

ARTICLE

Coastal and Marine Ecology

Environmental drivers of demography and potential factors limiting the recovery of an endangered marine top predator

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Funding information

National Science Foundation Graduate Research Fellowship Program

Handling Editor: Hunter S. Lenihan

Abstract

Understanding what drives changes in wildlife demography is fundamental to the conservation and management of depleted or declining populations, though making inference about the intrinsic and extrinsic factors that influence survival and reproduction remains challenging. Here we use mark–resight data from 2000 to 2018 to examine the effects of environmental variability on age-specific survival and natality for the endangered western distinct population segment (wDPS) of Steller sea lions (*Eumetopias jubatus*) in Alaska, USA. Though this population has been studied extensively over the last four decades, the causes of divergent abundance trends that have been observed across the wDPS range remain unknown. We developed a Bayesian multievent mark–resight model that accounts for female reproductive state uncertainty. Annual survival probabilities for male pups (0.44; 0.36–0.53), female yearlings (0.63; 0.49–0.73), and male yearlings (0.62; 0.51–0.71) born in the western portion of the wDPS range, estimated here for the first time, were lower than those in the eastern portion of the wDPS range, estimated as: male pups (0.69; 0.65–0.74), female yearlings (0.76; 0.71–0.81), and male yearlings (0.71; 0.65–0.78). There was a higher proportion of young female breeders in the western portion of the range, but overall natality was lower (0.69; 0.47–0.96) than in the eastern portion of the range (0.80; 0.74–0.84). Additionally, pup mass had a positive effect on pup survival in the eastern portion of the range and a negative effect in the western portion of the range, potentially due to earlier weaning of heavier pups. Local- and basin-scale oceanographic features such as the Aleutian Low, the Arctic Oscillation Index, the North Pacific Gyre Oscillation, chlorophyll concentration, upwelling, and wind in certain seasons were correlated with vital rates. However, drawing strong inferences from these correlations is challenging given that relationships between ocean conditions and an adaptive top predator in a dynamic ecosystem are exceedingly complex. This study provides the first demographic rate estimates for the western portion of the range where abundance estimates continue to decline. These results will advance efforts to identify factors driving

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regionally divergent abundance trends, with implications for population-level responses to future climate variability.

KEYWORDS

conservation, demography, environmental variability, hierarchical model, mark-resight, oceanographic conditions, Steller sea lion, survival, western distinct population segment

INTRODUCTION

Understanding the complex mechanisms linking environmental conditions to population dynamics is essential to developing effective conservation and management measures, but remains an ongoing challenge in most situations due to data availability and the complexities of making inferences across varying spatiotemporal scales. This is particularly true for top predators that inhabit vast and heterogeneous landscapes, where there is often a mismatch between the ecological question and the data that are available to examine the relevant hypotheses (Conn et al., 2014). Pinnipeds exhibit a range of responses to oceanographic variability, including changes in body condition, reproductive output, maternal attendance patterns, diet, the timing of pupping or weaning, foraging effort, and levels of stranding and mortality (Joy et al., 2015; Speakman et al., 2020; Sterling et al., 2014). While it is important to study these relationships at the scale that is most relevant to the species or ecological process of interest, this is often difficult or impossible to do (Mannocci et al., 2017; Wiens, 1989). The challenge that lies at the crux of this issue is how to scale inference from a small sample of individual behaviors or physiological outcomes to the population level, particularly given that prey and predator responses to biophysical changes may not be consistent in degree or duration across space and time. Our objective with this work was to examine environmental drivers of demography and fill existing knowledge gaps about the spatiotemporal variability of survival and reproduction for the western distinct population segment (wDPS) of Steller sea lions (*Eumetopias jubatus*).

Though the population dynamics of Steller sea lions have been studied extensively, understanding the factors affecting demography is an ongoing area of research. Over the last four decades, researchers have proposed numerous competing hypotheses to explain the precipitous decline of the species during the 1970s and the divergent recovery rates that have been observed across the species' range, including but not limited to nutritional stress (Atkinson et al., 2008; Pascual & Adkison, 1994; Trites & Donnelly, 2003) and reduced age-specific survival and fecundity (Holmes et al., 2007; Loughlin & York, 2000; York, 1994). However, existing demographic studies have

been conducted at relatively small spatiotemporal scales and have not included the central and western Aleutian Islands, where abundance continues to decline (Sweeney et al., 2018). Additionally, evaluations of the effects of oceanographic conditions have thus far focused on correlations with abundance rather than demographic rates (Lander et al., 2013; Trites et al., 2007).

Existing research about the impacts of environmental variability on Steller sea lions has largely focused on examining the effects of oceanographic conditions on body condition (Calkins et al., 1998), weaning (York et al., 2008), diet (Call & Loughlin, 2005; Sinclair et al., 2013), and foraging behavior (Lander et al., 2010, 2011, 2020). Those studies revealed that Steller sea lion diet varies by region (Call & Loughlin, 2005; Sinclair et al., 2013; Sinclair & Zeppelin, 2002), that female body condition and weaning age vary across oceanographic regimes (Calkins et al., 1998; York et al., 2008), that diet diversity may be lower in areas of population decline (Lander et al., 2009; Merrick et al., 1997), and that sea lions likely use biophysical features of the landscape to locate nearshore prey aggregations (Fadely et al., 2005; Lander et al., 2010, 2011, 2020). However, these behavioral and physiological outcomes have not yet been linked to changes in demography. Based on the assumption that seasonal and interannual variability in certain biophysical features affect the distribution and availability of Steller sea lion prey, we hypothesized that oceanographic features would be correlated with natality and survival of pups and young sea lions. Specifically, basin-scale processes such as the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and the Aleutian Low (AL) can cause localized changes in sea surface temperature (SST), upwelling, wind, and chlorophyll concentrations, which can affect the level of storminess or the distribution, density, and abundance of prey. The availability of prey can in turn affect foraging effort, energetic demands, the timing of weaning, reproductive output, and survival (Antonelis et al., 1997; Hastings et al., 2021; Trites & Porter, 2002). On the one hand, sea lions are flexible foragers with numerous target prey species and can therefore likely adapt to both short- and long-term environmental variability (Loughlin et al., 2003). On the other hand, sea lions are central and multiple-central place foragers

that rely to a great extent on the predictability of the distribution and quality of prey species near natal rookeries, which can be strongly affected by both static and dynamic oceanographic features (Raum-Suryan et al., 2004; Sinclair & Zeppelin, 2002).

In this study, we use mark–resight data from 2000 to 2018 for the wDPS of Steller sea lions in Alaska to estimate the effects of individual characteristics and oceanographic conditions on age- and sex-specific survival and natality while accounting for uncertainty in reproductive state. This work will improve our ability to make inference about the factors underlying population dynamics by investigating the effects of ocean conditions and comparing age- and sex-specific survival and natality over a greater spatiotemporal scale than has been examined to date. We report the first survival and natality estimates for individuals that breed in the far western Aleutian Islands where estimated abundance has continued to decline, and provide insights into the links between environmental conditions and the demographic rates that drive the abundance of this iconic top predator. Our results can inform conservation and management efforts in light of ongoing and future climatic change.

METHODS

Study system

The wDPS of Steller sea lions in the United States breeds on rookeries west of 144° W, an area that encompasses rookery and haul-out sites in the eastern, central, and western Gulf of Alaska and the eastern, central, and western Aleutian Islands (Figure 1). Each year, adult bulls establish territories beginning in May. Females reach reproductive maturity between the age of 3 and 6 (Pitcher & Calkins, 1981) and arrive at rookeries to give birth from late May to early July depending on the region (Kuhn et al., 2017; Pitcher et al., 2001). At a given rookery, most pups are born within a relatively short time period and nurse throughout the summer. Females make short foraging trips throughout the summer breeding season before leaving the rookery for the fall and winter (Trites & Porter, 2002), during which time their activities can vary depending on environmental conditions and local bathymetric features (Burkanov et al., 2011; Lander et al., 2011). Females exhibit a high degree of natal rookery site fidelity (Raum-Suryan et al., 2002), but recent research suggests a greater degree of movement between

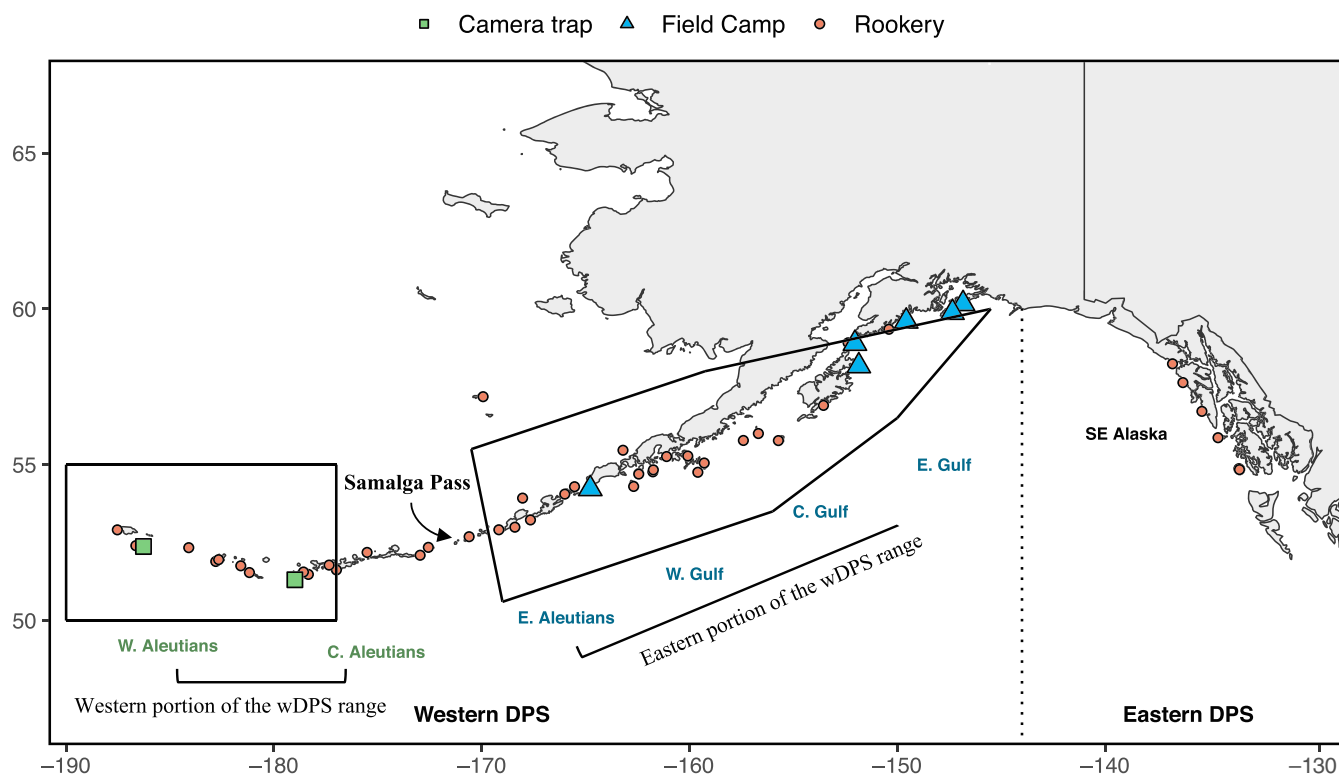


FIGURE 1 Steller sea lion branding locations in the eastern (blue triangles) and western (green squares) portions of the western distinct population segment (wDPS) range, and rookeries (red) throughout the wDPS (excluding Russia) and southeast Alaska (eastern distinct population segment (DPS) that extends along the US West Coast). Black polygons indicate locations from which satellite data were aggregated for use as covariates in the eastern (50°–58° N and 170–145° W) and western (50°–55° N and 190–176° W) portions of the wDPS range.

rookeries and regions within the Aleutian Islands and Gulf of Alaska, likely due to rookery-specific density dependence or prevailing environmental conditions (Fritz et al., 2016; Jemison et al., 2013).

The Aleutian Islands archipelago is a dynamic ecosystem that marks the boundary between the Pacific Ocean and the Bering Sea. The complex biological processes that drive primary production and foraging behavior of upper-level predators in the region are controlled largely by the dramatic bathymetry, hydrography, and biophysical characteristics of the numerous Aleutian passes, where heat exchange, nutrient mixing, and transport occur. While much remains unknown about this large region, researchers agree that the contrasting features to the east and west of Samalga Pass (~170° W) represent a notable ecological boundary (Ladd et al., 2005). To the east of Samalga Pass, narrow shallow passes are supplied by the warmer waters of the Alaska Coastal Current and are often characterized by high nutrient concentration and productivity that support coastal zooplankton species, a higher diversity of forage fish, and abundant nearshore and piscivorous seabirds. Sea lion genetics and diet composition also differ on either side of Samalga Pass, with diet in the eastern portion of the range being more diverse and dominated largely by walleye pollock (*Gadus chalcogrammus*) (O’Corry-Crowe et al., 2006; Sinclair & Zeppelin, 2002; Sinclair et al., 2005). In contrast, to the west of Samalga Pass, deep and wide passes are supplied by colder nutrient-rich waters of the Alaska Stream and are characterized by oceanic zooplankton, a lower diversity of potentially slower-growing forage fish (Hunt & Stabeno, 2005), planktivorous seabirds, and a lower diversity sea lion diet dominated by less densely aggregated Atka mackerel (*Pleurogrammus monopterygius*) (Rand et al., 2019; Sinclair et al., 2005). These generalized patterns likely oversimplify the fine-scale variability that occurs seasonally, interannually, and across island rookeries (Fadely et al., 2005; Mordy et al., 2005), particularly given the influence of mesoscale habitat features such as eddies (Lander et al., 2010, 2020; Miller et al., 2005) that influence the availability, abundance, and distribution of predators and their prey.

Sea lion data

Our study is based on mark–resight data of sea lions that were hot-branded with an individually unique mark and released as pups in June–July from rookeries in five US regions of the wDPS ($n = 2833$; 53% male). Approximately 13% of individuals were marked at Ulak and Agattu Island rookeries (hereafter, the “western portion of the wDPS range”) beginning in 2011 (Agattu Island) and 2013 (Ulak

Island), while the majority were marked in the eastern Aleutian Islands and central and eastern Gulf of Alaska (hereafter, the “eastern portion of the range”) beginning in 2000 (Table 1). Pups are weighed and measured prior to release, with pups having been heavier in the western versus eastern portions of the wDPS range during the period of data collection (Table 1). Resightings occurred May through August during dedicated field camps (eastern portion of the range only) and vessel- and land-based surveys, generating a total of approximately 39,300 and 25,150 sighting records of marked females and males, respectively (for more details, see Fritz et al., 2014). Capture histories for individuals marked in the western portion of the wDPS range were primarily based on remote camera data, as in Altukhov et al. (2015). Across the range, 41% of marked female pups and 46% of marked male pups were never resighted. Based on the differences in sample size and sampling effort in addition to the biogeographic divide at Samalga Pass and divergent abundance trends noted above, we estimated distinct vital rates for

TABLE 1 The number of marked and released pups per year in the eastern and western portions of the wDPS range and corresponding pup mass (mean with SD in parentheses) in the eastern and western portions of the wDPS range for each sex over the study period.

Year or sex	Eastern	Western
No. marked and released pups		
2000	258	...
2001	282	...
2002	194	...
2003	299	...
2004	185	...
2005	280	...
2006
2007
2008	178	...
2009	188	...
2010	178	...
2011	198	54
2012
2013	...	110
2014	191	...
2015	...	100
2016
2017	86	100
Pup mass (kg)		
Male	33.2 (5.5)	34.3 (6.2)
Female	28.2 (4.3)	29.5 (4.8)

individuals marked in the eastern versus western portions of the wDPS range.

In years when females were resighted, they were observed an average of six times. Multiple observations per season were collapsed into annual capture histories by adopting the observation with the greatest certainty in reproductive state (e.g., if a female was observed with a pup at any point in the season, that status was applied for the whole year). To simplify model structure, we assumed that false-positive identifications (pre-breeders or nonbreeders observed with pups) did not occur. In order to minimize this error, a female was only recorded as being with a pup if it was observed nursing or in very close physical contact with a single pup for a prolonged time (e.g., pup and female are sleeping together, or the pair reunites after female returns from foraging).

Oceanographic data

We examined metrics associated with both localized oceanographic conditions and basin-scale conditions as potential covariates on demographic rates, assuming these features directly (e.g., storminess) or indirectly (prey availability) affect survival and reproduction through several ecological mechanisms. Basin-scale indices included the Arctic Oscillation Index (AOI), PDO, NPGO, and the AL. The AOI characterizes Arctic climate patterns, where positive phases represent stronger winds and warmer temperatures in northern latitudes (Higgins et al., 2000). The PDO, which quantifies large-scale, interdecadal variability in SST, is associated with warm and cool phases that impact salinity, mixed layer depth, and ocean productivity (Mantua et al., 1997; Zhang & Levitus, 1997). The NPGO is associated with patterns in circulation and ocean currents, where positive phases are marked by lower SSTs and higher salinity, chlorophyll, and nutrients, and is thus often considered a driver of plankton dynamics (Di Lorenzo et al., 2008). The AL is a measure of the strength and position of the atmospheric low-pressure system that persists in the Aleutian Basin during fall through spring each year and is associated with the timing, location, and duration of regional storms (Rodionov et al., 2005; Seckel, 1993). Though years with stronger ALs have coincided with warmer winters, the mechanisms underlying this connection are not well understood (Rodionov et al., 2007). Time series of these variables were obtained at the monthly level from the National Oceanic and Atmospheric Administration (NOAA) National Center for Environmental Information (NOAA NCEI, 2020) and NOAA Physical Science Laboratory (NOAA PSL, 2020) and used in models for both the eastern and western portions of the wDPS range.

Localized environmental variables were obtained from satellite reanalysis products and included SST (in degrees Celsius), chlorophyll *a* concentration (in milligrams per cubic meter), geostrophic meridional (north–south) and zonal (east–west) wind (in meters per second), and the Bakun upwelling index (in cubic meters per second per 100 m of coastline). Data for SST and wind were obtained from the Copernicus Marine Environment Monitoring Service (Martin et al., 2019). Monthly composites of chlorophyll *a* concentration were obtained from Aqua MODIS and SeaWiFS satellite products (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, 2018) using the NOAA ERDDAP server (Simons, 2020). Monthly upwelling anomalies in the Gulf of Alaska (60° N, 149° W) were obtained from the NOAA Pacific Fisheries Environmental Laboratory.

All variables were obtained at monthly levels, aggregated to seasonal means, and converted to *Z*-scores (by subtracting the mean and dividing by the standard deviation) for the respective time series spanning the analyses for the western (2000–2018) and eastern (2011–2018) portions of the wDPS range. Sets of seasonal covariate values spanning the summer and fall of year *t* and the winter and spring of year *t* + 1 were applied to demographic rates in year *t* to coincide with the seasonal sea lion breeding cycle. Because there is a high degree of uncertainty about age-specific sea lion foraging patterns, separate broad spatial extents were selected as bounding boxes from which to obtain satellite data for individuals marked and resighted in the eastern portion of the wDPS range (50.3–58.1° N and 170.9–145° W) and those in the western portion of the wDPS range (49.8–55.4° N and 189.9–175.6° W) (Figure 1). Pairs of variables with high correlations ($r > 0.5$) were not included in the same model.

Statistical analyses

Age- or stage-specific demographic rates in wildlife populations can be estimated using multistate mark–recapture models (Brownie et al., 1993), where repeated sightings of marked individuals allow inference about the true latent state or ecological process based on a capture history that arises from an observation process with imperfect detection. However, biases can occur when the state of a marked individual is not observed with perfect certainty. Multievent models (Kendall et al., 2004; Pradel, 2005) allow for the estimation of parameters even when observations map to multiple true states and have led to improved parameter estimation compared with the strategy of dropping cases with state uncertainty (Kendall et al., 2004). Multievent models have been used extensively to assess reproductive status

and survival in species with simple life histories, but have also been increasingly used to examine vital rates and the effect of oceanographic conditions on demography for species with complex life histories (Champagnon et al., 2018; Fay et al., 2015; Fujiwara & Caswell, 2002; Himes Boor et al., 2002; Payo-Payo et al., 2016; Sanz-Aguilar et al., 2017; Tavecchia et al., 2016; Tomillo et al., 2017). Here we use a multievent model to account for reproductive state uncertainty, as a nursing female may be seen with or without her pup depending on a variety of circumstances. Below, we define the ecological and observation processes within the multievent model framework and then describe variable and model selection, model implementation in a Bayesian framework, and goodness of fit.

Ecological process model

True states were defined by an individual's age, sex, and reproductive state. Immature age classes included pups (young of year), age-1 yearlings, age-2 individuals, and

juveniles aged 3–5 that had not yet entered the breeding population (pre-breeders). Adult states included males aged 6+, reproductively mature females with pups aged 4+, and females aged 5+ that did not have a pup in a given year (non-pupping). Within the model, females that had not pupped by age 6 automatically transitioned into the non-pupping state (Figure 2). The state process model,

$$z_{i,t} | z_{i,t-1} \sim \text{Categorical}(\Omega_{z_{i,t-1}, i, t-1}),$$

describes the state z of individual i at occasion t , conditional on the individual's state at the previous occasion, modeled as categorically distributed according to transition array Ω , describing the probability of an individual being in state z conditional on its previous state and individual- and time-specific effects. This transition array is decomposed into survival ($\phi_{i,t}$) and pupping probability ($\psi_{i,t}$; the probability of a female that had a pup in year t having a pup in year $t + 1$ conditional on survival).

Interannual variability in survival and pupping probabilities was modeled as a function of environmental and

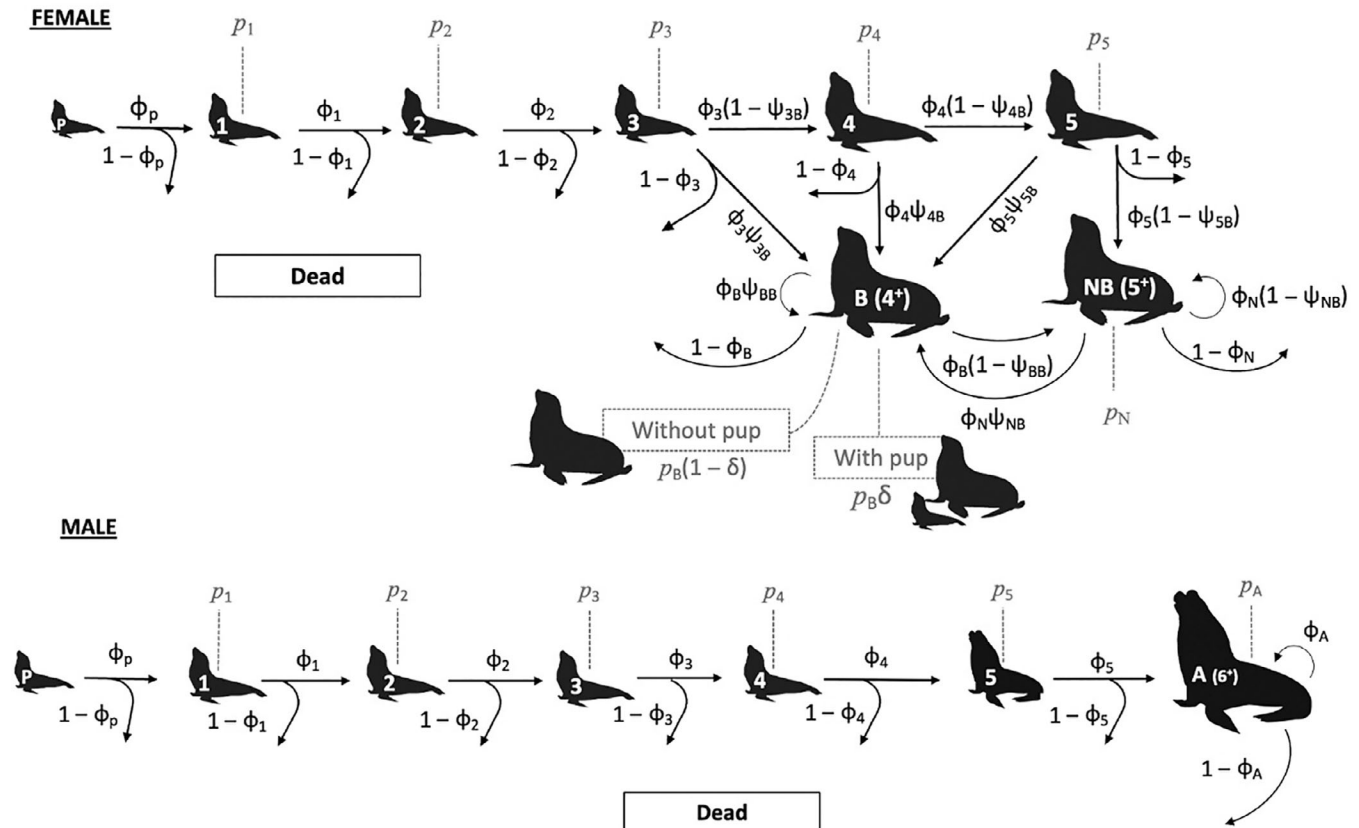


FIGURE 2 Life cycle diagram for female and male Steller sea lions, with true ecological states shown in white (pup [P], juveniles aged 1–3, pre-breeding subadults aged 4–5, breeding adult females [4+ B], non-pupping adult females [5+ NB], and adult males [6+ A]). Survival (ϕ) and pupping (ψ) probabilities denote transitions between true states (black lines) and detection probabilities (p) denote possible observation events for each age and female reproductive state (with or without pup) (gray dotted lines).

individual covariates and random effects of year. That is, for general demographic rate parameter γ ,

$$\text{logit}(\gamma_{a,s,t}) = \mu_{a,s}^\gamma + \mathbf{x}'\boldsymbol{\beta}_a^\gamma + \epsilon_{a,t}^\gamma,$$

where $\mu_{a,s}^\gamma$ is an age/state (a)- and sex (s)-specific intercept, \mathbf{x} is a vector of covariates with associated coefficients $\boldsymbol{\beta}_a^\gamma$, and $\epsilon_{a,t}^\gamma$ is an annual (t) random effect. The intercept $\mu_{a,s}^\gamma$ for a given demographic rate was given a logit-transformed uniform $U(0,1)$ prior distribution on the probability scale for individuals marked in the eastern portion of the wDPS range. For individuals marked in the western portion of the wDPS range where sample sizes were smaller, mean survival rates for each sex were estimated using an intrinsic Gaussian conditional autoregressive (CAR) model prior distribution that enforced autocorrelation by age,

$$\boldsymbol{\mu}_{\text{pup}:5,s}^\phi \sim N(\mathbf{0}, \sigma\mathbf{Q}^{-1}),$$

where \mathbf{Q} is the precision matrix of an intrinsic autoregression or order 2 (IAR(2); Speckman & Sun, 2003) scaled by σ . The IAR(2) correlation structure imposes a smoothness constraint that has two fewer degrees of freedom relative to independent random effects for each age. We used $\sigma \sim \text{Exp}(\lambda = 1)$ as a prior for the scaling parameter σ to penalize strong age effects, unless necessary for model fit (Simpson et al., 2017; van Erp et al., 2019).

To increase parameter estimability and regulate model complexity, we used the same penalized complexity approach as with the $\boldsymbol{\mu}_{\text{pup}:5,s}^\phi$ parameters for defining prior distributions on $\boldsymbol{\beta}_a^\gamma$ and $\epsilon_{a,t}^\gamma$. For fixed effects, a penalized complexity prior shrinks the coefficient toward zero in the absence of strong support for a covariate effect. The effect of each univariate covariate c (e.g., pup mass x_i and oceanographic variable x_t) on demographic rate $\gamma_{a,s}$ was drawn from a unique Gaussian distribution as $\beta_{a,c}^\gamma \sim N(0, \sigma_{a,c})$, with standard deviations distributed according to an exponential distribution with a fixed shrinkage rate $\sigma_{a,c} \sim \text{Exp}(\lambda = 1)$ to apply moderately strong shrinkage. Similarly, random year effects (estimated only for the eastern portion of the wDPS range) were drawn from a Gaussian distribution as $\epsilon_{a,t}^\gamma \sim N(0, \sigma_a^\gamma)$, with standard deviations σ_a^γ distributed according to an exponential distribution with a fixed shrinkage rate as described above. Age- and sex-specific intercepts were estimated for each demographic rate, but fixed effects of environmental conditions were shared across sexes and only estimated for pup survival (ϕ_p), age 1–2 survival (“young,” $\phi_{1:2}$), and first-time ($\psi_{3B,4B,5B}$) and repeat (ψ_{BB}) pupping, as we hypothesized that the survival of older individuals was likely to be relatively

unaffected by environmental variability due to much larger energy storage capacity and foraging experience. Separate fixed effects were examined for the effect of pup mass for each sex. For survival, shared temporal random effects were estimated for both sexes (except females with pups and adult males) and for juvenile individuals aged 3–5 (i.e., year-specific deviations from the mean were modeled in common for these groups). For pupping probabilities, shared random effects were estimated for all first-time breeding transitions for age 3–5 individuals ($\psi_{3B,4B,5B}$), with standard deviation σ_{PB}^W .

Age-specific natality (f) differs from pupping probability in that it is state independent (e.g., the number of offspring produced per female aged 4, 5, and 6⁺ in a given year, assuming only singleton births), whereas pupping probability is a state transition probability. Natality was calculated by taking the proportion of each female age class that had a pup at a given occasion according to the true z state. For the eastern portion of the wDPS range, age-specific and overall natality (proportion of females pupping in a given year) was calculated beginning in the seventh study year to allow for more than one marked cohort to have reached reproductive maturity. Due to the shorter study period and the biennial branding schedule in the western portion of the range, natality was calculated beginning in just the fourth year when at least one marked cohort had reached reproductive maturity.

Observation process model

Possible observations for adult females included being seen without a pup, seen with a pup, or not detected. These observations, combined with knowledge of an individual’s age, defined the events in the multievent model,

$$y_{i,t} | z_{i,t} \sim \text{Categorical}(\Theta_{z_{i,t},t}),$$

where an observation $y_{i,t}$ conditional on the true state $z_{i,t}$ is categorically distributed with probability array Θ . Components of detection probability for individual i at time t include the probability of detection, $p_{i,t}$, and the probability of correctly ascertaining the presence of a pup for breeders, $\delta_{i,t}$. Similar to demographic rates, detection probability was modeled as follows:

$$\text{logit}(p_{a,s}) = \mu_{a,s}^p + \beta^p + \epsilon_t^p,$$

where the mean intercept $\mu_{a,s}^p$ for each sex s and age a was estimated using a logit-transformed prior that was uniform $U(0,1)$ on the probability scale. For individuals in the eastern portion of the wDPS range, a categorical fixed effect parameter was included to account for

markedly lower resight survey effort in three years during the study period (2006, 2017, and 2018), where $\beta^p \sim N(0, 0.001)$ is drawn from a Gaussian distribution. Interannual variability in detection probability was estimated for the eastern portion of the wDPS range with random year effects drawn from a Gaussian distribution as $\epsilon_t^p \sim N(0, \sigma^p)$, with standard deviations σ^p estimated with shrinkage priors, distributed according to an exponential distribution with a fixed shrinkage rate as described above. For individuals in the western portion of the range, no temporal variance was modeled for detection probabilities. We expected that the probability of correctly ascertaining whether a female had a pup would be a function of the number of times a female was seen in a season, and so we used the number of sightings per individual per year (with pups or without) as a three-level categorical covariate for the multievent classification probability parameter, $\delta_{i,t}$, with levels defined as 1–2 resights per year, 3–8 resights, and 9+ resights.

Variable and model selection

To reduce the number of covariates to a reasonable number with which to use shrinkage priors as a variable selection technique, we eliminated covariates that were not supported based on a comparison between Watanabe–Akaike information criterion (WAIC; Watanabe, 2010) values of the null model versus models where each environmental variable was used as the sole covariate. We further eliminated some variables that did improve model fit based on WAIC values in order to avoid using highly correlated covariates in the same model. For demographic models for individuals marked in the eastern portion of the range, this process of elimination left the AL, AOI, NPGO, upwelling, northward wind, and chlorophyll concentration for use in the full covariate models. For the western portion of the range, the AOI, NPGO, upwelling, and northward wind were retained in the full covariate model.

Once the final set of environmental covariates was determined, we used WAIC to compare the null model, an interannual random effects-only model (no environmental covariates), and the set of full models (interannual random effects, pup body mass, and season-specific environmental covariates for each of the four seasons). Season-specific environmental covariates were examined together (i.e., all covariates were from the same season in each model run) due to the infeasibility of examining all possible combinations of the four seasonal values of each environmental covariate. We summarized the results of the full model according to the proportion of Markov chain Monte Carlo

(MCMC) chain samples for the environmental effects that were above versus below zero.

Model fitting

Models were fit using NIMBLE (de Valpine et al., 2019) within the R programming environment (R Core Development Team, 2022) using 20,000–40,000 iterations and 10,000–20,000 burn-in depending on the model, a thinning rate of 2 (to minimize the size of the resulting R object), and an adaptation rate of 10. We evaluated model convergence using visual inspection of chains and the Brooks–Gelman–Rubin statistic (Brooks & Roberts, 1998; Gelman & Rubin, 1992) $\hat{R} < 1.1$. After fitting full models, we evaluated goodness of fit using Bayesian p values, where we compared the number of observed versus predicted resightings of individuals by age at each occasion, and there were no indications of substantial lack of fit. The typical set of mark–recapture model assumptions applied in this study is as follows: we assumed that branding did not affect detection probability; individuals were independent with respect to survival and state transition probabilities; there were no identification errors; mortality during the sampling season was negligible; and there was no unmodeled heterogeneity in survival and detection probabilities.

RESULTS

Demography

Survival

Demographic rates reported in this section refer to those estimated using the null model to facilitate regional comparisons. Mean pup survival from 2000 to 2018 in the eastern portion of the wDPS range was 0.71 (95% credible interval = 0.67–0.76) and 0.69 (0.65–0.74) for females and males, respectively. Survival increased with age for both sexes, though survival for age-2 females (0.88; 0.82–0.92) was notably higher than that for age-2 males (0.76; 0.69–0.82; Figure 3, Table 2). Survival for females with a pup (0.94; 0.92–0.96) was higher than non-pupping females (0.83; 0.75–0.91; Figure 3, Table 2). Survival for individuals in the eastern portion of the wDPS range was most variable over years for pups and age-1 and age-2 individuals (Figure 4a). Mean annual male and female pup survival over the study period ranged from 0.31 to 0.95. Juvenile and pupping adult female survival remained relatively constant throughout the study period.

Age- and sex-specific survival rates for the western portion of the wDPS range from 2011 to 2018 had higher uncertainty than in the eastern portion of the wDPS range due to the smaller sample size. While female pup survival was similar to that in the east, male pup survival was 0.44 (0.36–0.53), which was significantly lower than that in the eastern portion of the wDPS range (Figure 3, Table 2). Additionally, female survival for age 1 through pre-breeding-age groups (age 3 to age 5) was notably lower compared with that of individuals marked in the eastern portion of the wDPS range. Estimates were similar between the eastern and western portions of the wDPS range for adult males and females.

Pupping and natality

For the eastern portion of the wDPS range, the probability of first-time pupping was highest for age-5 individuals (i.e., giving birth for the first time at age 5; ψ_{4B}) at 0.72 (0.62–0.8) and much lower for age-6 individuals

(ψ_{5B}) at 0.16 (0.01–0.38) and age-4 individuals (ψ_{3B}) at 0.13 (0.08–0.21) (Figure 3, Table 2). The probability of females with a young of year also pupping in the following year (ψ_{BB}) was high (0.98; 0.96–0.99) and remained relatively constant throughout the study period. The probability of pupping for females that had not given birth in the previous year (ψ_{NB}) was low (0.08; 0.03–0.16) and remained relatively low over the study period, with the exception of 2006–2007. Though estimated with a relatively high degree of uncertainty, the shared temporal standard deviation in pupping probabilities for first-time breeders was relatively high ($\sigma_{PB}^{\psi} = 1.26$), reflecting rates that fluctuated substantially throughout the study period (Figure 4b). Mean age-specific natality (calculated from the seventh year onward) was low for age-4 individuals (0.13; 0.04–0.28) and much higher for age-5 individuals (0.81; 0.7–0.9). Overall natality (f , proportion of breeding-age females with a pup each year) was 0.8 (0.74–0.84) from the seventh year onward (Table 2).

For the western portion of the wDPS range, age-specific pupping probabilities mirrored those in the eastern portion (higher probability for age-5 individuals

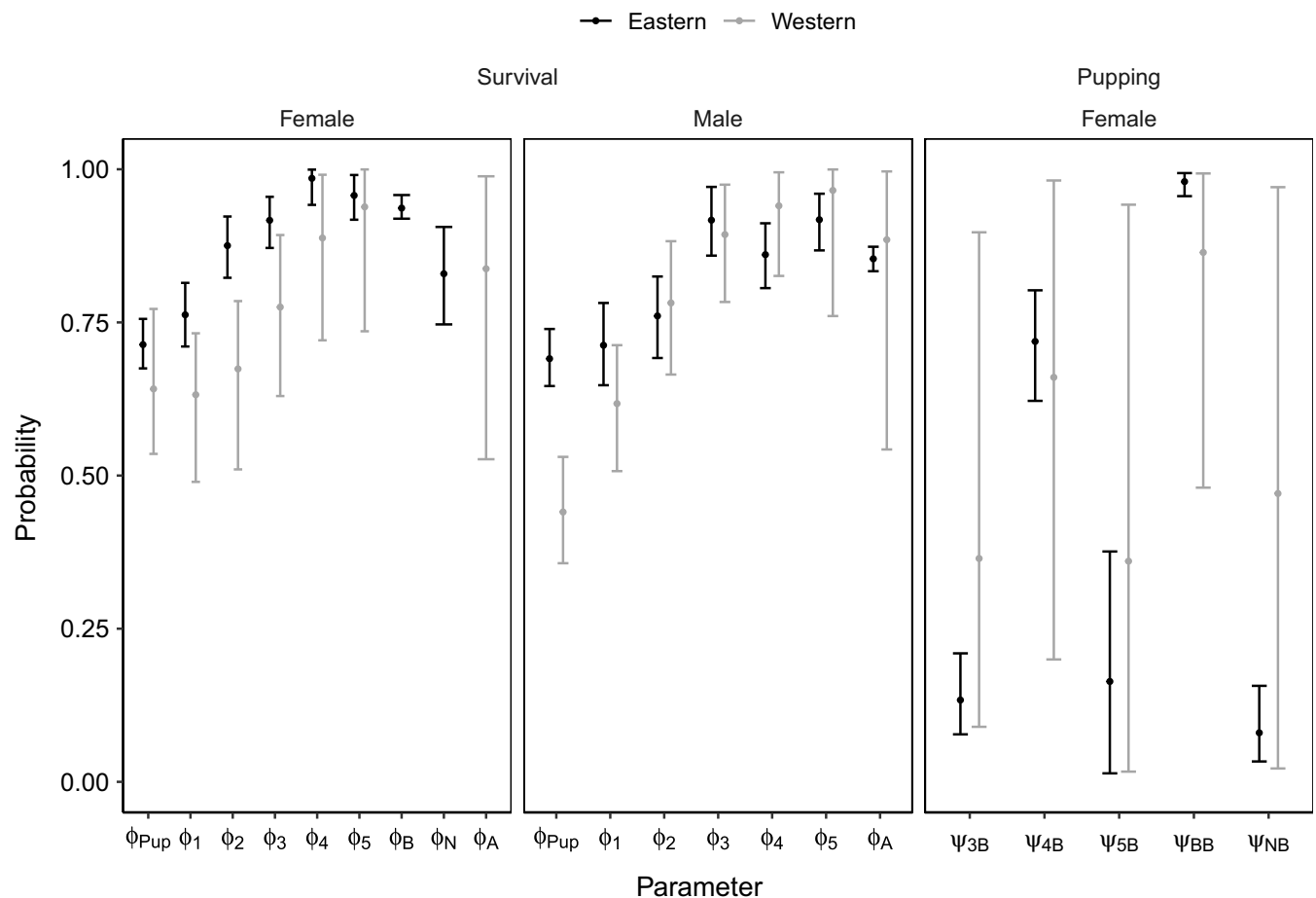


FIGURE 3 Posterior mean and 95% credible intervals for age- and sex-specific survival (ϕ) and pupping (ψ) probabilities for Steller sea lions in the eastern (black) and western (gray) portion of the western distinct population segment range.

TABLE 2 Posterior mean and 95% credible intervals (CIs) for age- and sex-specific (F, female; M, male) survival and natality (proportion of females with a pup) parameters for the eastern (2000–2018) and western (2011–2018) portions of the western distinct population segment.

Rate	Sex	Age	Eastern		Western	
			Mean	95% CI	Mean	95% CI
Survival	F	Pup	0.71	0.67–0.76	0.64	0.54–0.77
	M	Pup	0.69	0.65–0.74	0.44	0.36–0.53
	F	1	0.76	0.71–0.81	0.63	0.49–0.73
	M	1	0.71	0.65–0.78	0.62	0.51–0.71
	F	2	0.88	0.82–0.92	0.67	0.51–0.78
	M	2	0.76	0.69–0.82	0.78	0.66–0.88
	F	3	0.92	0.87–0.96	0.78	0.63–0.89
	M	3	0.92	0.86–0.97	0.89	0.78–0.97
	F	4	0.99	0.94–1.00	0.89	0.72–0.99
	M	4	0.86	0.81–0.91	0.94	0.83–1.00
	F	5	0.96	0.92–0.99	0.94	0.74–1.00
	M	5	0.92	0.87–0.96	0.97	0.76–1.00
	F	Adult with pup	0.94	0.92–0.96		
	F	Adult without pup	0.83	0.75–0.91		
	Natality	M	Adult	0.85	0.83–0.87	0.88
F		Adult	0.85	0.83–0.87	0.84	0.53–0.99
F		4	0.13	0.04–0.28	0.38	0.12–0.89
	F	5	0.81	0.7–0.90	0.76	0.49–1.00
	F	All	0.80	0.74–0.84	0.69	0.47–0.96

and existing breeders), though the mean probability of repeat pupping (ψ_{BB}) was slightly lower and credible intervals were much wider due to the smaller sample size (only two marked cohorts had reached reproductive maturity by the end of the study, which covered fewer years compared with that in the eastern portion of the wDPS range; Figure 3). Mean age-specific natality (calculated from the fourth year onward) was 0.38 (0.12–0.89) for age-4 individuals and 0.76 (0.49–1) for age-5 individuals. Natality for age-6⁺ individuals in the western portion of the wDPS range only included a single cohort and is therefore not directly comparable to natality estimated for the eastern portion of the range. Overall natality for the study period was 0.69 (0.47–0.96) from the fourth year onward (Table 2). Time-varying demographic rates were not estimated for individuals marked in the western portion of the range due to fewer marked individuals resighted over fewer occasions.

Detection

Detection probability increased with age for both males and females (Figure 5). Of note is that resightings in

the western portion of the range are the product of both opportunistic observations and remote cameras, and though less certain, mean age- and sex-specific detection probabilities were higher than those estimated from rookery-based field camps in the eastern portion of the range. The probability of correctly identifying females as having a pup ($\delta_{i,t}$) increased with resighting frequency, ranging from 0.41 (0.38–0.45) for individuals resighted once or twice per year to 0.71 (0.68–0.75) for those resighted more than nine times.

Individual and oceanographic covariates

The effect of individual characteristics and environmental conditions ($\beta_{c,a}$) are reported on the logit scale, where values above zero indicate a positive correlation and values below zero a negative correlation. We report both the logit-scale value of $\beta_{c,a}$, which indicates the strength of the correlation, and the proportion of MCMC samples that were above or below zero ($p(\beta_{c,a} > 0)$), which indicates the probability that the correlation was positive versus negative. In general, the uncertainty around coefficient effects increased with the

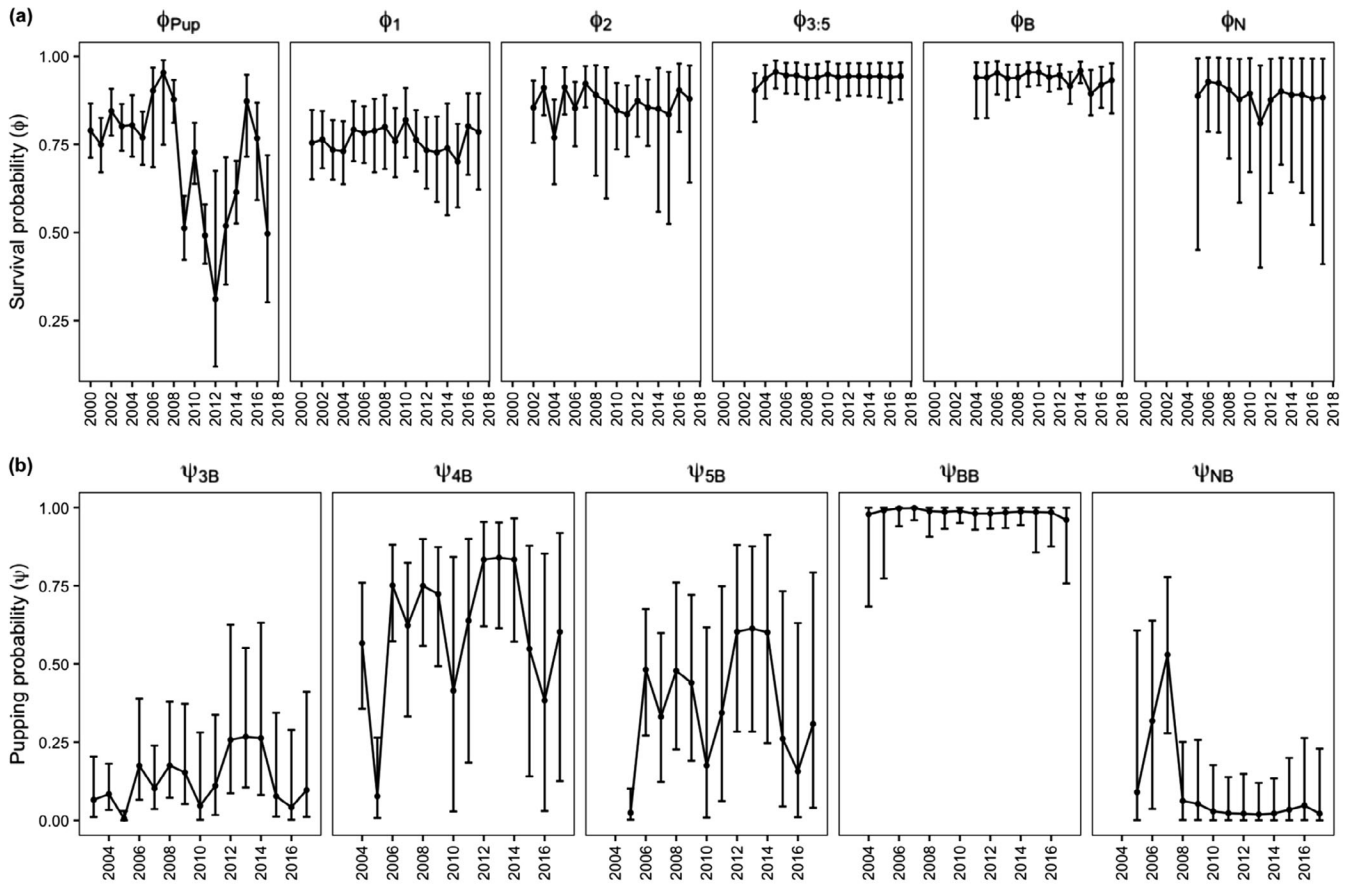


FIGURE 4 Posterior mean and 95% credible interval for time-varying age-specific (a) survival (ϕ) and (b) pupping (ψ) probabilities for female Steller sea lions marked in the eastern portion of the western distinct population segment range.

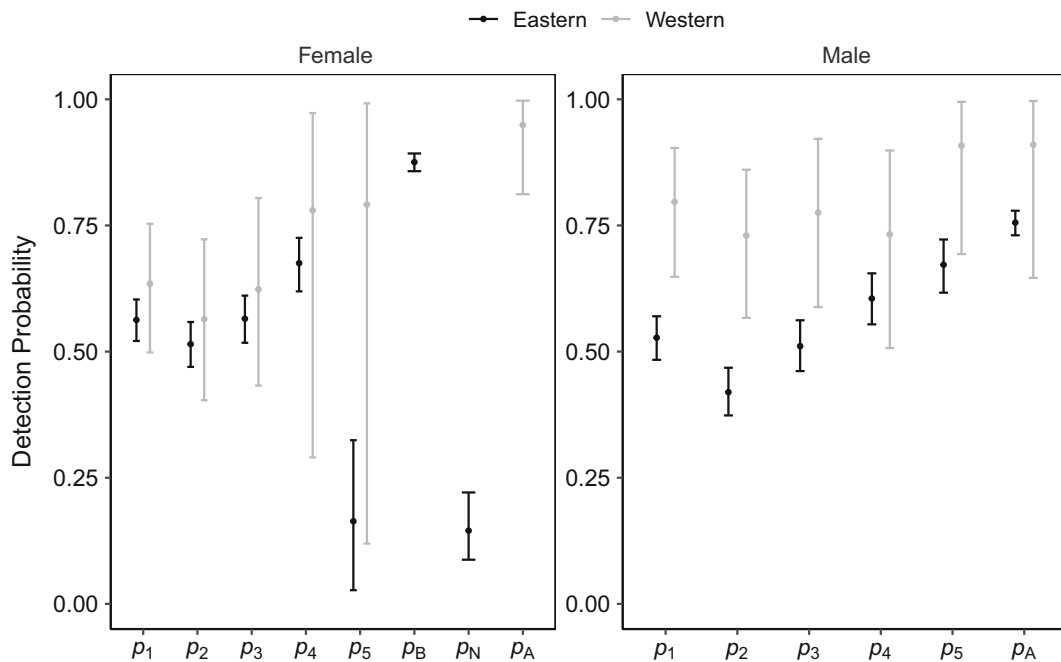


FIGURE 5 Posterior mean and 95% credible intervals for age- and sex-specific detection probabilities of Steller sea lions marked in the eastern (black) and western (gray) portion of the western distinct population segment range.

addition of random effects for vital rates and detection probabilities.

For individuals marked in the eastern portion of the wDPS range, pup mass had a positive effect on pup survival (ϕ_p) for both females ($\beta = 0.18$; 95% credible interval: 0, 0.37; $p(\beta > 0) = 0.98$) and males ($\beta = 0.29$; 0.12, 0.48; $p(\beta > 0) = 1$), and young females aged 1 to 2 ($\phi_{1,2}$) as well ($\beta = 0.07$; -0.06, 0.25; $p(\beta > 0) = 0.82$) (Figure 6). However, for individuals marked in the western portion of the range, pup mass had a negative effect on male pup

survival ($\beta = -0.26$; -0.59, 0.02; $p(\beta < 0) = 0.95$) and age 1–2 survival ($\beta = -0.14$; -0.66, 0.17; $p(\beta < 0) = 0.78$). Uncertainty in the estimates for the effect of pup mass on these various demographic rates is much greater for individuals marked in the western portion of the range. We did not detect an effect of pup mass on the probabilities of first-time pupping ($\psi_{3B,4B,5B}$; Figure 6).

For the eastern portion of the range, the full model included the AL, AOI, NPGO, chlorophyll concentration, meridional winds, and upwelling. Except for upwelling,

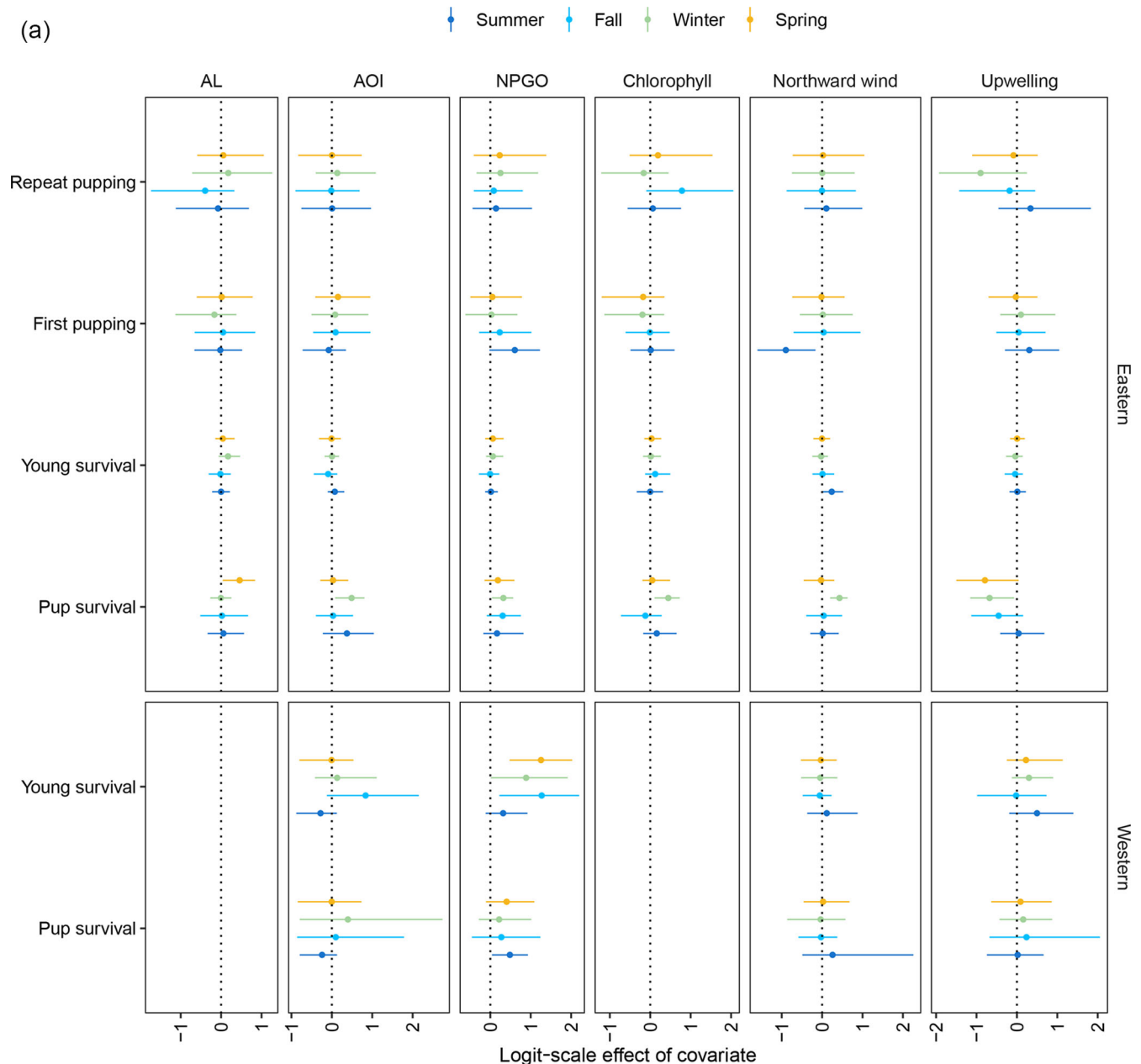


FIGURE 6 (a) Logit-scale posterior mean and 95% credible intervals for the fixed effects of environmental covariates in each season and pup mass at branding on pup and young (pooled effect for age 1–2) survival and (b) pupping probabilities for individuals marked in the eastern and western portions of the western distinct population segment range. AL, Aleutian Low; AOI, Arctic Oscillation Index; NPGO, North Pacific Gyre Oscillation.

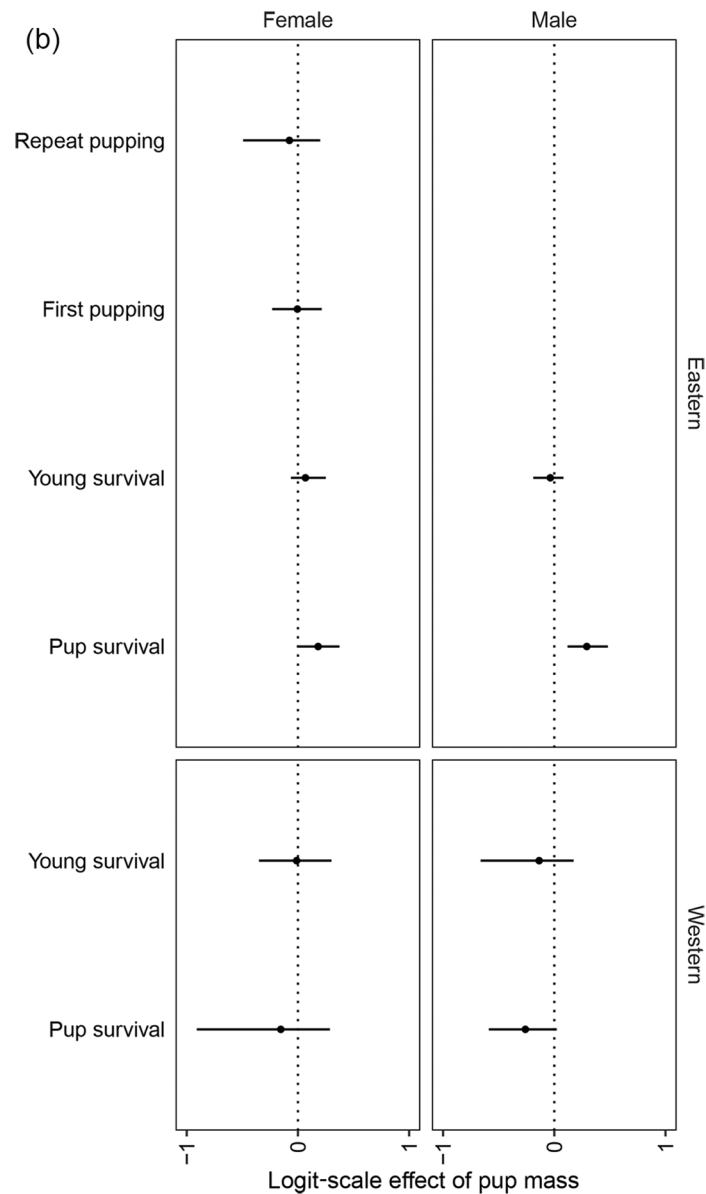


FIGURE 6 (Continued)

season-specific variables largely had a positive effect on the survival of pups (ϕ_p) that did not extend to individuals aged 1–2 (Figure 6). More specifically, pup survival was positively correlated with positive-phase AL in the spring ($\beta = 0.46$; 95% credible interval: 0.04, 0.84; $p(\beta > 0) = 0.99$), positive-phase AOI in the summer ($\beta = 0.37$; $-0.22, 1.04$; $p(\beta > 0) = 0.87$), and positive-phase NPGO in the summer ($\beta = 0.17$; $-0.17, 0.82$; $p(\beta > 0) = 0.81$) and fall ($\beta = 0.31$; $-0.09, 0.76$; $p(\beta > 0) = 0.91$) (Figure 6). In terms of more localized conditions, pup survival was positively correlated with chlorophyll concentration during the winter ($\beta = 0.45$; 0.11, 0.73; $p(\beta > 0) = 0.99$) and spring ($\beta = 0.05$; $-0.19, 0.49$; $p(\beta > 0) = 0.68$) and negatively correlated with increased upwelling, particularly in the fall ($\beta = -0.45$; $-1.13, 0.15$; $p(\beta < 0) = 0.91$)

and winter ($\beta = -0.68$; $-1.15, 0.07$; $p(\beta < 0) = 0.99$). In terms of reproduction, first-time pupping probability was positively correlated with summer positive-phase NPGO ($\beta = 0.61$; $-0.02, 1.23$; $p(\beta > 0) = 0.97$) and increased summer upwelling ($\beta = 0.31$; $-0.29, 1.05$; $p(\beta > 0) = 0.84$) and negatively correlated with stronger summer wind ($\beta = -0.9$; $-1.6, 0.16$; $p(\beta < 0) = 0.99$). Repeat pupping probability was positively correlated with chlorophyll concentrations in the fall ($\beta = 0.78$; $-0.1, 2.05$; $p(\beta > 0) = 0.93$), but showed little to no correlations with other environmental covariates.

For the western portion of the range, oceanographic variables included in the full model included the AOI, NPGO, wind, and upwelling, though their effects on pup and age 1–2 survival were estimated with less precision

due to the smaller sample size (Figure 6). Some environmental effects were similar to those estimated for individuals marked in the eastern portion of the range; however, a notable difference was that the effects were evident not for pup survival, but for age 1–2 survival ($\phi_{1,2}$). Specifically, positive-phase AOI in the fall ($\beta = 0.84$; $-0.12, 2.15$; $p(\beta > 0) = 0.92$) and positive-phase NPGO in the fall ($\beta = 1.27$; $0.23, 2.2$; $p(\beta > 0) = 0.99$), winter ($\beta = 0.89$; $0.01, 1.92$; $p(\beta > 0) = 0.98$), and spring ($\beta = 1.25$; $0.48, 2.03$; $p(\beta > 0) = 1$) exhibited strong evidence of a positive effect on age 1–2 survival. Stronger summer upwelling exhibited a positive correlation with age 1–2 survival ($\beta = 0.5$; $-0.19, 1.4$; $p(\beta > 0) = 0.9$) while stronger winds in spring and summer were correlated with lower survival probabilities. Environmental covariates were not included in the estimation of pupping probability for individuals marked in the western portion of the range due to the low sample size of reproductively mature individuals.

Model selection and evaluation

For the eastern portion of the range, both the models with time-varying demographic rates and the full seasonal models performed better than the null-model based on WAIC values (Table 3). Much of the improvement in the full models compared with the null model ($\Delta_{\text{WAIC}} = 310$) was attributable to the addition of random effects

TABLE 3 Watanabe–Akaike information criterion (WAIC) values for models of individuals marked in the eastern (null, random effects only, and seasonal full models) and western (null and seasonal full models) portions of the western distinct population segment range. The seasonal covariates used in the full models are noted in parentheses.

Model	WAIC	Δ_{WAIC}
Eastern		
Full (winter)	17,701.1	0.0
Random effects only	17,709.8	8.7
Full (summer)	17,710.4	9.3
Full (spring)	17,714.4	13.3
Full (fall)	17,715.3	14.3
Null	18,011.0	310.0
Western		
Full (spring)	919.2	0.0
Full (fall)	921.3	2.1
Full (winter)	922.9	3.7
Full (summer)	930.5	11.3
Null	933.7	14.5

($\Delta_{\text{WAIC}} = 8.7$), with much smaller but meaningful improvements with the addition of individual and environmental covariates (Table 3). The best-fit model was the full model that included environmental covariates from the winter season followed by the model that included covariates from the summer ($\Delta_{\text{WAIC}} = 9.3$). A consequence of the larger number of covariates accommodated by the penalized complexity shrinkage priors is that it is more challenging to attribute the improvement in model fit to a specific environmental variable. To elucidate the effects of each season-specific environmental covariate, we examined WAIC values for models where each covariate was used alone. This revealed that upwelling and the AL during winter and summer, the NPGO during the spring, and chlorophyll concentration over the entire non-breeding season explained the most variability when included alone (Appendix S1).

For demographic estimates in the western portion of the range, all full seasonal models performed better than the null model (Table 3). The best-fit model included covariates from the spring, followed closely by the model that included environmental variables from the fall season ($\Delta_{\text{WAIC}} = 2.1$). Similar to above, an examination of model fit with only one environmental covariate included at a time showed that these improvements in WAIC values could be attributed largely to the effect of spring and fall NPGO on age 1–2 survival, which had the lowest WAIC values when included alone (Appendix S1).

DISCUSSION

We used mark–resight data to estimate survival and natality and the effects of pup mass and oceanographic conditions for the wDPS of Steller sea lions in Alaska. This study provides the first demographic rate estimates for individuals marked in the western and central Aleutians where abundance continues to decline (Sweeney et al., 2018) and the first instance of examining correlations between environmental conditions and vital rates, providing insights into potential drivers of population dynamics for this population.

Demography

Regional comparisons

Researchers have hypothesized that the historical and ongoing decline in counts at rookeries in the western portion of the wDPS range may be due to a combination of demographic or environmental factors

(Holmes et al., 2007; Loughlin & York, 2000). With this study, we aimed to explore variation in age- and sex-specific vital rates to improve ecological understanding that can inform future management and recovery actions under the Endangered Species Act. In general, survival rates estimated in this study for the eastern portion of the wDPS range were similar to (or higher than) previous estimates (Fritz et al., 2014; Maniscalco et al., 2015; Pendleton et al., 2006; York, 1994) and those estimated for the eastern distinct population segment (DPS) (Hastings et al., 2011, 2021; Wright et al., 2017). However, survival rates for the western portion of the wDPS range (western and central Aleutian Islands) estimated here for the first time are notably lower than those in the eastern portion of the range, particularly for male pups, yearlings of both sexes, and juvenile females aged 2–5. Survival estimates for individuals aged 0–3 in the Asian stock of Steller sea lions in the Russian Far East (geographically closer to the western Aleutian Islands than other rookeries in the wDPS) ranged from approximately 0.6–0.8 (Altukhov et al., 2015), much higher than those estimated and reported here for the western and central Aleutians.

Though it is difficult to compare our natality estimates to those from previous studies that relied on proportions of observed breeders in aerial surveys, overall natality for the eastern portion of the wDPS range was similar to estimates from the late 2000s in the eastern Gulf of Alaska (Maniscalco et al., 2010, 2014) and those observed in stable or increasing pinniped populations (Lunn et al., 1994; McKenzie et al., 2005). In contrast, natality in the western portion of the wDPS range was lower. However, even though overall natality was lower, the proportion of age-4 individuals pupping for the first time was higher in the far west, which could contribute to lower pup survival rates if outcomes for offspring of inexperienced females are poorer. Though both survival and natality estimates for the western portion of the range had greater uncertainty compared with those for the eastern portion of the range, the differences are striking and could be limiting population growth. Additional years of data will reduce the uncertainty in adult survival and natality estimates, which will round out our understanding of the intrinsic factors limiting recovery, as those vital rates are often the dominant drivers of population dynamics for long-lived species (Heppell et al., 2000).

Age- and sex-specific comparisons

Examining patterns in age- and sex-specific survival rates can lend insight into life-history trade-offs, habitat

conditions and prey availability, and reproductive fitness. Age-specific survival generally increased with age from pups to adults for both males and females, as expected for long-lived mammals according to the demographic buffering hypothesis (Eberhardt, 2002; Gaillard et al., 1998; Pfister, 1998; Rotella et al., 2012) and similar to previous studies of this species (Altukhov et al., 2015; Hastings et al., 2011, 2018; Wright et al., 2017). However, this pattern was not uniformly observed for both sexes in each region. For males in the eastern portion of the range and females in the western portion of the range, a small drop was observed in survival for ages 1–2 compared with pups, as has also been previously observed (Altukhov et al., 2015; Fritz et al., 2014; Maniscalco, 2014; Pendleton et al., 2006). The effect of pup mass on survival was also different across sexes and regions, with a positive correlation in the eastern portion of the wDPS range versus a negative correlation (particularly pronounced for males) in the west. Taken together, these patterns in age-specific survival and the respective effects of pup mass likely stem from different maternal investment strategies and age at weaning across the range (Maniscalco, 2014).

Our results indicated that heavier pups had a higher probability of survival in their first year in the eastern portion of the wDPS range and a lower probability in the west. Larger pups might be able to forage more effectively (if they were still larger when independent foraging begins) or might be born earlier or to larger, more experienced females. Several authors have found this positive association between pup mass and first-year survival for this species (Hastings et al., 2011; Maniscalco, 2014; Wright et al., 2017) and for other pinnipeds around the world, particularly northern fur seals (*Callorhinus ursinus*; Boltnev et al., 1998) and Weddell seals (*Leptonychotes weddelli*; Hadley et al., 2007; Proffitt et al., 2010). However, females can compensate for smaller pup size by increasing maternal investment and/or weaning later (Lee et al., 1991; Trillmich, 1990), providing support for the assertion that maternal care influences first-year survival more than birth mass for otariids (Boyd, 1990; McMahan & Hindell, 2003). Hastings et al. (2021) found that in certain rookeries in both the eastern and western DPSs, earlier weaned yearlings had a lower probability of survival and that heavier pups were more likely to wean by one year of age. Applying these concepts to our findings, it is possible that the larger pups in the western portion of the range incur a larger burden on lactating females (as was found in South American sea lions, *Otaria flavescens*, who foraged longer for heavier pups; Drago et al., 2021) and may habitually be weaned sooner and therefore ultimately experience lower survival rates despite their larger size. It could also be that resource

limitations in the far western regions lead females to spend more time foraging during the summer and therefore less time nursing pups. With additional years of data, a closer examination of the region-specific life-history strategies for breeding females could lend insight into the trade-offs inherent in maximizing reproductive fitness given prevailing environmental conditions and physiological constraints.

Oceanographic effects

We examined numerous local- and basin-scale oceanographic indices to identify potential correlations between environmental features and demography based on the hypothesis that these dynamic biophysical conditions either directly (e.g., through increased storminess) or indirectly (e.g., bottom-up forcing mechanisms that affect the quality, quantity, or distribution of prey species) impact survival and natality. Oceanographic conditions are known to be correlated with foraging, health, maternal investment, and reproductive success in pinnipeds. Studies have shown that other otariids, primarily fur seals, associate with certain frontal features while foraging or migrating (Joy et al., 2015; Ream et al., 2005; Speakman et al., 2020; Sterling et al., 2014), but few studies have linked these features to demography. Existing examples include correlations between sea ice and recruitment in Weddell seals (Hadley et al., 2007), SSTs and first-year survival for subantarctic fur seals (*Arctocephalus tropicalis*; Beauplet et al., 2005), and El Niño conditions and first-year survival in southern elephant seals (*Mirounga leonina*; McMahon & Burton, 2005). In this study, we found that the NPGO, AL, AOI, northward wind, and chlorophyll concentration were positively correlated with pup and age 1–2 survival and that summer upwelling in the previous season was positively correlated with fecundity. Taken together, these results could indicate that lower SSTs, higher chlorophyll and nutrient concentrations (during positive-phase NPGO), and stronger winds and decreased storminess (during positive-phase AOI) represent conditions that may be more favorable for pup survival and reproductive success. However, the effects of these localized and basin-scale conditions were age, region, and season specific. Namely, the AL had the strongest effect in the spring while the AOI, chlorophyll concentration, and wind mattered more in the summer and winter for individuals marked in the eastern portion of the wDPS range. These seasons are likely important in terms of life-history events, as research has shown that pups are more vulnerable during their first winter (Trites & Porter, 2002), where survival outcomes

are likely largely dependent on foraging mothers' access to prey. In the spring, environmental cues could be signaling adult females whether to wean their pups or continue nursing, and in the summer, lactating females would likely benefit from higher prey densities close to rookeries.

While identifying the precise mechanisms by which these features affect demography was outside the scope of this study, our findings improve our understanding of the population's response to environmental variability. Demographic rates in both regions were positively correlated with the NPGO, which has exhibited correlations with salmon productivity in the Gulf of Alaska (Jones et al., 2021) and may also influence plankton dynamics (Di Lorenzo et al., 2008) that affect both the availability and quality of groundfish and forage fish species. The NPGO was predominantly in a negative phase from 2013 to 2018, coinciding with a persistently low groundfish body condition index seen in bottom trawls in the Aleutian Islands (North Pacific Fisheries Management Council, 2020). Notably absent from the group of variables that showed some degree of correlation with demographic rates is SST, which has been shown to be correlated with foraging behavior (Lander et al., 2010) and have lasting ecosystem effects long after marine heatwave events (Arimitsu et al., 2021; Suryan et al., 2021). It may be that SST is more important at a highly localized scale as a behavioral cue rather than at broad regional scales. The fact that the effect of ocean conditions was limited to pup survival in the eastern portion of the range is likely an indication that these variables either directly affect pup survival (i.e., through increased storminess or maternal separation) or indirectly by affecting maternal investment (i.e., fat storage, weaning, nutrient transfer, and prey quality). In contrast, the more notable effect of ocean conditions on yearling and age-2 individuals in the western portion of the range could be due to earlier weaning of those heavier pups by their first summer, in which case, yearling individuals could be strongly affected by prevailing ocean and foraging conditions.

When examining the complex relationships between environmental conditions and demography for an adaptive top predator, it is important to examine the effects of environmental variability and habitat features at the scale that is relevant to the species (Mannocci et al., 2017), though this is complicated by several factors. First, multiple spatiotemporal scales are likely important to sea lions, as both local- and region-scale environmental conditions influence the quantity and quality of prey, for which data are patchily available. Second, the relationships between climate indices and the species they affect can themselves exhibit decadal-scale changes, as has been

shown with the NPGO (Litzow et al., 2018, 2020). These complex issues of scale-matching and nonstationary relationships make it challenging to identify mechanistic pathways by which environmental variables affect demography. We know that dynamic and static habitat features are important, but it is difficult to quantify precisely how they matter due to spatiotemporal and individual heterogeneity. In addition to these inferential obstacles, the sea lions themselves present an additional challenge in that they are, by nature, adaptive and have evolved to maximize fitness in dynamic and variable environments. For example, nursing females can compensate for unfavorable foraging conditions or smaller pup birth mass by extending lactation or changing foraging behavior (Maniscalco et al., 2014; Trites & Porter, 2002; York et al., 2008). While this flexibility may be particularly important in high-latitude environments with strong seasonality (Varpe, 2017), it does make it difficult to disentangle the effects of pup body size, maternal characteristics, regional differences, and environmental variability.

Future work could address some of these complexities through an individual-based integrated model combining mark–resight observations that included maternal attendance and suckling of dependent young, telemetry data that could better inform the spatial extent of environmental covariates, localized measures of prey availability (though these are not readily available), and proxies for other stressors such as natural predation or contaminant exposure that may also vary across the range. These observational datasets could be used to estimate the effects of environmental variability within a stochastic antecedent model framework (Ogle et al., 2015) that could examine the lag time, duration, and intensity of the effects of ocean conditions. This framework could better account for the effects of maternal versus pup characteristics and would address the uncertainty about the strength, relative importance, and timing of the effects of seasonal environmental variability.

This study has highlighted demographic differences that may inform ongoing investigation into the divergent abundance trends that have been observed across the species range. We provide insights into ecological processes that may affect Steller sea lion survival and natality, but highlight the complexities of identifying causal mechanisms underlying changes in demography for this and other highly mobile, long-lived top predators. This research has provided important information for the conservation and management of this species and will be foundational to future analyses of population viability and extinction risk that will inform decision-making in light of ongoing and anticipated future climate variability.

CONCLUSION

We examined interannual variability in age- and sex-specific demographic rates and the effects of pup mass and oceanographic conditions on survival and natality for the wDPS of Steller sea lions. Our results provide the first demographic rate estimates for individuals marked in the central and western Aleutian Islands, where low survival of male pups and young sea lions of both sexes may be contributing to or driving the continued declining abundance trends that contrast the stable or increasing trends at rookeries to the east of Samalga Pass. One of the strengths of this study is its broad spatiotemporal scope, which has facilitated the estimation of demographic rates with reasonable precision in the eastern portion of the wDPS range and highlighted the importance of continued survey effort in the central and western Aleutians to reduce the uncertainty in age 1–2 survival and enable more robust estimates of natality and adult survival, as those vital rates may also be factors limiting recovery. Pup mass had a positive effect on pup survival in stable or increasing population areas and a negative effect in the far western rookeries, potentially indicating differing maternal investment strategies between the two regions.

For both the eastern and western portions of the wDPS range, we found correlations of varying strength and degree between sea lion vital rates and seasonal oceanographic conditions. Namely, the spring ALs, summer and winter AOI and wind velocities, fall and winter chlorophyll concentrations, and NPGO and upwelling throughout the year exhibited age- or region-specific effects on survival and natality. However, because the effects of ocean conditions are dynamic, vary over time and three-dimensional space, and are complicated by potential lag effects of unknown duration, the design of this study precluded specifically identifying the mechanisms underlying these observed correlations. Even so, improving our understanding of demography and the environmental factors that influence survival and natality across rookeries in the wDPS will enhance our ability to estimate population viability and trends in abundance and inform ongoing conservation and management strategies for this and other endangered species.

ACKNOWLEDGMENTS

The authors would like to thank the countless field technicians who collected the mark–resight and camera-based observations. We would also like to express our gratitude to Marine Mammal Laboratory staff who provided feedback during study development and manuscript review. The manuscript benefited from reviews by P. B. Conn and two anonymous reviewers. Amanda J. Warlick was supported by the National Science Foundation Graduate

Research Fellowship Program. The fieldwork associated with the marking and resighting of sea lions was conducted under Marine Mammal Protection Act and Endangered Species Act permit numbers 782-1532-00, 782-1532-01, 782-1532-02, 782-1532-03, 782-1768-00, 782-1768-01, 782-1889, 14326, 14326-01, 14326-02, and 18528-00 and animal care and use committee approvals A/NW 2010-4, A/NW 2013-2, and A/NW 2016-3. The findings and conclusions of the National Oceanic and Atmospheric Administration (NOAA) authors in the paper are their own and do not necessarily represent the views of the National Marine Fisheries Service or NOAA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Warlick and Converse, 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.7379560>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Warlick, Amanda J., Devin S. Johnson, Tom S. Gelatt, and Sarah J. Converse. 2022. "Environmental Drivers of Demography and Potential Factors Limiting the Recovery of an Endangered Marine Top Predator." *Ecosphere* 13(12): e4325. <https://doi.org/10.1002/ecs2.4325>