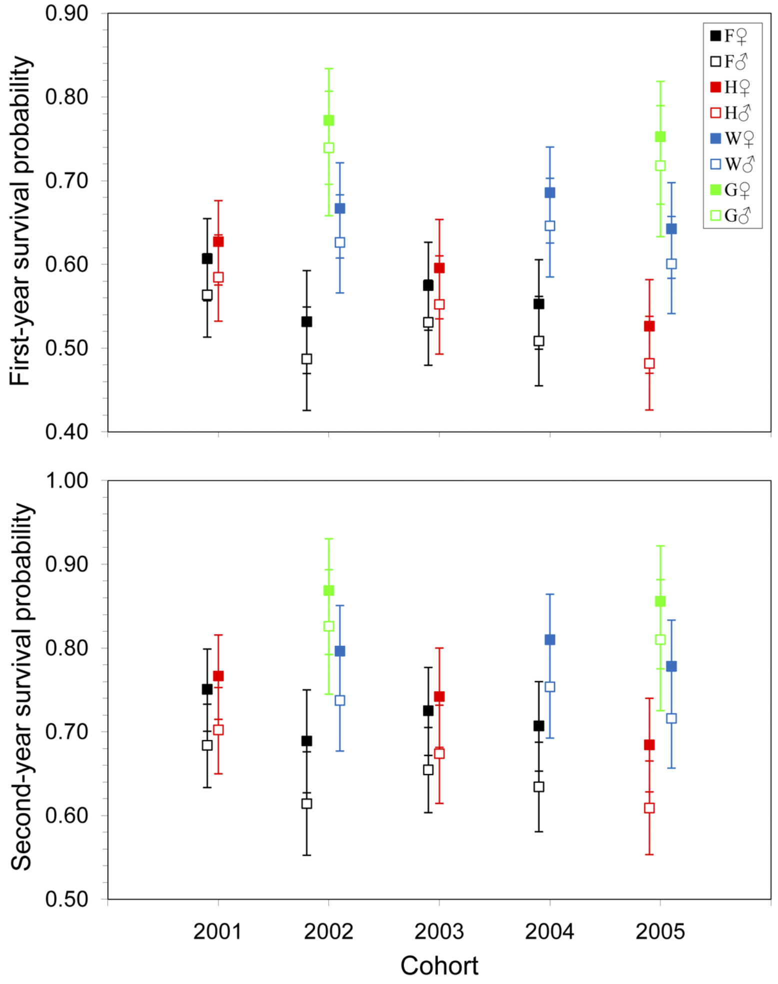

Fig. 5. Cohort variation in first- and second-year survival of Steller sea lions from Southeast Alaska, 2001–2005. Symbols are as in Fig. 3. Estimates (±95% CI) were taken from the best model in Table 2C.

ern Alaska (1,001 non-pups at Graves Rock and 1,156 non-pups at White Sisters in 2002; Pitcher et al. 2007) with high population growth (8.2%/yr; Mathews et al. 2011), had larger body size at approximately one month of age and higher survival for all ages, but particularly for juveniles. Average body mass-at-capture was ~2 kg (~7%) higher for pups born at northern rookeries and body condition was also highest for Graves Rock pups (Fig. 3). Sea lions born at northern rookeries were 2–2.75 times as likely to survive to 7 yrs of age compared to sea lions born at southern rookeries. Our survival estimates for Graves Rock-born animals are the highest observed yet for this species.

Cohorts with reduced survival also had reduced average body size at capture (Figs. 3, 5). However, body size did not explain temporal or spatial variation in survival suggesting a correlation rather than a cause, or some confounding among explanatory variables. Because birth dates of pups were unknown, pups with higher mass may have been older, and the effects of body size, age and maternal effects cannot be separated. However, the benefit of larger body size to survival beyond the first year argues against strictly age-at-capture effects, which would have only benefitted first-year survival by potentially excluding some early mortality. Possible maternal effects correlated to offspring body size include maternal age, size and/or quality (Bernardo 1996). At Forrester Islands from 2005–

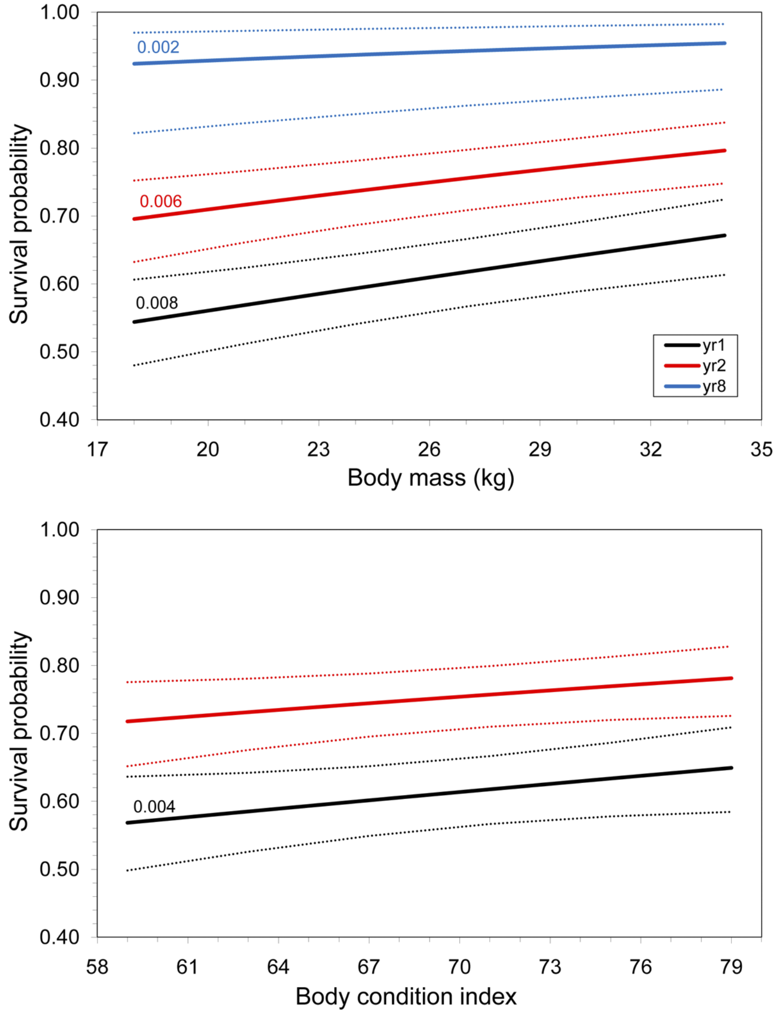

Fig. 6. Effect of body mass and condition at capture on future survival probability for Steller sea lion pups from Southeast Alaska. Lines are predicted effects (±95% CI) based on estimates of coefficients from the best models in Table 2D–E. The slopes of the lines are included. Pups were ~2–4 weeks old when captured. Data for females born at Forrester Islands in 2001 are shown.

2009, 5–7-yr-old branded females were on average first seen with their pups 3–10 days later than females 12+ yrs (ADFG, *unpublished data*). If younger females give birth later than older females, maternal effects rather than or in addition to effects of early body size may underlie survival patterns. Maternal effects may be particularly influential in this species, as offspring may be nutritionally supported by their mothers up to 3 years of age and support into the second year is not uncommon (Calkins and Pitcher 1982, Trites et al. 2006).

Correlations among demographic parameters and pup body size suggest environmental conditions may by favorable for sea lions in northern southeastern Alaska. Favorable conditions in this region were also suggested by (1) improved survival for southern-born sea lions that dispersed to this region as non-pups, (2) higher natal site fidelity for sea lions born at Graves Rock that rarely used other areas than the Cross Sound to Icy Straits region in summer (ADFG, *unpublished data*, Fig. 2), and (3) recent use of this area by western population sea lions dispersing from the central and western Gulf of Alaska and occasionally pupping and raising

Table 4. Model selection results for the multi-state model to examine effects of geographic areas on estimates of survival (S), resighting (p) and movement (Ψ) probabilities for Steller sea lions marked from 2001–2005 in southeastern Alaska.

Model	nPar	AICc	Weight
1. **S: CJS + NSE + Out(male)**; p: best; Ψ: best	181	34998.11	0.26
2. S: CJS + Out(male); p: best; Ψ: best	180	34998.50	0.21
3. S: CJS + NSE; p: best; Ψ: best	180	34998.90	0.18
4. S: CJS + NSE (female) + Out(male); p: best; Ψ: best	181	35000.22	0.09
5. S: CJS + NSE (FH female) + Out(male); p: best; Ψ: best	181	35000.55	0.08
6. S: CJS; p: best; Ψ: best	179	35000.60	0.08
7. S: CJS + NSE (FH) + Out(male); p: **CJS + Out (male) + BC*sex + SSE*sex (*BEST*);** Ψ: best	181	35000.65	0.07
8. S: CJS; p: CJS + area*sex Ψ: best	182	35002.81	0.02
9. S: CJS; p: CJS + area; Ψ: best	178	35004.87	0.01
10. S: CJS; p: CJS + area*nr; Ψ: best	189	35016.56	0.00
11. S: CJS; p: CJS + Out (male) + BC*sex; Ψ: best	177	35016.67	0.00
12. S: CJS; p: CJS + area*nr*sex; Ψ: best	200	35023.83	0.00
13. S: CJS; p: CJS; **Ψ: area*to area*sex*nr3*age3 (*BEST*)**	174	35059.13	0.00
14. S: CJS; p: CJS; Ψ: area*to area*sex*nr3*yr1	112	35086.87	0.00
15. S: CJS; p: CJS; Ψ: area*to area*sex*nr3*age2	158	35177.53	0.00
16. S: CJS; p: CJS; Ψ: area*to area*sex*nr3	96	35261.89	0.00
17. S: CJS; p: CJS; Ψ: area*to area*sex*nr	104	35262.90	0.00
18. S: CJS; p: CJS; Ψ: area*to area*male*nr2 + area*to area*female*nr3	76	35292.48	0.00

Notes: All models fit are shown. Model notation is as in Table 2. Area: 5 broad geographic regions, BC, S-SE, MidSE, N-SE (NSE), and Outside (Out; see Fig. 2). nr = 4 natal rookeries (F = Forrester Islands, H = Hazy Islands, W = White Sisters, G = Graves Rock); nr3 = 3 natal rookery groups (F, H, W+G); nr2 = 2 natal rookery groups (F+H and W+G). Age for Ψ: yr1 = first-year differing from 1+ yrs (2 age-classes), age2: juvenile yrs (0–3) differing from adult yrs (3+ yrs; 2 age-classes), and age3: first-year, juvenile (1–3) and adult (3+) yrs differing (3 age-classes). Effects fit only in males, females, N-SE, Out or Forrester or Hazy-born animals (FH) are in parentheses and italics. The best models for S, p, and Ψ are in boldface. CJS = the best CJS model without cohort effects (Table 2C, 8th model in list; S: nr + sex*age4, p: sex*age + time, with age4 = 4 age-classes: 0–1 yr, 1–2 yrs, 2–3 yrs, and annual survival 3+ yrs).

Table 5. Absolute difference in annual survival probability of non-pups (1+ yrs) using geographic areas Outside and North-SE (N-SE) versus those using British Columbia, South-SE, or Mid-SE.

	Age		
Natal rookery	1–2	2–3	3+
Females: N-SE			
F	+0.045	+0.022	+0.012
H	+0.045	+0.021	+0.012
W	+0.039	+0.017	+0.009
G	+0.028	+0.011	+0.006
Males: N-SE			
F	+0.047	+0.033	+0.022
H	+0.047	+0.033	+0.022
W	+0.041	+0.027	+0.018
G	+0.030	+0.018	+0.011
Males: Outside			
F	−0.105	−0.081	−0.058
H	−0.104	−0.080	−0.056
W	−0.096	−0.068	−0.046
G	−0.074	−0.046	−0.030

Notes: Differences in survival probabilities were calculated as the difference in survival estimates from the best model without cohort effects (Table 2C, 8th model in list) and the area-specific estimates from the best multi-state model in Table 4. See Fig. 2 for geographic areas. Natal rookeries are as in Table 1.

dependent offspring there in the summer and winter (O'Corry-Crowe et al. 2005, 2006, Gelatt et al. 2007, Pitcher et al. 2007; ADFG/NMFS, *unpublished data*). Glacier Bay in northern southeastern Alaska has undergone rapid deglaciation over the last 225 yrs resulting in new habitat which has become a productive marine ecosystem (reviewed by Mathews et al. 2011).

More study is needed to understand the extrinsic drivers that underlie the regional and temporal patterns of sea lion survival we identified, particularly the role of population density versus prey dynamics on demography. A geographic comparison would provide a strong contrast, as probability of survival to age 7 yrs varied by up to a factor of 2.75 among rookeries but only up to 1.20 among cohorts. The role of prey dynamics in population change is a central issue to large mammal population dynamics, and a focus of Steller sea lion research (National Research Council 2003). The population decline coincided with the 1976/77 oceanic regime shift in the North Pacific and with population declines in several other top predator species, suggesting a link between population dynamics and prey conditions (reviewed by Trites et al. 2007).

Research has not provided definitive answers as to the role of food versus other factors, such as direct take by humans, in the decline. However, greater diet diversity and temporal stability and spatial diversity in sea surface temperatures have been associated with areas of population growth in the west, such as the Unimak Pass area in the western Gulf of Alaska and eastern Aleutian Islands (Merrick et al. 1997, Sinclair and Zeppelin 2002, Winship and Trites 2006, Lander et al. 2009). Recent modeling suggested population response to prey dynamics (Guenette et al. 2006), including a potential positive effect of total prey availability on first-year survival and a negative effect of the fraction of the prey that is walleye pollock (*Theragra chalcogramma* Pallas 1814) on fecundity and first-year survival (Wolf and Mangel 2008).

Effects of early conditions on population dynamics of sea lions

Conditions during early life can greatly influence individual fitness and population dynamics in many species, not only through short-term responses but through long-lasting influences throughout life, such as adult body size, reproductive performance, survival, and longevity (Lindstrom 1999, Beckerman et al. 2003, Gaillard et al. 2003, Descamps et al. 2008). These delayed life-history (or delayed quality) effects can be synchronized among cohorts (Beckerman et al. 2003) creating "cohort effects" which may linearize density-dependence in vital rates. Cohort effects tend to destabilize stable population dynamics and stabilize unstable dynamics, creating an averaging effect (Lindstrom and Kokko 2002, Beckerman et al. 2003). For example in stable populations, cohort effects tend to increase population fluctuations much like environmental variation whereas in populations with variable dynamics, cohort effects reduce temporal variation (Lindstrom and Kokko 2002).

We observed multiple delayed life-history effects as (1) effect of birth rookery on annual survival up to 7–8 yrs of age, (2) effect of early body size (mass at approximately one month of age) on annual survival at 1+ yrs with effect size nearly 0 by age 8 yrs (Fig. 6), and (3) effect of conditions in the birth year influencing survival into the second year of life, with survival from 0–1 yr and 1–2 yrs affected equally by birth year conditions (Fig. 5). This implies that Steller sea lions may be less able to catch up in subsequent years to poor early conditions in life, such as being born late, smaller, or in a populous area or poorer environment. Similarly, good early conditions may produce a compounding of benefits to future fitness. However, movements to potentially more productive, safer, or less populated areas may alleviate a poor start and provide a mechanism for spatial structure for sea lion populations. These delayed life-history effects, including cohort effects, should be incorporated in future population models and may exacerbate spatial variation in population trends.

Parameter estimates and comparison to other populations

Estimates of survival for sea lions in southeastern Alaska were high for all ages, consistent with moderate population growth. Our survival estimates matched estimates of population trend from count data. We fit a simple Leslie matrix model using our survival estimates, together with the only available estimates for mean annual reproductive rate (0.630 for male and female pups, or 0.315 for female pups) and mean age of first reproduction (1 + mean age of first pregnancy = 6 yrs) available for this species (from an assumed stable population in the Gulf of Alaska from 1975–1978, Pitcher and Calkins 1981). Values for Forrester- and Hazy-born females produced a stable to slightly increasing population ($\hat{r}$ = 0.009 and 0.016, respectively), consistent with estimates from count data for Forrester Islands ($\hat{r}$ = 0–0.006, Pitcher et al. 2007). Survival estimates for Graves Rock- and White Sisters-born females produced populations growing at 8.0% and 4.9%/year, respectively, with the Graves Rock estimate similar to that for the Glacier Bay/Icy Straits/Cross Sound region based on non-pup counts (8.2%/yr; Mathews et al. 2011).

In our study, temporal variation in conditions was significant to juveniles in particular, especially given the potential for cohort effects for long-term studies. Therefore, studies of juveniles require several years of monitoring to ensure adequate sampling, and temporal variation in juvenile survival should be incorporated in stochastic population models. We expected greater temporal variation in juvenile than adult survival. This is a common pattern for long-lived birds and mammals due to the higher susceptibility of juveniles to environmental insult (Goodman 1979) associated with having smaller body sizes, higher mass-specific metabolic rates and reduced foraging efficiencies, coupled with having higher energy requirements needed for growth. Our inability to detect temporal variation in survival of Steller sea lions after age two years agrees with other research that demonstrated reduced variability of fitness components most influential to population growth rates, especially adult survival for long-lived birds and mammals (Stearns and Kawecki 1994, Eberhardt 2002, Gaillard and Yoccoz 2003).

Our current estimates from southeastern Alaska are similar to estimates from the 1970s in the Gulf of Alaska before this portion of the population declined (Calkins and Pitcher 1982, York 1994). Our estimates are also similar to those from southeastern Alaska during the 1990s (Pendleton et al. 2006). Similarly, survival of females from marking to 7 yrs at the Kozlova Cape, Kamchatka, Russia (1996–1999 cohorts) was estimated at 0.33 (Burdin et al. 2009), just slightly higher than our estimates for females born at southern rookeries in southeastern Alaska (Table 3). Survival estimates of juvenile and adult females, but not males, from the central Gulf of Alaska in the late 1980s continue to stand-out as particularly low compared to other survival estimates for female Steller sea lions (York 1994, Pendleton et al. 2006, Table 3).

Compared to mark-recapture estimates for other sea lion species, our estimates for sea lions from White Sisters were similar to estimates from an increasing population of California sea lions (*Zalophus californianus* Lesson 1828) in Mexico, although annual variation in first year survival was higher in their study compared to ours (0–1 yr = 0.56–1.0; 1–4 yrs = 0.90; 5–9 yrs = 0.90 males and 0.97 females, Hernandez-Camacho et al. 2008), perhaps due to greater environmental variation such as that caused by El-Niño (Aurioles-Gamboa and Le Boeuf 1991). Estimates from a declining population of New Zealand sea lions (*Phocarctos hookeri* Gray 1844) were much reduced for juveniles compared to our estimates for Steller sea lions (0–1 yr = <0.35, 1–2 yr = 0.50–0.70, 2–3 yr = 0.70–0.80; Chilvers and MacKenzie 2010). Annual adult male survival was also unusually high (0.98), and adult female survival varied annually (4+ yr = 0.89–0.95; Chilvers and MacKenzie 2010, Chilvers et al. 2010).

Sex effects

We expected lower survival of males than females for this polygynous, sexually-dimorphic pinniped (Pistorius et al. 1999, Pendleton et al. 2006). Sex differences in survival have been observed for California and New Zealand sea lions but only among adults and not juveniles (Hernandez-Camacho et al. 2008, Chilvers and MacKenzie 2010). The magnitude of difference between the sexes as adults (4–5+ yrs) was similar between our study (absolute difference of 0.08 per age) and the California and New Zealand sea lion studies (0.07); however the pattern was reversed among sexes in New Zealand sea lions (Hernandez-Camacho et al. 2008, Chilvers and MacKenzie 2010).

Although some males, but not females, incurred mortality risk due to long-range dispersal, this was not a large factor in the differential survival between sexes. Because few males made these movements (ADFG, *unpublished data*), male survival estimates were nearly identical in the Cormack-Jolly-Seber model which ignored long-range dispersal, and in the multi-state model which accounted for it. Instead greater energy requirements, greater sensitivity to reduced prey availability, and/or sex-specific physiological factors that increase vulnerability of males relative to females may explain differential survival between sexes. Compared to females, male Steller sea lions are larger at birth (Merrick et al. 1995, Brandon et al. 2005) and maintain this difference throughout life (Winship et al. 2001). Males are noticeably larger than females at 5–7 yrs of age due to a higher growth rate from 2–5 yrs and a pronounced growth spurt in mass at 5–7 yrs (Winship et al. 2001). Males also experience greater seasonality in growth patterns than females and acquire energy for growth mainly from November to March, unlike females who maintain more consistent weight year-round (Winship et al. 2001). This higher growth, body size, and seasonal dependency of growth for males, particularly at 4–8 yrs of age, may reduce the ability of males to meet their higher energy requirements in a fluctuating environment and increase male mortality risk.

Males are sexually mature by 4–7 yrs (Calkins and Pitcher 1982) although they may not successfully hold territories with females until 9 yrs of age or older. We observed males at 5–8 yrs frequenting the periphery of rookeries or very rarely among females for short periods (<1 day) during the breeding season. Of 23 males branded in 1994–1995 that were seen holding territories with adult females from 6–14 yrs of age, only 4% were first sighted holding territories at <9 yrs of age (compared to 83% at 9–11 yrs and 13% at >11 yrs; ADFG, *unpublished data*). Similarly, Thorsteinson and Lensink (1962) reported 87% of territorial bulls were 9–13 yrs. Therefore reduced male survival due to increased male-male aggression likely did not affect males at the ages in our study. However, testosterone levels increase with the onset of sexual maturity in male pinnipeds (Lydersen and Kovacs 2005) and reduced immunity associated with testosterone production (Mills et al. 2009) compounded with stress from high pubertal growth may increase mortality risk for males from 4–8 yrs. Other sex-specific physiological factors such as reduced immunity and ability to utilize fat during food shortages for males compared to females (Widdowson 1976, Hill et al. 1986, Chin et al. 2005) may be detrimental to males of all ages. Finally, reduced survival due to greater inquisitiveness, playfulness and incautious behavior by males may be suggested by the greater incidence of entanglement by males than females in marine debris or fishing gear (12 of 14 entangled branded sea lions were male; Raum-Suryan et al. 2009).

Of males that moved long-distances in our study, 98% went north into the western population (only 2% moved south into Oregon and Washington, USA), perhaps using the strong, northerly Alaska Coastal Current in summer. Males that travelled outside southeastern Alaska and northern British Columbia had reduced survival to 7 yrs compared to males remaining within southeastern Alaska and British Columbia, suggesting that males incur survival costs for long-distance dispersal, in contrast to enhancing survival by dispersal to northern southeastern Alaska for both sexes.

Male Steller sea lions more often make long-range movements as juveniles than as adults (Raum-Suryan et al. 2004), yet survival costs of dispersal are highest for this age-class (Table 5). Juveniles have greater mass-specific energy demands than adults due to higher growth rates and smaller body size, such that dispersing while young may be particularly risky. Body size of males is only slightly larger than females at <4 yrs (Winship et al. 2001) suggesting similar energy requirements between sexes at these ages. Due to sex-specific physiologies, juvenile males may be more susceptible to food shortages than juvenile females in many mammals, even when sexes are similar in body size (Widdowson 1976). Large movements by males may be due both to simple sex-specific behavioral tendencies, and a stronger behavioral response to unmet nutritional needs by males relative to females. Males born at the larger southern rookeries with lower survival were more likely to make long-distance movements than males born at the smaller northern rookeries with high survival (ADFG, *unpublished data*), suggesting male dispersal tendency may be linked to environmental conditions in the birth area. This may establish a behavior that carries into adulthood and improves male fitness by providing familiarity with large geographic regions that may be required to find predictable, rich prey patches in winter.

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