

AN ABSTRACT OF THE THESIS OF

Norma A. Vazquez for the degree of Master of Science in Wildlife Science presented on September 27, 2013

Title: Spatial and Temporal Distribution of Juvenile Steller Sea Lion (*Eumetopias jubatus*) Predation Events in the Gulf of Alaska

Abstract approved:

Markus Horning

The first objective of this study was to quantify the intensity of space use of 70 juvenile (12-26 months old) Steller sea lions (SSLs) from the western Distinct Population Segment (DPS) in the Kenai Fjord(KF)/Prince William Sound (PWS) region of Alaska as derived from externally attached ARGOS satellite transmitter tags. A Bayesian state-space model (SSM) approach was used to process and interpolate the ARGOS-based locations. The resulting tracks were then used to quantify the spatio-temporal distribution of SSLs by way of a gridded utilization distribution (UD) in the study area. Each of six combined two-month UDs had an average of 24 ± 4.16 animals (range: 20-30) contributing around $5,090 \pm 1,879$ filtered locations (range: 2,757-7,593).

Results of the bimonthly UDs show juvenile SSL remained within the KF/PWS study region during the tracking period, with the exception of one individual, TJ16 (male), who crossed the 144° W Meridian separating the western and eastern DPS. Furthermore, results revealed that juveniles exhibit different spatial distributions depending on the time of year. They remain confined to a relatively smaller area (6,500-12,075 km²) in the 100% UD months of March through August compared to a larger area of 11,300-22,575 km² in the 100% UD

months September through February. In general, in winter (November-April) 90% of observations fell within 30km of the nearest haul-out, whereas in summer (May-October) 90% fell within 20km. A multifactor analysis of covariance (MANCOVA) revealed a significantly higher percent time spent at sea from November through April than May through October ($n=63$; age as covariate $F_1=3.796$, $p=0.056$; season as factor $F_1=13.147$, $p=0.001$). Thus, while age contributed to the observed variance, the main effect was clearly by season.

The second objective of this study was to characterize the density effects of predator-prey interactions based on the spatial distribution of actual juvenile Steller sea lion predation events in relation to their utilization distribution. Fifteen predation events were detected from archival Life History Transmitter (LHX) tags implanted into a subset of $n=36$ of the 70 juvenile SSLs. A Bayesian SSM approach was used to process and interpolate the ARGOS locations received post-mortem from LHX tags. The processed tracks were then used to extrapolate the most likely locations of predation events.

All 15 predation events occurred in the western DPS from 2008 through 2013. We expected predation events to occur uniformly in all areas for non-specialized predators, and more often in areas of high utilization such as near rookeries and haul-outs for predators that are specialized on SSLs and focus hunting efforts on high use areas. Results suggest the opposite, with four of the 15 predation events occurred in the 91-100% UD, or areas of the lowest relative frequency distribution of animal locations, 3 events occurred in the 81-90% UD, and only 1 event in the 21-30% UD corresponding to an area of higher relative frequency distribution of animal locations. Seven of the 15 predation events occurred outside the UD range, and therefore in areas likely of the lowest relative frequency distribution of animal locations.

The winter predation rate was twice that of summer, with 10 predation events during the winter periods (November-April), and 5 events during the summer periods (May-October). Six predation events occurred in January-

February. One predation event occurred in March-April, 2 events in May-June, 1 event in July-August, 2 events in September-October, and 3 events in November-December. A Rayleigh test for circular distribution showed a significant difference from uniformity with a mean ordinal date of January 6th (for n=7 animals \leq 22 months of age), $p=0.016$).

Studying predation in the marine environment comes with many challenges due to limitations in locating and tracking highly mobile marine predators over a long period of time and over a wide geographic range. Previous Steller sea lion studies looking at predation have inherent biases due to only sampling during the summer months and only near rookeries and haul-outs. Our study shows that we can detect predation all year round, including winter, and far away from rookeries and haul-outs. Since juvenile survival is low, and thus poses a significant risk for population-level survival, increased knowledge of the specifics of juvenile SSL space utilization patterns is of vital importance to assessing the importance of predation risk as one of the main drivers of their survivability. This is the first study to relate actual predation events to the intensity of space use of juvenile SSLs in a declining population in the KF/PWS region of Alaska.

Key words: Steller sea lion, utilization distribution, predation, state-space model, spatial distribution, juvenile, Prince William Sound, Kenai Fjords, Alaska, telemetry

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Spatial and Temporal Distribution of Juvenile Steller Sea Lion (*Eumetopias jubatus*)
Predation Events in the Gulf of Alaska

by
Norma A. Vazquez

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Spatial and Temporal Distribution of Juvenile Steller Sea Lion (*Eumetopias jubatus*) Predation Events in the Gulf of Alaska

CHAPTER 1: GENERAL INTRODUCTION AND THESIS OVERVIEW

The Steller sea lion (*Eumetopias jubatus*) (Scheffer 1958) was described by the German physician/theologian George Wilhelm Steller in 1742 and is the largest member of the family Otariidae (Loughlin et al. 1987). Paleontological evidence from early Miocene times suggests that polygynous breeding and sexual dimorphism has been a long-standing characteristic of otariid biology (Bartholomew 1970) (Figure 1.1). Males weigh up to 1,120 kg and can measure up to 3.4 m in standard length, in contrast, females can weigh up to 350 kg and measure up to 2.9 m (Loughlin et al. 1987). Pup weight at birth is 16-23 kg and pups are born with brown fur that molts after about 3 months of age, around the time they begin to range from their birth site (Calkins & Pitcher 1982, Raum-Suryan et al. 2004). Adult fur color varies between a light buff to reddish brown (Loughlin et al. 1987).



Figure 1.1: A Steller sea lion haul-out showing adult females and at least one male (center). Note the sexual dimorphism between the male and all the surrounding females (Picture source: Norma Vazquez).

The geographic distribution of the Steller sea lion extends around the North Pacific Ocean rim from the Kuril Islands and Okhotsk Sea in Russia, through the Aleutian Islands and central Bering Sea, to the southern coast of Alaska, and south to California (Calkins & Pitcher 1982, Loughlin et al. 1984, 1987) (Figure 1.2). Seal Rocks in Prince William Sound, Alaska is the northernmost (60°09'N) rookery and Año Nuevo Island, California, the southernmost (37°06'N) (Loughlin et al. 1987).

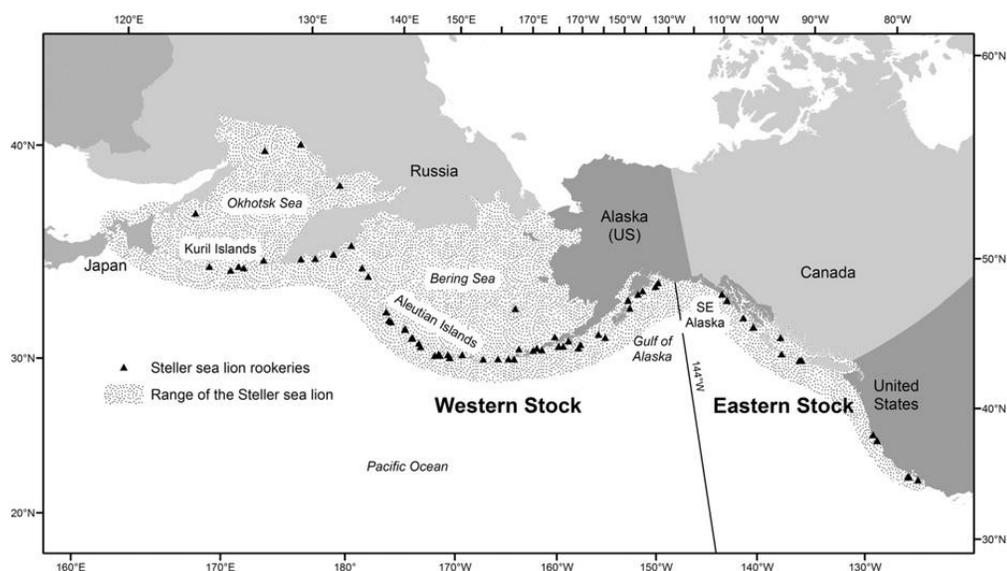


Figure 1.2: Distribution of Steller sea lions (shaded light gray). Major rookeries are depicted (triangles). The population is divided into western and eastern stocks at 144° W (black line). (Adapted from NOAA's National Marine Fisheries Service: www.nmfs.noaa.gov)

Steller sea lions are described as gregarious animals that gather annually at widely dispersed known rookeries and haul-outs (Pitcher & Calkins 1981) (Figures 1.1, 1.2). A rookery is defined as a terrestrial site where adult males actively defend territories and where adult females congregate for breeding, pupping, and rearing young while haul-outs are terrestrial sites where Steller sea lions of all age classes (except pups) visit on a regular basis to rest (Calkins & Pitcher 1982). Steller sea lions are not known to migrate in the traditional sense, but utilization of these two different land based locations depends on the time of year, concentrating on rookeries during the period of May-Oct and dispersing widely to many haul-outs during their first few years and during the non-breeding season (Calkins & Pitcher

1982, Loughlin et al. 1987). Like many pinnipeds but unlike any other marine mammal, they combine offshore marine feeding and terrestrial sites (Bartholomew 1970) to meet their vital needs, a strategy known as central place foraging (Orians & Pearson 1977). The use of central place terrestrial sites and marine foraging sites depends on suitable substrate and exposure, seasonal resource availability, conspecific competition, fisheries competition, and perceived predation risk (Raum-Suryan et al. 2004).

In 1997 two separate stocks of Steller sea lions were recognized for management purposes based on geographic distribution, population dynamics, and genotypic differences: an eastern stock, which includes animals east of Cape Suckling, Alaska (144° W), and a western stock, west of Cape Suckling through the Aleutian Islands (Bickham et al. 1996, Baker et al. 2005, Allen & Angliss 2012). Kenyon and Rice (1961) summarized aerial surveys in the Aleutian Islands from the late 1950s and early 60s and estimated that the total Steller sea lion population numbers (eastern and western stocks combined) were between 240,000 and 300,000. However, their populations suffered a significant decline in the following decades, with only 116,000 present in 1989 (Loughlin et al. 1992). Similarly, the western stock population was estimated at 177,000 in the 1960s (Baker et al. 2005) but numbered only 45,916 between 2008 and 2011 (Allen & Angliss 2012). The collapse of Steller sea lions from the western Distinct Population Segment (DPS) starting in the late 1970s prompted the National Marine Fisheries Service (NMFS) to list them under the Endangered Species Act (ESA) and scientists to question the causes of the precipitous decline (Springer et al. 2003, NMFS 2008).

Numerous studies have put forward various hypotheses to explain the sharp decline. For example, nutritional stress due to fisheries competition (Alverson 1992, Osterblom et al. 2008) or nutritional stress due to regime shifts (Loughlin 1998), by-catch (Perez & Loughlin 1991), hunting (Perez & Loughlin 1991, Loughlin & York 2000), contamination (Lee et al. 1996, Atkinson et al. 2008), and predation by killer whales (Springer et al. 2003) have all been posed as potential threats and

impacts to Steller sea lion recovery but very little is known about the role of juvenile mortality by predation as a factor. Specifically, we lack baseline information on quantifying predation risk in relation to juvenile sea lion's probability of occurrence at each point in space in the declining western DPS.

To describe an animal's space use pattern, an individual must be located and position recorded at successive points in time (Ford & Krumme 1979). Biologging has revolutionized the study of animal movement with the introduction of VHF telemetry, light-level geolocation, GPS tracking, and one of the most widely used in marine studies, ARGOS satellite telemetry (Hazen et al. 2012). Furthermore, advances in telemetry devices such as the implantable Life History Transmitter (LHX) tag have made it possible to gradually overcome obstacles in collecting data from animals that occupy extensive ocean ranges and to directly measure mortality and predation (Horning & Hill 2005). LHX tags provide information on end-of-life locations to allow assessment of long-term emigration patterns and spatial information about predation events (Horning & Mellish 2009). Since juvenile survival is low (York 1994, Holmes & York 2003, Noren et al. 2009), and thus poses a significant risk for population-level survival, increased knowledge of the specifics of juvenile Steller sea lion space utilization patterns is of vital importance to assessing the viability of predation risk as one of the main culprits to their survivability (Frid et al. 2009, Curtice et al. 2011).

The primary objectives of the research described in this thesis were to (1) characterize the utilization distribution of juvenile Steller sea lions in the Kenai Fjords/Prince William Sound region of Alaska relative to seasonal changes (Chapter 2), and (2) characterize the density effects of predator-prey interactions based on time spent at sea by juvenile Steller sea lions and the spatial distribution of actual predation events in relation to their utilization distribution (Chapter 3). Jointly, results from these studies are critical to understanding (or considering) the predation hypothesis of the decline of the juvenile Steller sea lion from the western DPS in Alaska.

I provide a general introduction and overall discussion in Chapters 1 and 4, respectively. Based on the discussion and knowledge gained from this study, I present research recommendations for future studies of Steller sea lions in Chapter 4. Chapters 2 and 3 in this thesis are intended for submission as individual manuscripts to peer-reviewed journals. Therefore, those two chapters include an abstract and some of the introductory text may be repeated throughout all chapters in thesis.

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CHAPTER 2: SPATIO-TEMPORAL VARIANCE IN SPACE-USE PATTERNS OF
JUVENILE STELLER SEA LION (*Eumetopias jubatus*) IN THE GULF OF ALASKA

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Abstract

The ability of highly mobile marine predators such as the Steller sea lion (SSL) (*Eumetopias jubatus*) to range over extensive geographic areas depends in part on their life history characteristics and biology. In a non-migratory species, access to terrestrial resting sites as well as marine foraging areas is critical to the survival of the developing juvenile. The main objective of this study was to quantify the intensity of space use of 70 weaned juvenile (12-26 months old) sea lions in the Kenai Fjord/Prince William Sound region of Alaska as derived from satellite transmitter tags and assess associations, if any, between season and the distance to nearest haul-out. Using the free software packages R version 2.15.2 and WinBUGS, we fit a state-space model (SSM) to all of the pre-processed ARGOS locations of each sea lion track. The model yielded an estimate of the most probable path of a sea lion at 4-hr intervals, while accounting for non-Gaussian ARGOS location error. Juveniles remain confined to a relatively smaller area (6,500-12,075 km²) in the % UD months of March through August compared to a larger area of 11,300-22,575 km² in the 100% UD months of September through February. Furthermore, in winter (November-April) 90% of observations fell within 30km of the nearest haul-out, whereas in summer (May-October) 90% fell within 20km. A multifactor analysis of covariance (MANCOVA) revealed a significantly higher percent time spent at sea from November through April than May through October (n=63; age as covariate $F_1=3.796$, $p=0.056$; season as factor $F_1=13.147$, $p=0.001$). Thus, age does contribute to the observed variance, but the main effect is clearly by season.

Key words: satellite telemetry, state-space model, utilization distribution, seasonal effects, juvenile Steller sea lion.

Introduction

The ability of highly mobile marine predators such as the Steller sea lion (or northern sea lion; *Eumetopias jubatus*) to range over extensive geographic areas depends in part on their life history characteristics and biology. Steller sea lions are the largest species of the family Otariidae and are central place foragers (Orians & Pearson 1977), depending on terrestrial sites (rookeries and haul-outs) for parturition, caring for young, molting, and resting (Bartholomew 1970) and on the marine environment for foraging trips. In a non-migratory species, access to terrestrial resting sites and marine foraging areas is critical to the survival of the developing juvenile (Raum-Suryan et al. 2004). The weaning process of Steller sea lion pups is not well defined but it is believed they wean gradually as early as 4 months old up to three years of age (Pitcher & Calkins 1981). In most pinniped species, juveniles are more prone to post-weaning dispersal than adults, who exhibit a high fidelity to their natal rookeries for finding mates and breeding (Raum-Suryan et al. 2004).

The Steller sea lion ranges from Russia and Japan into the Gulf of Alaska, and south to California (Kenyon & Rice 1961, Call et al. 2007) (Figure 2.1). The population has been divided into two stocks for management purposes based primarily on genetic differences: an Eastern Population Stock (EPS) (east of Cape Suckling, Alaska; longitude 144°W) and a Western Population Stock (WPS) (west of Cape Suckling, Alaska; longitude 144°W) (Figure 2.1) (Bickham et al. 1996, Baker et al. 2005). Over the past 4 decades these two stocks have shown opposing population trends. Overall, the WPS has declined by over 80% (Loughlin et al. 1992); the largest declines occurring in the Gulf of Alaska and western Aleutian Islands, areas that historically were the hub of distribution and abundance (Kenyon & Rice 1961, Loughlin et al. 1987), whereas the EPS has been steady or increasing about 3% per year during the same time period (Pitcher et al. 2007). This extreme drop in numbers led to the WPS to be listed as “endangered” in 1997 under the United States Endangered Species Act (Baker et al. 2005, Call et al. 2007).

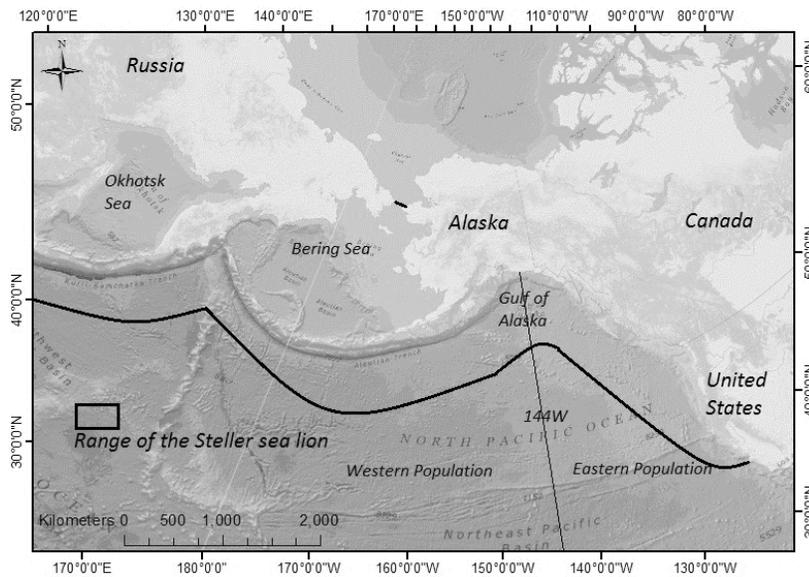


Figure 2.1: Map of the Steller sea lion range (thick black line). Thin line depicting the division between the Western and Eastern Distinct Population Segment at 144°W.

Of the multitude of hypotheses behind the past and present decline of the WPS of Steller sea lions (Springer et al. 2003, Trites & Donnelly 2003, Atkinson et al. 2008), the study of life history parameters (i.e. fecundity, survivability, mortality, etc) are of paramount importance in relation to trying to explain what factors may be affecting current population trends. However, it has not been proven that a single factor can account for the ultimate reason for the past nor present trends. Slow changes in a populations' response to perturbations of important life history parameters such as fecundity and mortality rates make it challenging to detect what causes the most detrimental impact and in turn, hinders management and conservation efforts (Holmes & York 2003). This slow detection of change is compounded by a lack of knowledge involving juvenile Steller sea lion space use patterns as they relate to the declining WPS.

It has always been logistically difficult to track marine animals over long periods of time because they move extensively beyond boundaries of direct observation (Boyd et al. 2004, Naito 2004). Thus, the use of platform transmitter terminals (PTT) attached to an animal made it possible to incorporate the

measurement of spatial and temporal distribution to answer questions like: How do animals use space and time, Are there any age/sex-specific patterns in the type of habitats used, etc. (Boyd et al. 2004, Kooyman 2004). The main objective of this study was to quantify the intensity of space use of 70 juvenile (12-26 months old) Steller sea lions in the Kenai Fjord (KF)/Prince William Sound (PWS) region of Alaska as derived from satellite transmitter tags.

Methods

Steller Sea Lion Captures and Data Collection

Seventy free-ranging (FR) and transient juvenile (TJ) Steller sea lions from the WPS were captured within Resurrection Bay and Prince William Sound (PWS), AK (Figure 2.2). “Free-ranging” juveniles refers to the animals that were captured, sampled, and released immediately in the field as a control comparison while “Transient” juveniles were captured, sampled, transported to the Alaska SeaLife Center (ASLC), and then released after approximately 20-60 days in quarantined, temporary captivity (Mellish et al. 2006). Captures were performed by SCUBA divers using a baited pole and noose to bring the animal into a restraint box aboard a capture skiff (Raum-Suryan et al. 2004, Mellish et al. 2006). Following an initial health assessment under inhalant gas anesthesia on a larger research vessel, TJ sea lions (n=57) were transported to a quarantine facility at the Alaska SeaLife Center (ASLC) within 48 hours of capture for temporary holding of 6 to 12 weeks (Mellish et al. 2006, Thomton et al. 2008). FR (n=13) and TJ (n=57) sea lions were released with Satellite tags (SPLASH n=22, SDR-T16 n=48; Wildlife Computers) that were glued to the pelage along the midline of the back with fast-setting epoxy (Titan™ epoxy #332, and/or Devcon™ 5-min or 10-min epoxy) (Thomton et al. 2008). Furthermore, single (n=2) or dual Life History Transmitter (LHX) tags (n=34) were surgically implanted into the abdominal cavity of TJs n=36 out of the 70 sea lions under gas anesthesia (Horning & Hill 2005, Horning et al. 2008, Horning & Mellish 2009). All animals were then continually monitored post-surgery while minimizing handling and human interaction (Mellish et al. 2006). Steller sea lion captures,

temporary captivity, tag implantation, and post-release monitoring were conducted under federal permits issued under the MMPA/ESA (NMFS Permits #881-1890, #881-1668 & #14335, as well as Institutional Animal Care and Use Permits (IACUP) #02-015, 03-007, 05-002, 06-001, & 08-005).

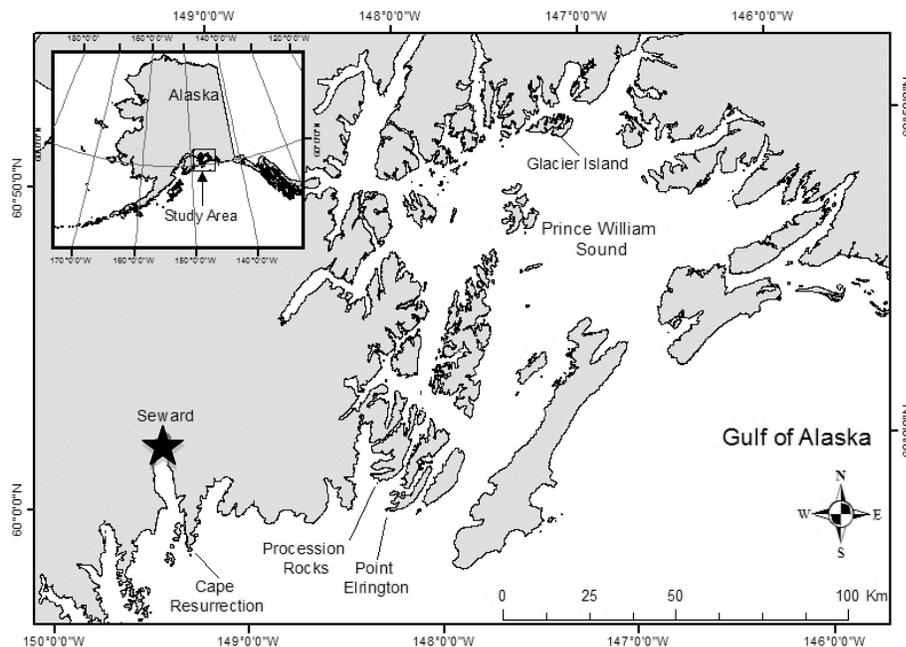


Figure 2.2: Study area and capture locations. Transient and free-ranging juvenile Steller sea lions were released either at the capture locations (Cape Resurrection, Procession Rocks, Point Elrington, and Glacier Island) or at the Alaska SeaLife Center in Seward, Alaska (Black star) near Resurrection Bay.

Satellite Location Pre-Processing

The SDR-T16 tags are designed to provide both at-sea and on-land locations through the Service ARGOS system by using a combination of known satellite positions, known position of the Earth's surface, and the distance between the SDR and the satellite as measured from the Doppler shift of the transmitter signal (Rehberg & Small 2001, Vincent et al. 2002, Service ARGOS 2011). There are 7 location classification schemes: location class (LC) 3 is accurate to <150m, LC 2 (error 150-350m), LC 1 (error 350-1000m), LC 0 (error >1000m), and LCs A, B have no assigned accuracy range and LC Z are invalid (Vincent et al. 2002, Loughlin et al. 2003, Costa et al. 2010). At least four successive uplinks during a single satellite

pass are necessary for a location to be assigned an accuracy of 0 or better. The least accurate positions (A, B, and Z) need at least 2 or 3 uplinks and are the most common for many marine animals tracking studies, complicating estimation of the animals' true position and behavioral state (Vincent et al. 2002).

Satellite locations were first extracted from Service ARGOS (CLS America Inc.) data files using the WC-DAP (Wildlife Computers Data Analysis Programs) software package v3.0 (Wildlife Computers, Inc. 2010). Service ARGOS provides two possible lat/lon locations, therefore the secondary location pairs were manually examined against the primary ARGOS location pairs to see if they provided a more likely solution to the transmission. The coordinates and associated LCs were switched if it was obvious that the primary ARGOS lat/lon pairs were biologically impossible compared to the secondary lat/lon pairs, such as being in a different hemisphere, etc. Finally, all z-location classes were removed.

State-Space Model

State-space models (SSMs) maximize use of all available location and quality information by combining an observation error model (i.e. telemetry precision) with a process model (movement through time and space) of animal movement and solving them together. In other words, SSMs predict the future location of an animal based from its current states probabilistically (Patterson et al. 2008, Maxwell et al. 2011). A Bayesian state-space model (SSM) developed by Jonsen et al. (2005, 2007) and modified by Bailey et al. (2009) was fit to all of the pre-processed ARGOS locations of each sea lion track using R version 2.15.2 (R Development Core Team, 2012) and WinBUGS software (Lunn et al. 2000) which uses Markov Chain Monte Carlo (MCMC) methods to address the observation error issue and improve data retention (Jonsen et al. 2007). The SSM was applied to regularize the observations into evenly spaced pseudo-locations (Jonsen et al. 2007). We estimated locations and associated credible limits at four-hour intervals (6 loc/day), as it represents half the average number of ARGOS locations per day for these animals. The maximum

gap over which we interpolated was 51 days where one individual's external tracking had 51 consecutive days missing.

Transition Equation (Process Model)

Finding the “true” path of an animal's movement is very problematic since animals change their behavior patterns over time and space (Anderson-Sprecher & Ledolter 1991). State-space time series models describe a dynamic Markov process where the state of a process that cannot be directly observed evolves over regular time intervals based on its previous state, process variability, and biological parameters; this is known as the transition equation/process model (Anderson-Sprecher & Ledolter 1991, Jonsen et al. 2005, Bailey et al. 2009). We based the transition equation on a first-difference correlated random walk model (DCRW) (Jonsen et al. 2005). The random walk model is based on two parameters: mean turning angle (θ) and autocorrelation in speed and direction (γ ; Jonsen et al. 2005) (Bailey et al. 2009, Jonsen et al. 2007). Thus the process model is written as:

$$\mathbf{d}_t \sim N_2 [\gamma \mathbf{T}(\theta)\mathbf{d}_{t-1}, \mathbf{\Sigma}]$$

where \mathbf{d}_{t-1} is the difference between \mathbf{x}_{t-1} (unobserved coordinate states) and \mathbf{x}_{t-2} (lat/lon locations) and N_2 is a bivariate Gaussian distribution with mean 0. $\mathbf{T}(\theta)$ is a transitional matrix that describes the rotational component of the correlated random walk and $\mathbf{\Sigma}$ is the covariance matrix (Jonsen et al. 2005, 2007, Bailey et al. 2009):

$$\mathbf{T}(\theta_b) = \begin{bmatrix} \cos(\theta_b) & -\sin(\theta_b) \\ \sin(\theta_b) & \cos(\theta_b) \end{bmatrix}, \quad \mathbf{\Sigma} = \begin{bmatrix} \sigma_{lon}^2 & \rho\sigma_{lon}\sigma_{lat} \\ \rho\sigma_{lon}\sigma_{lat} & \sigma_{lat}^2 \end{bmatrix}, \quad 0 \leq \gamma_b < 1$$

Where b denotes behavioral mode 1 or mode 2, σ_{lon}^2 and σ_{lat}^2 are the process variances in longitude and latitude, respectively, and ρ is the correlation coefficient. To allow for variability in the autocorrelation, we add the term γ , with $\gamma = 0$ representing a simple random walk and $0 < \gamma < 1$ representing a random walk with correlation in both direction and move speed (Jonsen et al. 2005, 2007). A lack of overlap between these parameters confirms that use of the model is appropriate (Bailey et al. 2008, Maxwell et al. 2011).

Measurement Equation (Observation model)

The second component of the state-space model, the measurement equation, relates the unobserved states predicted by the transition equation to the observed data (Jonsen et al. 2007). The measurement equation assumes that the observations are made over regular time intervals that correspond to the time step modeled in the transition equation, however, ARGOS data are observed irregularly through time, with variable quality classes and non-Gaussian errors (Jonsen et al. 2005, 2007) due to an animal's diving behavior, sea state, satellite availability or transmission issues, etc (Jonsen et al. 2012). Therefore, utilizing state-space filtering methods on ARGOS data are more appropriate because it allows the irregularly observed data ("noisy" data) to be modeled directly within the state-space framework. Since ARGOS position errors can be strongly non-Gaussian (Jonsen et al. 2005), they are modeled with generalized t-distributions, which are robust to extreme values (Jonsen et al. 2007). Rather than estimating the parameters for each t distribution directly within the state-space model, the measurement equation estimation error for each location class were derived from published data from tags on captive gray seals, *Halichoerus grypus* (Vincent et al. 2002).

Two chains were run in parallel, each for a total of 30,000 MCMC samples, the first 10,000 were discarded as a burn-in to ensure convergence and the remaining 20,000 samples were thinned, retaining every fifth sample to reduce autocorrelation. Thus, posterior distributions for the movement parameter θ , mean turning angle, and γ , autocorrelation in speed and direction were output from the model and based on 20,000 samples from each chain giving a total of 4,000 independent samples (Bailey et al. 2008, 2009).

Utilization Distribution of Steller sea lions

Utilization distributions (Van Winkle 1975, Worton 1989) were used to quantify space use of juvenile Steller sea lions within the waters of Prince William Sound and Kenai Fjords in Alaska. How intensely an animal or a group of animals

use different areas within their home range can be referred to as their utilization distribution (Kranstauber et al. 2012) and can be quantified as a multi-dimensional relative frequency distribution of animal locations (Kie et al. 2010). To approximate the utilization distribution of sea lions, we followed the analysis of Maxwell et al. (2011) and Womble (2012). A first-difference correlated random walk model was used to predict positions at 4-hour intervals using the observed raw ARGOS locations and an animal's expected behavior as parameterized by the mechanistic equation (Jonsen et al. 2005, 2007, Maxwell et al. 2011).

After determining the most probable path using the SSM, we pooled the resulting locations to estimate the combined utilization distribution of all sea lions at two-month intervals (Jan-Feb, Mar-Apr, May-June, July-Aug, Sept-Oct, Nov-Dec), or 6 different time periods. We chose 6 time periods as the temporal scale of analysis to try to get an equal distribution of locations per animal for each time period. The grid cell method has advantages over traditional home range/utilization distribution methods such as minimum convex polygons (MCP) and kernel density estimation (KDE) in home range construction because MCPs over-estimates the home range of an animal when there are many outliers and KDE analysis would result in over-smoothed results given the fine scale of our data (Getz & Wilmers 2004, Maxwell et al. 2011). Gridding allowed us to see finer scale measurement of animal distribution even if data were combined across animals and across years (Maxwell et al. 2011). A grid cell size of 25km² was chosen as the spatial scale of analysis to allow for detection of small-scale movements (Maxwell et al. 2011) as well as yield smooth contours between grid cells since our data was grouped across animals travelling at different speeds.

Grid cells (25km²) were created in the freely available Geospatial Modeling Environment (GME) platform (version 0.7.2.0, Beyer 2012) using the command "genvecgrid" (Generate Vector Grid) and saving the output feature data source as a shapefile for ease of transition to ArcMap. Sea lion locations for each of the six 2-month period were spatially joined in ArcGIS (Version 10 ESRI 2011) with grid cells

(25km²) generated in GME in order to get a count of the total number of points found in each cell. To get the proportion of total locations per grid cell for each of the 6 time periods, we divided the number of sea lion locations in each cell by the total number of locations for that time period. These proportions were sorted from largest to smallest in order to calculate the cumulative proportions from which the utilization distributions values were based on in ArcGIS. The utilization distribution was symbolized in ArcGIS as categories where values were grouped by tens (i.e. 91-100, 81-90, 71-80, 61-70, 51-60, 41-50, 31-40, 21-30, 11-20, 1-10) using a yellow-red color ramp to display each category in descending order. This method identified all grid cells where a sea lion location was observed and quantified the probability of detecting a sea lion in a given grid cell within a specified time period (i.e. Jan-Feb). As an example, grid cells included in the 100% utilization distribution represent grid cells with the lowest intensity of use by sea lions. In contrast, a grid cell with 10% utilization distribution represents a grid cell with the highest intensity of use or the highest proportion of sea lion locations for a grid cell for that time period. Core areas were consequently defined as UDs of 50% or less (Maxwell et al. 2011).

Time At Sea

The Satellite-linked Time-depth recorder (models SPLASH and SDR-T16, Wildlife Computers Inc., Redmond, WA, USA) tags are designed to provide both at-sea and on-land locations (Wildlife Computers 2000). Data is encoded into three types of messages: “histograms”, “timelines”, and “status messages”, which are useful in providing information on animal behavior and tag functionality. Timeline messages provide information on when an animal was hauled-out given a reading of “dry” for the conductivity sensor. Each timeline message covers a 24 hour period which is divided into 72 20-minute increments. Each of the 72 bins reports whether the majority (>50%) of the conductivity readings during that 20-minute period were “wet” or “dry” and assigns a 1 or 0 respectively. Since tag-to-satellite communications are uni-directional, even with redundant transmissions for each

timeline, not all timelines transmitted by a tag are received. Duplicate timelines were removed from the analysis.

We sub-sampled 8 timeline messages from each animal to have equal representation. This resulted in samples from 66 of 70 animals, four animals with fewer than 8 timelines received were excluded from analysis. The percent time spent at sea (“wet”) within the first 8 timelines (days) was calculated by dividing the total time “wet” (in first 8 timelines[days]) by 192 hours (the total hours in 8 timelines[days]). We ran a multifactor analysis of covariance (MANCOVA) to test for significance effects between time at sea, age (covariate), and season (factor) (coded as 1=winter months; 2=summer months).

Results

Seventy free-ranging (FR) and transient juvenile (TJ) Steller sea lions were captured within Resurrection Bay and Prince William Sound, AK (Figure 2.2) in 2003 (n=4 sea lions captured; Sept., Oct., Nov.), 2004 (n=13; May, July, Sept.), 2005 (n=11; Apr., Aug., Nov.), 2006 (n=4; Apr.), 2007 (n=6; Oct.), 2008 (n=10; Apr., May, Nov.), 2009 (n=5; July, Aug.), 2010 (n=5; Nov., Dec.), 2011 (n=7; May, June), and 2012 (n=5; Aug) (Table 2.1). Animals were released at ages averaging $16.6 \pm .93$ months (SD) (range: 12-26mo). There were a total of 56,833 raw ARGOS locations transmitted during 4,911 deployment days (9/10/03-11/02/12) (Table 2.1). The average deployment period for satellite-linked transmitters (SPLASH n=22, SDR-T16 n=48) was 70.15 ± 11.5 days (range: 10-215). The average number of locations per day for all 70 animals was 12.33 ± 1 (range: 4.57-23.57). There were a total of 46 males to 24 females, resulting in a ratio of 1.92:1.

Table 2.1: Steller sea lions (n=70) tagged with satellite-linked transmitters (36 of them also equipped with LHX tags) (SPLASH, SDR-T16, Wildlife Computers) in Prince William Sound, AK between 2003 and 2012.

ID#	PTT	LHX	Age at release (months)	Sex	Capture Location	Release Date	Date of Last Location	Total Deploy Days
FR010	44591	no	13	M	---	07/28/04	09/28/04	62
FR011	44590	no	13	F	---	07/28/04	08/09/04	12
FR013	44594	no	13	F	---	07/29/04	08/13/04	15
FR014	44595	no	13	F	---	07/29/04	08/27/04	29

Table 2.1: (Continued). Steller sea lions (n=70) tagged with satellite-linked transmitters (36 of them also equipped with LHX tags) (SPLASH, SDR-T16, Wildlife Computers) in Prince William Sound, AK between 2003 and 2012.

ID#	PTT	LHX	Age at release (months)	Sex	Capture Location	Release Date	Date of Last Location	Total Deploy Days
FR015	44596	no	13	M	---	07/29/04	08/13/04	15
FR63	61762	no	12	F	---	06/01/11	07/20/11	49
FR64	61766	no	12	F	---	06/01/11	07/10/11	39
FR65	61782	no	12	M	---	06/01/11	07/20/11	49
FR66	61781	no	14	M	---	08/08/12	09/13/12	17
FR67	61782	no	14	F	---	08/08/12	09/05/12	29
FR68	61783	no	14	M	---	08/08/12	11/02/12	86
FR69	61784	no	26	M	---	08/08/12	08/31/12	23
FR70	61785	no	14	M	---	08/09/12	08/23/12	15
TJ01	6559	no	14	M	Cape Resurrection	09/10/03	11/30/03	81
TJ02	6569	no	15	F	Cape Resurrection	10/02/03	10/16/03	14
TJ03	44585	no	17	M	Procession Rocks	12/08/03	04/15/04	129
TJ04	44586	no	17	F	Procession Rocks	12/08/03	05/05/04	149
TJ05	41790	no	23	F	Glacier Island	05/26/04	06/27/04	32
TJ06	43760	no	23	F	Glacier Island	05/26/04	07/05/04	40
TJ07	41791	no	23	F	Glacier Island	05/26/04	06/27/04	32
TJ08	43764	no	23	M	Glacier Island	05/26/04	06/16/04	21
TJ09	43759	no	15	M	Cape Resurrection	09/28/04	02/20/05	145
TJ10	43761	no	15	M	Cape Resurrection	09/28/04	12/21/04	84
TJ11	44624	no	15	F	Pt. Erlington	09/28/04	02/11/05	136
TJ12	44625	no	15	M	Glacier Island	09/28/04	03/08/05	161
TJ13	44606	no	22	M	Lowell Pt.	04/28/05	06/16/05	49
TJ14	44607	no	22	F	Lowell Pt.	04/28/05	06/13/05	46
TJ15	44608	no	22	M	Lowell Pt.	04/28/05	07/26/05	89
TJ16	44609	no	22	M	Lowell Pt.	04/28/05	06/19/05	52
TJ17	44605	no	13	M	Lowell Pt.	08/04/05	10/09/05	66
TJ18	44619	no	13	M	Lowell Pt.	08/04/05	09/09/05	36
TJ19	44621	no	13	F	Lowell Pt.	08/04/05	09/01/05	28
TJ20	44622	no	13	F	Lowell Pt.	08/04/05	10/28/05	85
TJ21	44620	no	17	F	Lowell Pt.	11/22/05	03/27/06	125
TJ23	44599	yes	17	M	Lowell Pt.	11/22/05	02/02/06	72
TJ24	34158	yes	22	M	Lowell Pt.	04/17/06	07/05/06	79
TJ25	34154	yes	22	M	Lowell Pt.	04/17/06	06/29/06	73
TJ26	34152	yes	22	M	Lowell Pt.	04/17/06	07/31/06	105
TJ27	37114	yes	22	M	Lowell Pt.	04/17/06	06/26/06	70
TJ32	61770	yes	15	M	Lowell Pt.	10/10/07	02/23/08	136
TJ33	61773	yes	15	M	Lowell Pt.	10/10/07	02/11/08	124
TJ34	61772	yes	15	M	Lowell Pt.	10/09/07	03/31/08	174
TJ35	61759	yes	15	M	Lowell Pt.	10/09/07	02/08/08	122

Table 2.1: (Continued). Steller sea lions (n=70) tagged with satellite-linked transmitters (36 of them also equipped with LHX tags) (SPLASH, SDR-T16, Wildlife Computers) in Prince William Sound, AK between 2003 and 2012.

ID#	PTT	LHX	Age at release (months)	Sex	Capture Location	Release Date	Date of Last Location	Total Deploy Days
TJ36	61763	yes	15	M	Lowell Pt.	10/09/07	02/23/08	137
TJ37	61754	no	15	M	Lowell Pt.	10/10/07	01/13/08	95
TJ38	61766	yes	22	M	Lowell Pt.	04/29/08	05/28/08	29
TJ39	61793	yes	22	F	Lowell Pt.	04/29/08	06/12/08	44
TJ40	61777	yes	22	M	Lowell Pt.	04/29/08	06/20/08	52
TJ41	61771	yes	22	M	Lowell Pt.	04/29/08	06/26/08	58
TJ43	61761	yes	16	F	Lowell Pt.	11/12/08	04/03/09	142
TJ44	61769	yes	16	M	Lowell Pt.	11/11/08	11/21/08	10
TJ45	61695	yes	16	M	Lowell Pt.	11/12/08	01/05/09	54
TJ46	61696	yes	16	M	Lowell Pt.	11/11/08	02/17/09	98
TJ47	61694	yes	16	F	Lowell Pt.	11/11/08	01/17/09	67
TJ48	61698	yes	16	M	Lowell Pt.	11/11/08	06/14/09	215
TJ50	61757	yes	13	M	Seward Marine Center	07/29/09	09/01/09	34
TJ51	61756	yes	13	F	Lowell Pt.	07/21/09	08/15/09	25
TJ52	61764	yes	25	M	Seward Marine Center	07/29/09	10/12/09	75

Utilization Distribution of Steller Sea Lions Using State-Space Modeling

Each of the six bimonthly utilization distributions (UD) (Figures 2.3-2.8) had an average of 24 ± 4.16 animals (range: 20-30) contributing around $5,090 \pm 1,879$ processed locations (range: 2,757-7,593) (Table 2.2). The locations of seventeen animals encompassed only one UD, 31 animals encompassed 2 UD, 19 animals encompassed 3 UD, and 3 animals encompassed 4 UD. The July-August UD has 238 more locations and 8 more animals than the September-October UD however, September-October has a more extensive area by $4,500 \text{ km}^2$. The 100% UD of juvenile Steller sea lions was most extensive in November-December ($22,575 \text{ km}^2$) and January-February ($17,525 \text{ km}^2$) (Figures 2.8, 2.3, respectively, Table 2.3). May-June ($12,075 \text{ km}^2$) and September-October ($11,300 \text{ km}^2$) 100% UD were the second most extensive areas (Figures 2.5, 2.7, respectively, Table 2.3). The least extensive 100% UD were during the months of March-April ($6,500 \text{ km}^2$) and July-August ($6,800 \text{ km}^2$) (Figures 2.4, 2.6, respectively, Table 2.3). The area of high-intensity (50% UD) use occurring consistently across all 6 bimonthly utilization

distribution was at the haul-outs called Cape Resurrection and Rugged Island within Resurrection Bay, Glacier Island, Perry Island, and Grotto Island (Figures 2.9, 2.10). Other areas of high-intensity use but less consistent across all 6 utilization distributions include Procession Rocks, the Needle, Cape Junken, Cape Fairfield, Chiswell Island, and Aialik Cape, haul-outs and rookeries in the Kenai-Fjords/Prince William Sound area of Alaska.

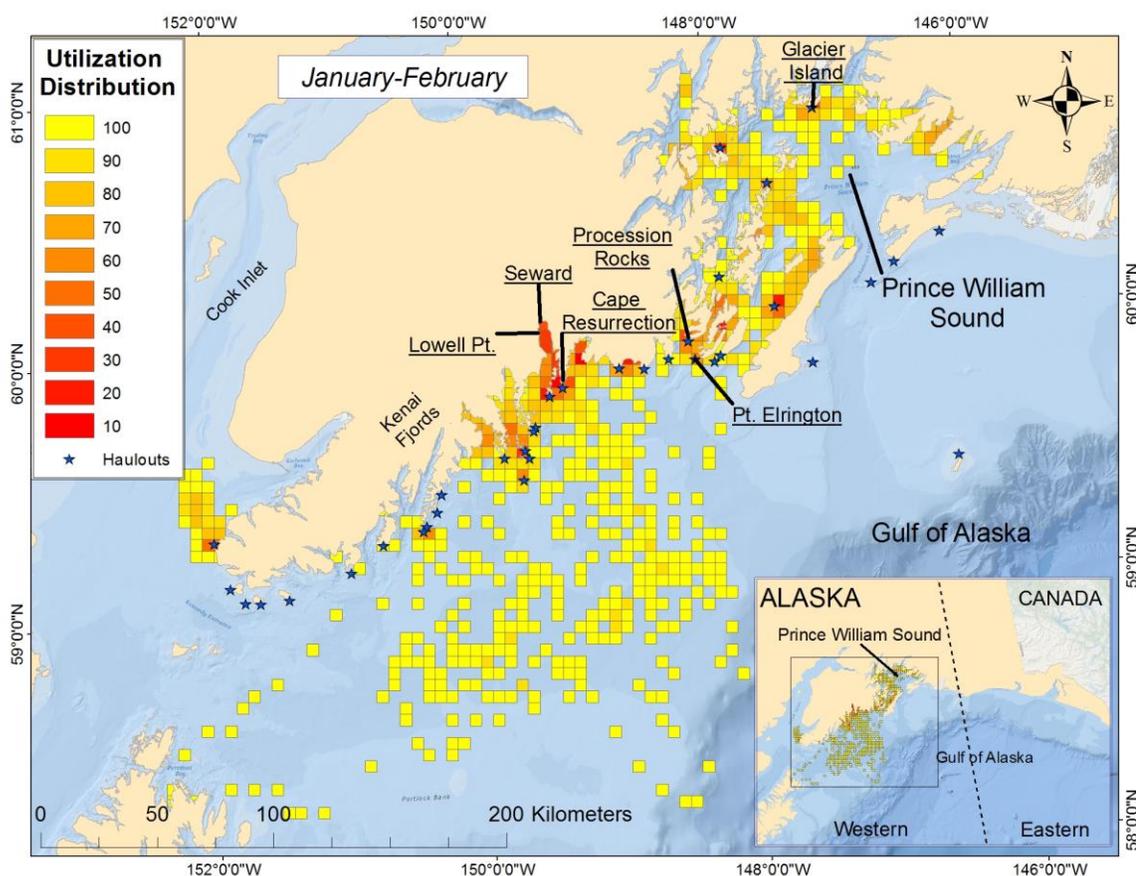


Figure 2.3: Utilization distribution of juvenile Steller sea lions during January and February between 2003 and 2011. Steller sea lions were captured and released at one of the underlined locations on the map. Stars indicate major haul-outs. Grid cell size is 25km². Yellow grid cells represent low-intensity use and red grid cells represent high-intensity use. Bathymetric data are from ESRI Ocean Basemap layer (2012). Map projection is Alaska Albers, map datum is NAD 1983.

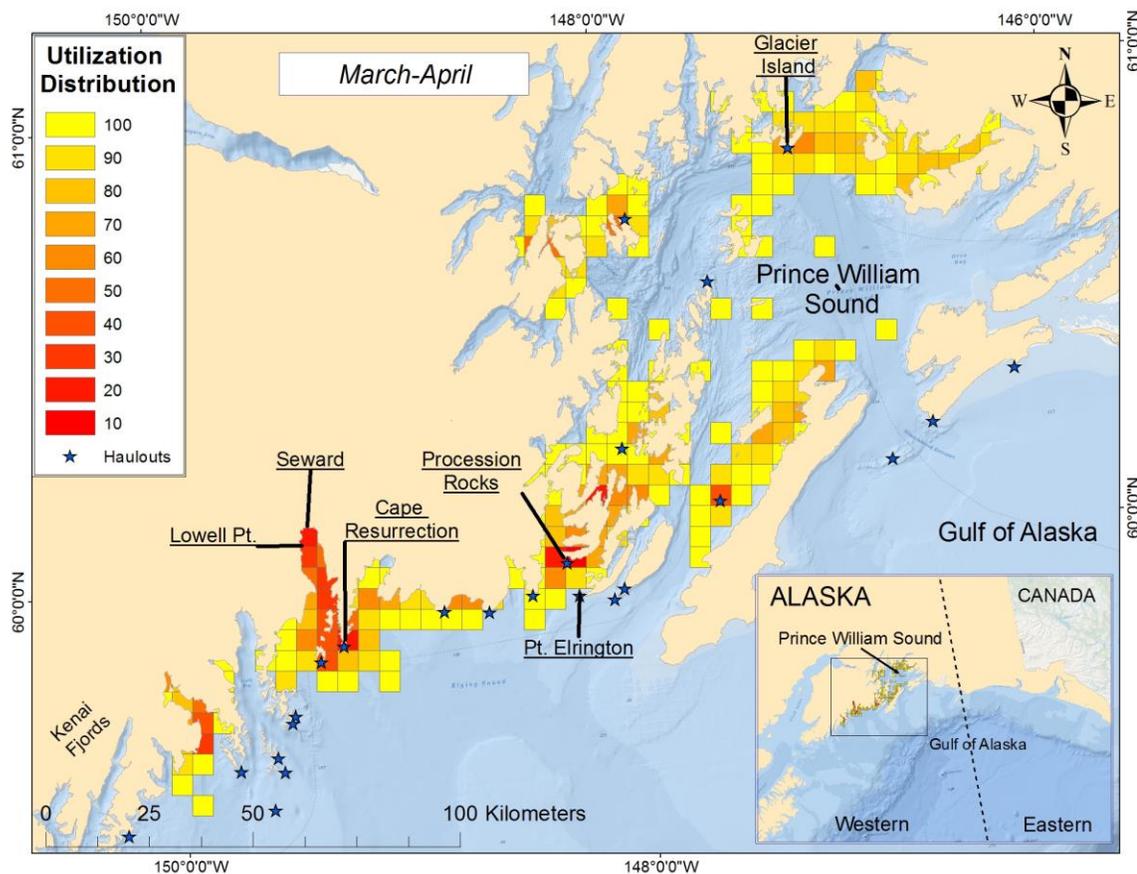


Figure 2.4: Utilization distribution of juvenile Steller sea lions during March and April between 2003 and 2011. Steller sea lions were captured and released at one of the underlined locations on the map. Stars indicate major haul-outs. Grid cell size is 25km². Yellow grid cells represent low-intensity use and red grid cells represent high-intensity use. Bathymetric data are from ESRI Ocean Basemap layer (2012). Map projection is Alaska Albers, map datum is NAD 1983.

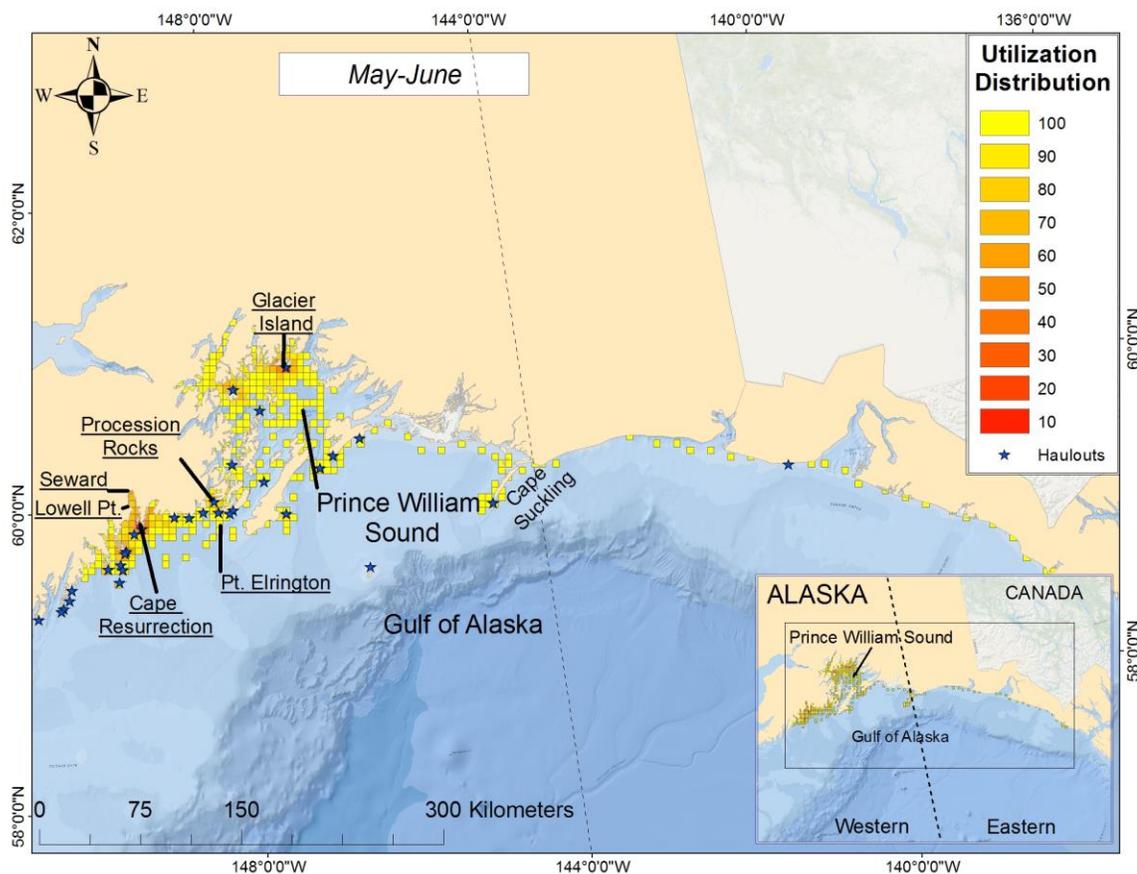


Figure 2.5: Utilization distribution of juvenile Steller sea lions during May and June between 2003 and 2011. Steller sea lions were captured and released at one of the underlined locations on the map. Stars indicate major haul-outs. Grid cell size is 25km². Yellow grid cells represent low-intensity use and red grid cells represent high-intensity use. Bathymetric data are from ESRI Ocean Basemap layer (2012). Map projection is Alaska Albers, map datum is NAD 1983.

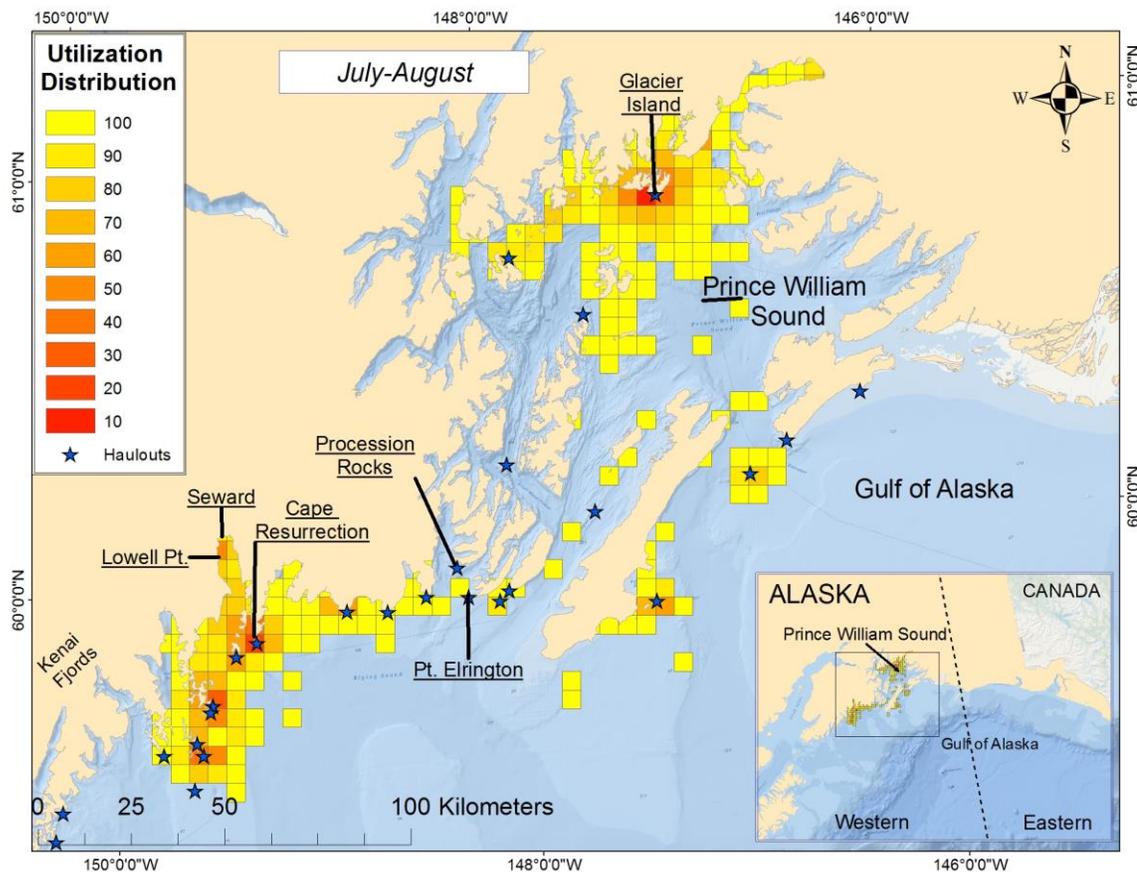


Figure 2.6: Utilization distribution of juvenile Steller sea lions during July and August between 2003 and 2012. Steller sea lions were captured and released at one of the underlined locations on the map. Stars indicate major haul-outs. Grid cell size is 25km². Yellow grid cells represent low-intensity use and red grid cells represent high-intensity use. Bathymetric data are from ESRI Ocean Basemap layer (2012). Map projection is Alaska Albers, map datum is NAD 1983.

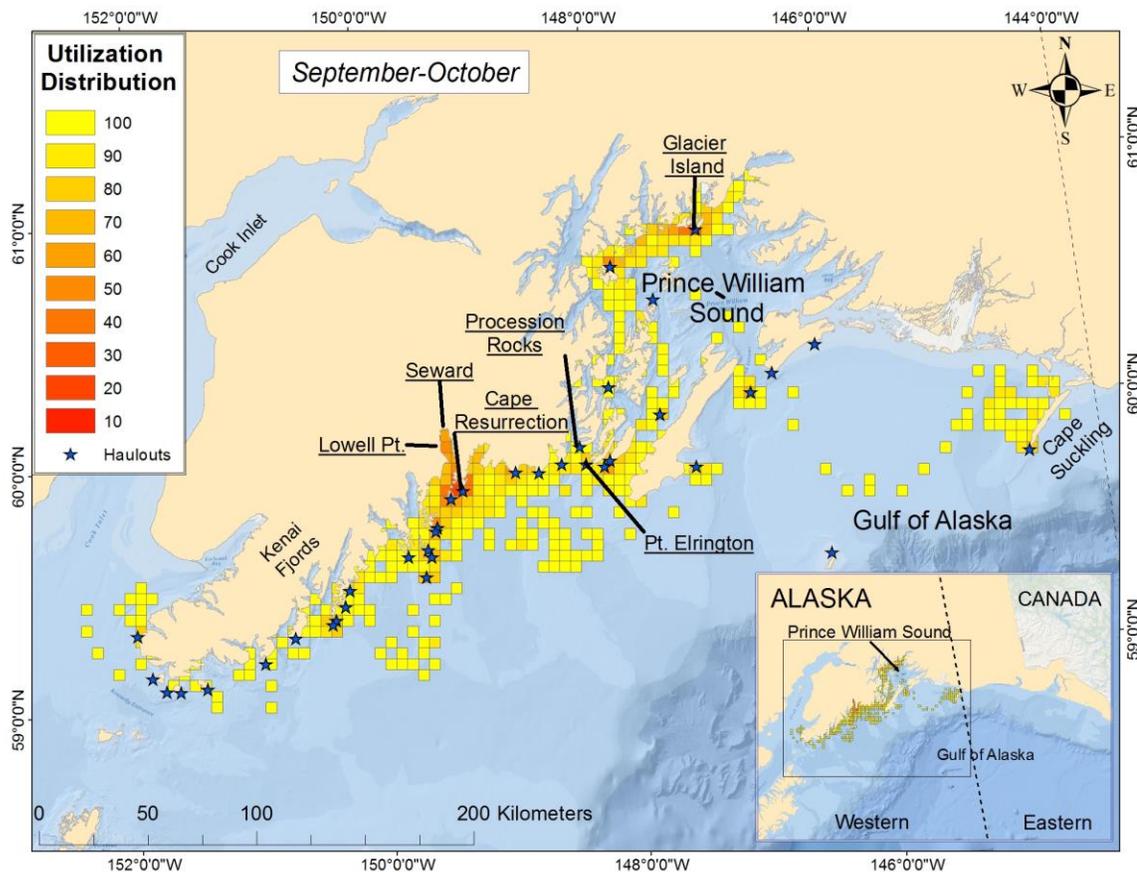


Figure 2.7: Utilization distribution of juvenile Steller sea lions during September and October between 2003 and 2012. Steller sea lions were captured and released at one of the underlined locations on the map. Stars indicate major haul-outs. Grid cell size is 25km². Yellow grid cells represent low-intensity use and red grid cells represent high-intensity use. Bathymetric data are from ESRI Ocean Basemap layer (2012). Map projection is Alaska Albers, map datum is NAD 1983.

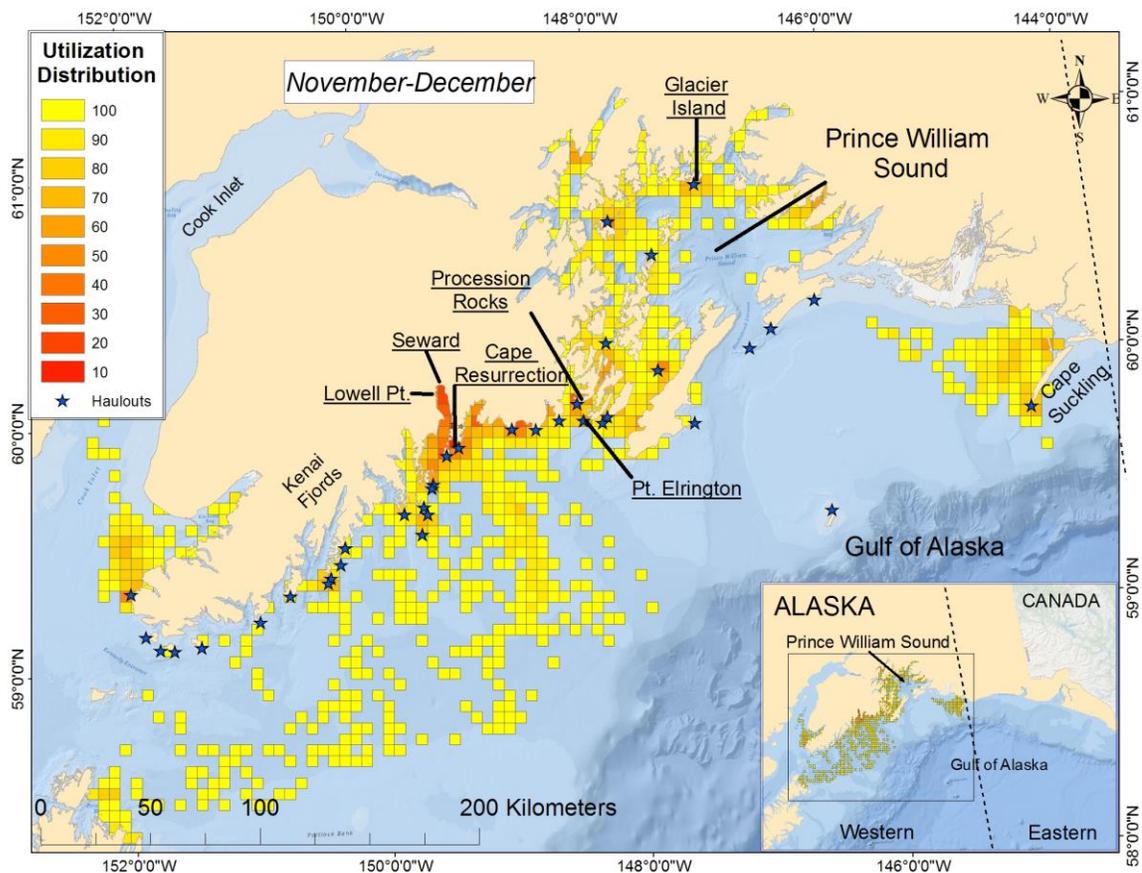


Figure 2.8: Utilization distribution of juvenile Steller sea lions during November and December between 2003 and 2012. Steller sea lions were captured and released at one of the underlined locations on the map. Stars indicate major haul-outs. Grid cell size is 25km². Yellow grid cells represent low-intensity use and red grid cells represent high-intensity use. Bathymetric data are from ESRI Ocean Basemap layer (2012). Map projection is Alaska Albers, map datum is NAD 1983.

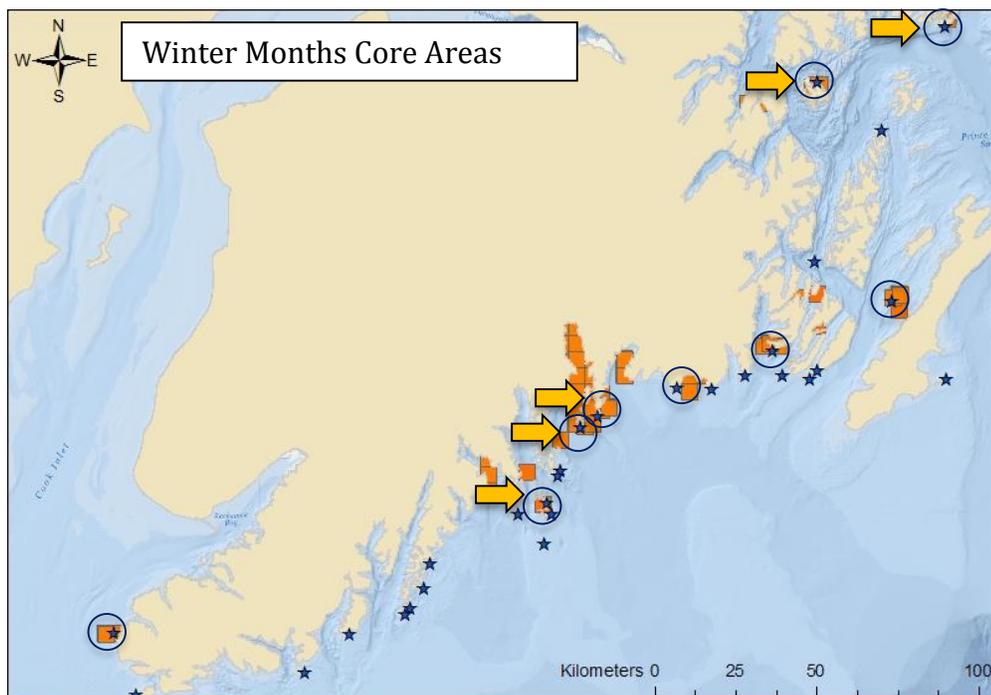


Figure 2.9: Core Areas (50% UD) for winter months (November-April). Stars represent haul-outs and stars within a circle are the haul-outs that overlap the core use areas. Arrows represent haul-outs that occur in both seasons.

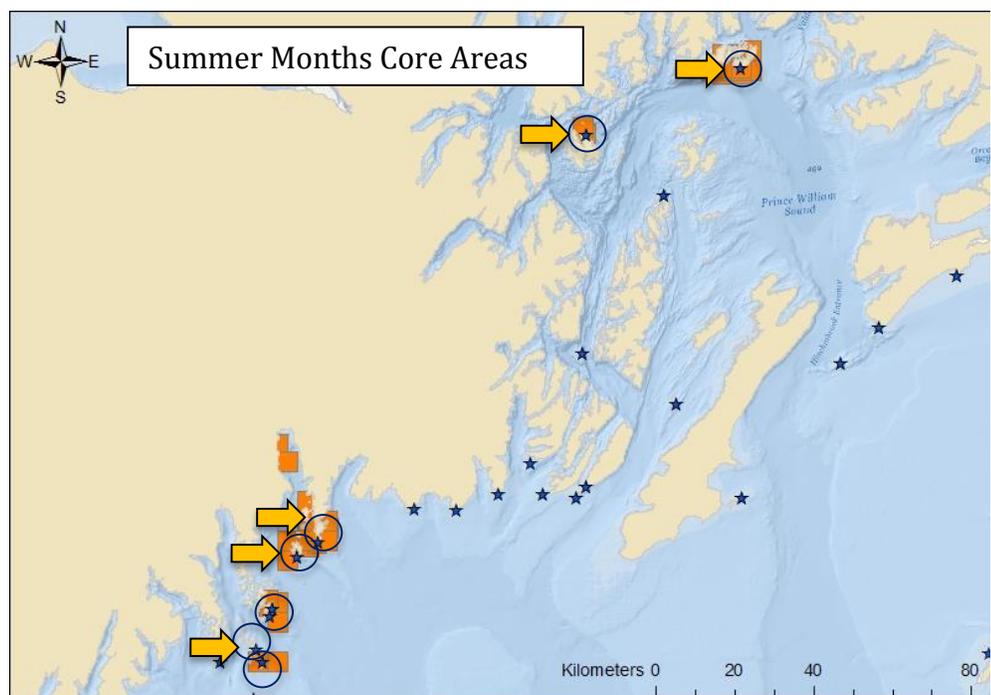


Figure 2.10: Core Areas (50% UD) for summer months (May-October). Stars represent haul-outs and stars within a circle are the haul-outs that overlap the core use areas. Arrows represent haul-outs that occur in both seasons.

Table 2.2: Summary of the number of processed SSM locations each animal contributed to each of the 6 bimonthly utilization distributions. Total number of animals and locations in each UD are summarized.

ID#	Number of locations & Animals in each UD					
	Jan-Feb	Mar-Apr	May-June	July-Aug	Sept-Oct	Nov-Dec
	23 Animals 6,384 Locations	20 Animals 2,757 Locations	25 Animals 5,634 Locations	30 Animals 4,157 Locations	22 Animals 3,919 Locations	29 Animals 7,593 Locations
FR010	---	---	---	219	162	---
FR011	---	---	---	65	---	---
FR013	---	---	---	86	---	---
FR014	---	---	---	174	---	---
FR015	---	---	---	85	---	---
FR63	---	---	194	119	---	---
FR64	---	---	182	52	---	---
FR65	---	---	182	113	---	---
FR66	---	---	---	150	75	---
FR67	---	---	---	150	21	---
FR68	---	---	---	144	381	7
FR69	---	---	---	137	---	---
FR70	---	---	---	86	---	---
TJ01	---	---	---	---	325	180
TJ02	---	---	---	---	84	---
TJ03	375	282	---	---	---	119
TJ04	375	381	20	---	---	119
TJ05	---	---	199	---	---	---
TJ06	---	---	219	25	---	---
TJ07	---	---	191	---	---	---
TJ08	---	---	128	---	---	---
TJ09	294	---	---	---	213	381
TJ10	---	---	---	---	207	315
TJ11	256	---	---	---	213	381
TJ12	369	45	---	---	207	381
TJ13	---	19	286	---	---	---
TJ14	---	19	268	---	---	---
TJ15	---	13	381	157	---	---
TJ16	---	13	309	---	---	---
TJ17	---	---	---	182	237	---
TJ18	---	---	---	182	52	---
TJ19	---	---	---	172	---	---
TJ20	---	---	---	182	359	---
TJ21	369	159	---	---	---	250
TJ22	369	159	---	---	---	250
TJ23	186	---	---	---	---	250
TJ24	---	75	382	26	---	---
TJ25	---	82	364	---	---	---
TJ26	---	82	381	183	---	---
TJ27	---	82	346	---	---	---
TJ32	336	---	---	---	125	382

Table 2.2: (Continued). Summary of the number of processed SSM locations each animal contributed to each of the 6 bimonthly utilization distributions. Total number of animals and locations in each UD are summarized.

ID#	Number of Locations & Animals in Each UD					
	Jan-Feb 23 Animals 6,384	Mar-Apr 20 Animals 2,757	May-June 25 Animals 5,634	July-Aug 30 Animals 4,157	Sept-Oct 22 Animals 3,919	Nov-Dec 29 Animals 7,593
	Locations	Locations	Locations	Locations	Locations	Locations
TJ33	260	---	---	---	119	381
TJ34	375	192	---	---	125	382
TJ35	237	---	---	---	125	382
TJ36	332	---	---	---	125	382
TJ37	78	---	---	---	125	382
TJ38	---	13	169	---	---	---
TJ39	---	---	267	---	---	---
TJ40	---	13	309	---	---	---
TJ41	---	---	355	---	---	---
TJ43	369	207	---	---	---	313
TJ44	---	---	---	---	---	65
TJ45	26	---	---	---	---	313
TJ46	297	---	---	---	---	319
TJ47	103	---	---	---	---	319
TJ48	369	381	275	---	---	319
TJ50	---	---	---	194	1	---
TJ51	---	---	---	153	---	---
TJ52	---	---	---	213	257	---
TJ54	---	---	---	127	---	---
TJ55	---	---	---	213	381	53
TJ56	---	---	---	---	---	161
TJ57	369	239	---	---	---	238
TJ58	265	---	---	---	---	250
TJ59	369	301	---	---	---	244
TJ60	6	---	---	---	---	75
TJ62	---	---	13	198	---	---
TJ63	---	---	57	90	---	---
TJ64	---	---	57	102	---	---
TJ65	---	---	100	177	---	---

Table 2.3: Summary of the intensity of use of the study area by juvenile Steller sea lions from 2003-2012 using gridded utilization distribution (UD). Grid cell size is 25km².

Months	Season	Area in 10%	Area in 50%	Area in 80%	Area in 100%
		UD (km ²)	UD (km ²)	UD (km ²)	UD (km ²)
January-February	Winter	50	700	3,300	17,525
March-April	Winter	25	525	1,850	6,500
May-June	Summer	25	225	1,600	12,075
July-August	Summer	25	275	1,200	6,800
September-October	Summer	0	300	1,675	11,300
November-December	Winter	25	625	3,975	22,575

The frequency distribution of the total number of SSM-generated observations as a function of distance to the nearest rookery or haul-out is shown for each time period in Figures 2.11 and 2.12. The percentages shown in Figures 2.11 and 2.12 reflect the mean proportion of time spent at different distances to haul-out locations, across the year. Animals on average spent more time at a greater distance from rookeries or haul-outs during the November through March periods, than during April through October periods. However, these distributions include the proportion of time spent hauled out in a dry state. We used a threshold of 5km as a proxy to estimate the proportion of at-sea locations only as a function of distance from rookeries and haul-outs. This threshold was based on the lowest quality LC with an assigned accuracy (LC 0), though we used an empirically determined LC 0 error of 4.2km (Costa et al., 2010) rather than the value of >1km (as indicated by the ARGOS service provider). The resulting distributions are shown in Figures 2.13 and 2.14, and are based on the assumption that locations with a distance from the nearest rookery or haul-out >5km are likely at sea, whereas for closer locations this assumption cannot necessarily be made. Since SSM generated locations are equally spaced in time at 4 hour intervals, the mean number of locations per animal and day spent at a distance greater than 5 km from the nearest rookery or haul-out as shown in Table 2.4 suggests that most of the seasonal differences for time spent within 10 km (Fig. 2.11, 2.12) are driven by the proportion of time spent dry (hauled out) versus wet (at sea).

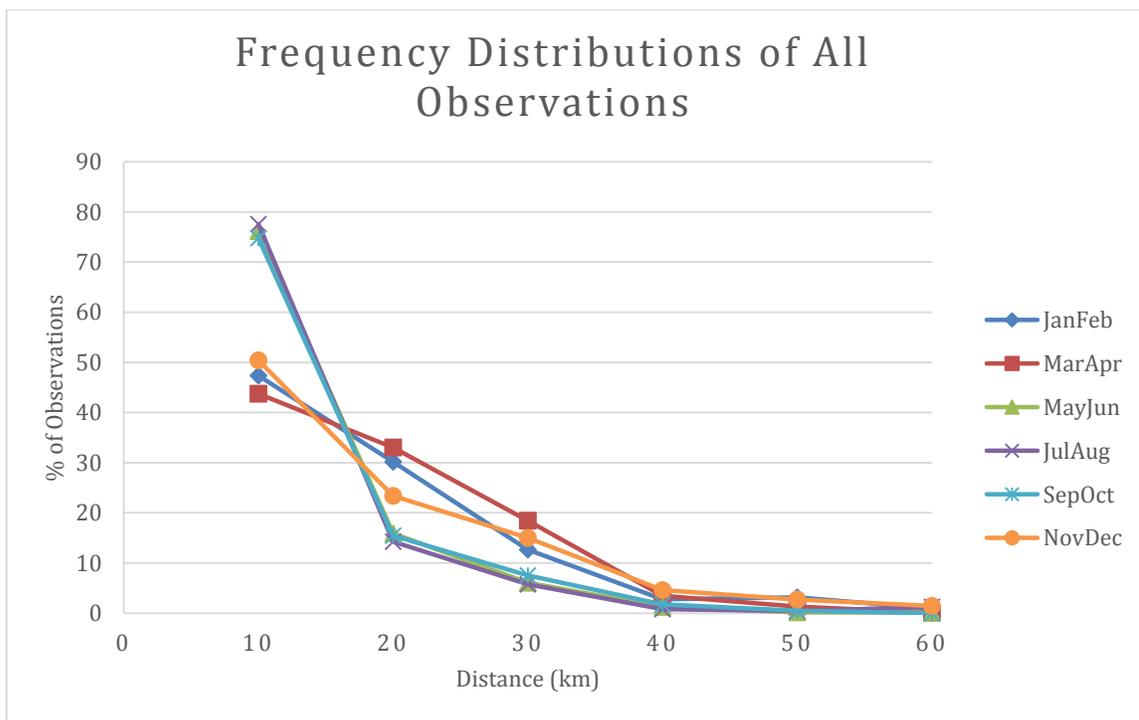


Figure 2.11: Frequency distribution of all observations vs distance (km) to nearest haul-out.

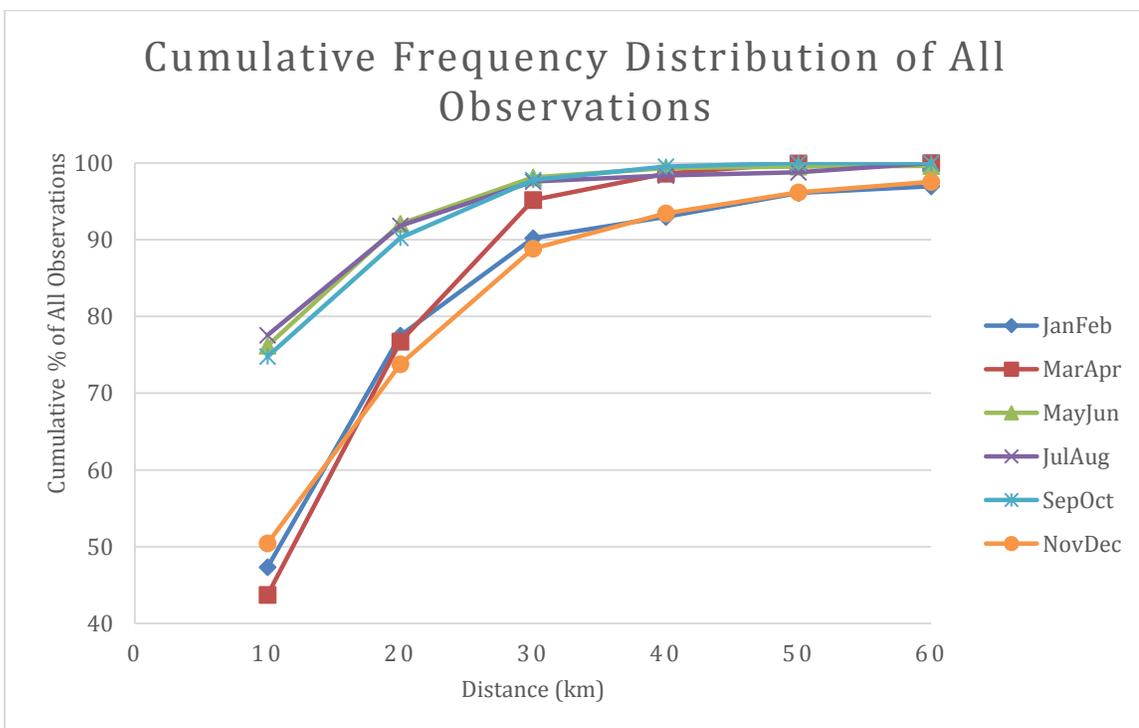


Figure 2.12: Cumulative frequency distribution of all observations vs distance (km) to nearest haul-out.

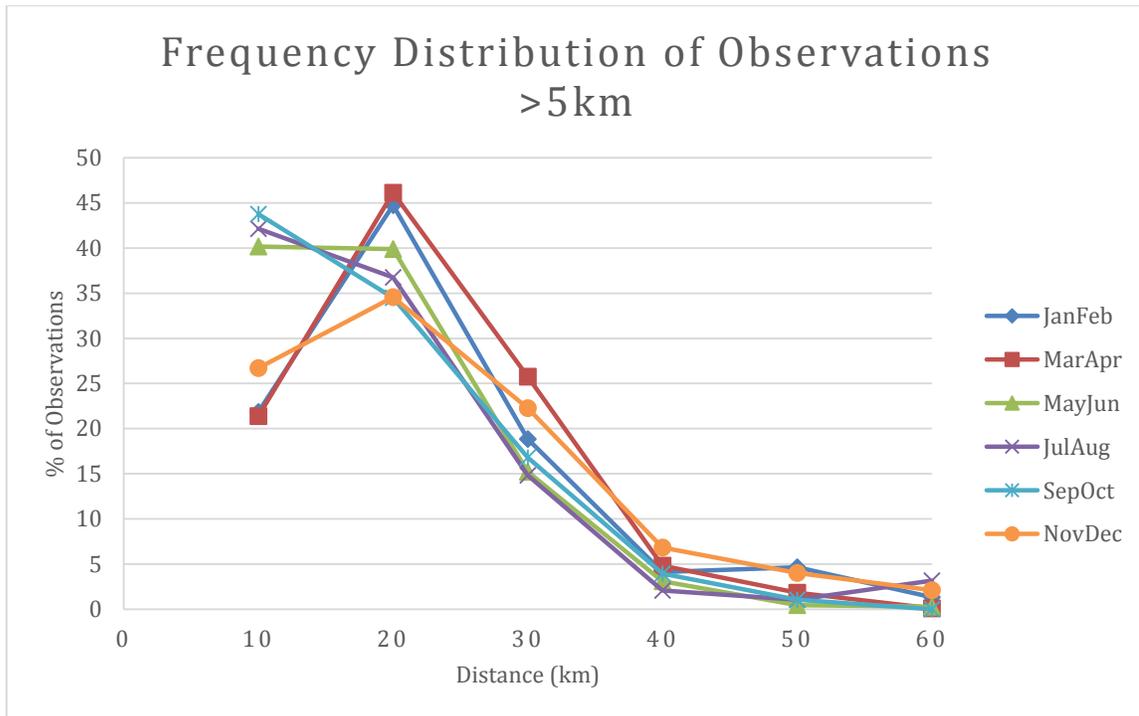


Figure 2.13: Frequency distribution of observations >5km vs distance (km) to nearest haul-out.

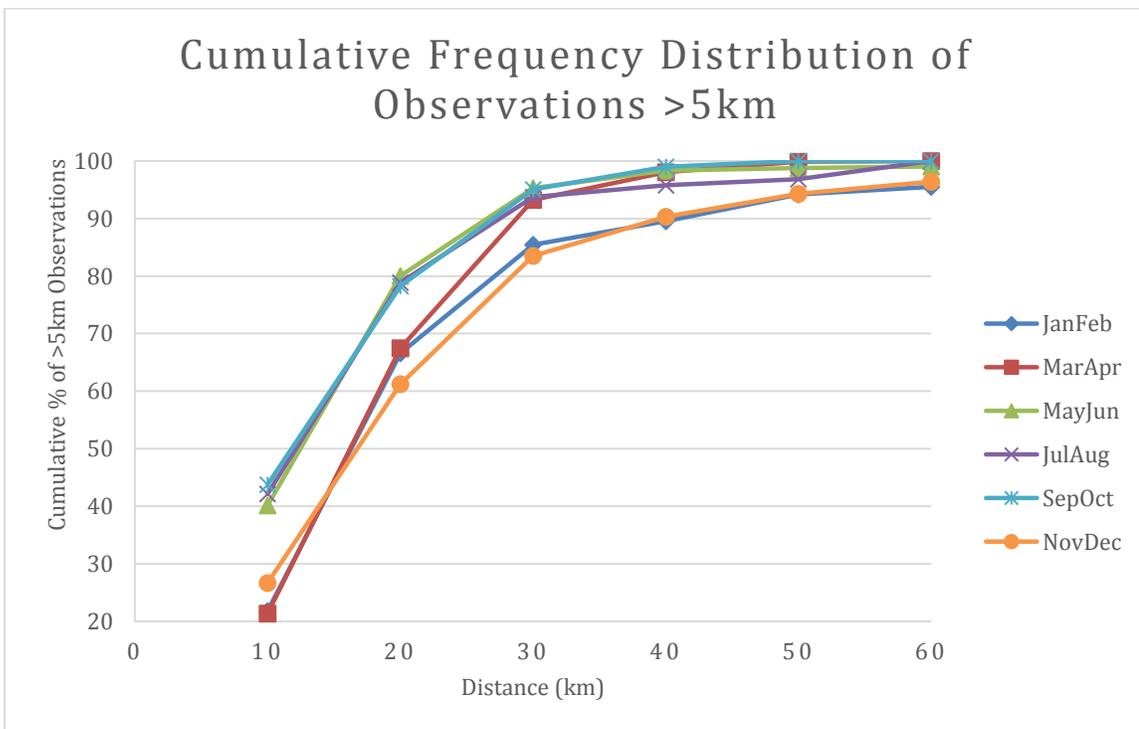


Figure 2.14: Cumulative frequency distribution of observations >5km vs distance (km) to nearest haul-out.

Table 2.4: Mean number of locations per day and animal for each 2-month time period for all observations and for a subset of observations >5km from nearest rookery or haul-out.

	Jan-Feb	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec
All Obs	6.22	6.18	6.22	6.17	6.21	6.24
Obs >5km	4.74	4.55	2.89	3.07	3.18	4.3

Time At Sea: Age Effects

The mean age at release for the 66 animals was $16.66 \pm .96$ months (range: 12-26 months). The mean percent time at sea (“wet”) for all 66 animals is 40.45 ± 4.94 (range: 7-96%) and the mean estimated total days spent at sea is 30.28 ± 6.98 days (range: 2.1-123.54 days) (Table 2.5). Given the difference in percentage of observation spent within 5 and 10km from rookeries and haul-outs, respectively, between two apparent groupings (November-April, and May-October, see Figures 2.11 and 2.13) we tested for significant effects between season and age, and time at sea. A multifactor analysis of covariance (MANCOVA) revealed a significantly higher percent time spent wet from November through April than May through October ($n=63$; age as covariate $F_1=3.796$, $p=0.056$; season as factor $F_1=13.147$, $p=0.001$).

Table 2.5: Summary of the 66 animals used in the statistical analysis.

Animal ID	Percent Time “Wet” in First 8 Timelines/Days	Total Deployment Days	Estimated Days Spent at Sea “Wet”	Age at Release (months)
FR010	45	62	27.9	13
FR013	40	15	6	13
FR014	39	29	11.31	13
FR015	16	15	2.4	13
FR63	31	49	15.19	12
FR64	29	39	11.31	12
FR65	48	49	23.52	12
FR66	54	17	9.18	14
FR67	34	29	9.86	14
FR68	61	86	52.46	14
FR69	65	23	14.95	26
FR70	40	15	6	14
TJ01	20	81	16.2	14
TJ03	33	129	42.57	17
TJ04	27	149	40.23	17
TJ05	7	32	2.24	23
TJ06	8	40	3.2	23
TJ07	10	32	3.2	23
TJ08	10	21	2.1	23
TJ09	20	145	29	15

Table 2.5: (Continued). Summary of the 66 animals used in the statistical analysis.

Animal ID	Percent Time "Wet" in First 8 Timelines/Days	Total Deployment Days	Estimated Days Spent at Sea "Wet"	Age at Release (months)
TJ10	41	84	34.44	15
TJ11	61	136	82.96	15
TJ12	48	161	77.28	15
TJ13	46	49	22.54	22
TJ14	38	46	17.48	22
TJ15	33	89	29.37	22
TJ16	46	52	23.92	22
TJ17	29	66	19.14	13
TJ18	11	36	3.96	13
TJ19	32	28	8.96	13
TJ20	32	85	27.2	13
TJ21	47	125	58.75	17
TJ22	36	125	45	17
TJ23	23	72	16.56	17
TJ24	16	79	12.64	22
TJ25	18	73	13.14	22
TJ26	37	105	38.85	22
TJ27	19	70	13.3	22
TJ32	26	136	35.36	15
TJ33	20	124	24.8	15
TJ34	71	174	123.54	15
TJ35	10	122	12.2	15
TJ36	15	137	20.55	15
TJ37	45	95	42.75	15
TJ39	68	44	29.92	22
TJ40	39	52	20.28	22
TJ41	59	58	34.22	22
TJ43	49	142	69.58	16
TJ44	45	10	4.5	16
TJ45	96	54	51.84	16
TJ46	87	98	85.26	16
TJ47	44	67	29.48	16
TJ48	52	215	111.8	16
TJ50	51	34	17.34	13
TJ51	39	25	9.75	13
TJ52	47	75	35.25	25
TJ54	39	21	8.19	13
TJ55	35	104	36.4	13
TJ56	64	26	16.64	17
TJ57	70	136	95.2	17
TJ58	63	81	51.03	17
TJ59	76	146	110.96	17
TJ60	84	13	10.92	18
TJ62	56	34	19.04	12
TJ63	38	24	9.12	12
TJ64	32	26	8.32	12

Discussion

Telemetry-based studies of marine animal movement generally involve three analytical components: 1) error corrections; 2) calculation of summary movement metrics from interpolated tracks; and 3) biological inference (Jonsen et al. 2012). Reviews (Patterson et al. 2008, Schick et al. 2008) have shown that adaptation of state-space modeling methods has become more prominent in movement ecology, offering a major advantage by integrating these three analysis phases in one method. A Bayesian state-space modeling framework was applied to juvenile Steller sea lion telemetry to calculate their utilization distribution in the Kenai Fjords (KF)/Prince William Sound (PWS) region of Alaska within the western Distinct Population Segment (DPS). Results of the bimonthly utilization distribution show non-uniformity such that some grids are not adjacent to one another but actually isolated in some circumstances. A reason for this might be a result of the combination of the low interpolation rate used for the state-space model and relatively fast swim speeds of individual juvenile sea lions.

Space use was highest in close proximity to and around haul-outs and rookeries. In general, 90% of all observations in the winter occurred within 30 km from nearest haul-out and within 20 km in the summer. Fifty percent of locations (core area) occurred near Glacier Island, Perry Island, the Needle, Procession Rocks, Cape Junken, Cape Fairfield, Cape Resurrection, Rugged Island, and Grotto Island for the winter months (November-April). The core areas (50% UD) visited during the summer months (May-October) include Glacier Island, Perry Island, Cape Resurrection, Rugged Island, Aialik Cape, Grotto Island, and Chiswell Island. Therefore, the haul-outs and rookeries that were the most prominent high-use areas year-round include Glacier Island, Perry Island, Cape Resurrection, Rugged Island, and Grotto Island, none of which are rookeries. This makes sense since these animals are presumed to be weaned, thus not yet sexually mature.

Animals spent more time at sea in winter than summer, and at a greater mean distance from rookeries and haul-outs. Thus two distinct seasons emerge in the data

we analyzed, with a transitional period between winter and summer. The reasons for the observed differences are not readily apparent within the data, but may relate to biotic and abiotic environmental characteristics not sampled here, such as bathymetry, temperature, prey distribution and abundance (Womble et al. 2009), predation pressure (Frid et al. 2009), or others.

March-April merits more discussion as it illustrates mixed characteristics. As seen in Figures 2.12-2.15, between 80% and 100%, it follows the same spatial pattern as the summer groups. However, by 50% it shows different values between summer and winter groups, and eventually converges with the winter months. Call et al. (2007) studied the at-sea and haul-out patterns of juvenile Steller sea lions in Prince William Sound and found that the variability in their study of juveniles may be due to individual differences in development and shifts in oceanic conditions during April-June that result in an increase of primary production and thus increase near-shore prey availability, which also coincides with weaning. This indicates near-shore areas adjacent to haul-outs are critical to the developing juvenile.

The fact that there were 2 distinct groups and one transitional period between the six 2-month intervals during the extent of the study might reflect the timing of changes in physiological requirements as juveniles are making more independent trips and transitioning into adulthood to forage. For example, Womble et al. (2009) found that seasonal attendance patterns of sea lions were commonly associated with the changes of available prey, thus suggesting seasonal foraging patterns. In the fall and winter, Steller sea lions tend to forage on salmon (*Oncorhynchus* spp.) and herring (*Clupea pallasii*) aggregations, respectively, while in the spring and summer, they forage on forage fish and salmon as well (pollock (*Theragra chalcogramma*) and Pacific hake (*Merluccius productus*) throughout the year) (Womble et al. 2009). However, the scope of our inferences and interpretations is limited because we did not analyze at-sea behavior in this study but only had a broad measurement of total time spent at-sea based on the state-

space model location estimates and timeline data, it limits the scope of our inferences and interpretations.

Analysis of space use using state-space model track estimates not only revealed that juvenile Steller sea lions in the PWS/KF region of Alaska utilize different areas depending on the time of year, but also show different spatial extents. They remain confined to a relatively smaller area (6,800-12,075 km²) in the 100% UD months of May through October compared to a larger area of 6,500-22,575 km² in the 100% UD months of November through April. One potential explanation for this pattern may be that the absence of prey from areas near winter haul-outs forces individuals to expand their foraging range both horizontally (longer trip lengths) and vertically (deeper dives) (Merrick & Loughlin 1997). Mellish et al. (2007) and Thomton et al. (2008) found significantly deeper mean dive depths in winter than summer, for an early subset of these study animals.

Furthermore, the utilization distribution illustrates that most of the juveniles from the western DPS were confined to a discrete region within PWS, KF, and around the Kenai Peninsula, with the exception of a single individual crossing the 144° stock boundary. This individual, TJ16, traveled east from its release location of Lowell Point as far as the eastern edge of Icy Strait Point, Alaska. It is unknown if this emigration was permanent since the observation days ended outside of the study area so we cannot make any inferences on interchangeability between the western and eastern DPS.

Information regarding species movement and how they use their habitats is necessary in attempting to discern any potential threats for a species of high conservation concern such as the Steller sea lion from the western DPS. The findings of our study have implications for other telemetry-based research on Steller sea lions. The primary efforts of juvenile sea lion research has been in the development of diving, movement, and distribution at sea (Merrick and Loughlin 1997, Raum-Suryan et al. 2004, Pitcher et al. 2005), however, intensity of space use patterns as young sea lions mature provide important information regarding

implications for their survival as it is the most critical time of their lives as they move toward independence and ultimately, reproduce.

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CHAPTER 3: CHARACTERIZATION OF PREDATION EVENTS OF JUVENILE STELLER SEA LION IN THE GULF OF ALASKA (2003-2013)

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Abstract

Without current information on at-sea behavior and predation risk of juvenile Steller sea lions in the Kenai Fjords (KF)/Prince William Sound (PWS) region of Alaska, it is difficult to assess whether predation by killer whales or sharks is a potential factor in the continued decline of the Steller sea lion (SSL) in the western Distinct Population Segment (DPS). The objective of this study was to characterize the density effects of predator-prey interactions based on the spatial distribution of actual juvenile Steller sea lion predation events in relation to their utilization distribution. A Bayesian state-space model approach was used to process and interpolate the ARGOS locations received post-mortem from Life History Transmitter (LHX) tags. The processed tracks were then used to extrapolate the most likely locations of predation events. Four of the 15 predation events occurred in the 91-100% UD, or areas of the lowest relative frequency distribution of animal locations, 3 events occurred in the 81-90% UD, and only 1 event in the 21-30% UD corresponding to an area of higher relative frequency distribution of animal locations. Seven of the 15 predation events occurred outside the UD range, and therefore in areas likely of the lowest relative frequency distribution of animal locations. The winter predation rate was twice that of summer, with 10 predation events during the winter periods (November-April), and 5 events during the summer periods (May-October). A Rayleigh test for circular distribution showed a significant difference from uniformity with a mean ordinal date of January 6th, ($n=7$, $p=0.016$). Since juvenile survival is low, and thus poses a significant risk for population-level survival, increased knowledge of the specifics of juvenile SSL space utilization patterns is of vital importance to assessing the viability of predation risk as one of the main culprits to their survivability.

Key words: satellite telemetry, Life History Transmitter, state-space model, predation, predation risk, utilization distribution.

Introduction

The mechanisms behind population control have been an important topic when addressing the nature of the upper-trophic structure of an ecosystem and how populations respond to environmental disturbances (Hunt & McKinnell 2006). Large apex predators, through size, mobility, and nutritional requirements can exert substantial forces on lower trophic levels, which could lead to temporary or permanent changes in the structure and function of ecosystems (Estes et al. 1998, Williams et al. 2004). Furthermore, the potential effect on populations at lower trophic levels may be influenced by the requirements for profitable foraging of top predators, the abundance of preferred prey species and the foraging habitat range of the predator (William et al. 2004, Hunt & McKinnel 2006). For example, if foraging is focused where most or all of the prey population occurs in high densities, the predator can have a significant impact on populations of their prey (Hunt & McKinnell 2006).

The recent collapse of Steller sea lions (SSL) (*Eumetopias jubatus*) from the western Distinct Population Segment (DPS) (from Prince William Sound west through the Aleutian Islands) has prompted the National Marine Fisheries Service (NMFS) to list them under the Endangered Species Act (ESA) and scientists to question the causes of the precipitous decline (NMFS 2008). Very little information exists on juvenile Steller sea lion survival or their contribution to overall population trajectories (York 1994). Most studies on juveniles have focused on bottom-up population control (i.e. resource scarcity) as a potential link to the population decline (Merrick & Loughlin 1997, Loughlin et al. 2003, Noren et al. 2009, Womble et al. 2009, Calkins et al. 2013). Horning & Mellish (2012) suggested that age-structured predation focused on juveniles could potentially affect reproductive output and trajectory of a population. Frid et al. (2009) provided the foundation for further model developing and testing of the hypothesis that juvenile Steller sea lion predation risk (direct and/or indirect) and prey distribution are not mutually exclusive and affect foraging decisions by the endangered sea lions. However, the

studies mentioned above do not characterize predation on Steller sea lions in relation to their likely density at sea.

The implantable Life History Transmitter (LHX) tags (Figure 3.1) were developed by Horning & Hill (2005) to overcome limitations associated with existing experimental approaches for survival analysis such as the classic mark-recapture methods (Horning & Hill 2005). The main difference is that the LHX tag allows one to determine when and where a mortality event occurs, which is not possible with mark-recapture models relying on relatively infrequent re-sighting information. LHX tags detect mortality events when temperature of the host drops below a preset threshold (24°C) and determines cause of death from temperature profile across the mortality event. Failure to accurately recognize these state transitions makes the estimation of the location of predation events highly variable, which is compounded by the fact that 1) the implantable LHX tag monitors and archives sensor data without transmitting while inside the host body, 2) only begins transmitting after the tag is extruded from the decomposing or dismembered carcass, and 3) transmissions may not necessarily be received for hours or even days after mortality. After an animal's death, the stored data is then transmitted through the ARGOS system aboard polar orbiting environmental satellites. The LHX tag provides temporally and spatially unrestricted sampling effort, and as a result can accurately assess survival and predation rates (Horning & Hill 2005, Horning & Mellish 2009, 2012). LHX tags provide data on causes of mortality, and for non-traumatic mortalities can provide estimates of body mass at time of death (Horning & Mellish 2009).

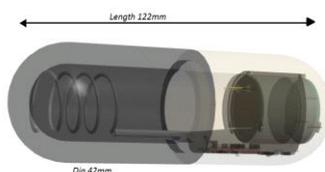


Figure 3.1: 3D view of Life History Tag. Dimensions and configuration (Wildlife Computers 2000).

Without current information on at-sea behavior and predation risk of juvenile Steller sea lions, it is difficult to assess whether predation by killer whales or sharks is a potential factor in the continued decline of the Steller sea lion in the western DPS. Specifically, we lack baseline information on characterizing the relationship of predation and juvenile sea lion's probability of occurrence at each point in space in the declining western DPS. The objective of this study was to characterize the density effects of predator-prey interactions based on the spatial distribution of actual juvenile Steller sea lion predation events determined from archival Life History Transmitter (LHX) tags in relation to their utilization distribution. We hypothesize that predation events occur uniformly in all areas for non-specialized predators, and more often in areas of high utilization such as near rookeries and haul-outs for predators that are specialized on SSLs and focus hunting efforts on high use areas.

Methods

Study Area, Animal Captures, and Tagging

Seventy weaned juvenile (12-25 months) Steller sea lions were captured via an underwater noose method (see Mellish et al. 2006) in the Prince William Sound (PWS) and Kenai Fjords (KF) region of Alaska, (Figure 3.2) between 2001 and 2012. All 70 animals were instrumented with ARGOS satellite transmitters (SDR-T16 and SPLASH tags, Wildlife Computers, Redmond, WA) glued midline to the dorsal fur, between the scapulae. Details regarding the capture method and satellite tag deployments are given in Vazquez et al. (2013).

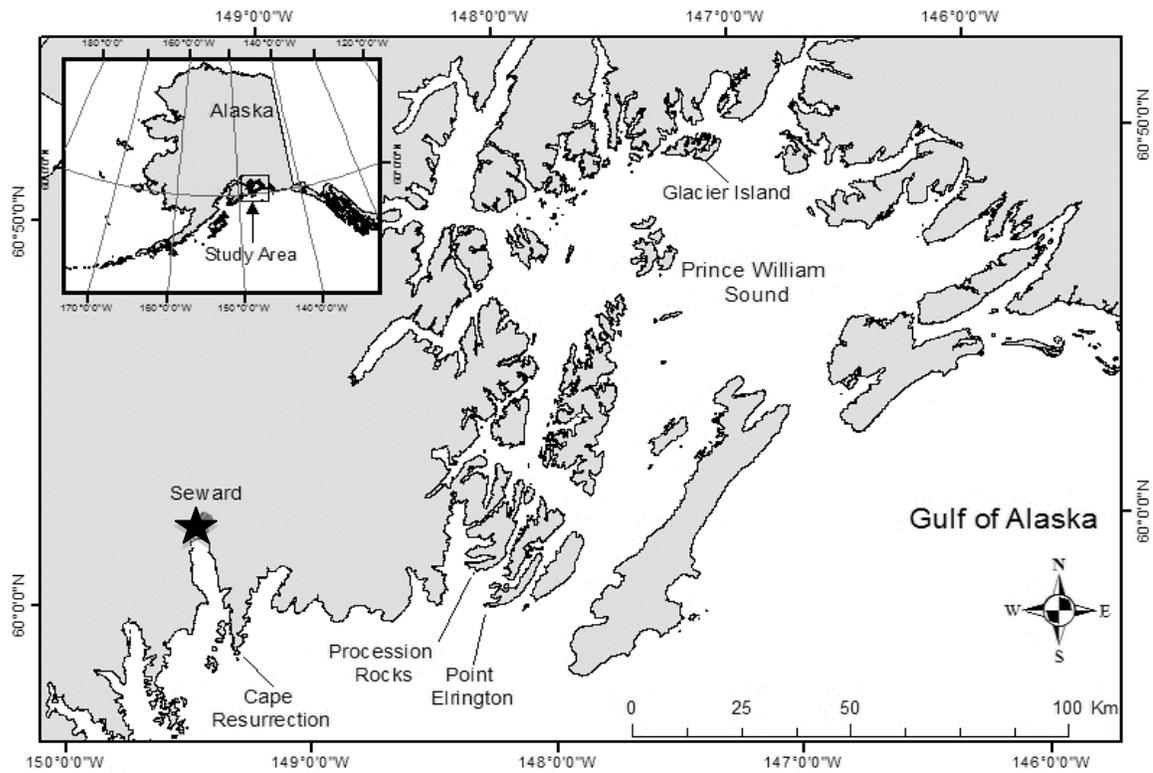


Figure 3.2: Study area and capture locations. Transient and free-ranging juvenile Steller sea lions were released either at the capture locations (Cape Resurrection, Procession Rocks, Point Elrington, and Glacier Island) or at the Alaska SeaLife Center in Seward, Alaska (Black star) near Resurrection Bay.

Characterizing Predation from Life History Transmitter (LHX) Tags

To directly measure mortality and predation in the juvenile Steller sea lion, Life History Transmitter (LHX) tags were deployed in 36 juveniles (N=8 females and N=28 males) from 2005-2011 (Horning et al. 2008, Horning & Mellish 2012). Single (N=2) or dual (N=34) LHX tags were surgically implanted into the animals. The concept of dual tags was instrumental for the calculation of cumulative tag failure rates and to increase data recovery likelihood and estimate event detection probability (Horning & Hill 2005, Horning & Mellish 2012). The tags may uplink with some delay after death, based on fate of animal and tags, and uplinks may occur at varying intervals based on programming and ambient conditions (sea state, etc.) for periods ranging from a few days to several months.

LHX tags determine two Tag State Transitions in order to correctly initiate transmissions, since the tag does not transmit while inside the host body: (1) transition between being in a live animal versus a deceased one, followed by (2) transition from being inside the host's abdominal cavity to being outside in the ocean elements (Horning & Hill 2005). Failure to identify these state transitions will delay or prevent transmissions. An acute death (dismemberment) at sea by major trauma such as an attack by a predator leads to: (1) the immediate extrusion of implanted LHX tag or (2) the LHX tag getting lodged within chunks of smaller body parts (Horning & Mellish 2009). An acute/non-traumatic event other than predation should lead to algor mortis (gradual body cooling) and delayed tag extrusion as the body slowly decomposes (Horning & Mellish 2009).

In principle, state transitions are determined based on temperatures outside a user-defined physiological temperature range (24 – 43°C), light levels or detecting air. The first state transition (live to dead) is evaluated every 30 minutes. Date and time of death is therefore determined, stored and later transmitted with a 30 minute resolution. The second state transition (extrusion and/or reaching surface) is evaluated once every 24 hours at 12:00 noon Greenwich Mean Time (GMT). If a tag is extruded and in a position to transmit (at the ocean surface or ashore) shortly after 12:00pm, the first LHX transmission may be delayed by up to 24 hours, affecting the accuracy of the estimated mortality location. Once transmissions from a tag are being received, initial location (those closest in time to the mortality event) estimates computed by the ARGOS service provider (CLS America, Inc.) are often of lower accuracy (i.e. location classes 0, A or B), sequential location estimates generally improve in accuracy. As LHX tags continue to transmit, subsequent location estimates should reflect the movement of tags floating on the ocean surface (in case of mortalities at sea, and until tags are washed up at shore). Movements of floating tags should be influenced by surface currents, tides and winds. Transmissions allow estimation of the position from which tags are uplinking, and they also include data on date and time of death, and temperature profiles across

the mortality event that are subsequently used to classify detected mortalities into predation and non-predation events (Horning & Mellish 2009).

State Space Model

Using the free software packages R version 2.15.2 (R Development Core Team, 2012) and WinBUGS (Lunn et al. 2000), we fit the Bayesian state-space model (SSM) developed by Jonsen et al. (2005, 2007) and modified by Bailey et al. (2009) to all of the raw ARGOS locations of each sea lion track (See Vazquez et al. 2013) and to the raw Life History Transmitter (LHX) tag locations. The model yielded an estimate of the most probable path of a sea lion at 4-hr intervals, while accounting for non-Gaussian ARGOS location error. For the LHX tag, we used an hourly time-step. See Vazquez et al. (2013) for details of SSM code and analysis.

Utilization Distribution

Six bimonthly utilization distributions (UD) representing the number of animals per area were used in order to relate the locations of detected predation events to the animals' space use. The UD's were calculated from temporally interpolated external transmitter locations of individual tracks as described in Vazquez et al. (2013).

Estimating Mortality Location and Error

We used the Bayesian State-Space Modeling (SSM) described in Vazquez et al. (2013) to process all raw ARGOS locations and location error covariates obtained from LHX tags. We subsampled the raw LHX ARGOS locations to only the first 7 days post mortem to estimate the most likely location for the date and time when the first state transition was recorded (the death time stamp), in two steps. First, we maximized the accuracy of the location estimate of the initial post-mortem uplink. Since SSM output accuracy progressively increases as more locations are considered, we ran the model in reverse to use all available information from the first 7 days post-uplink. The model was set to produce output (pseudo-locations) in 1 hour increments. Next, we extrapolated to an earlier time from this improved first uplink location estimate. Extrapolation occurred over varying time periods that

corresponded to the time difference between the death time stamp and the first uplink.

From post-uplink SSM tracks, sequential SSM movement vector sets were selected to cover an equivalent period of time (where each vector within a set corresponds to the SSM output in form of distance and bearing over a 1 hour period). As many different such sequential vector sets as could be obtained from within the 7 days subsample were then applied to the improved first uplink location estimate. This yielded multiple backward-extrapolated locations.

We used the library (geosphere) in R to calculate the new positions originating from the first LHX location every time using the final distance and bearing. These new locations were plotted in ArcGIS and we used the “Central Feature” command to identify the most centrally located feature in the point distribution. This centrally located feature was calculated within ArcGIS by measuring the distances from each feature centroid to every other feature centroid and summing them. Then the feature associated with the shortest accumulative distance to all other features is selected and copied to a newly create output feature class, resulting in the estimated mortality location. The mean variance in the backward extrapolation was two orders of magnitude lower than the mean 95% credible area for the SSM-based improved first uplink location estimate. Therefore, since we did not want to add the negligible vector-based error to the SSM-based error, we used the 95% credible limit from the reverse state space model output for the first uplink location.

Distribution Test for Age At Death: Seasonal Effects

Circular mean and standard deviation of age at time of death and season were calculated using a Rayleigh test for uniformity (Moore 1980, Zar 1996). Since data are rhythmic, one cannot perform linear tests so a test for circular distribution is appropriate. Ordinal dates (where Jan 1st= 1 and Dec 31st= 365) were converted to a phase angle (a value between 0 and 360 degrees) in order to be able to run the test.

Results

Characterizing Predation and LHX Tags Summary

Of the 36 LHX tagged animals, 17 mortalities were detected between the first release in November of 2005, and August of 2013. The event detection probability was previously estimated at >98%, suggesting that within the sample of 36 animals no mortalities were undetected (Horning & Mellish, in review). Two of the 17 detected mortalities (TJ27, TJ43) yielded insufficient data to allow a determination of causes of mortality. All fifteen events with complete temperature data sets were classified as predation since the tags recorded immediate extrusion and/or cold-water temperatures (Horning & Mellish, in review). Their deployment information is summarized in Table 3.1.

Table 3.1: Summary of 15 predation events detected via LHX tags. Underlined animal IDs represent events with time gaps between mortality and first uplink locations > 4 days. Dates and times are in GMT.

ID	Days Tracked PR (Ext. Tag)	Days Alive PR	Last Ext. Loc. Date & Time	Mortality Date & Time	1st Usable LHX Loc. Date & Time	LC 1st LHX	Distance to Nearest Haul-out (km ²)	Mortality Region & 95% Credible Limit Error Area (km ²)
<u>TJ32</u>	136	138	02/23/08 23:32:05	02/25/08 22:00:00	03/12/08 14:30:00	2	9.7	KF (W of Rugged Is) N/A
TJ33	124	124	02/11/08 17:10:50	02/11/08 22:30:00	02/12/08 21:03:00	0	10	KF (N of Fox Is) 3,807
<u>TJ35</u>	122	221	02/08/08 0:30:09	05/18/08 11:00:00	05/23/08 5:48:00	1	56.4	KF (Cook Inlet) N/A
TJ44	10	361	11/21/08 11:30:31	11/7/09 20:00:00	11/08/09 23:22:00	1	20	V/C (N of Busby Is) 1
TJ46	98	421	02/17/09 14:54:13	01/06/10 12:00:00	01/06/10 20:07:00	A	28.1	GoA (W of Kodiak Is) 18,889 PWS
TJ47	67	67	01/17/09 13:50:29	01/17/09 17:30:00	01/17/09 20:34:00	B	6.3	(Elrington Passage) 580
TJ51	25	92	08/15/09 11:37:14	10/22/09 6:00:00	10/22/09 21:16:00	B	9.4	KF (NE of Rugged Is) 181,794

Table 3.1: (Continued). Summary of 15 predation events detected via LHX tags. Underlined animal IDs represent events with time gaps between mortality and first uplink locations > 4 days. Dates and times are in GMT.

ID	Days Tracked PR (Ext. Tag)	Days Alive PR	Last Ext. Loc. Date & Time	Mortality Date & Time	1st Usable LHX Loc. Date & Time	LC 1st LHX	Distance to Nearest Haul-out (km²)	Mortality Region & 95% Credible Limit Error Area (km²)
<u>TJ52</u>	75	738	10/12/09 21:49:09	08/06/11 14:30:00	08/21/11 20:57:00	2	12.5	KF (Nuka Passage) N/A
<u>TJ54</u>	21	295	08/11/09 7:21:30	05/12/10 17:00:00	05/16/10 11:51:00	A	24.6	KF (E of Rabbit Is) N/A
<u>TJ57</u>	136	307	04/09/11 3:08:40	09/27/11 17:30:00	09/27/11 23:10:00	B	39.9	PWS (NW of Hinchinbrook Is) 574,610
<u>TJ58</u>	81	81	02/12/11 11:59:37	02/12/11 22:00:00	02/13/11 21:05:00	B	13.1	PWS (Knight Is Passage) 6,054
<u>TJ59</u>	146	431	04/18/11 8:40:13	01/28/12 16:30:00	01/28/12 22:13:00	A	63.3	GOA (NE of Kodiak Is) 85,068
<u>TJ62</u>	34	624	08/2/11 11:44:59	03/15/13 05:30:00	03/15/13 22:48:00	2	4.5	KF (NE of Harbor Is) 15,767
<u>TJ63</u>	24	163	07/16/11 6:12:04	12/02/11 22:00:00	12/03/11 20:03:00	A	15	PWS (E of Perry Is) 15,767
<u>TJ64</u>	26	165	07/18/11 2:39:50	12/04/11 20:00:00	12/09/11 21:19:00	A	14	PWS (SE of Glacier Is) N/A

PR=post release; Ext.=External; LHX=Life History Transmitter; LC=Location Class; PM=post-mortem; UL=uplink; KF=Kenai Fjords; PWS=Prince William Sound; V/C=Valdez/Cordova; GoA=Gulf of Alaska

From the 15 predation events, 10 individuals (TJs 44, 46, 47, 51, 57, 58, 59, 62, 63, 64) had both LHX tags uplink at some point post-mortem and 5 individuals (TJs 32, 33, 35, 52, 54) only had one of the LHX tags uplink. Partial or full data sets were physically recovered from some of the tags that did not uplink, and not all tags that uplinked provided locations within the first 7 days after initial uplink. Tags from at least three individuals (TJ 52, TJ63 and TJ64) appeared to have been ingested by a predator, resulting in substantial delays to initial uplink (Horning & Mellish, in review). The external transmitters of TJs 33, 47, and 58 were still

transmitting up until shortly before the time of mortality. For example, TJ33's last external tag uplink was on 2/11/2008 at 17:10 GMT and the actual mortality time-stamp occurred on 2/11/2008 at 22:30 GMT, however the LHX tag didn't begin uplinking until 2/12/2008 at 21:03 GMT. Therefore, for those three individuals, we almost had a continuous track leading up to the actual mortality location. The other 7 animals lost their external transmitters well before actual mortality (Table 3.1). Five animals had time gaps between mortality and first uplink of at least 4 days (Table 3.1). For these animals no mortality location extrapolation was attempted, and the first uplink locations was used instead. These 5 remaining predation events will be described anecdotally but no statistical analysis will be performed on them.

Utilization Distribution of Steller Sea Lions Relative to Predation Events

Overlaying the estimated predation locations on their associated 2-month period utilization distribution allowed us to identify at which relative density of animal observations each predation event occurred (Figures 3.3-3.8). All 15 predation events occurred within the region of the western DPS spanning from 2008 through 2013. Six predation events (TJs 32, 33, 46, 47, 58, 59) occurred in January-February (Figure 3.3). One predation event (TJ 62) occurred in March-April, 2 events (TJs 35, 54) in May-June, 1 event (TJ 52) in July-August, 2 events (TJs 51, 57) in September-October, and 3 events (TJs 44, 63, 64) in November-December (Figures 3.4, 3.5, 3.6, 3.7 & 3.8, respectively).

Four of the 15 events occurred in the 91-100% UD, 3 events occurred in the 81-90% UD, and 1 event in the 21-30% UD (Figure 3.9). Seven of these predation locations occurred outside the UD range, meaning they did not overlap any of the grid cells. Furthermore, we could calculate the straight-line distance between the estimated predation location and the nearest haul-out within the western DPS (Table 3.1). An example of the x-y vector locations and mean predation location estimate based on the central feature in ArcGIS is shown in Figure 3.10. The error area for the estimated predation locations are summarized in Table 3.2.

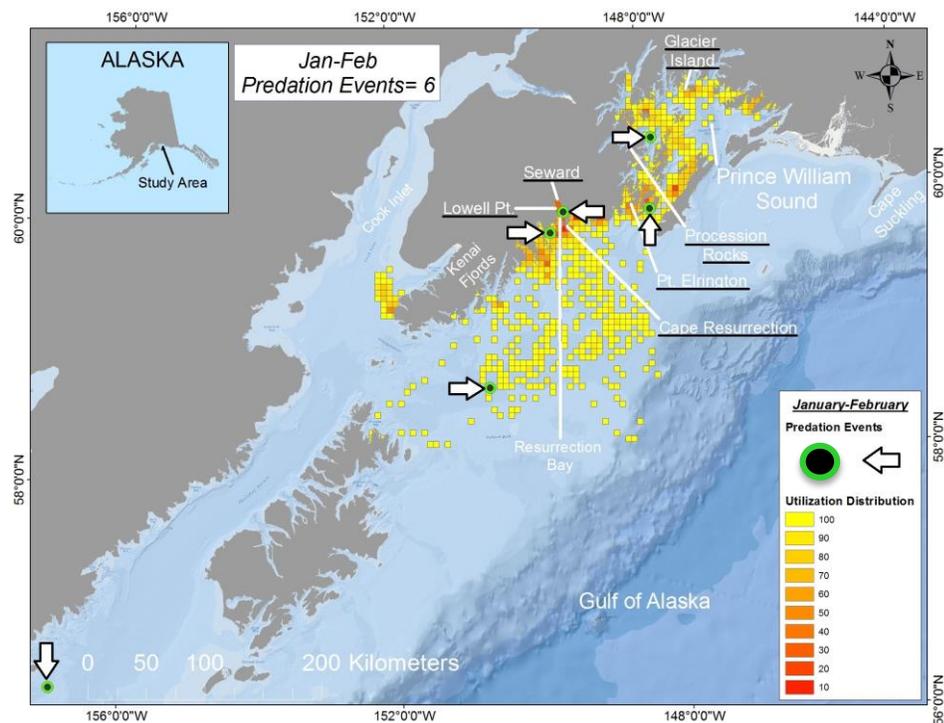


Figure 3.3: Overlay of the estimated predation locations on the January-February utilization distribution. Arrows point to estimated predation location.

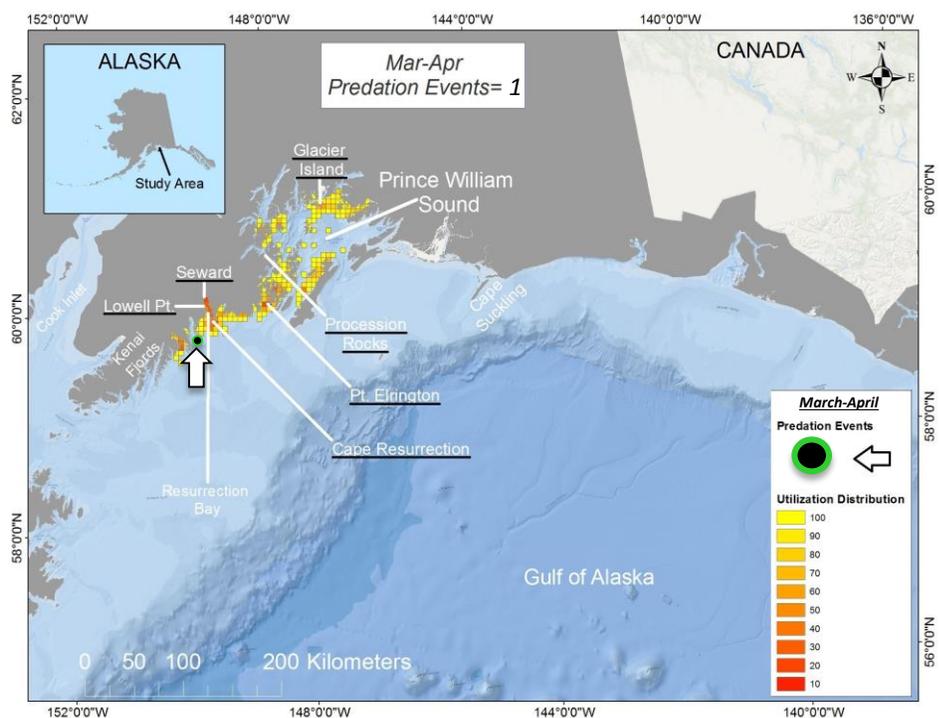


Figure 3.4: Overlay of the estimated predation locations on the March-April utilization distribution. Arrow points to estimated predation location.

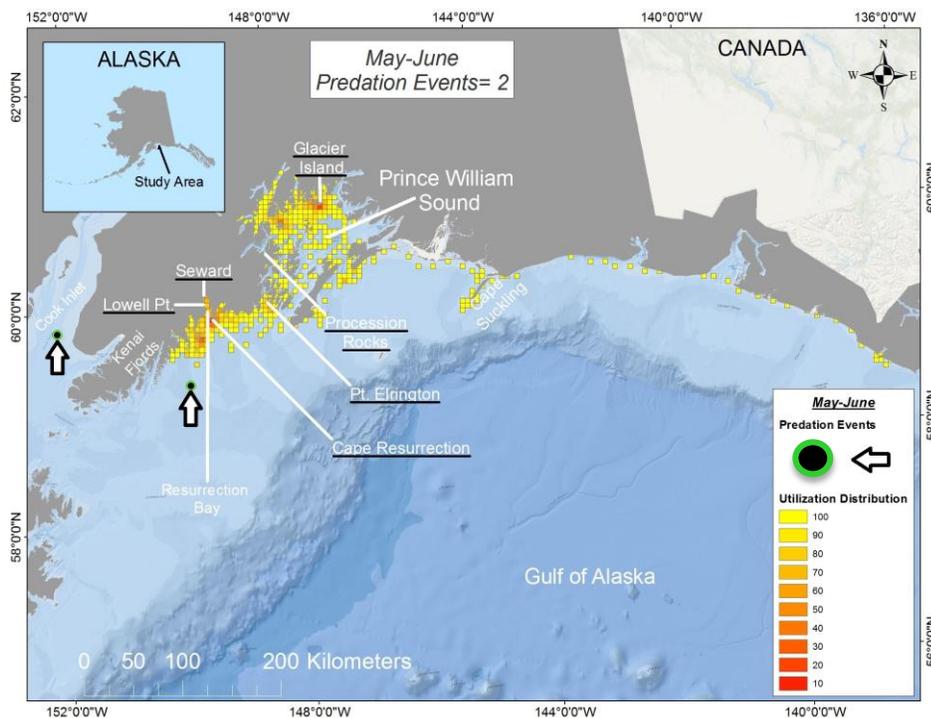


Figure 3.5: Overlay of the estimated predation locations on the May-June utilization distribution. Arrows point to estimated predation location.

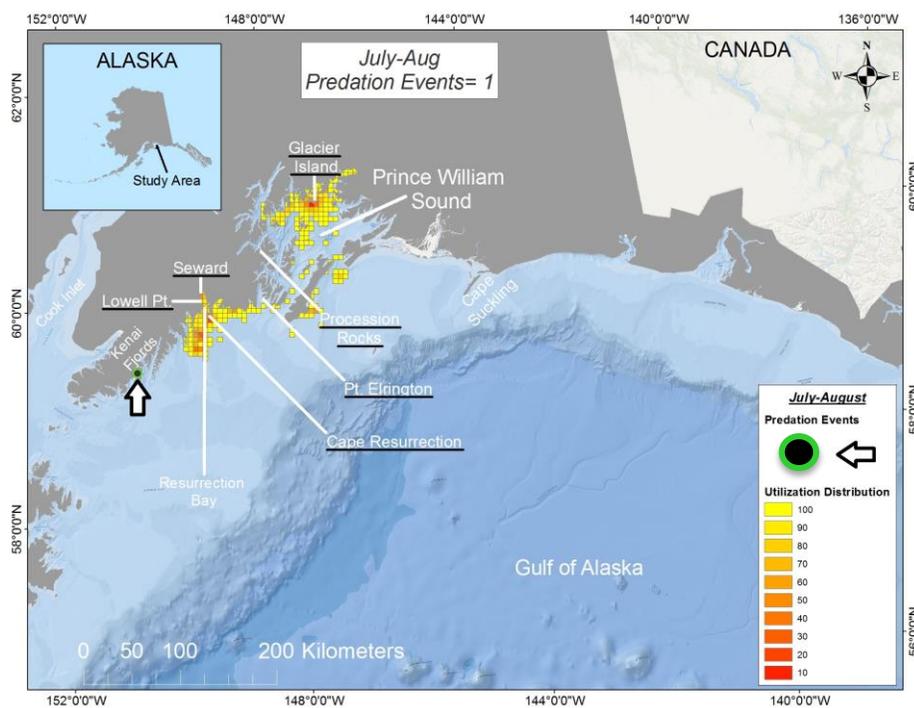


Figure 3.6: Overlay of the estimated predation locations on the July-August utilization distribution. Arrows point to estimated predation location.

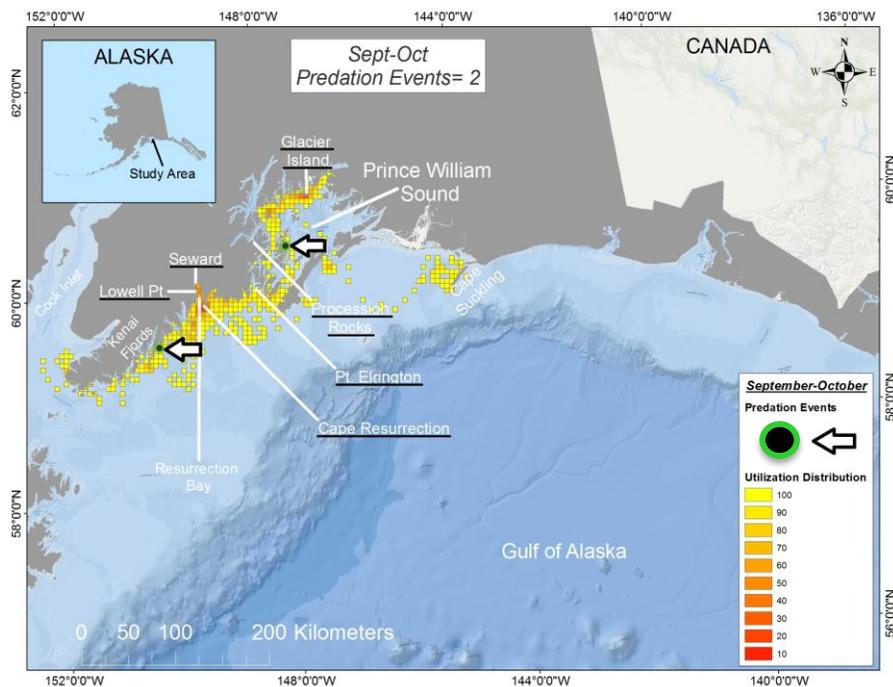


Figure 3.7: Overlay of the estimated predation locations on the September-October utilization distribution. Arrows point to estimated predation location.

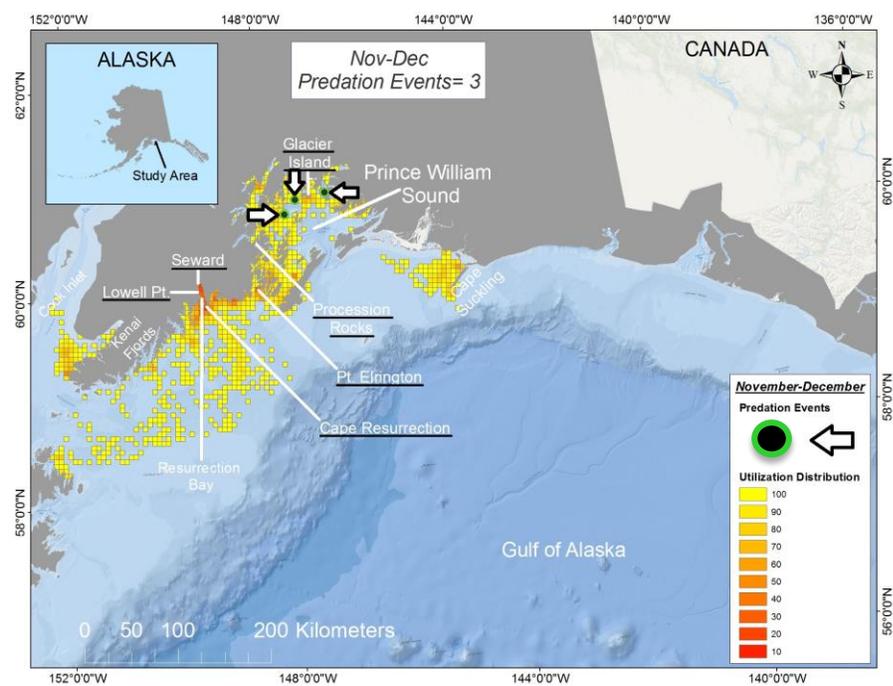


Figure 3.8: Overlay of the estimated predation locations on the November-December utilization distribution. Arrows point to estimated predation location.

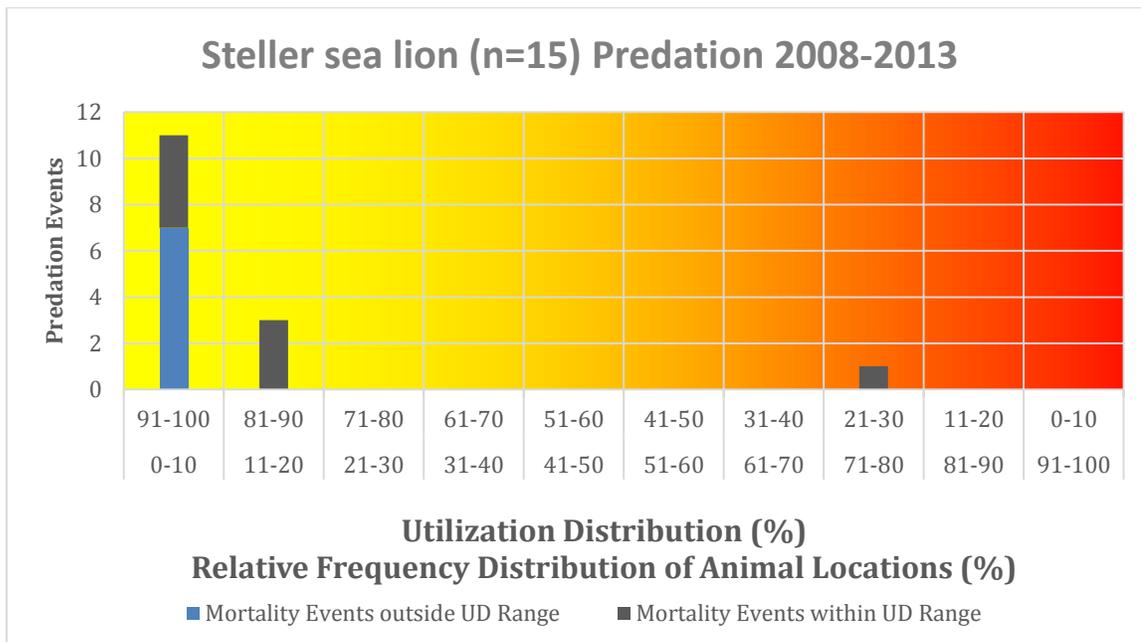


Figure 3.9: Number of predation events as a function of percent Utilization Distribution and relative frequency distribution of animal locations.

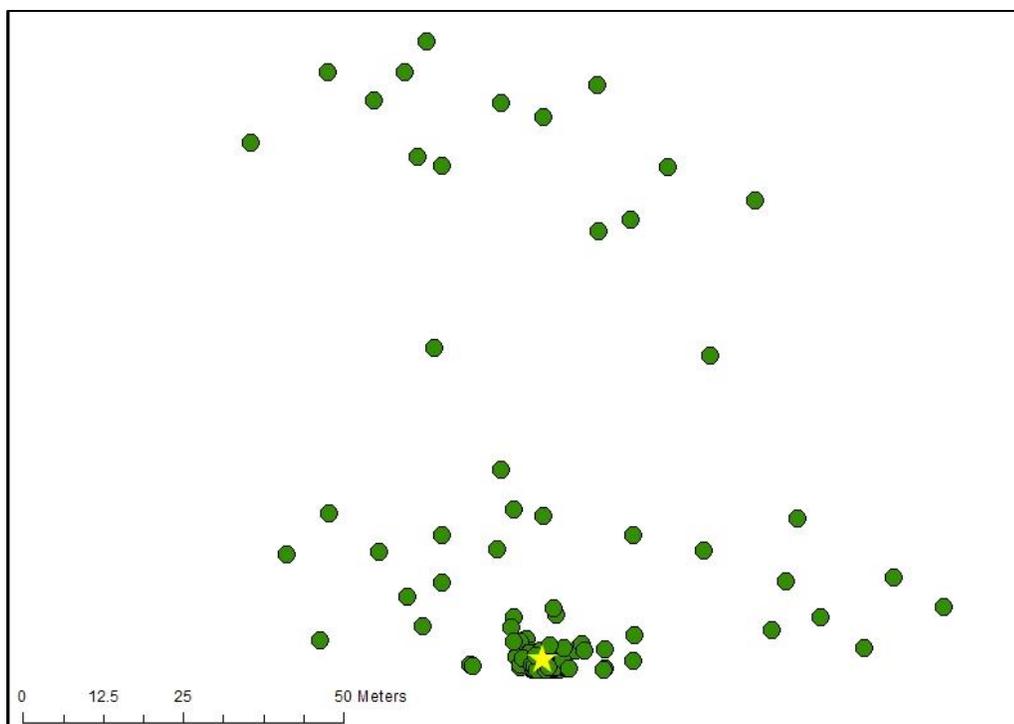


Figure 3.10: Example of x-y vector locations (green circles) and mean predation location estimate based on central feature in ArcGIS (Yellow star). Scale is in meters.

Table 3.2: Summary of the 95% error area using the x-y vector component method versus the 95% credible limit of the state-space model location outputs. Both in km².

Animal ID	95% error area based on vector extrapolations (km²)	95% credible error area based on SSM-based locations (km²)
TJ33	0.000707	3,807
TJ44	0.000209	1
TJ46	0.003757	18,889
TJ47	0.632372	580
TJ51	---	181,794
TJ57	0.000287	574,610
TJ58	0.001877	6,054
TJ59	0.000305	85,068
TJ62	0.000668	15,767
TJ63	0.000195	15,767

To identify patterns in the distribution of age at death (≤ 22 months) and time of year, we performed a Rayleigh test for uniformity in a circular distribution (Moore 1980, Zar 1996). We limited our analysis to animals 22 months of age and younger, and thus to an $n=7$, because most of the tracking data is from animals within those age ranges. For 22 months of age at death and below, the test revealed a significant difference from a uniform distribution ($n=7$, $\theta=5.5$, $p=0.016$). During the winter months (including the transitional months of March-April, see Vazquez et al. 2013 chapter 2) there are 10 predation events, and during the summer months (May-October) there are 5 predation events. Therefore, predation rates double in winter versus summer.

Discussion

Studying predation in the marine environment comes with many challenges due to limitations in locating and tracking highly mobile marine predators over a long period of time and over a wide geographic range (Dahlheim & White 2010), and due to difficulty of remotely detecting predation events (Williams et al. 2004). Furthermore, predator-prey interactions are difficult to discern, particularly when multiple prey or multiple predators may be involved (Ferguson et al. 2012). Tagging 70 juvenile Steller sea lions (SSLs) from the western Distinct Population Segment (DPS) has advanced our capabilities on obtaining data on their utilization

distribution, and application of LHX tags has allowed classifying mortality events by cause and locations in the marine environment.

Estimating the predation locations from post-mortem LHX transmissions is challenging, largely due to the fact that tag programming was not optimized to provide immediate, high-quality locations. As a result, a substantial and highly variable delay was introduced between actual mortalities and initial transmit locations. Furthermore, initial uplink locations were often of a lower quality than subsequent locations. We were able to reduce the location quality effect by way of state-space modeling (SSM) since this method maximizes the use of all available location and quality information. By applying SSM modeling in reverse, we were able to generate evenly spaced (in time) interpolated locations with reduced 95% credible limits. However, the 95% credible limit associated with the SSM track estimates were still unrealistically large, in particular when the reverse SSM method was used to further extrapolate in time to the actual mortality event. Some errors spanned an area almost as large as the state of Alaska, which is not only biologically infeasible for an animal to move that fast but also environmentally unrealistic for winds and currents to drift the tag at those speeds. Instead, we applied an estimation of mean post-mortem tag drift rates to the best available initial LHX transmit location as obtained from reverse SSMs. The resulting uncertainties however remain large, and it is likely that with improved methods these could be reduced. Our interpretations, which result from both strengths and weaknesses of the dataset, provide a novel attempt to consider spatial and temporal characteristics of post-weaning predation on juvenile SSLs in a declining population in the Kenai Fjord (KF)/Prince William Sound (PWS) region of Alaska (Figure 3.2).

The detected predation rate on juvenile sea lions is very high. The winter predation rate was twice that of summer, with 10 predation events during the winter periods (November to April), and 5 events during the summer periods (May through October). For animals within the age range for which UDs were derived from post-release tracking (under 22 months), the annual distribution of events was

significantly different from a uniform distribution, with a mean date of January 6, supporting the interpretation that there are seasonal differences in regards to predation rates. The winter time ranging behavior also differed considerably from summer, with animals spending more time at sea, and at a greater distance from rookeries and haul-outs. While not analyzed here, Mellish et al. (2007) and Thomson et al. (2008) previously found significantly deeper mean juvenile sea lion dive depths in winter than summer, for an early subset of the 70 animals used in this study.

Frid et al. (2009) supports the notion of seasonal effects on the foraging decisions made by juveniles SSLs in PWS with respect to predation risk by way of a risk-benefit model between juvenile SSLs, transient Killer whales (*Orcinus orca*) and Pacific sleeper sharks (*Somniosus pacificus*). The model suggests that in the summer, there may be elevated predation risk around inshore herring aggregations where transient Killer whales are most likely to occur whereas in the winter, there may be higher predation risk in the open basin of PWS, where sea lion prey, walleye pollock, and their predator, Pacific sleeper sharks, overlap spatially (Frid et al. 2009).

No conclusive data exist on what predators are responsible for the majority of predation events detected in our study. Evidence that transient Killer whales prey on Steller sea lions in Alaska have been reported by Ford et al. (1998), Heise et al. (2003), Maniscalco et al. (2007) and Durban et al. (2010) where remote-video monitoring systems, vessel observations, photography and sea lion flipper tags recovered from killer whale stomachs were used to identify the presence of killer whales and confirm predation events. On the other hand, preliminary and indirect data suggests that some actual predation events may be attributed to Pacific sleeper sharks (Horning & Mellish, in review). Furthermore, during repeated vertical migrations, Pacific sleeper sharks tend to spend majority of their night-time above 100 m depth compared to other times of the day, which coincides with diving thresholds of juvenile Steller sea lions at night (Hulbert et al. 2006).

Analyzing where predation events occurred in relation to the juveniles' utilization distribution provided surprising results. Our expectation was that 1) predation events should occur more often in areas of high utilization such as near rookeries and haul-outs, with the assumption that predators that are specialized on SSLs such as transient killer whales should have a higher success rate near terrestrial sites, or 2) that predation events should occur uniformly throughout the sea lions' range in the case of non-specialized, opportunist predators such as sharks. With 10 predation events being considered, the null model would suggest one event per UD interval. Results suggest the opposite, with four of the 15 predation events occurring in the 91-100% UD, or areas of the lowest relative frequency distribution of animal locations, 3 events occurring in the 81-90% UD, and only 1 event in the 21-30% UD corresponding to an area of higher relative frequency distribution of animal locations. Seven of the 15 predation events occurred outside the UD range, and therefore in areas likely of the lowest relative frequency distribution of animal locations.

The fact that there is no effect of increased predation in areas of high utilization may suggest that the predator in question are not specialized on juvenile SSLs or if there are multiple predators, then a relatively large component of them are generalists. However, we do not have a completely random effect on where predation events occur. If predators were distributed randomly in the study area, we would expect to see predation events distributed evenly across all UDs. This is not the case, so other factors are likely affecting where predation events occur that affect the predators' spatio-temporal distribution. Species-specific characteristics and predator behavior may be driven by bathymetry, water temperatures, abundance of alternate prey, etc. Therefore, further analysis effort is necessary to identify the predator/s species and consider additional factors affecting predation locations.

Studies of at-sea behavior have attempted to explain the role of resource scarcity in the population declines of the endangered Steller sea lion (Merrick &

Loughlin 1997) while other studies focus solely on the relationship of physiological and environmental changes that may impact the transition into adulthood (Call et al. 2007). Despite the importance of all these drivers, they are usually treated as independent factors and don't take predation into account. As central place foragers, they must optimize the trade-offs associated with energy gain versus risk of mortality by underutilizing resources (in quantity and/or quality) (Frid et al. 2009). The importance of predation has gained recent recognition as a potential driver of juvenile survivability (Horning & Mellish 2012), and understanding is still required of how foraging behavioral mechanisms might influence the current population parameters.

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Many top predators have the ability to switch among alternative prey due to interplay between behavioral ecology and population dynamics (Ferguson et al. 2012), thus their ability to shape ecosystems through top-down control may depend on the degree of specialization and the diversity of alternate prey species available (Hunt & McKinnell 2006). The population dynamics of the long-lived Steller sea lion (SSL) (*Eumetopias jubatus*) have received a lot of attention for over three decades due to the rapid and inexplicable decline (as high as 15% per year) of the endangered western Distinct Population Segment (DPS). The pattern and rate of decline in abundance varies greatly across different time periods and within the six sub-regions used to monitor the population: the eastern, central, and western Gulf of Alaska and the eastern, central, and western Aleutians (Guenette et al. 2006, Calkins et al. 2013). Various hypotheses have been investigated to explain the decline (Trites & Donnelly 2003, Springer et al. 2003, Dillingham et al. 2006, Atkinson et al. 2008,) but none have been accepted as the ultimate cause for the lack of recovery, making it a major challenge for their conservation and management.

Investigations of age-structured population changes suggest that the rapid decline in the 1980s was associated with a large drop in juvenile SSL survival, together with smaller declines in adult survival and natality (Holmes & York 2003, Holmes et al. 2007). Recent studies support this finding of high juvenile mortality with the aid of implantable, satellite-linked post-mortem data transmitters, or Life History Transmitter (LHX) tags (Horning & Hill 2005, Horning & Mellish 2009, 2012). LHX tags provide spatially explicit data of predation on individual sea lions. Despite this huge advance in technology, the inconclusive results of whether the present decline is due to top-down and/or bottom-up forces is compounded by a lack of knowledge of juvenile SSL utilization distribution patterns as they relate to the western DPS. Increased knowledge from this study should help managers and scientists plan more efficient study designs to assess the predation hypothesis of the

current SSL population in the Kenai Fjords (KF)/Prince William Sound (PWS) region of Alaska.

Prince William Sound is located along the alpine coast of southern Alaska, bordered by the Gulf of Alaska and a rugged coastline. PWS is a combination of multiple deep basins (deepest is 350 m with one area being 700m), large, complex, fjord-type estuarine, channels, islands, and inlets with freshwater input to the sound (Niebauer et al. 1994, Wang et al. 2001). Acquisition of high accuracy satellite locations is not always guaranteed due to the many topographic features of PWS obstructing the polar orbiting satellites' visibility window. Notwithstanding low-accuracy (obstruction by mountain ranges), large data gaps (can't transmit/receive signals underwater), and potential autocorrelation associated with ARGOS satellite locations, the use of a Bayesian State Space Modeling (SSM) approach and gridded utilization distribution (UD) method is a robust method to analyze the dataset in this study. State-space models encompass a range of time series methods that estimate the state of an unobservable process from an observed data set, while accounting for measurement error; thus it is a more rigorous and powerful tool (Jonsen et al. 2012).

Chapter 2 examined the spatio-temporal distribution of 70 juvenile (12-26mo) SSLs post-weaning in the KF/PWS region of Alaska (2003-2012), which is extremely difficult to assess with direct observation due to their rapid movements and large ranges. Results of the bimonthly UD's show juveniles remained within the KF/PWS study region during the tracking period, with the exception of one individual, TJ16 (male), who crossed the 144° W Meridian separating the western and eastern DPS. It is unknown if this emigration was permanent since the tracking period ended outside of the study area so we cannot make any inferences on interchangeability between the western and eastern DPS.

Space use was highest in close proximity to haul-outs and rookeries. In general, in winter (November-April) 90% of observations are within 30km of the nearest haul-out, whereas in summer (May-October) 90% are within 20km. This

indicates near-shore areas adjacent to haul-outs are critical to the developing juvenile. A multifactor analysis of covariance (MANCOVA) revealed a significantly higher percent time spent wet from November through April than May through October ($n=63$; age as covariate $F_1=3.796$, $p=0.056$; season as factor $F_1=13.147$, $p=0.001$). In other words, age does account for a good portion of the observed variance, but the main effect is clearly with season.

Juveniles exhibit different spatial extents depending on the time of year. They remain confined to a relatively smaller area (6,500-12,075 km²) in the 100% UD months of March through August compared to a larger area of 11,300-22,575 km² in the 100 % UD months of September through February. One potential explanation for this pattern may be that the absence of prey from areas near winter haul-outs forces individuals to expand their foraging range both horizontally (longer trip lengths) and vertically (deeper dives) (Merrick & Loughlin 1997).

The second objective of this study (Chapter 3) was to characterize the density effects of predator-prey interactions based on the spatial distribution of actual juvenile Steller sea lion predation events in relation to their utilization distribution. Data received post-mortem from 17 animals from 2008-2013 suggest mortality for 15 juveniles was due to predation in the eastern Gulf of Alaska region, representing about 88% of total mortalities. The winter predation rate was twice that of summer, with 10 predation events during the winter periods (November-April), and 5 events during the summer periods (May-October). The annual distribution of events was significantly different from a uniform distribution, with a mean date of January 6, supporting the interpretation that there are seasonal differences in regards to predation rates.

Analyzing where predation events occurred in relation to the juveniles' utilization distribution provided surprising results. Our expectation was that predation events should occur more often in areas of high utilization such as near rookeries and haul-outs, with the assumption that predators are specialized on SSLs and have a higher success rate near terrestrial sites. Alternatively, predation events

should occur uniformly across all areas in case of non-specialized, opportunist predators. Results suggest the opposite, with four of the 15 predation events occurring in the 91-100% UD, or areas of the lowest relative frequency distribution of animal locations, 3 events occurring in the 81-90% UD, and only 1 event in the 21-30% UD corresponding to an area of higher relative frequency distribution of animal locations. Seven of the 15 predation events occurred outside the UD range, and therefore in areas likely of the lowest relative frequency distribution of animal locations.

The fact that there is no effect of increased predation in areas of high utilization may suggest that the predator in question are not specialized on juvenile SSLs or if there are multiple predators, then a relatively large component of them are generalists. However, we do not have a completely random effect on where predation events occur. If predators were distributed randomly in the study area, we would expect to see predation events distributed evenly across all UDs. With 10 predation events being considered, the null model would suggest one event per UD interval. However, with neither expectation being met, other factors are likely affecting where predation events occur. Such factors may relate to the predators' spatio-temporal distribution, and may include bathymetry, water temperatures, abundance of alternate prey, etc. Therefore, further analysis effort is necessary to identify the predator/s species and consider additional factors affecting predation locations.

Without the joint application of telemetry and geographic information system methods to examine animal movement, the quantification of important life-history parameters such as space use patterns and predation would not be possible. This study represents the first effort to combine implantable archival satellite tags (LHX) with external telemetry to quantify the utilization distribution of 70 juvenile Steller sea lions in the western DPS and relate it to actual predation events. LHX tags are a powerful tool that allow assessment of long-term emigration patterns and

spatial information about predation events, therefore it may be of interest to be able to instrument a higher number of individuals as well as other marine vertebrates.

The forcing mechanism(s) that led to the early 1980s collapse may not be the same as those impeding the rebound of abundance now. Nonetheless, whether the factors are top-down and/or bottom-up in nature, reduced juvenile survival appears to be a contributing factor of the decline and lack of recovery in the Alaskan sea lion population (Merrick & Loughlin 1997). Given high predation events at different density levels, it would be pertinent to investigate multiple predator-prey relationships as opposed to a single-species, as this may provide the most robust conservation and management efforts for an endangered species.

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