**The Effects of Ocean Conditions on Survival and Natality in the Western Distinct Population Segment of Steller Sea Lions**

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### 0.0.1 **Abstract**

Understanding what drives changes in wildlife demography over time is fundamental to the conservation and management of depleted or declining populations. The factors that influence survival and reproduction can be extrinsic or intrinsic and can change over time and space. Here we use almost 20 years of mark-resight data from 2000-2018 to examine the effects of environmental variability on age-specific survival and natality for the endangered western distinct population segment 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 range of this population remain unknown. We developed a Bayesian multi-event mark-resight model that accounts for female reproductive state uncertainty. Results indicated that survival rates for male pups (0.41; 0.33-0.52) and juveniles of both sexes (0.60; 0.42-0.76) born in the western portion of the range, estimated here for the first time, were lower than those estimated for pups (0.70; 0.67-0.76) and juveniles (0.74; 0.71-0.81) born in the eastern portion of the range. 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. 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 exhibited correlations with vital rates. However, strong inference is challenging given that relationships between ocean conditions and an adaptive top predator in a highly dynamic ecosystem are exceedingly complex. This study provides the first demographic rate estimates for the western portion of the population range where abundance estimates continue to decline. This work can inform ongoing research and management and will advance efforts to identify factors driving regionally divergent abundance trends with implications for population-level responses to future climate variability.

KEYWORDS: Steller sea lion, demography, survival, oceanographic conditions, environmental variability, conservation, mark-resight, hierarchical model, western Distinct Population Segment

### 0.0.2 **Introduction**

Though the population dynamics of Steller sea lions (*Eumetopias jubatus*) 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. Factors that have been examined include nutritional stress (Pascual & Adkison 1994, Trites & Donnelly 2003, Atkinson et al. 2008) and reduced age-specific survival and fecundity (York 1994, Loughlin & York 2000, Holmes et al. 2007). However, existing demographic studies have been conducted on relatively small spatio-temporal scales and have not included the central and western Aleutian Islands, where abundance seemingly continues to decline (Sweeney et al. 2018). Additionally, evaluations of the effects of oceanographic conditions have thus far focused on correlations with trends in abundance rather than demography. There has yet to be a comprehensive examination of factors that have been hypothesized to affect demography and therefore drive trends in abundance.

Pinnipeds exhibit a range of responses to oceanographic variability, including reduced body condition, lower reproductive output and changed maternal attendance patterns, shifts in diet and the timing of pupping or weaning, increased foraging effort, and higher levels of stranding and mortality. Existing research about the impacts of environmental variability on Steller sea lions has largely focused on examining 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) spanning oceanographic regime shifts and the heterogenous landscape created by the Aleutian Island passes. However, even though we have learned that Steller sea lion diet varies by region and over time (Sinclair & Zeppelin 2002, Call & Loughlin 2005), that female body condition and weaning age have varied across oceanographic regimes (Calkins et al. 1998, York et al. 2008), that diet diversity has traditionally been lower in areas where the population continues to decline (Merrick et al. 1997), and that sea lions likely use biophysical features of the landscape to locate nearshore prey aggregations (Loughlin et al. 2003, Fadely et al. 2005, Lander et al. 2010, 2011, 2020), these behavioral and physiological findings have not yet been linked to changes in demography.

Understanding the complex mechanisms linking environmental conditions to patterns in population dynamics is challenging and requires addressing the difficulties of making inference across differing spatio-temporal scales. This is particularly true for top predators that inhabit vast and heterogenous 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). While it is important to study these relationships at the scale that is most relevant to the species or ecological process of interest, this can oftentimes be difficult or impossible to do (Wiens 1989, Mannocci et al. 2017). 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 bridge the gap in understanding how Steller sea lion demography is responding to oceanographic variability over time and space. Based on the assumption that seasonal and interannual variability in certain biophysical features affects the distribution and availability of prey, we hypothesized that these 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, upwelling, wind, and chlorophyll concentration that can affect the level of storminess or the distribution, density, and abundance of forage fish, which in turn can affect foraging effort, energetic demands, the timing of weaning, reproductive output, and survival. On the one hand, sea lions are flexible foragers with numerous target prey species that can likely adapt in response to both short- and long-term environmental variability (Loughlin et al. 2003). On the other hand, sea lions are 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 (Sinclair & Zeppelin 2002).

In this study, we use mark-resight data from 2000-2018 for the western distinct population segment (DPS) 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 providing estimates of the effects of ocean conditions and comparing age- and sex-specific survival and natality over a greater spatio-temporal 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 abundance estimates have continued to decline, and provide insights into the links between environmental conditions and the demographic rates that drive abundance of this iconic top predator. Our results can inform conservation and management efforts in light of ongoing and future climatic change.

### 0.0.3 **Methods**

*Study system*  
The western DPS of Steller sea lions breeds on rookeries west of 144W, 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 male bulls establish territories beginning in May. Females reach reproductive maturity between the ages of 3 and 6 (Pitcher & Calkins 1981) and arrive at rookeries to give birth from late May to early July depending on the region (Pitcher et al. 2001, Kuhn et al. 2017). At a given rookery, the majority of pups are born within a relatively short time period and nurse throughout the summer before going out to sea with females for the fall and winter (Raum-Suryan et al. 2002). Females make short foraging trips throughout the summer breeding season, though their activities can vary depending on environmental conditions and local bathymetric features (Lander et al. 2010, Lander et al. 2011). Females exhibit a high degree of natal rookery site fidelity (Pitcher & Calkins 1981), but recent research suggests a greater degree of movement between regions within the Gulf of Alaska than was previously believed to occur (Fritz et al. 2016).

The Aleutian Islands archipelago is a vast, heterogenous, and 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 and biophysical characteristics of the numerous Aleutian passes, where nutrient mixing and transport occur. While much remains unknown about this region, which spans more than 2,000 km of ocean, researchers agree that the contrasting features to the east and west of Samalga Pass (~170W) represent a notable ecological boundary (Ladd et al. 2005a, Stabeno et al. 2005, Stabeno & Hunt 2005). Specifically, narrow, shallow passes to the east of Samalga Pass 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 genetic phylogeographic differentiation and diet composition also vary 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, the deep, wide passes to the west of Samalga Pass 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*) (Sinclair et al. 2005, Rand et al. 2019). These generalized patterns likely oversimplify the fine-scale spatio-temporal variability that occurs seasonally, interannually, and across island rookeries (Mordy et al. 2005, Fadely et al. 2005), particularly given the influence of micro-scale habitat features such as eddies (Stabeno et al. 1999, Hunt et al. 1999, Ladd et al. 2005b) that influence the availability, abundance, and distribution of predators and their prey.

*Data*  
Sea lion resights – In this study, we included observations of sea lions that have been branded with an individually unique mark, weighed, measured, and released as pups from rookeries in five regions in the western DPS (*n* = 2,833). Of the total marked individuals, approximately 13% were marked in the western portion of the range (Ulak and Agattu rookeries) beginning in 2011 (Agattu Is.) and 2013 (Ulak Is.), while the remainder were marked in the eastern portion of the range beginning in 2000 (Figure 1). Resighting 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. Capture histories for the western portion of the range were primarily based on remote camera data. Of the total number of marked pups across the range, 41% of females and 46% of males were not resighted.

In years when females were resighted, they were observed an average of six times. For each sighting, whether females were seen interacting with or in close proximity to pups was recorded as an indication of reproductive status, and only records with strong evidence of an association with a pup (e.g., nursing) were assumed to be definitive evidence of pupping. 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 non-breeders 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 very close physical contact with a single pup for a prolonged time (e.g., pup and female are sleeping together or the pair reunite after female returns from foraging).

Oceanographic data –- We examined metrics associated with both localized oceanographic conditions and basin-scale conditions as potential covariates on demography, assuming that these features directly (e.g., storminess) or indirectly (forage fish availability) affect survival and reproduction through several ecological mechanisms. Basin-scale indices included the Arctic Oscillation Index (AOI), Pacific Decadal Oscillation (PDO), the North Pacific Gyre Oscillation (NPGO), and the Aleutian Low (AL). The AOI characterizes Arctic climate patterns, where positive phases represent stronger winds, warmer temperatures, and decreased storminess (Higgins et al. 2000). The PDO is a metric based primarily on sea surface temperature and pressure (Zhang et al. 1997, Mantua et al. 1997), with warm and cool phases that impact salinity, mixed layer depth, and ocean productivity. The NPGO measures patterns in circulation and ocean currents, where positive-phases are marked by lower sea surface temperatures 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 low-pressure system that persists in the Aleutian Basin fall through spring each year and can impact the timing, location, and duration of regional storms (Seckel 1993, Rodionov et al. 2005). 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 NOAA National Center for Environmental Information (NOAA NCEI 2020) and NOAA Physical Science Laboratory (NOAA PSL 2020).

Localized environmental variables were obtained from satellite reanalysis products and included sea surface temperature (SST; C), chlorophyll-a concentration (mg/m), geostrophic meridional (north-south) and zonal (east-west) wind (m/second), and the Bakun upwelling index (m/second/100 m of coastline). Data for SST and wind were obtained from the Copernicus Marine Environment Monitoring Service (Martin et al. 2019). Monthly composite chlorophyll-a concentration was obtained from Aqua MODIS and SeaWiFS satellite products (NASA 2018) using the NOAA ERDDAP server (Simons 2020). Monthly upwelling anomalies in the Gulf of Alaska (60N, 149W) were obtained from the NOAA Pacific Fisheries Environmental Laboratory.

All variables were obtained at monthly levels, aggregated to seasonal means, and Z-scored over the time series. Because there is a high degree of uncertainty surrounding age- and sex-specific sea lion foraging patterns, the spatial extent of the bounding box for obtaining satellite data on environmental variables was relatively broad and encompassed waters surrounding the Aleutian chain (46.3 to 58.1N and -177.9 to -159W). However, for models examining the effects of ocean conditions on individuals marked and resighted in the western portion of the range, a smaller spatial extent was used for satellite data to reflect the smaller foraging range of those individuals (49.8 to 55.4N and 169.9 to 175.6E) (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 multi-state 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. Multi-event models (Kendall 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 & Nichols 2002, Lebreton & Pradel 2002, Kendall 2004). Multi-event models have been used extensively to assess reproductive status and survival in species with simple life histories, but have been increasingly used to examine vital rates and the effect of oceanographic conditions on demography for species with complex life histories (Fujiwara & Caswell 2002, Fay et al. 2015, Johnson et al. 2016, Tavecchia et al. 2016, Payo-Payo et al. 2016, Guery et al. 2017, Santidrian Tomillo 2017, Sanz-Aguilar et al. 2017, Champagnon et al. 2018, Himes Boor et al. *in review*). Here we use a multi-event 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.

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

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 , describing the probability of an individual being in state *z* conditional on its previous state and individual- and time-specific effects (Eq. (1)). For Steller sea lions, this transition array is decomposed into survival () and pupping probability (; the probability of a female that bred in year *t* having a pup in year *t+1* conditional on survival).

Interannual variability in survival and pupping probabilities for individuals marked in the eastern portion of the range were modeled as functions of environmental and individual covariates and random effects of year. That is, for general demographic rate parameter ,

where is an age (*a*) and sex (*s*)-specific intercept, is a vector of covariates with associated coefficients , and is an annual (*t*) random effect (Eq. (2)). The intercept for a given demographic rate was estimated using a logit-transformed uniform U(0,1) prior distribution on the probability scale. To increase parameter estimability and regulate model complexity, we applied penalized complexity approach (Simpson et al. 2017, van Erp et al. 2019) for defining prior distributions on and . Using 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 and oceanographic variable ) on demographic rate was assumed to be drawn from a unique Gaussian distribution as , with standard deviations distributed according to an exponential distribution with a fixed shrinkage rate to apply moderately strong shrinkage. Similarly, random year effects were assumed to be drawn from a Gaussian distribution as , with standard deviations 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 (), age 1-2 survival (“young”, ), and first-time () and repeat () 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, correlated random effects were assumed between sexes (except females with pups and adult males) and were also assumed for juvenile individuals ages 3-5 (i.e., year-specific deviations from the mean were modeled in common for these groups). For pupping probabilities, correlated random effects were assumed for all first-time breeding transitions for age 3-5 individuals ().

To assist in the estimation of age-specific survival for pups through age-5 individuals () in the western portion of the range where sample sizes were smaller, mean survival rates were modeled as,

where is an intrinsic autoregression or order 2 (IAR(2); Speckman and Sun 2003) scaled by and MVN represents a multivariate normal distribution (Eqs. (3)-(4)). The IAR(2) model imposes a smoothness constraint that is orthogonal to a quadratic fixed effect over the ages. Thus, it is equivalent to estimating two fewer parameters relative to *independent* age random effects. As with the previous penalized complexity priors, we used as a prior for the scaling parameter .

Age-specific natality (*f*, the number of offspring produced per female ages 4, 5, and 6+, assuming only singleton births) 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 range, age-specific and overall natality (proportion of females pupping in a given year) were calculated beginning in the 7th 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 4th year when at least one marked cohort had reached reproductive maturity.

Observation 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, define the events in the multi-event model,

where an observation conditional on the true state is categorically distributed with probability array (Eq. (5)). Components of detection probability for individual *i* at time *t* include the probability of detection, , and the probability of correctly ascertaining the presence of a pup for breeders, . Similar to demographic rates, detection probability was modeled as,

where the mean intercept for each sex *s* and age *a* was estimated using a logit-transformed prior that was uniform U(0,1) on the probability scale (Eq. (6)). For individuals marked in the eastern portion of the 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, 2018), where is drawn from a Gaussian distribution. Interannual variability in detection probability was estimated for the eastern portion of the range with random year effects assumed to be drawn from a Gaussian distribution as , with standard deviations estimated with shrinkage priors, distributed according to an exponential distribution with a fixed shrinkage rate as described above. 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 categorical covariate for the multi-event classification probability parameter, .

Variable and model selection – To reduce the number of covariates down 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 (Supplemental information). 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” model. For the western portion of the range, the AOI, NPGO, chlorophyll concentration, and northward wind were retained in the full 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 a set of full models (interannual random effects, pup body mass, and season-specific environmental covariates). 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 MCMC chain sample estimates for the environmental effects that was above versus below zero.

Models were fit using NIMBLE (NIMBLE Development Team 2019) within the R programming environment (R Core Development 2018) using 20,000-40,000 iterations and 10,000-20,000 burn-in depending on the model, a thinning rate of 1, and an adaptation rate of 10. We evaluated model convergence using visual inspection of chains and the Brooks-Gelman-Rubin statistic (Gelman & Rubin 1992; Brooks & Roberts 1998) < 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 problematic lack of fit. The typical set of mark-recapture model assumptions applied in this study, where it was assumed that branding did not affect detection probability, that survival and the reproductive state of individuals were independent, there were no identification errors, mortality during the sampling season was negligible, and that there was no unmodeled heterogeneity in survival and detection probabilities.

### 0.0.4 **Results**

*Demographic rate estimation*

##### 0.0.4.0.1 Survival

Eastern portion of the range – Mean pup survival across years in the eastern portion of the 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 similarly for both sexes, though survival for age-2 females (0.88; 0.82-0.92) was notably higher than that of age-2 males (0.76; 0.69-0.82; Figure 3, Table 1). 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 1). Survival for individuals marked in the eastern portion of the range was most variable over years for pups, age-1, and age-2 individuals (Figure 4a). Male and female pup survival over the study period ranged from approximately 0.27-0.95. Juvenile and pupping adult female survival remained relatively constant throughout the study period.

Western portion of the range – All age- and sex-specific survival rates for the western portion of the range from 2011-2018 were estimated with much greater uncertainty compared to those in the eastern portion of the range due to the smaller sample size. Mean female pup survival in the western and central Aleutians (Agattu and Ulak island rookeries) was 0.66 (0.55-0.8), similar to that in the east. However, mean male pup survival was 0.44 (0.36-0.56), which was significantly lower than males in the eastern portion of the range and females in either region (Figure 3, Table 1). Additionally, female survival for age-1 through pre-breeding age groups (age-3 to age-5) was notably lower compared to that of individuals marked in the eastern portion of the range. Estimates were similar between the eastern and western regions for adult males, but lower for females in the western portion of the range (0.84; 0.52-0.99).

##### 0.0.4.0.2 Pupping and natality

Eastern portion of the range – The probability of first-time pupping was highest for age-5 individuals (i.e., giving birth for the first time at age 5; ) at 0.72 (0.62-0.8) and much lower for age-6 individuals () at 0.16 (0.01-0.38) and age-4 individuals () at 0.13 (0.08-0.21) (Figure 5, Table 1). The probability of females with a young of year also pupping in the following year () was high (0.98; 0.96-0.99). The probability of pupping for females that had not given birth in the previous year () was low (0.08; 0.03-0.16). Though estimated with a relatively high degree of uncertainty, the temporal standard deviation in pupping probabilities for first-time breeders was relatively high ( = 1.26), reflecting rates that fluctuated substantially throughout the study period (Figure 4b). The probability of females pupping given an individual also had a pup in the previous year remained relatively constant throughout the study period. The probability of pupping given an individual did not have a young of year in the previous year remained relatively low over the study period, with the exception of 2006-2007, with an overall temporal standard deviation of = 0.8. Mean age-specific natality (calculated from the 7th year onward) was low for age-4 individuals (0.13; 0.04-0.28) and much higher for age-5 (0.81; 0.7-0.9). Overall natality (*f*, proportion of breeding-age females with a pup each year) was calculated as approximately 0.8 (0.74-0.84) in the last few years of the study period (Table 1).

Western portion of the range – Age-specific pupping probabilities in the western portion of the range mirrored that in the eastern portion (higher probability for age-5 individuals and existing breeders), though the mean probability of repeat pupping () 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 to that in the eastern portion of the range; Figure 5). Mean age-specific natality (calculated from the 4th year onward) was 0.38 (0.12-0.88) for age-4 individuals and 0.76 (0.49-1) for age-5 individuals. Natality for age-6+ in the western portion of the 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 approximately 0.7 (0.47-0.96; Table 1). Time-varying demographic rates were not examined for individuals marked in the western portion of the range due to fewer marked individuals resighted over fewer occasions.

##### 0.0.4.0.3 Detection

Detection probability increased with age for both males and females (Figure 6). 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 () 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.

##### 0.0.4.0.4 Individual and oceanographic covariates

The effect of individual characteristics and environmental conditions () 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 that indicates the strength of the correlation, and the proportion of MCMC samples that were above or below zero (p), which indicates the probability that the correlation was positive versus negative. In general, the uncertainty around coefficient effects increased with the addition of random effects for vital rates and detection probabilities.

*Effect of pup body mass*  
For individuals marked in the eastern portion of the range, pup mass had a positive effect on pup survival () for both females ( = 0.18; 0-0.37; p( = 0.98)) and males ( = 0.29; 0.12-0.48; p( = 1)), and young females age-1 to age-2 () as well ( = 0.07; -0.06-0.25; p = 0.82) (Figure 7). However, for individuals marked in the western portion of the range, pup mass had a negative effect on male pup survival ( = -0.26; -0.59-0.02; p = 0.95) and age 1-2 survival ( = -0.14; -0.66-0.17; p = 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 first-time pupping probability (; Figure 7).

*Effect of environmental conditions*  
For the eastern portion of the range, the full model included the AL, AOI, NPGO, chlorophyll concentration, meridional winds, and upwelling. With the exception of upwelling, season-specific variables largely had a positive effect on the survival of pups () that did not extend to individuals age 1-2 (Figure 8). More specifically, pup survival was positively correlated with positive-phase AL in the spring ( = 0.46; 0.04-0.84; p = 0.99), positive-phase AOI in the summer ( = 0.37; -0.22-1.04; p = 0.87) and positive-phase NPGO in the summer ( = 0.17; -0.17-0.82; p = 0.81) and fall ( = 0.31; -0.09-0.76; p = 0.91) (Figure 8). In terms of more localized conditions, pup survival was positively correlated with chlorophyll concentration during the winter ( = 0.45; 0.11-0.73; p = 0.99) and spring ( = 0.05; -0.19-0.49; p = 0.68) and negatively correlated with increased upwelling, particularly in the fall ( = -0.45; -1.13-0.15; p = 0.91) and winter ( = -0.68; -1.15–0.07; p = 0.99). In terms of reproduction, first-time pupping probability was positively correlated with summer positive-phase NPGO ( = 0.61; -0.02-1.23; p = 0.97) and increased summer upwelling ( = 0.31; -0.29-1.05; p = 0.84) and negatively correlated with stronger summer wind ( = -0.9; -1.6–0.16; p = 0.99). Repeat pupping probability was positively correlated with chlorophyll concentrations in the fall ( = 0.78; -0.1-2.05; p = 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 exhibited 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 9). 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 (). Specifically, positive-phase AOI in the fall ( = 0.84; -0.12-2.15; p = 0.92) and positive-phase NPGO in the fall ( = 1.27; 0.23-2.2; p = 0.99), winter ( = 0.89; 0.01-1.92; p = 0.98), and spring ( = 1.25; 0.48-2.03; p = 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 ( = 0.5; -0.19-1.4; p = 0.9) while stronger winds in spring and summer were correlated with lower survival rates. 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 in terms of lower WAIC values (Table 2). Much of the improvement in the full models compared with the null model ( = 310) was attributable to the addition of random effects ( = 8.7), with much smaller but meaningful improvements with the addition of individual and environmental covariates (Table 2). 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 ( = 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 Aleutian Low 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 (Supplemental information).

For demographic estimates in the western portion of the range, all full seasonal models performed better than the null model (Table 2). The best-fit model included covariates from the spring, followed closely by the model that included environmental variables from the fall season ( = 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 value could be attributed largely to the effect of spring and fall NPGO on age 1-2 survival, which in fact had the lowest WAIC value when included alone (Supplemental information).

### 0.0.5 **Discussion**

We used mark-resight data to estimate survival and natality and the effects of pup weight and oceanographic conditions for the western DPS of Steller sea lions in Alaska. This study provides the first demographic rate estimates for individuals marked in the western and central Aleutians where populations continue 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.

*Demographic comparisons*  
Regional comparisons – One consistent finding in many Steller sea lion studies is that survival estimates vary both between and within regions as well as over time, oftentimes complicating direct comparison of results from different studies. However, in general, survival rates estimated for the eastern portion of the range in this study were similar to (or higher than) previous estimates (York 1994, Pendleton et al. 2006, Fritz et al. 2014, Maniscalco et al. 2015) and to those estimated for the eastern DPS (Hastings et al. 2011, 2021, Wright et al. 2017). Though natality is an important component of demography that can influence population dynamics, less is known about this vital rate for this population and it is difficult to compare our results to most previous estimates that relied on proportions of observed breeders in aerial surveys, where the proportion of individuals hauled out at a given time and the proportion of pups that had been born or already died were unknown. In this study, our estimates of overall natality were approximately 0.8 in the eastern portion of the range, which is similar to that estimated in the late 2000s in the eastern Gulf of Alaska (Maniscalco et al. 2010, 2014). These rates are within the range of those observed in stable or increasing pinniped populations (McKenzie et al. 2005, Testa 1987, Lunn et al. 1994) compared with rates of below 0.55 that have been associated with declining populations (Pitcher et al. 1998, Dabin et al. 2005).

Researchers have hypothesized that the historical and ongoing decline in counts at rookeries in the western portion of the range may be due to a combination of demographic or environmental factors (Loughlin & York 2000, Holmes et al. 2007). 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. Survival rates for the western portion of the 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 age-2 females. Overall natality was also lower in the western portion of the range at 0.7. Though these estimates have a higher degree of uncertainty due to the smaller sample size, these differences are striking and could be limiting population growth for these regions of the western DPS. Mean male pup survival for individuals born in the western portion of the range was 0.44. Survival estimates for individuals age 0-3 in the Asian stock of Steller sea lions that resides in the Russian Far East (geographically closer to the western Aleutian Islands than other rookeries in the western DPS) ranged from approximately 0.6 to 0.8 (Altukhov et al. 2015), much higher than reported here. 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, Gaillard et al. 2003).

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 reproductive fitness. Age-specific survival generally increased with age from pups to adults for both males and females, which is what would be expected for long-lived mammals according to the demographic buffering hypothesis (Gaillard et al. 1998, Pfister 1998, Eberhardt 2002, Rotella et al. 2012) and what has been noted in previous studies of this species for both the eastern and western DPSs (Maniscalco et al. 2010, Hastings et al. 2011, 2018, Altukhov et al. 2015, 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 that of pups, which has also been observed by others (Pendleton et al. 2006, Fritz et al. 2014, Maniscalco et al. 2014, Altukhov et al. 2015). The effect of pup mass was also different across sexes and regions, with a positive correlation in the eastern portion of the 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 differential maternal investment strategies and age-at-weaning across the range.

Our results indicated that heavier pups had a higher probability of survival in their first year in the eastern portion of the range and a lower probability in the west, the effects of which were not strongly evident past the first year. Larger pups might be able to forage more effectively 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 the eastern DPS (Hastings et al. 2011, Wright et al. 2017) and for other pinniped species around the world, particularly fur seals (Boltnev et al. 1998) and Weddell seals (Thomas & DeMaster 1993, Hadley et al. 2007, Proffitt et al. 2010). However, females can compensate for smaller pup size by increasing maternal investment and/or weaning later (Trillmich 1990, Lee et al. 1991, Pitcher et al. 1998), providing support for the assertion that maternal care is more influential than birth mass for otariids (Boyd 1990, McMahon & Hindell 2003). Hastings et al. (2021) found that in certain rookeries in both the eastern and western DPSs, females were weaned sooner than males, that earlier weaned yearlings had a lower probability of survival, that heavier pups were more likely to wean by one year of age, and that pup body mass had a positive effect on survival. In applying these concepts to our findings, it is possible that larger pups in the western portion of the range are weaned sooner and therefore ultimately have lower survival. 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 influence many aspects of foraging, health, maternal investment, and reproductive success in pinnipeds. Studies have shown that other otariids, primarily fur seals, associate with certain frontal features or oceanographic niches while foraging or migrating (McCafferty et al. 1998, Loughlin 1999, Georges et al. 2000, Guinet et al. 2001, Ream 2005, Sterling et al. 2014, Joy et al. 2015, Speakman et al. 2020), 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), sea surface temperatures and first-year survival for subantarctic fur seals (Beauplet et al. 2005), and El Niño conditions and first-year survival in southern elephant seals (McMahon & Burton 2005). In this study, we found that there was strong evidence that the NPGO, the Aleutian Low, the AOI, northward wind, and chlorophyll concentration were positively correlated with pup or age 1-2 survival and that upwelling was positively correlated with fecundity. Taken together, these results could indicate that lower sea surface temperatures, 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 Aleutian Low was most impactful 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 range. These seasons are likely important in terms of life history events, as research has shown that pups are most vulnerable during their first winter (York 1994, Trites & Larkin 1996), as they are limited to shallower diving and the physiological constraints of their smaller body size (Trites & Porter 2002). 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. For example, stronger spring Aleutian Lows may be associated with higher wind stress, stronger downwelling eddies, and increased chlorophyll concentrations (Prants et al. 2018) that could affect the aggregation of prey species and favorable foraging conditions for lactating females in the summer and milder conditions during a pup’s first winter. 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. 2020) and may also influence plankton dynamics (Di Lorenzo et al. 2008) that affect both the availability and quality of forage fish. Notably absent from the group of variables that showed some degree of correlation with demographic rates is sea surface temperature, which has been shown to affect 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 sea surface temperature 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 earlier weaning) or indirectly by affecting maternal investment (i.e., fat storage, nutrient transfer, 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), but in this case, that is complicated by several factors. First, multiple spatio-temporal 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 non-stationary relationships make it challenging to identify mechanistic pathways by which environmental variables affect demography. We know that landscape features are important, it is just that the reasons why they matter simultaneously vary by individual sea lion, rookery, region, season, and year. 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. Nursing females can compensate for unfavorable foraging conditions or smaller pup birth weights by extending lactation or changing foraging behavior (Stearns 1976, Trites & Porter 2002, York et al. 2008, Maniscalco et al. 2014, Balme et al. 2017). While this flexibility may be particularly important in high-latitude environments with strong seasonality (Varpe et al. 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, and localized measures of prey availability (though these are not readily available). 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 age- and sex-specific differences in base demographic rates that may inform ongoing investigation into the divergent abundance trends that have been observed between the eastern and western portions of the western DPS. Our results emphasize the improvement in precision that can be achieved with a longer-term dataset and the benefits of continued focus on obtaining additional years of data for the western portion of the range. Though the current study design precluded the identification of specific mechanisms by which ocean conditions affect demography, we have highlighted correlations that provide insight into ecological processes and patterns over the nearly 20-year study that could be explored further in future studies. This research has provided important information for the conservation and management of this species, particularly for portions of this endangered population that show continued evidence of decline, 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.

### 0.0.6 **Conclusion**

This study 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 western DPS 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 spatio-temporal scope, which has facilitated the estimation of demographic rates with reasonable precision in the eastern portion of the range and highlight the importance of continued survey effort in the central and western Aleutians to reduce the uncertainty in age 1-2 survival probabilities and enable a more robust estimate 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 western DPS range, we found correlations of varying strength and degree between sea lion vital rates and seasonal oceanographic conditions. Namely, the spring Aleutian Lows, summer and winter AOI and wind velocities, fall and winter chlorophyll concentrations, and NPGO and upwelling throughout the year exhibited age- or region-specific positive or negative 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 western DPS will enhance our ability to estimate population viability and trends in abundance and inform ongoing conservation and management strategies for this endangered species.

### 0.0.7 **Acknowledgments**

[placeholder - get permit numbers] The findings and conclusions of the NOAA and USGS authors in the paper are their own and do not necessarily represent the views of the National Marine Fisheries Service, NOAA or United States Geological Survey. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

### 0.0.8 **Figures and Tables**

![](data:application/pdf;base64,) Figure 1: Steller sea lion field camps (blue triangles) in the eastern portion of the range, remote cameras (green squares) in the western portion of the range, and rookeries (red) throughout the western distinct population segment (DPS) (excluding Russia) and southeast Alaska (eastern DPS that extends along the U.S. West Coast). Black rectangles indicate locations from which satellite data were aggregated for use as covariates in the eastern (46.3 to 58.1^∘N and -177.9 to -159^∘W) and western (49.8 to 55.4^∘N and 169.9 to 175.6^∘E) portions of the range. Table shows the number of marked and released pups in each region over the study period.

![](data:application/pdf;base64,) Figure 2: Life cycle diagram depicting ecological state process parameters for females and males, with states for females including pre-breeding ages 3-5, pupping state for ages 4+, and non-pupping state for ages 5+. Females that have not pupped by age 6 automatically transition into a non-pupping state.

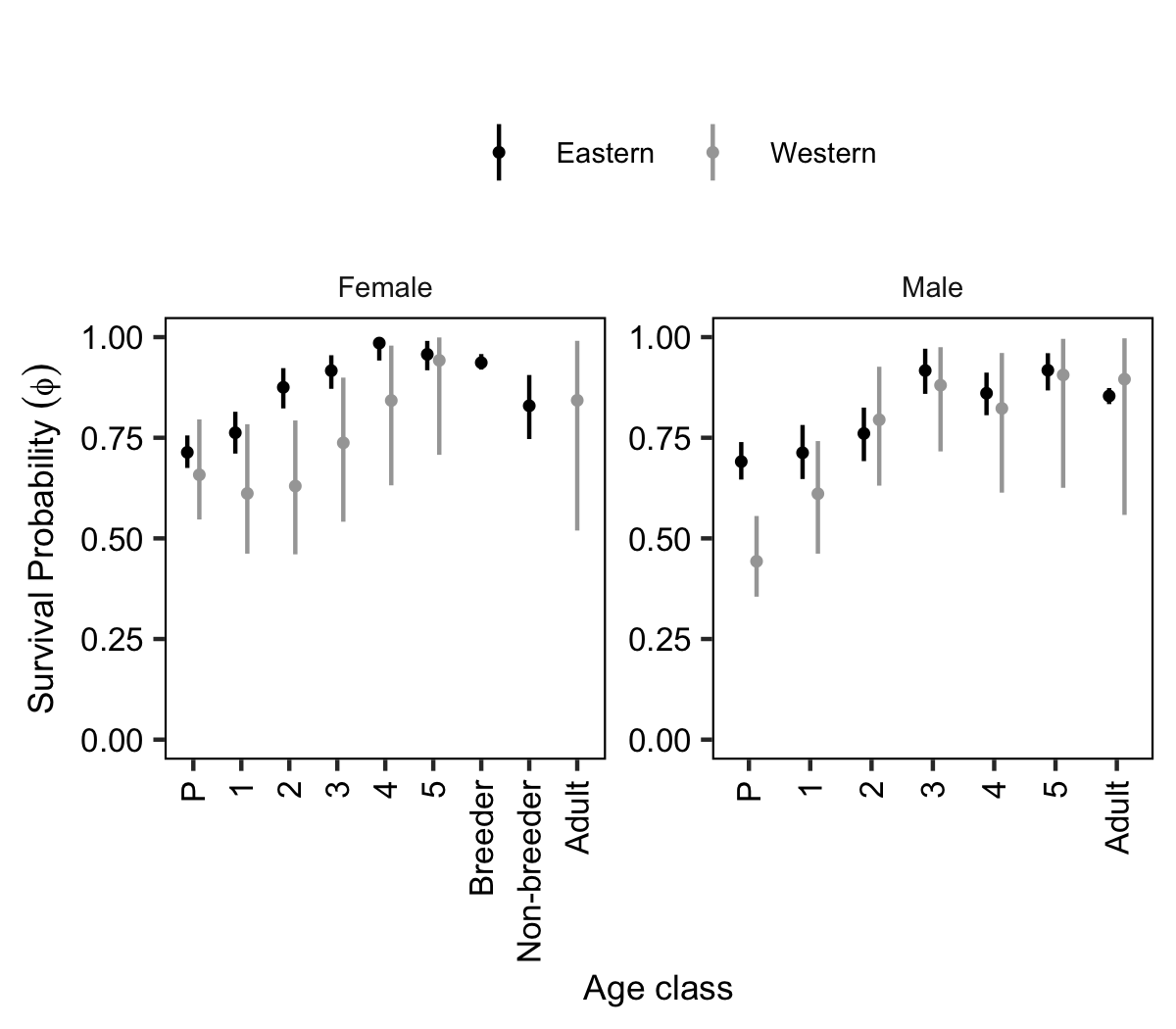


Figure 3: Posterior mean and 95% credible intervals for age- and sex-specific survival of Steller sea lions in the eastern (black) and western (grey) portion of the range.

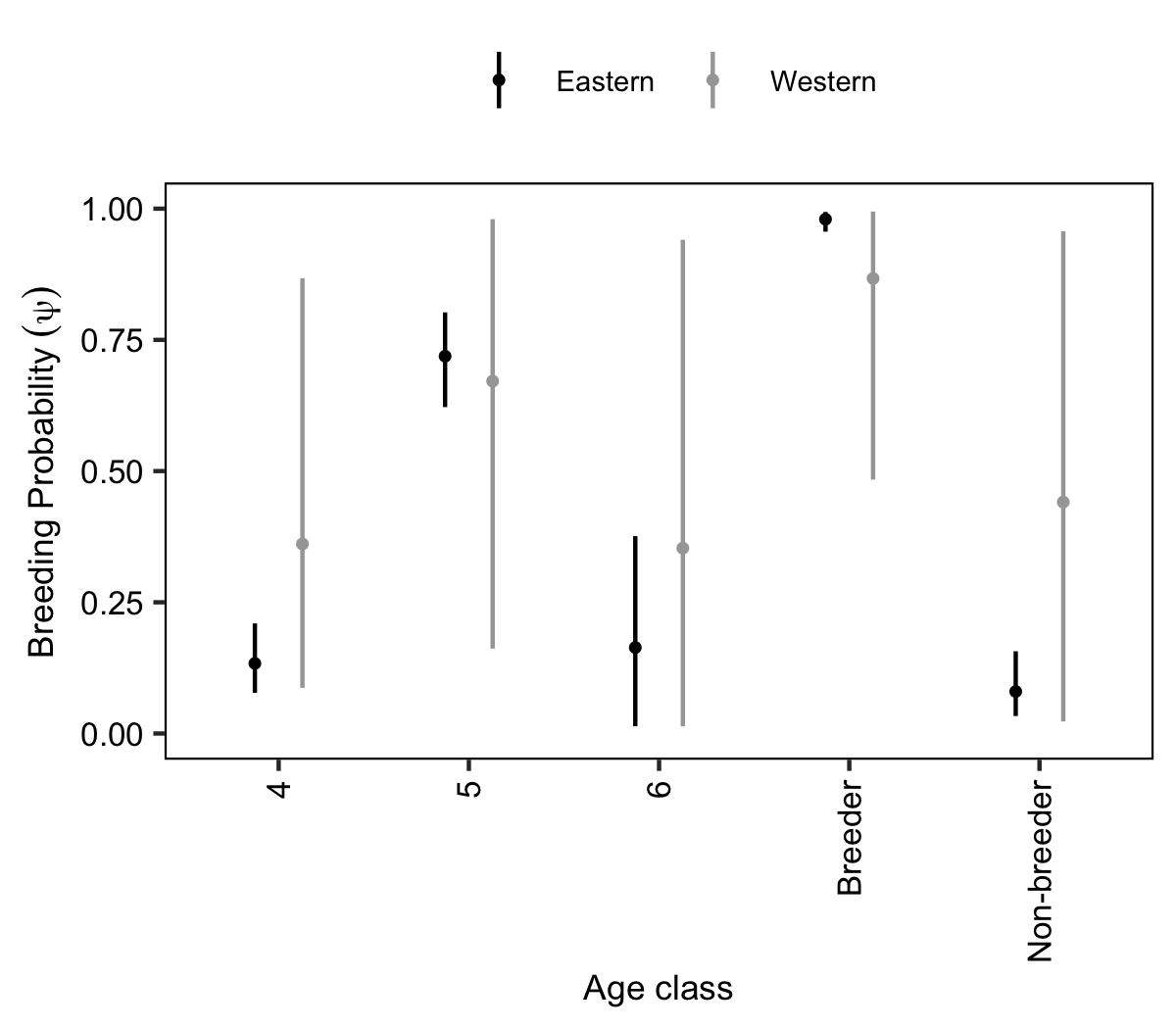


Figure 5: Posterior mean and 95% credible intervals for age-specific pupping probability for female Steller sea lions in the eastern (black) and western (grey) portion of the range.

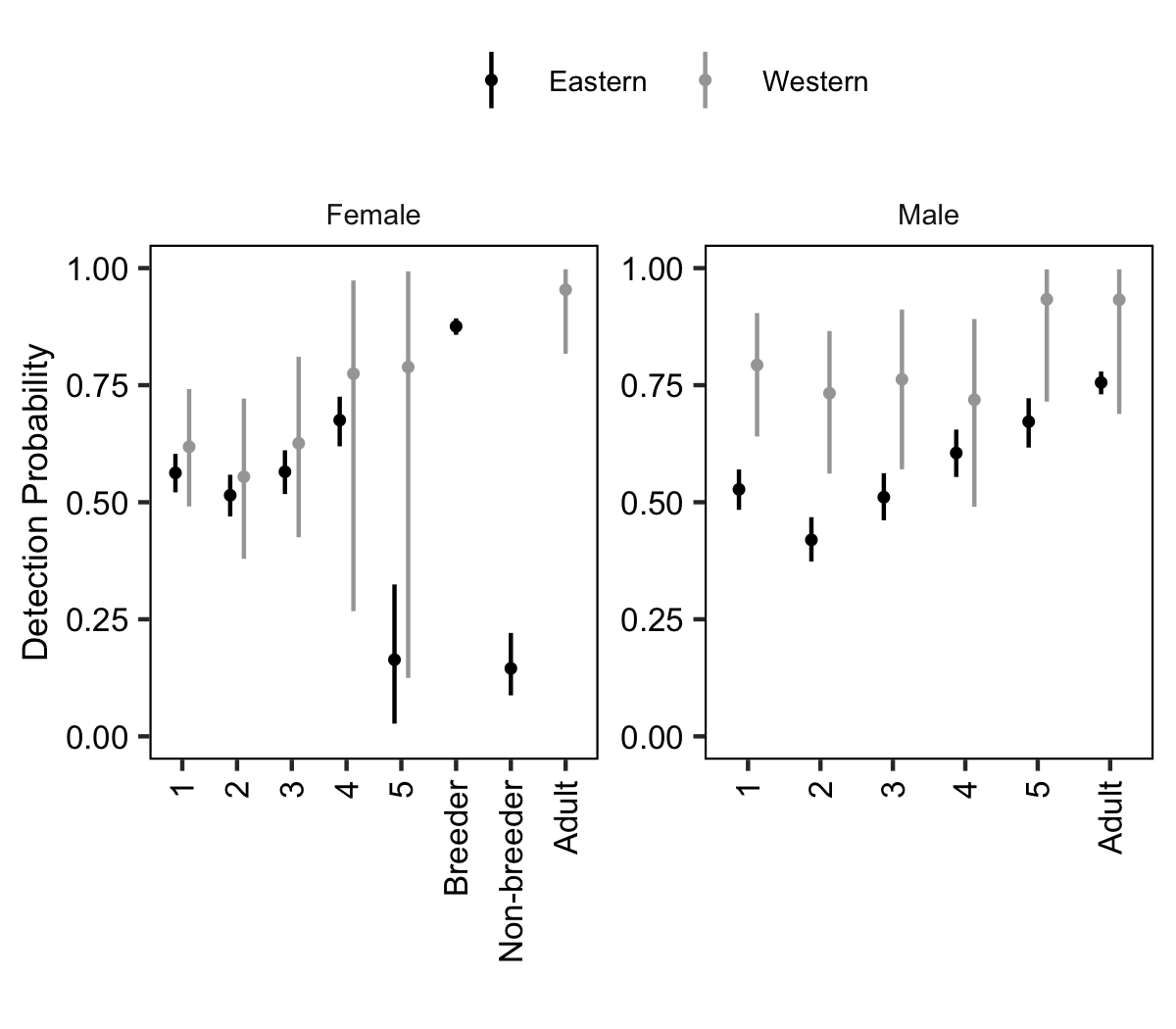


Figure 6: Posterior mean and 95% credible intervals for age- and sex-specific detection probability of Steller sea lions marked in the eastern (black) and western (grey) portion of the range.

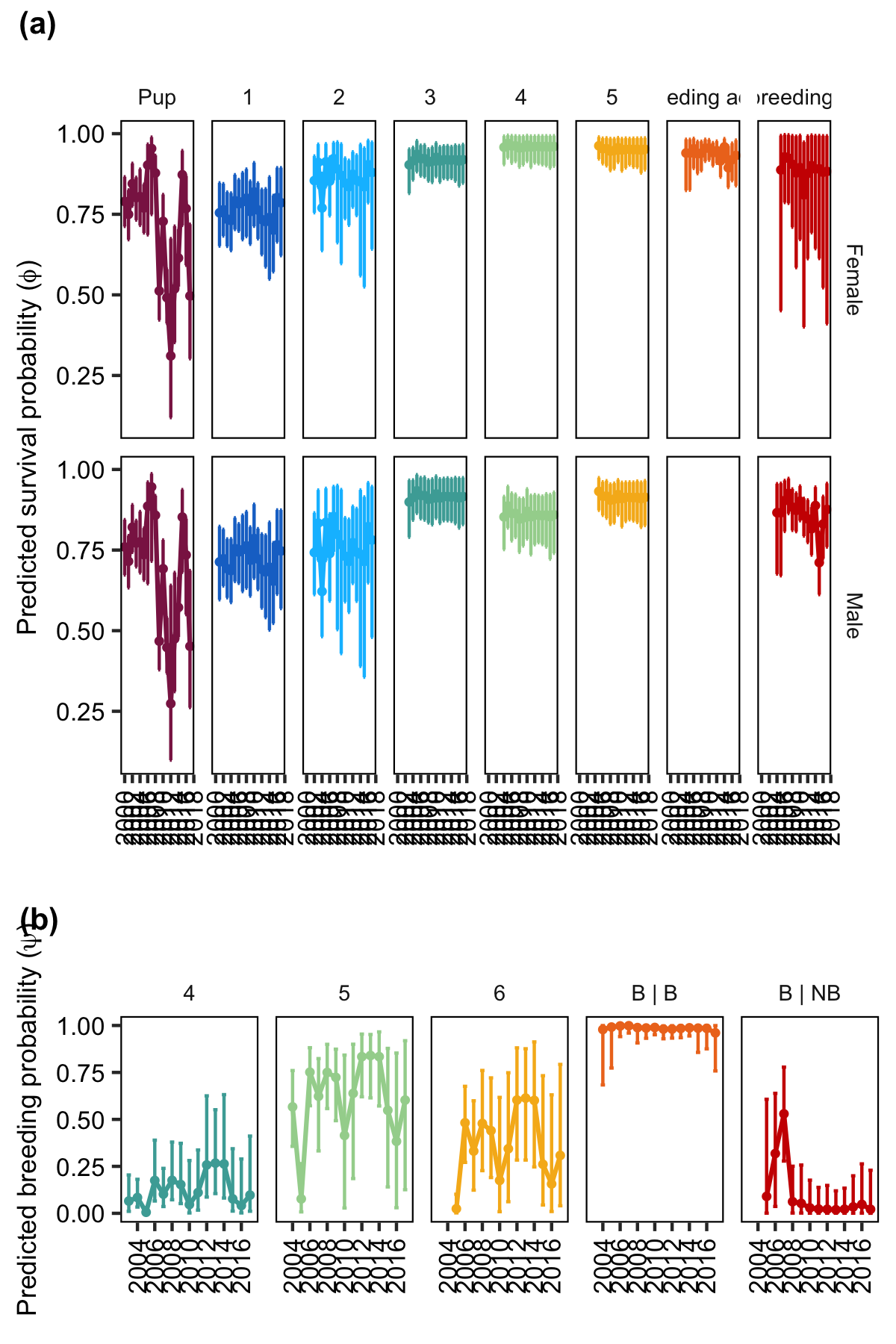


Figure 4: Posterior mean and 95% credible interval for predicted time-varying age-specific (a) survival and (b) pupping probability for Steller sea lions marked in the eastern portion of the range.

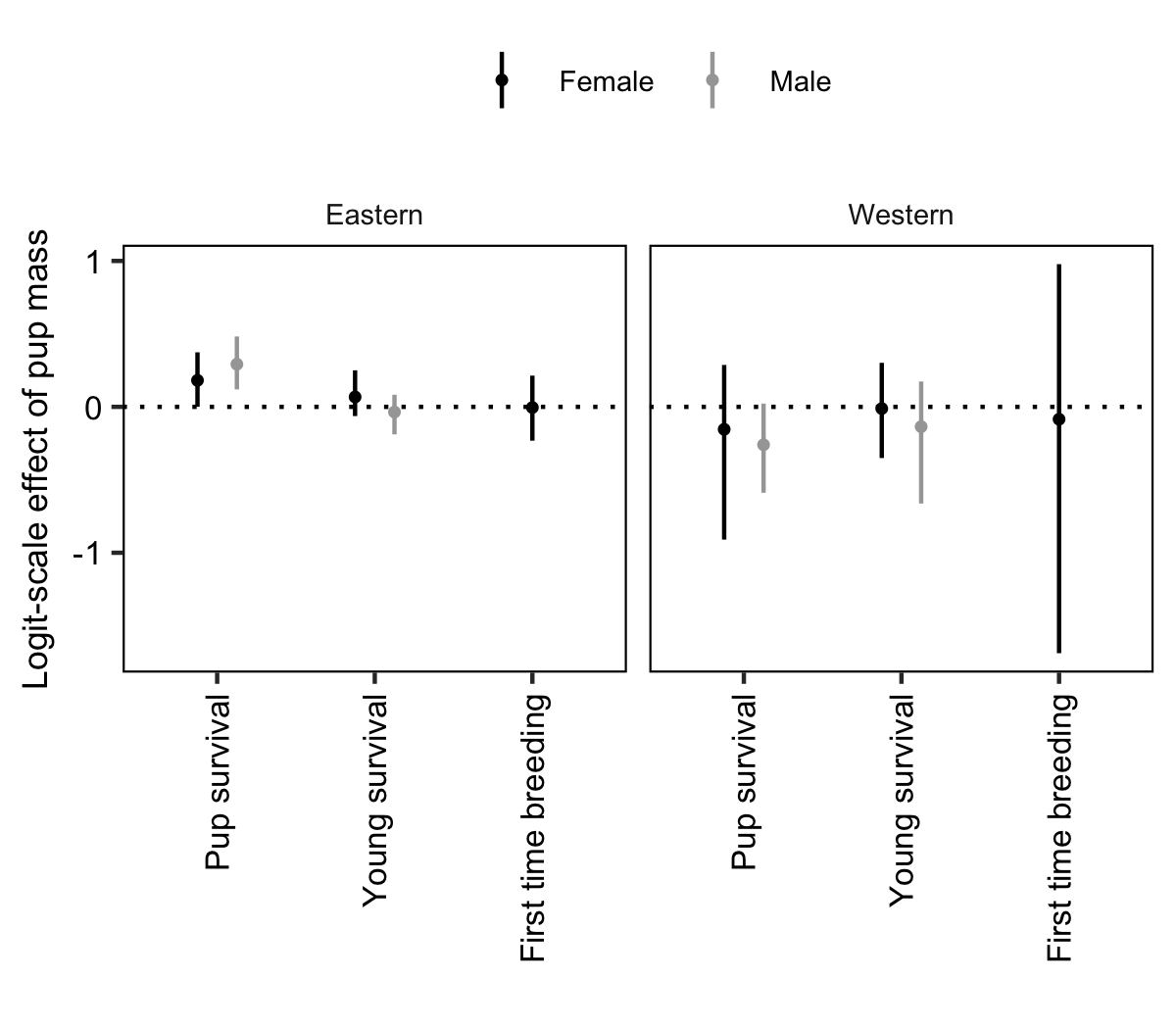


Figure 7: Logit-scale posterior mean and 95% credible intervals for the fixed effects of pup mass at branding on male (grey) and female (black) pup and age 1-2 survival and first-time pupping probability for individuals marked in the eastern and western portions of the range.

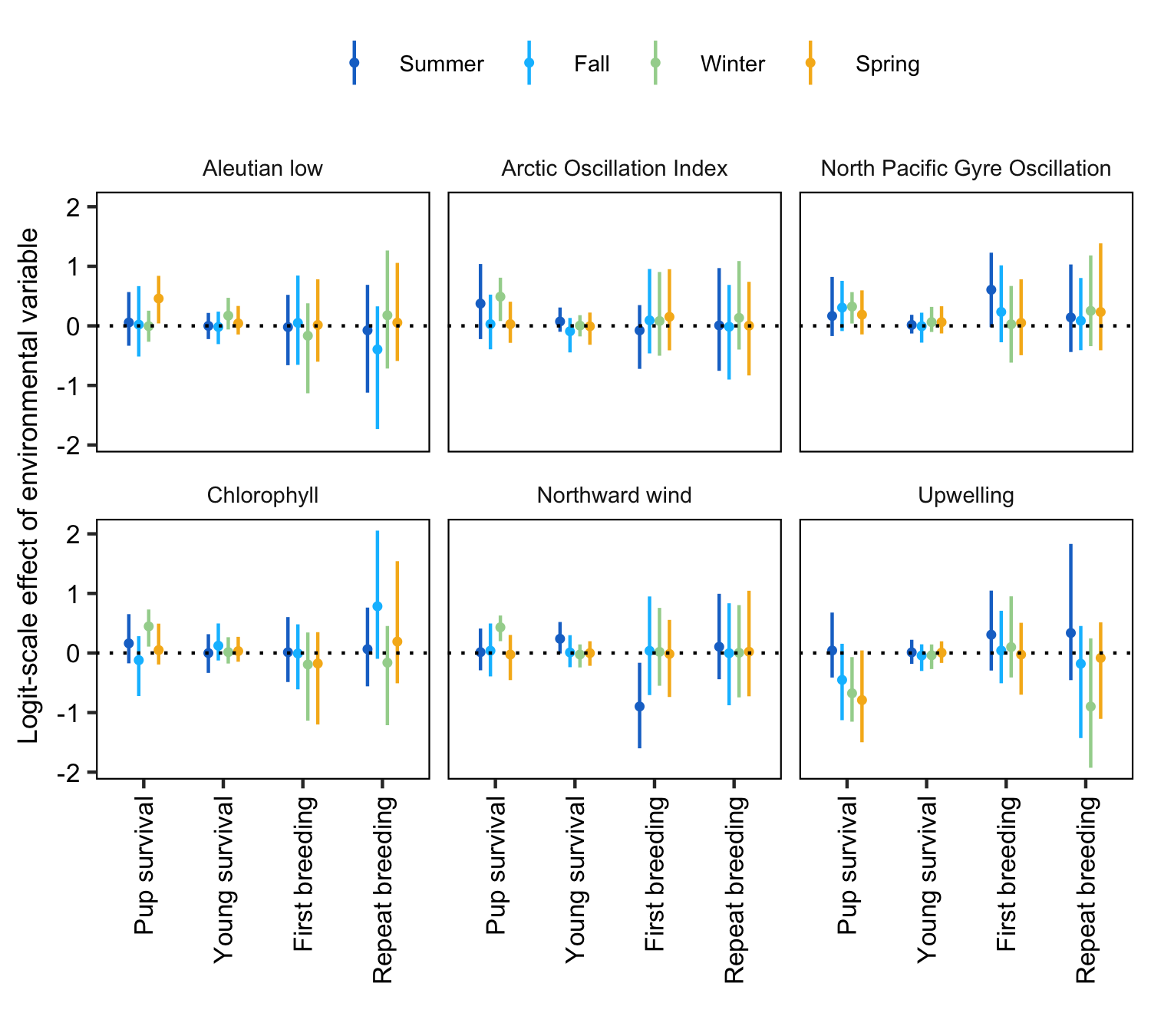


Figure 8: Logit-scale posterior mean and 95% credible intervals for the fixed effects of season-specific environmental covariates on pup and age 1-2 survival and first-time and repeat pupping probabilities for individuals marked in the eastern portion of the range.

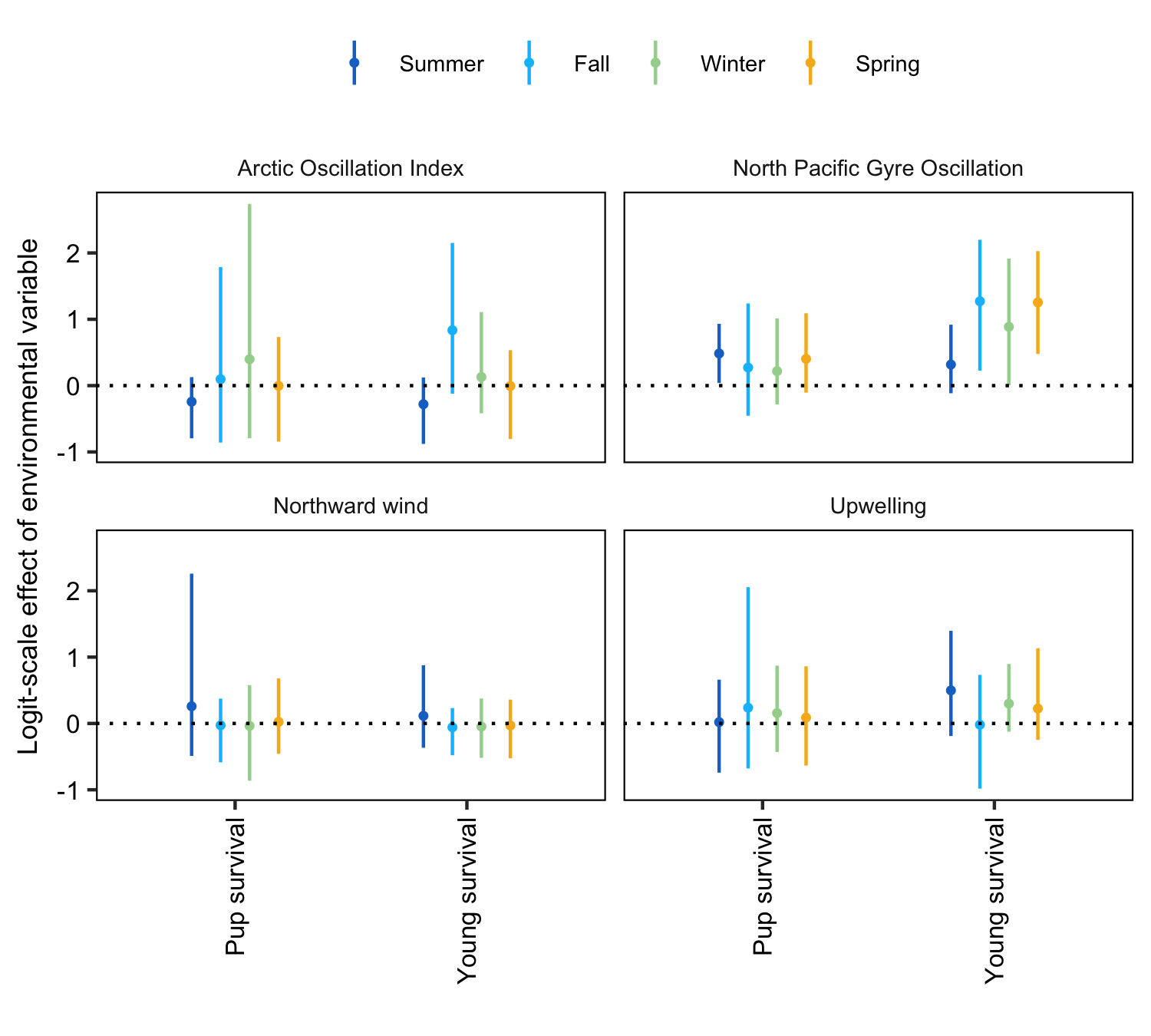


Figure 9: Logit-scale posterior mean and 95% credible intervals for the fixed effects of season-specific environmental covariates on pup and age 1-2 survival for individuals marked in the western portion of the range.

Table 1: Posterior mean and 95% credible intervals for age- and sex-specific (M = male; F = female) survival (phi edit) and natality (f) parameters.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Parameter | Age class | Eastern | 95% CI | Western | 95% CI |
|  | P | 0.71 | 0.67-0.76 | 0.66 | 0.55-0.8 |
|  | P | 0.69 | 0.65-0.74 | 0.44 | 0.36-0.56 |
|  | 1 | 0.76 | 0.71-0.81 | 0.61 | 0.46-0.78 |
|  | 1 | 0.71 | 0.65-0.78 | 0.61 | 0.46-0.74 |
|  | 2 | 0.88 | 0.82-0.92 | 0.63 | 0.46-0.79 |
|  | 2 | 0.76 | 0.69-0.82 | 0.79 | 0.63-0.93 |
|  | 3 | 0.92 | 0.87-0.96 | 0.74 | 0.54-0.9 |
|  | 3 | 0.92 | 0.86-0.97 | 0.88 | 0.72-0.98 |
|  | 4 | 0.99 | 0.94-1 | 0.84 | 0.63-0.98 |
|  | 4 | 0.86 | 0.81-0.91 | 0.82 | 0.61-0.96 |
|  | 5 | 0.96 | 0.92-0.99 | 0.94 | 0.71-1 |
|  | 5 | 0.92 | 0.87-0.96 | 0.91 | 0.63-1 |
|  | Breeder | 0.94 | 0.92-0.96 | NA | NA |
|  | Non-breeder | 0.83 | 0.75-0.91 | NA | NA |
|  | Adult | 0.85 | 0.83-0.87 | 0.90 | 0.56-1 |
|  | Adult | NA | NA | 0.84 | 0.52-0.99 |
|  | 4 | 0.13 | 0.04-0.28 | 0.38 | 0.12-0.88 |
|  | 5 | 0.81 | 0.7-0.9 | 0.76 | 0.49-1 |
|  | all | 0.80 | 0.74-0.84 | 0.70 | 0.47-0.96 |

Table 2: WAIC values for models of individuals marked in the eastern (null, random effects only, seasonal full models) and western (null and seasonal full models) portions of the range.

|  |  |  |  |
| --- | --- | --- | --- |
| Region | Model | WAIC | delWAIC |
| Eastern | Full (Winter) | 17,701.1 | 0.0 |
| Eastern | Random effects only | 17,709.8 | 8.7 |
| Eastern | Full (Summer) | 17,710.4 | 9.3 |
| Eastern | Full (Spring) | 17,714.4 | 13.3 |
| Eastern | Full (Fall) | 17,715.3 | 14.3 |
| Eastern | Null | 18,011.0 | 310.0 |
| Western | Full (Spring) | 919.2 | 0.0 |
| Western | Full (Fall) | 921.3 | 2.1 |
| Western | Full (Winter) | 922.9 | 3.7 |
| Western | Full (Summer) | 930.5 | 11.3 |
| Western | Null | 933.7 | 14.5 |

### 0.0.9 **Literature Cited**

Atkinson, S., D.P. Demaster, and D.G. Calkins. 2008. Anthropogenic Causes of the Western Steller Sea Lion Eumetopias Jubatus Population Decline and Their Threat to Recovery. Mammal Review 38 (1): 1–18. <doi:10.1111/j.1365-2907.2008.00128.x>.

Benson, A.J., and A.W. Trites. 2002. Ecological Effects of Regime Shifts in the Bering Sea and Eastern North Pacific Ocean. Fish and Fisheries 3 (2): 95–113. <doi:10.1046/j.1467-2979.2002.00078.x>.

Boltnev AI, York AE, Antonelis GA. 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. Candian Journal of Zoology 76:843–854.

Boyd IL. 1990. State-dependent fertility in pinnipeds: contrasting capital and income breeders. Functional Ecology 14:623–630.

Brooks, S.P. & Roberts, G.O. 1998. Convergence assessment techniques for Markov chain Monte Carlo. Statistics and Computing, 8, 319-335.

Conn, P.B., D.S. Johnson, L.W. Fritz, and B.S. Fadely. 2014. Examining the Utility of Fishery and Survey Data to Detect Prey Removal Effects on Steller Sea Lions (Eumetopias Jubatus). Canadian Journal of Fisheries and Aquatic Sciences 71 (8): 1229–42. <doi:10.1139/cjfas-2013-0602>.

Copernicus Marine Environment Monitoring Service, 2020. <https://resources.marine.copernicus.eu/documents/PUM/CMEMS-MOB-PUM-015-002.pdf>

de Valpine, P., D. Turek, C.J. Paciorek, C. Anderson-Bergman, D. Temple Lang, an Bodik. NIMBLE Development Team. 2019. Programming with models: writing statistical algorithms for general model structures with NIMBLE. Journal of Computational and Graphical Statistics 26: 403-413. <DOI:10.1080/10618600.2016.1172487>.

Di Lorenzo E., Schneider N., Cobb K. M., Chhak, K, Franks P. J. S., Miller A. J., McWilliams J. C., Bograd S. J., Arango H., Curchister E., Powell T. M. and P. Rivere, 2008: North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys. Res. Lett., 35, L08607, <doi:10.1029/2007GL032838>.

Fritz, L., K. Sweeney, D. Johnson, M. Lynn, T. Gelatt, and J. Gilpatrick. 2013. Aerial and ship- based surveys of Steller sea lions (Eumetopias jubatus) conducted in Alaska in June-July 2008 through 2012, and an update on the status and trend of the western distinct population segment in Alaska. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC- 251, 92 p.

Fritz L., R. Towell, T. Gelatt, D. Johnson, and T. Loughlin. 2014. Recent increases in survival of western Steller sea lions in Alaska and implications for recovery. Endang. Spec. Res. 26(1):13–24. doi: 10.3354/esr00634.

Fritz, L., K. Sweeney, R. Towell, and T. Gelatt. 2016. Aerial and ship- based surveys of Steller sea lions (Eumetopias jubatus) conducted in Alaska in June-July 2013 through 2015, and an update on the status and trend of the western distinct population segment in Alaska. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-321, 72 p. <doi:10.7289/V5/TM-AFSC-321>.

Gelman, A. & Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. Statist. Sci., 7, 457-472.

Higgins, R. W., A. Leetmaa, Y. Xue, and A. Barnston, 2000: Dominant factors influencing the seasonal predictability of U.S. precipitation and surface air temperature. J. Climate, 13, 3994-4017.

Himes Boor, G., McGuire, T.L., Warlick, A.J., Taylor, R.L., Converse, S.J., McClung, J.R., and A.D. Stephens. *In review*. Estimating a reproductive rate when offspring ages are uncertain: a novel multievent mark-recapture model applied to an endangered beluga whale population.

Holmes, E.E., L.W. Fritz, A.E. York, and K. Sweeney. 2007. Age-Structured Modeling Reveals Long-Term Declines in the Natality of Western Steller Sea Lions. Ecological Applications 17 (8): 2214–32. <doi:10.1890/07-0508.1>.

Kuhn, C.E., K.C., D. Johnson, and L. Fritz. 2017. A Re-Examination of the Timing of Pupping for Steller Sea Lions Eumetopias Jubatus Breeding on Two Islands in Alaska. Endangered Species Research 32: 213–22. <doi:10.3354/esr00796>.

Lander, M., T. Loughlin, M. Logsdon, G. VanBlaricom, and B. Fadely. 2010. Foraging Effort of Juvenile Steller Sea Lions Eumetopias Jubatus with Respect to Heterogeneity of Sea Surface Temperature. Endangered Species Research 10 (March): 145–58. <doi:10.3354/esr00260>.

Lander, M.E., M.L. Logsdon, T.R. Loughlin, and G. Van Blaricom. 2011. Spatial Patterns and Scaling Behaviors of Steller Sea Lion (Eumetopias Jubatus) Distributions and Their Environment. Journal of Theoretical Biology 274 (1): 74–83. <doi:10.1016/j.jtbi.2011.01.015>.

Lander, M.E., Fadely, B.S., Gelatt, T.S., Sterling, J.T., Johnson, D.S., Pelland, N.A., 2020. Mixing it up in Alaska: Habitat use of adult female Steller sea lions reveals a variety of foraging strategies. Ecosphere 11, e03021. <https://doi.org/10.1002/ecs2.3021>

Lee PC, Majluf P, Gordon IJ. 1991. Growth, weaning and maternal investment from a comparative perspective. Journal of Zoology 225:9–114.

Loughlin, T.R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. Molecular Genetics of Marine Mammals 3:159-171.

Loughlin, T.R., and A.E. York. 2000. “An Accounting of the Sources of Steller Sea Lion, Eumetopias Jubatus, Mortality.” Marine Fisheries Review, 6.

Maniscalco, J.M., Springer, A.M., Parker, P., 2010. High Natality Rates of Endangered Steller Sea Lions in Kenai Fjords, Alaska and Perceptions of Population Status in the Gulf of Alaska. PLOS ONE 5, e10076. <https://doi.org/10.1371/journal.pone.0010076>

Maniscalco, J.M., A.M., Springer, P. Parker, M.D. Adkinson. 2014. A longitudinal study of Steller sea lion natality rates in the Gulf of Alaska with comparisons to census data. PLOS One 9:e111523.

Maniscalco, J.M., 2014. The Effects of Birth Weight and Maternal Care on Survival of Juvenile Steller Sea Lions (Eumetopias jubatus). PLOS ONE 9, e96328. <https://doi.org/10.1371/journal.pone.0096328>

Mannocci, L., A.M. Boustany, J.J. Roberts, D.M. Palacios, D.C. Dunn, P.N. Halpin, S. Viehman, et al. 2017. Temporal Resolutions in Species Distribution Models of Highly Mobile Marine Animals: Recommendations for Ecologists and Managers. Diversity and Distributions 23 (10): 1098–1109. <doi:10.1111/ddi.12609>.

Mantua, N. J., S. R. Hare, Y., Zhang, J. M. Wallace, and R. C. Francis, 1997: A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Met. Soc., 76, 1069-1079.

Martin, M., McLaren, A., Good, S., 2019. PRODUCT USER MANUAL For Global Ocean GMPE Sea Surface Temperature Multi Product Ensemble SST\_GLO\_SST\_L4\_NRT\_OBSERVATIONS\_010\_005 16.

McMahon CR, Hindell MA. 2003. Twinning in southern elephant seals: implications of resource allocation by mothers. Wildlife Research 30:35–39.

McMahon, C.R., Burton, H.R., 2005. Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, Mirounga leonina, pup survival. Proceedings of the Royal Society B: Biological Sciences 272, 923–928. <https://doi.org/10.1098/rspb.2004.3038>

Merrick, R.L., M.K. Chumbley, and G.V Byrd. 1997. Diet Diversity of Steller Sea Lions (Eumetopias Jubatus) and Their Population Decline in Alaska: A Potential Relationship. Canadian Journal of Fisheries and Aquatic Sciences 54 (6): 1342–8. <doi:10.1139/f97-037>.

NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. 2018. Sea-viewing Wide Field-of-view Sensor (SeaWiFS) R2018.0 Chlorophyll Data; NASA OB.DAAC, Greenbelt, MD, USA. doi: <https://dx.doi.org/10.5067/ORBVIEW-2/SEAWIFS/L3M/CHL/2018>.

NOAA NCEI, 2020. NOAA Climate monitoring teleconnections: Arctic Oscillation. <https://www.ncdc.noaa.gov/teleconnections/ao/> accessed July 1, 2020.

NOAA PSL, 2020. NOAA Physical Sciences Laboratory: Gridded Climate Datasets. <https://psl.noaa.gov/data/gridded/tables/ocean.html> accessed July 1, 2020.

O’Corry-Crowe, G., Taylor, B.L., Gelatt, T., Loughlin, T.R., Bickham, J., Basterretche, M., Pitcher, K.W., DeMaster, D.P., 2006. Demographic independence along ecosystem boundaries in Steller sea lions revealed by mtDNA analysis: implications for management of an endangered species. Can. J. Zool. 84, 1796–1809. <https://doi.org/10.1139/z06-167>

Pascual, M.A., and M.D. Adkison. 1994. The Decline of the Steller Sea Lion in the Northeast Pacific: Demography, Harvest or Environment? Ecological Applications 4 (2): 393–403. <doi:10.2307/1941942>.

Pitcher, K.W., and D.G. Calkins. 1981. Reproductive Biology of Steller Sea Lions in the Gulf of Alaska. Journal of Mammalogy 62 (3): 599–605. <doi:10.2307/1380406>.

Pitcher, K.W., V.N. Burkanov, D.G. Calkins, B.J. Le Boeuf, E.G. Mamaev, R.L. Merrick, and G.W. Pendleton. 2001. Spatial and Temporal Variation in the Timing of Births of Steller Sea Lions. Journal of Mammalogy 82 (4): 1047–53. <doi:10.1644/1545-1542(2001)082><1047:SATVIT>2.0.CO;2.

Pfister CM. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecologi- cal implications. Proc Nat Acad Sci. 1998; 95: 213–218. PMID: 9419355

Proffitt KM, Rotella JJ, Garrott RA. 2010. Effects of pup age, maternal age, and birth date on pre-weaning survival rates of Weddell seals in Erebus Bay, Antarctica. Oikos 119:1255–1264.

Raum-Suryan, K.L., K.W. Pitcher, D.G. Calkins, J.L. Sease, and T.R. Loughlin. 2002. Dispersal, Rookery Fidelity, and Metapopulation Structure of Steller Sea Lions (Eumetopias Jubatus) in an Increasing and a Decreasing Population in Alaska. Marine Mammal Science 18 (3): 746–64. <doi:10.1111/j.1748-7692.2002.tb01071.x>.

Rodionov, S.N., Bond, N.A., Overland, J.E., 2007. The Aleutian Low, storm tracks, and winter climate variability in the Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography 54, 2560–2577. <https://doi.org/10.1016/j.dsr2.2007.08.002>

Rodionov, S.N., Overland, J.E., Bond, N.A., 2005. Spatial and temporal variability of the Aleutian climate. Fisheries Oceanography 14, 3–21. <https://doi.org/10.1111/j.1365-2419.2005.00363.x>

Rotella JJ, Link WA, Chambert T, Stauffer GE, Garrott RA. 2012. Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark-recapture data. J Anim Ecol. 2012; 81: 162–173. doi: 10.1111/j.1365-2656.2011.01902.x PMID: 21939440

Seckel, G.R. 1993. Zonal gradient of the winter sea level atmospheric pressure at 50 N: an indicator of atmospheric forcing of North Pacific surface conditions. J. Geophys. Res. 98:22615–22628.

Simons, R.A. (2019). ERDDAP. <https://coastwatch.pfeg.noaa.gov/erddap>. Monterey, CA: NOAA/NMFS/SWFSC/ERD.

Sinclair, E.H., Zeppelin, T.K., 2002. Seasonal and Spatial Differences in Diet in the Western Stock of Steller Sea Lions (Eumetopias Jubatus). Journal of Mammalogy 83, 973–990. <https://doi.org/10.1644/1545-1542(2002)083><0973:SASDID>2.0.CO;2

Sinclair, E. H., D. S. Johnson, T. K. Zeppelin, and T. S. Gelatt. 2013. Decadal variation in the diet of Western Stock Steller sea lions (Eumetopias jubatus). U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-248, 67 p.

Speckman, P.L. and Sun, D., 2003. Fully Bayesian spline smoothing and intrinsic autoregressive priors. Biometrika. 90:289–302.

Sweeney, K., Towell, R., Gelatt, T. 2018. Results of Steller Sea Lion Surveys in Alaska, June-July 2017. NOAA Fisheries Alaska Fisheries Science Center Marine Mammal Laboratory, Seattle, WA. <https://media.fisheries.noaa.gov/dam-migration/ssl_aerial_survey_2018_final.pdf>

Thomas JA, DeMaster DP. 1983. Parameters affecting survival of Weddell seal pups (Leptonychotes weddelli) to weaning. Canadian Journal of Zoology 61:2078–2083.

Trillmich F. 1990. The behavioral ecology of maternal effort in fur seals and sea lions. Behaviour 114:3–20.

Trites, A. W., and C. P. Donnelly. 2003. “The Decline of Steller Sea Lions Eumetopias Jubatus in Alaska: A Review of the Nutritional Stress Hypothesis.” Mammal Review 33 (1): 3–28. <doi:10.1046/j.1365-2907.2003.00009.x>.

York, A.E. 1994. The Population Dynamics of Northern Sea Lions, 1975-1985. Marine Mammal Science 10 (1): 38–51. <doi:10.1111/j.1748-7692.1994.tb00388.x>.

York, A. E., J. R. Thomason, E. H. Sinclair, and K.A. Hobson. 2008. Stable carbon and nitrogen isotope values in teeth of Steller sea lions: Age of weaning and the impact of the 1975- 1976 regime shift in the North Pacific Ocean. Can. J. Zool. 86: 33-44.

Watanabe, S., 2010. Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory. Journal of Machine Learning Research 11.

Wiens JA .1989. Spatial scaling in ecology. Funct Ecol 3: 385 – 397.

Wright, B.E., Brown, R.F., DeLong, R.L., Gearin, P.J., Riemer, S.D., Laake, J.L., Scordino, J.J., 2017. Survival rates of Steller sea lions from Oregon and California. J Mammal 98, 885–894. <https://doi.org/10.1093/jmammal/gyx033>

Zhang, R.H. and S. Levitus, 1997: Structure and cycle of decadal variability of upper-ocean temperature in the North Pacific. J. Climate, 10, 710-727.