APPLYING NOVEL APPROACHES TO OLD DATASETS:

UTILIZING OPPORTUNISTIC OBSERVATIONS AND BAYESIAN ESTIMATION TO DESCRIBE SPATIAL USE PATTERNS FOR STELLER SEA LIONS

by

Gina Kristine Himes Boor

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

August 2010

APPROVAL

of a dissertation submitted by

Gina Kristine Himes Boor

This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

Dr. Daniel Goodman

Approved for the Department Ecology

Dr. David W. Roberts

Approved for the Division of Graduate Education

Dr. Carl A. Fox

STATEMENT OF PERMISSION TO USE

Gina Kristine Himes Boor

August 2010

ACKNOWLEDGEMENTS

The NOAA National Marine Fisheries Service, National Marine Mammal Lab, Alaska Fisheries Science Center, 7600 Sand Point Way N.E. F/AKC3 Seattle, WA 98115-6349, provided access to their Platforms of Opportunity database and telemetry data for use in this study. Additional telemetry data were provided by the Alaska Department of Fish and Game Division of Wildlife Conservation 333 Raspberry Road Anchorage, AK 99518-1599.

TABLE OF CONTENTS

TABLE OF CONTENTS – CONTINUED

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES – CONTINUED

LIST OF FIGURES – CONTINUED

ABSTRACT

Despite two decades of satellite telemetry studies conducted on Steller sea lions, scientists still lack basic spatially-explicit knowledge about Steller sea lion habitat use. The Platforms of Opportunity data collected by the National Marine Fisheries Service contain Steller sea lion sighting records throughout the species' entire range and have the potential to fill the critical gap in knowledge about what areas Steller sea lions are using. The Platforms of Opportunity data have not previously been used to identify marine mammal habitat because they contain sightings without associated effort records (e.g. time spent surveying or area sampled). In this study a novel approach was used to overcome this issue through development of an effort index that allowed for calculation of effort-corrected Steller sea lion encounter rates. A Bayesian negative binomial model was used to quantify both the encounter rate and the uncertainty surrounding that rate within 15 km^2 grid cells across the species' entire range. Year-round encounter rate estimates were derived in addition to breeding and non-breeding season encounter rates. Although the results of this analysis confirmed many of the areas known to be important Steller sea lion habitat, several previously unrecognized high-use areas were identified. Current critical habitat designated areas only encompass about 37% of high use areas estimated using this methodology.

CHAPTER 1

INTRODUCTION

The Alaskan population of Steller sea lions has declined by more than 80% over the last 40 years (Braham et al. 1980; Fritz et al. 2008a; Loughlin 1998). It is generally believed that the decline has been caused by a combination of factors including nutritional stress (DeMaster and Atkinson 2002; Loughlin 1998; Loughlin and York 2000; Merrick 1995). Despite many years of intensive research, the scientific community still lacks both detailed and broad scale information about Steller sea lion habitat use and feeding ecology. The diet of Steller sea lions is fairly well understood, but where sea lions search for and obtain the food they are consuming is not. Satellite telemetry units have been deployed on more than 300 animals over the course of 30 years. Data from these units have contributed significantly to our understanding of SSL at-sea movement, but age- and sex-biases in deployment subjects, limited spatial distribution, high levels of error in location data, as well as possible biases in the data themselves have limited their use in making inferences about Steller sea lion habitat use. In this document I present a methodology for utilizing opportunistic marine mammal sighting data to estimate Steller sea lion encounter rates throughout their entire range, thus significantly expanding our knowledge of Steller sea lion spatial use patterns.

As a result of the lack of effort associated with opportunistic data, they cannot be used in their raw form to estimate Steller sea lion use patterns. To overcome this obstacle, I developed an effort index from other marine mammal sightings in the database of opportunistic sightings. Using the sea lion counts and the effort index, I applied a

Bayesian negative binomial model to estimate Steller sea lion encounter rates across their entire range. The Bayesian estimation approach also provides a measure of uncertainty surrounding those encounter rate estimates.

Steller sea lion biology, population size and status, and feeding ecology are presented in Chapter 2 as background information. Chapter 3 summarizes our current understanding of Steller sea lion spatial and habitat use derived from satellite telemetry and other studies. The limitations of our current knowledge and the problems associated with previous studies are also outlined in Chapter 3 in preparation for presentation of my own analysis. Chapter 4 contains a full description of the Bayesian analysis of the Platforms of Opportunity (POP) data, including description of the data themselves, data analysis methodologies, model results, and discussion of the patterns found. Finally, Chapter 5 summarizes the results of the Bayesian model, presents a discussion of the implications of these findings, and suggests future work that could further elucidate Steller sea lion habitat use patterns.

CHAPTER 2

STELLER SEA LION BIOLOGY AND ECOLOGY

Taxonomy and General Description

Steller sea lions, *Eumetopias jubatus*, are marine mammalian carnivores in the Order Carnivora, suborder Caniformia (“dog-like”), and Pinnipedia clade. Unlike the other group of marine mammals, whales and dolphins (Order Cetacea), pinnipeds are amphibious, giving birth, molting, breeding, and resting on land, but foraging and traveling at sea. The Pinnipedia clade distinguishes aquatic carnivores from their terrestrial cousins, and is composed of three monophyletic families: Otariidae, the eared seals; Odobenidae, walruses; and Phocidae, “true” or earless seals (Berta and Sumich 2003; Feldhamer *et al*. 2007). Sea lions and fur seals make up the Otariidae family and are distinguished from the Phocids by a number of characteristics. The most obvious anatomical distinguishing features include the presence of external pinnae (ear flaps), the ability to rotate their pelvis to bring the hind flippers forward for use in walking on land, extended and flattened fore flippers, and use of those fore flippers for propulsion in water (Berta 2002; Boness 2002; Feldhamer *et al*. 2007). Sea lions can be distinguished from their closer relatives, the fur seals, by their pelage and facial features. Sea lions have a single layer of hair, while fur seals have a dense layer of fine waterproof underfur in addition to an outer layer of longer stiff guard hairs (Gentry 2002). Sea lions also have blunt noses in relation to the more pointed noses of fur seals (Feldhamer *et al*. 2007).

Steller sea lions are the largest of the otariids and exhibit strong sexual dimorphism. On average, males grow to 282 cm and weigh 566 kg, while females measure 228 cm and weigh 263 kg (Loughlin 2002). At birth pups are about 1 m in length and weigh 16 to 23 kg (Loughlin *et al*. 1987). Pups are born with chocolate brown fur, while adult pelage tends to be lighter colored, from light buff to reddish brown. An annual molt occurs in early fall but individual timing varies from late summer to early winter (Calkins and Pitcher 1982). Males have longer course hair on their neck, chest and shoulders giving them their eponymous mane (the specific epithet of their Latin name, *jubatus*, means "having a mane") (Loughlin 2002). While females may live as long at 30 years, male Steller sea lions are thought to live only into their mid- to late teens (Loughlin 2002).

Distribution

Steller sea lions range throughout the north Pacific rim from California up through British Columbia and Alaska, along the Aleutian Islands into the Bering Sea, and to eastern Russia and Hokkaido in northern Japan (Loughlin *et al*. 1987). Alaska is the center of abundance of the population.

Steller sea lions use two types of land-based sites, rookeries and haul-outs. Both are used as resting sites throughout the year but rookeries are used primarily for breeding, birthing, and rearing young pups in the summer months (Loughlin *et al*. 1984). During the breeding season haul-out sites are generally occupied by the non-breeding portion of the population (Hoover 1988; Loughlin *et al*. 1984). Seasonal shifts in distribution occur throughout the range, with breeding and non-breeding individuals alike dispersing in the late fall presumably to exploit seasonal prey abundances in other areas (Calkins and Pitcher 1982; Kenyon and Rice 1961; Loughlin *et al*. 1987; Raum-Suryan *et al*. 2004;

Womble *et al*. 2009).

The same rookery and haul-out sites tend to be used consistently from year to year and are located on isolated off-shore islands or rocks. Of the 51 identified rookeries the southern-most is located on Año Nuevo Island, California (37°06'N), and the northern-most is Seal Rocks in Prince William Sound, Alaska (60°09'N) (Loughlin *et al*. 1984; Loughlin 2002) (Figure 2-1). While the majority are concentrated in Alaska, rookeries also occur in California, Oregon, British Columbia, and Russia. More than 250 haul-out sites have been identified throughout the Steller sea lion range (Sease *et al*. 2001).

Population Structure

The population is divided into at least two genetically distinct populations. Multiple studies using both mitochodrial DNA (mtDNA) polymorphisms as well as nuclear microsatellite markers have found significant genetic divergence between populations lying west and east of Cape Suckling in the Gulf of Alaska along the 144°W meridian (Bickham *et al*. 1996; Baker *et al*. 2005; Hoffman *et al*. 2006). Long-term observations of marked individuals also support this eastern and western division in the population (Raum-Suryan *et al*. 2002). Some evidence suggests that the westernmost rookeries in the range may be a distinct Asian stock (Baker *et al*. 2005), although one recent study found little support for such separation (Hoffman *et al*. 2006). The two populations are currently referred to as western and eastern Distinct Population Segments (DPS) (Figure 2-2).

Finer scale divisions of the western DPS have also been suggested. Genetic differences were found between what were termed continental "shelf rookeries",

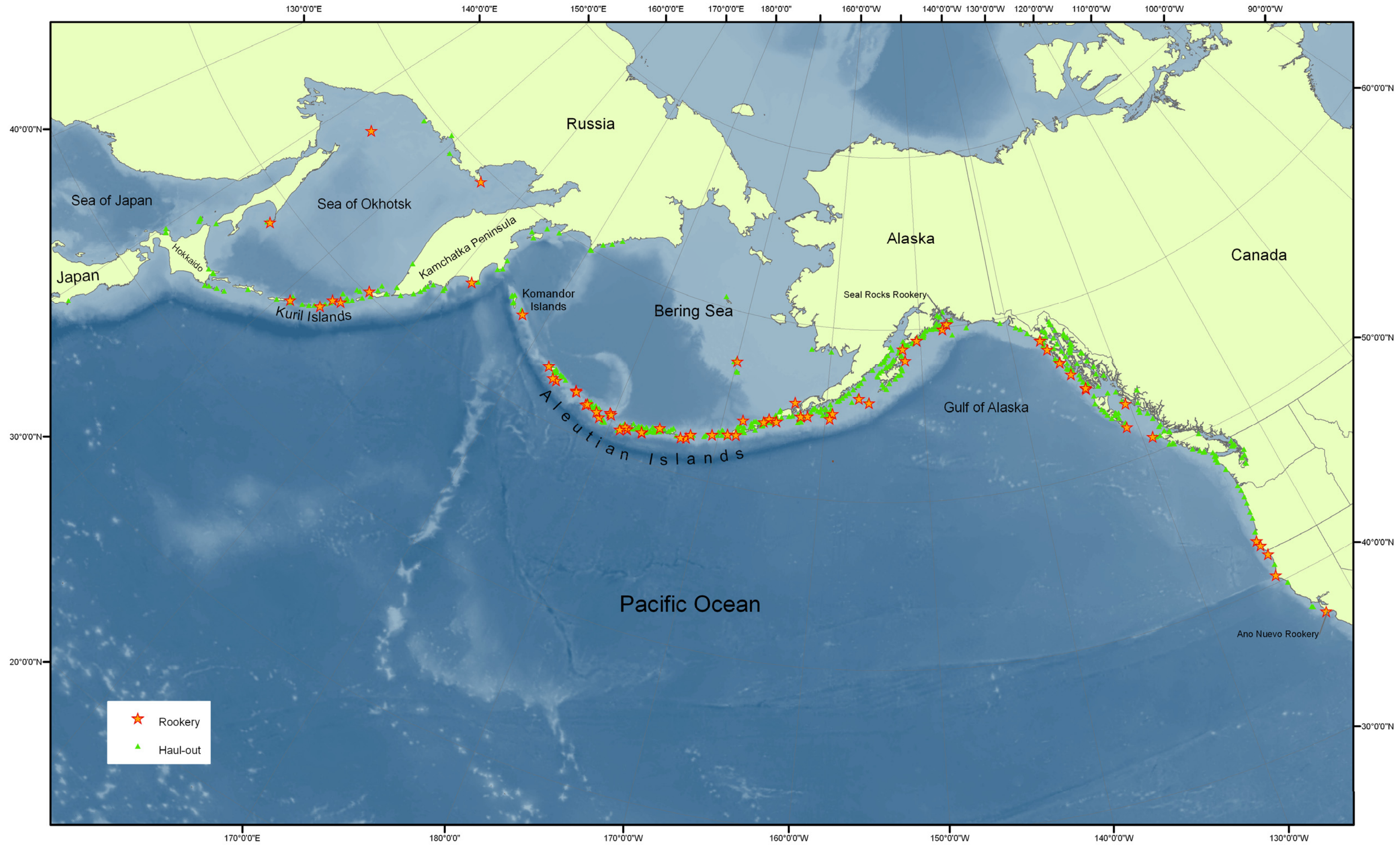

Figure 2-1. Steller sea lion rookeries and haul-outs.

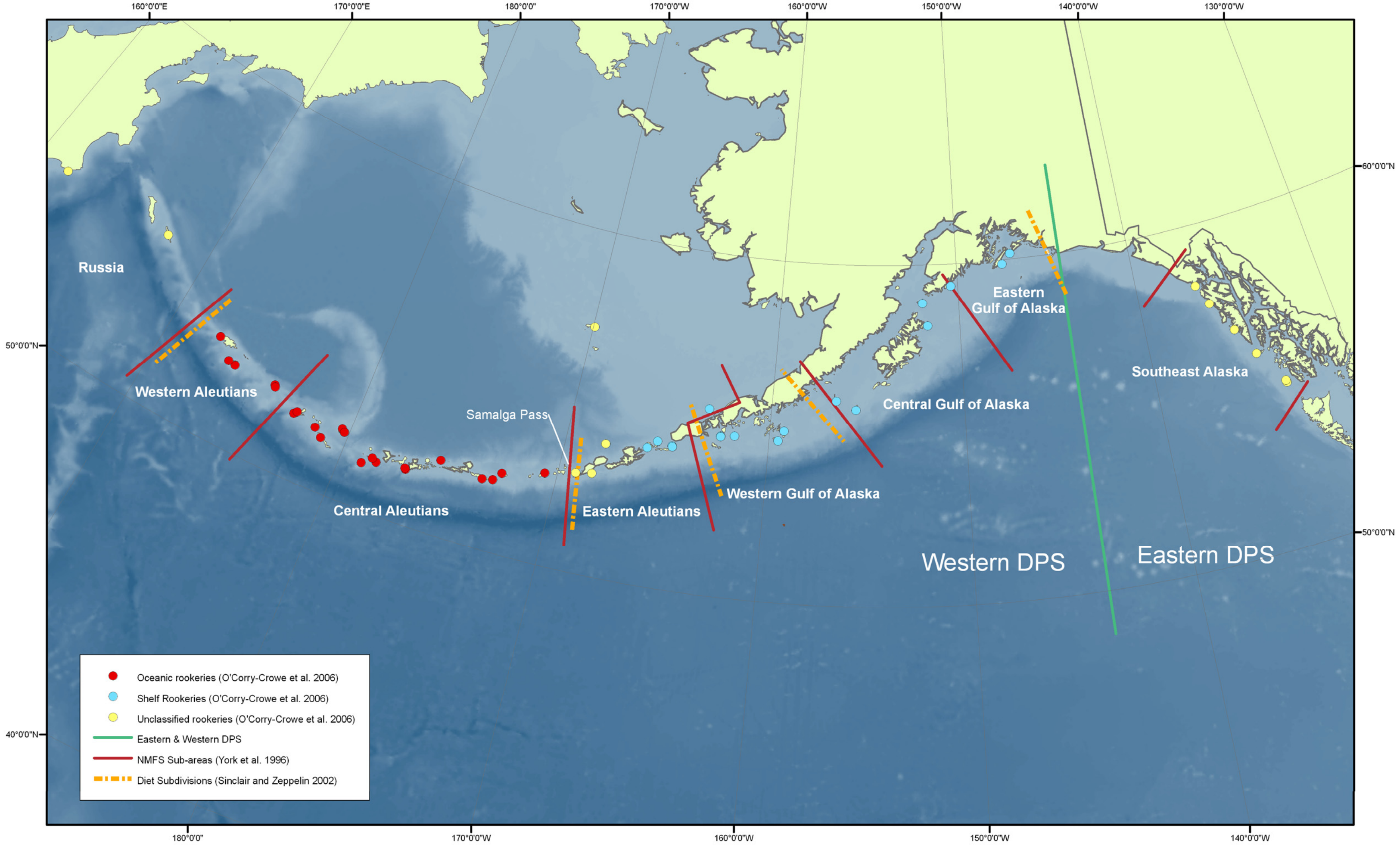

Figure 2-2. Suggested sub-regions of the Steller sea lion population based on diet, genetics, and population trajectories; includes the boundary between the western and eastern Distinct Population Segments (DPSs).

including those in the Gulf of Alaska and the eastern Aleutians, and “oceanic rookeries”, including those in the central and western Aleutians (Figure 2-2) (O’Corry-Crowe *et al*. 2006). Unlike the phylogeographic-level divergence of mtDNA and nuclear microsatellite markers found between the western and eastern DPS, the frequency-level genetic divergences found by O’Corry-Crowe *et al*. (2006) between the sub-regions of the western DPS do not represent evolutionary time-scale divergences but rather reduced immigration between the sub-regions over ecological time scales.

Subdivisions of the western DPS based on population trends and diet have also been noted. Significant differences in population trajectories in different sub-regions have been recognized (York *et al*. 1996) and have resulted in the National Marine Fisheries Service assessing bi-annual population counts and resulting trends separately for 6 sub-regions in the western DPS: eastern, central, and western Gulf of Alaska, and eastern, central, and western Aleutians (Figure 2-2) (Sease and Gudmundson 2002). Diet composition varies regionally as well, with distinct boundaries between regions that closely correspond to sub-area divisions defined by population trajectories, and suggests that local population growth is tied to foraging success and local prey populations (Figure 2-2) (Merrick *et al*. 1997; Sinclair and Zeppelin 2002; Sinclair *et al*. 2005). The western-most dietary division defined by Sinclair and Zeppelin (2002) lies at Samalga Pass which also marks the division between the western Gulf of Alaska and eastern Aleutians population sub-areas (York *et al*. 1996) and corresponds to the general location of the division defined by O’Corry-Crowe *et al*. (2006) between shelf and oceanic sub-populations. The consistency in the boundaries between sub-regions of the western DPS based on very different datasets and analyses suggests that long term ecological differences may be present between sub-regions.

Population Size and History

Once abundant throughout their range, Steller sea lion populations have experienced large declines over the past 50 years particularly in the western DPS. The first wide-scale Steller sea lion population surveys were conducted in the 1950s and 60s and yielded an estimate of 240,000 to 300,000 animals (Kenyon and Rice 1961). Since then the population has experienced a decline of over 80%, with the most rapid declines occurring in the 1980s. Although the exact start of the decline has been difficult to identify, declines in the eastern Aleutians and western and central Gulf of Alaska had begun prior to 1975 (Loughlin *et al*. 1984; Braham *et al*. 1980). Loughlin *et al*. (1992) documented declines in all areas of the Steller sea lion range except Southeastern Alaska by 1977. When the most complete range-wide survey of SSL was conducted in 1989, the world SSL population had fallen to about 116,000 animals (Loughlin *et al*. 1992). By 1994, the population estimate was about 100,000 (Loughlin 2002).

The dramatic overall population declines, however, did not occur uniformly range-wide, and in fact all of the declines occurred solely in the western DPS. Southeast Alaska and British Columbia populations of the eastern DPS grew during this period, experiencing an average annual growth of about 3.2% between the 1970's and 2000's (Pitcher *et al*. 2007). Relative to estimates in the early part of the 20th century, population sizes in Washington, Oregon, and California are much reduced but have been growing or remained static since the 1970's (Pitcher *et al*. 2007). In the western DPS the populations declined overall by about 15% per year in the 1980’s and by about 5% per year through the 1990’s, although rates of decline varied among sub-areas (Loughlin *et al*. 1992; NMFS 2008; Sease and Loughlin 1999; Sease *et al*. 2001; Trites and Larkin 1996)

Following the declines in the latter portion of the 20th century the U.S. portion of the western DPS experienced the first region-wide increases since standardized surveys began in the 1970’s with about 3% annual growth between 2000 and 2004 (Fritz *et al*. 2008b). Between 2004 and 2008 (the last year for which data are available) the western DPS population remained static or declined slightly (Fritz *et al*. 2008a ; Fritz *et al*. 2008b). As in other periods, regional variability in the population trajectories continues. The western Aleutian and central Gulf of Alaska sub-populations have consistently experienced declining numbers throughout the first part of the 21st century (Fritz *et al*. 2008a; NMFS 2008). Although the central Aleutian sub-population had experience about 10% growth between 2000 and 2004, it declined by an estimate 16% between 2004 and 2008 (Fritz *et al*. 2008b; NMFS 2008). The eastern Aleutian sub-area has consistently increased since 2000, with an increase of about 7% between 2004 and 2008 (Fritz *et al*. 2008b).

The most current estimate of the number of Steller sea lions in the eastern DPS is between 46,000 and 58,000 (Pitcher *et al*. 2007). Based on surveys conducted between 2006 and 2008, a minimum of 18,000 Steller sea lions populate Russian rookeries and haul-outs (Burkanov 2009). A minimum population of about 41,000 Steller sea lions are estimated for the Alaska portion of the western DPS based on data from 2004 to 2008

(Allen and Angliss 2009). At present, a minimum current estimate of the number of Steller sea lions world-wide is about 105,000.

Status Under the Endangered Species Act

In response to the precipitous drop in population size, Steller sea lions were listed as threatened under the Endangered Species Act (ESA) in 1990. Following the initial listing, genetic studies suggested the presence of two distinct stocks of Steller sea lions, a western and an eastern distinct population segment (Bickham *et al*. 1996). The western DPS has experienced the most decline, and in 1997 its status was changed to endangered under the ESA. Since the early 1980s the eastern DPS has experienced slow but steady growth overall, although the California subpopulation has failed to recover from early declines. As a result, the eastern DPS remains listed as threatened. Although the Steller sea lion population was once most concentrated in the western portion of the range, the eastern DPS has now surpassed the western DPS in total number of sea lions.

Reproduction

Both males and females reach sexual maturity between the ages of 3 and 8, although males do not reach physical maturity until age 9 to 11 (Loughlin 2002; Loughlin *et al*. 1987; Raum-Suryan *et al*. 2002). Breeding and pupping season occurs between May and July primarily on rookeries (Loughlin 2002). Steller sea lions are polygynous and in early May dominant males, usually between 9 and 13 years of age, establish breeding territories at the rookeries (Loughlin *et al*. 1987; Hoover 1988). The territories are maintained for up to 68 days during which time the presiding males do not leave the rookery (Hoover 1988). The rigors of fasting during this period and fighting to establish and maintain breeding territories are thought to contribute to the shorter life span of males (Loughlin 2002).

Females give birth to a single pup between mid-May to mid-July with the peak of the pupping season occurring in early to mid-June (Pitcher and Calkins 1981). Females undergo a brief period of estrus between 6 and 16 days post-parturition during which time mating occurs (Gentry 1970). After egg fertilization, female Steller sea lions experience delayed implantation of about three months, with active gestation beginning in late September to October and lasting approximately 9 months (Pitcher and Calkins 1981).

Following a perinatal period of 2 to 17 days (mean of 9 to 10) when sea lion mothers remain on the rookery attending to and nursing their pup, they resume foraging trips at sea (Maniscalco et a. 2006; Milette and Trites 2003; Sandgren 1970). Early foraging trips last about 1 day (Gentry 1970; Maniscalco *et al*. 2006; Merrick and Loughlin 1997; Milette and Trites 2003; Sandegren 1970). Generally, between-trip bouts on land also last about 1 day but can be up to 3 days (Gentry 1970; Maniscalco *et al*. 2006; Merrick and Loughlin 1997; Milette and Trites 2003; Sandegren 1970). As the pups get older, mothers tend to spend more time at sea foraging (Merrick and Loughlin 1997; Mansicalco *et al*. 2006; Milette and Trites 2003). The length of shore visits between foraging trips tends to remain the same or decrease slightly as the pup ages (range 15-27 hrs) (Merrick and Loughlin 1997; Milette and Trites 2003; Trites and Porter 2002), although one study found that time on shore between trips increased between summer and autumn months (Maniscalco *et al*. 2006). From August to October mother-pup pairs disperse from natal rookeries presumably to exploit seasonal concentrations of prey elsewhere (Calkins and Pitcher 1982; Raum-Suryan *et al*. 2002).

Breeding Strategy

Female Steller sea lions are income breeders, meaning that they must forage for food to provision themselves while concurrently nursing pups (Costa 1993). Within about 9 or 10 days of parturition Steller sea lions resume foraging trips between bouts of provisioning their young (Maniscalco *et al*. 2006; Milette and Trites 2003; Sandgren 1970). This strategy, employed by all otariids, contrasts with the capital breeding strategy employed by most phocids, wherein energy needed for provisioning young is acquired and stored throughout the year prior to giving birth, and foraging resumes only after weaning occurs. The income breeding approach is thought to have evolved in animals that have had access to a consistent and close food source, whereas capital breeders may have evolved in environments where forage is less predictable in time and space (Costa 1993). Although some have argued that the income breeding pattern is less economical than capital breeding, tradeoffs exist between the two strategies, with one advantage of income breeding being that animals can invest more in their offspring and exhibit significantly more plasticity in the age at which pups are weaned. Steller sea lion mothers nurse their young for anywhere from 1 to 3 years (Gentry 1970; Pitcher and Calkins 1981; Hoover 1988; Sandegren 1970). In terms of foraging strategies, this has several implications. For successful reproduction and survival of the mother and pup, sufficient sources of sea lion prey must be available near rookeries throughout the breeding season. Because of the plasticity in weaning age, however, low prey productivity throughout the year may have less impact on pup and juvenile survival if Steller sea lion mothers are able to continue nursing until prey resources are more easily obtained by juvenile animals.

Diet and Foraging Ecology

Prey Species

Steller sea lions are opportunistic foragers, feeding on a wide variety of fishes and cephalopods, and to a lesser extent on crustaceans, gastropods, and occasionally birds and other pinnipeds (Merrick *et al*. 1997; Pitcher 1981; Sigler *et al*. 2009; Sinclair and Zeppelin 2002; Trites *et al*. 2007). The specific composition of Steller sea lion diet appears to be dependent on region, season, sex, age, and even year depending on oceanic conditions (Ficus and Baines 1966; Gende and Sigler 2006; Lander *et al*. 2009; Merrick and Calkins 1996; Merrick *et al*. 1997; Pitcher 1981; Sigler *et al*. 2009; Sinclair and Zeppelin 2002; Trites and Calkins 2008; Trites *et al*. 2007). In Alaska, walleye pollock (*Theragra chalcogramma*) is one of the primary prey items in most regions, with Atka mackerel (*Pleurogrammus monopterygius*), Pacific salmon (*Oncorhynchus* spp.) and Pacific cod (*Gadus macrocephalus*) also comprising a large portion of the diet (*ibid*). Octopus, squid, Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), flatfishes (order Pleuronectiformes), sculpins (family Cottidae), rockfishes (family Scorpaenidae), and eulachon (*Thaleichthys pacificus*) also play major or minor roles in the Steller sea lion diet depending on the region and season (*ibid*). A wide variety of other fishes and invertebrates are also consumed in smaller quantities (*ibid*).

Population and Diet

Regional population trajectories appear to be tied at least in part to Steller sea lion diet. Diet diversity has been shown to be lowest in regions where sea lions have experienced declining populations, and highest in areas of stable or increasing populations (Merrick *et al*. 1997; Trites *et al*. 2007). The regions defined by differences in diet composition identified by Sinclair and Zeppelin (2002) also closely align with regions identified by York *et al*. (1996) based on their differing population trajectories. These correlative links between diet and population trajectories suggest a link between the availability of prey and the growth or decline of the nearby population.

Foraging Behavior and Strategies

Several adaptations enable sea lions to more easily find and consume prey underwater. All pinnipeds have an acute sense of smell and highly sensitive whiskers, a well developed tapetum lucidem that allows them to see well in low light conditions, and excellent hearing underwater (Berta and Sumich 2003; Feldhamer *et al*. 2007). The large forward-pointing eyes of pinnipeds indicates that visual detection of prey is important, but prey can also be detected with whiskers that are very sensitive to touch and slight water movements (Heithaus and Dill 2002).

As a central place forager, Steller sea lion foraging forays are restricted by their need to return to a rookery or haul-out to rest, and for reproductively active females, to provision young. Sea lions tend to do most of their foraging at night, preferring to haul-out during midday (Gentry 1970; Loughlin and Nelson 1986; Loughlin *et al*. 1998; Loughlin *et al*. 2003; Rehberg *et al*. 2009; Rehberg and Burns 2008; Sandegren 1970;

Sigler *et al*. 2009; Trites and Porter 2002), although differences in this pattern have been noted in some regions and seasons (Call *et al*. 2007; Fiscus and Baines 1966; Rehberg and Burns 2008; Sigler *et al*. 2009). The prevalence of nighttime foraging may be driven by either avoidance of predators that hunt visually, such as the orca (*Orcinus orca*)(Frid *et al*. 2007), or targeting preferred prey that vertically migrate to shallower depths at night (Sinclair and Zeppelin 2002), or both.

Adult females with pups spend about half of their time at sea during summer months, but that proportion increases during the winter and may be as much as 90%, varying with lactation status and age of dependent young (Maniscalco *et al*. 2006; Merrick and Loughlin 1997; Milette and Trites 2003; Rehberg *et al*. 2009; Trites and Porter 2002). Young-of-the-year animals in the winter and spring spend between 38% and 46% of their time at sea (Merrick and Loughlin 1997; Rehberg and Burns 2008; Trites and Porter 2002).

Consistent with the opportunistic nature of their foraging, Steller sea lions exploit densely schooled prey in spawning or migratory aggregations when available. Sightings of large groups of foraging sea lions have been associated with areas of concentrated prey species (Fiscus and Baines 1966; Gende and Sigler 2006; Loughlin and Nelson 1986; Marston *et al*. 2002; Sigler *et al*. 2004; Sigler *et al*. 2009). Spikes in the frequency of occurrence of Pacific herring, Pacific cod, sand lance, and Pacific salmon in the diets of Steller sea lions correspond spatially and temporally with spawning aggregations and migratory movements of these fish species (Sigler *et al*. 2009; Sinclair and Zeppelin 2002; Womble and Sigler 2006). In addition, seasonal abundance patterns of Steller sea lions at haul-outs and rookeries have been correlated with seasonal aggregations of prey species and sea lions have been shown to move to different haul-outs to exploit seasonal aggregations of various prey species (Gende *et al*. 2001; Sigler *et al*. 2004; Sigler *et al*. 2009; Womble *et al*. 2005; Womble and Sigler 2006; Womble *et al*. 2009). Interestingly however, Gende and Sigler (2006) found that the year-to-year persistence of forage fish hot-spots was more predictive of Steller sea lion presence than the density of the schooling fish (*ibid*). Sea lions also switch prey in response to changes in prey abundance near their haul-out location (Sigler *et al*. 2009). In areas where walleye pollock and Atka mackerel occur nearshore year-round, these species compose a large portion of the diet of Steller sea lions year-round (*ibid*; Sinclair and Zeppelin 2002).

Just as their diet is quite varied, Steller sea lion foraging strategies are also variable. They have been found to forage both in large groups and individually, preferring group foraging when exploiting schooling prey, but hunting individually or in small groups of 2 to 5 when feeding on non-schooling, slow moving, or sessile prey (Fiscus and Baines 1966; Gende and Sigler 2006; Gentry 1970; Riedman 1990; Sigler *et al*. 2009). Gende *et al*. (2001) observed several instances of remarkable cooperative feeding behavior by 75 to 300 Steller sea lions over the course of 4 years at the beginning of the Eulachon (*Thleichthys pacificus*) spring spawning run in Berners Bay, in southeast Alaska (58°45’N, 135°00’W). Two other observations of synchronous diving by groups of Steller sea lions have been recorded (Orr and Poulter 1967; Sigler *et al*. 2004), but it is unclear whether groups of sea lions consistently forage cooperatively or are simply all exploiting the same concentrated prey patch. While some studies report that groups of foraging Steller sea lions tend to be composed of females and sub-adult males, with adult males tending to be observed alone (Hoover 1988; Loughlin and Nelson 1986; Loughlin 2002; Orr and Poulter 1967), others report foraging groups consisting of mixed age- and sex-classes including adult males (Fiscus and Baines 1966; Gende *et al*. 2001).

Steller sea lions are relatively shallow divers in relation to phocids and other marine mammals. The deepest dives by female Alaska Steller sea lions are generally less than 250 meters, although deeper dives have been recorded during winter months (Loughlin *et al*. 1998, Merrick and Loughlin 1997; Rehberg *et al*. 2009). Adult female in Alaska have a mean dive depth between 20 and 30 meters (Merrick and Loughlin 1997; Rehberg *et al*. 2009), while females studied in Russian waters exhibited a mean dive depth of 53 meters (Loughlin *et al*. 1998). Rehberg *et al*. (2009) also found that dive depth differed significantly between individuals and ranged from 19.2 to 47.1 meters. Dive duration for adults is most often less than 2 minutes but can be more than 16 minutes (Loughlin *et al*. 1998, Merrick and Loughlin 1997; Rehberg *et al*. 2009).

In young sea lions diving ability and therefore dive duration and dive depth develops with age (Fadely *et al*. 2005; Loughlin *et al*. 2003; Pitcher *et al*. 2005) Young-of-the-year (YOY) mean dive depth is generally less than 10 meters (Fadely *et al*. 2005; Loughlin *et al*. 2003; Merrick and Loughlin 1997; Pitcher *et al*. 2005). Measures of juvenile (1-3 years old) mean dive depth vary considerably between studies with Alaska animals averaging between 13 and 29 meters (*ibid*; Rehberg and Burns 2008), and juveniles in Washington averaging around 40 meters (Loughlin *et al*. 2003). Loughlin *et al*. (2003) speculated that the dive depth difference between Washington and Alaska animals may be related to the local habitat conditions in which juveniles are foraging; this may also be true for the other studies, although this has not been explored. YOY individuals spend less than 1 minute on average in any one dive, whereas juvenile dives generally last between 1 and 2 minutes (Fadely *et al*. 2005; Loughlin *et al*. 2003; Merrick and Loughlin 1997; Pitcher *et al*. 2005; Rehberg and Burns 2008). Although most dives by young animals are shorter and shallower than those of adults, maximum depths by some individual juveniles rival those of adult animals (max depths: 288-452 meters)(Loughlin *et al*. 2003; Pitcher *et al*. 2005; Sigler *et al*. 2009). By about 1.5 years of age, juveniles appear to be capable of diving to similar depths as adults (Pitcher *et al*. 2005).

Through foraging, prey, and dive studies, we have developed a relatively clear picture of how and on what Steller sea lions prey, and how those foraging strategies and skills develop in pups and juveniles. Less in known, however, about exactly where they forage, what areas are of importance, and what the habitat characteristics are of those areas. In the next chapter I will detail what is currently known about Steller sea lion habitat use and foraging areas.

CHAPTER 3

STELLER SEA LION HABITAT USE: A LITERATURE REVIEW

Introduction

The diving and movement of Steller sea lions at sea has been studied most intensively over the last 20 years. Throughout this period, the dominant source of information about spatial and habitat use has come from satellite telemetry data. Indirect inferences about at-sea use can also be made from studies on Steller sea lion diet, on-land observation of attendance patterns, and through predictive habitat modeling. The aim of this chapter is to summarize current knowledge of Steller sea lion at-sea movement and habitat use by describing and synthesizing the findings of these studies. In addition, I will explore the limitations of these sources of information as they relate to a complete understanding of Steller sea lion habitat use. The information needed for adequate management and recovery of Steller sea lion populations will also be discussed.

Our Current Knowledge Of At-Sea Movement and Habitat Use

Telemetry Data

Background. Satellite telemetry units have been used in the study of Steller sea lions since 1990 when the first units were deployed as a test of their functionality (Merrick *et al.* 1994). Since then over 300 units have been deployed and have provided a range of data on Steller sea lion patterns of diving and movement.

To obtain satellite telemetry data from Steller sea lions, animals must be captured either on land or underwater (Loughlin *et al.* 2003; McAllister *et al.* 2001). Once captured, telemetry units are attached with quick-setting epoxy to the pelage on the animal's back or head. Prior to 1996, animals were captured and chemically immobilized from afar using a dart and a pneumatic gun; since that time animals have been captured manually and physically restrained (Loughlin *et al.* 2003). The discontinuation of sedation marked the end of adult deployments since adult animals are too large to be captured and restrained.

The unit attached to the Steller sea lion collects various data that are transmitted to polar orbiting satellites which then transmit the data back to receiving stations. Animal location data are not collected by the telemetry unit itself, but are determined only when a transmission to an orbiting satellite (uplink) occurs. Location of a transmitter is calculated from the Doppler shift in the frequency of the transmission signal as the satellite moves overhead. Since various factors such as movement of the animal during transmission, oscillator stability, and number of transmissions to the satellite, among other issues affect the accuracy of location calculations, different combinations of these factors will result in varying degrees of accuracy of the estimated locations (White and Garrott 1990). To account for this, each estimated location is assigned to an accuracy class (3 to 0, and A, B, Z, in diminishing order) that indicates the estimated level of error associated with that location. Estimated accuracies for Class 3 range from 150 m to 400 m (Fadely *et al.* 2005; Raum-Suryan *et al.* 2004; Rodgers 2001; Vincent *et al.* 2002), while accuracy for the lowest classes (0-B) range from about 1 km to 20 km (Fadely *et al.* 2005; Raum-Suryan *et al.* 2004; Rodgers 2001; Vincent *et al.*

2002; White and Sjoberg 2002). Class Z locations are categorized as invalid positions.

The data collected by telemetry units vary from study to study but generally include metrics on dive duration, dive depth, time at depth, and an indicator of wet or dry status of the unit. In all recent deployments, Steller sea lion telemetry units have been programmed to summarize 6 hours of dive data into histograms, such that dives cannot be assessed individually. Time at depth is also binned into histograms and can be used to determine how much time an animal spent at or near the surface versus how much time it spent diving below some threshold, usually 4 or 6 meters (m). The time spent below 4 or 6 m is usually interpreted as the amount of time an animal spent foraging. The wet/dry data indicates when an animal is on land or at-sea, and thus can be used to identify individual trips to sea as well as the overall proportion of time spent at sea. Because dive data are binned and because animal locations are calculated only when data uplinks to a satellite occur, there is no direct link between location data and foraging activity. It is in fact possible and relatively common in the telemetry data for an animals to spend multiple hours at sea with no locations recorded in that period.

Deployments. The Alaska Department of Fish and Game (ADFG) and the National Marine Fisheries Service (NMFS) have deployed the largest numbers of satellite telemetry units on Steller sea lions. At least 262 telemetry units were deployed between 1992 and 2005 by the two agencies (Table 3-1). Of those, 163 were deployed on young-of-the-year (YOY) animals, 62 were deployed on juveniles 1-3 years of age, and 37 were deployed on adult animals over the age of 3. In the immature age classes males and females have been evenly sampled, but of the 37 adult animals all were female.

Table 3-1. Satellite telemetry deployments by Alaska Department of Fish and Game and the National Marine Fisheries Service, 1992-2005 (published and unpublished data).

		Breeding Season (May-Aug)				Non-Breeding Season (Sept-Apr)				
DPS	Region	YOY	Juv	Adults	Total	YOY	Juv	Adults	Total	TOTAL
Eastern	WA	2	0	0	2	0	6	0	6	8
	SEA	10	28	0	38	18	29	0	47	85
Western	EGOA	4	0	0	4	7	13	0	20	24
	CGOA	4	7	5	16	32	8	8	48	64
	WGOA	0	0	4	4	2	0	0	2	6
	EAI	0	0	4	4	26	8	3	37	41
	CAI	3	0	4	7	16	2	0	18	25
	WAI	0	0	1	1	0	0	0	0	1
	Russia	0	0	8	8	0	0	0	0	8
	TOTAL	23	35	26	84	101	66	11	178	262

Abbreviations: WA=Washington state, SEA=Southeast Alaska, EGOA=Eastern Gulf of Alaska, CGOA=Central Gulf of Alaska, WGOA=Western Gulf of Alaska, EAI=Eastern Aleutians, CAI=Central Aleutians, WAI=Western Aleutians

Approximately 32% (n=84) of the telemetry tags were deployed in the breeding season, defined herein as the period from May through August, while the remaining 63% (n=178) were deployed during the non-breeding season from September to April.

Data from an additional 88 telemetry deployments on Steller sea lions by entities other than ADFG and NMFS have been reported in peer-reviewed scientific literature (Lander *et al.* 2009; Lander *et al.* 2010; Rehberg and Burns 2008; Rehberg *et al.* 2009). Eleven (11) of these were deployed on adult animals while the remaining 77 were attached to immature animals, including both YOY and juveniles (Table 3-2). Many of the studies grouped YOY and juvenile animals together, so separate counts of each could not be determined. Of the 77 immature animals 4 were categorized by Rehberg and Burns (2008) as sub-adults, three of which were between the ages of 30 and 32 months and one of which was a male aged 45 months. For simplicity and consistency, in

Table 3-2. Satellite telemetry units deployed by entities other than ADFG and NMFS and reported in the scientific literature, 1992-2005.

		Age Class		
DPS	Region	Immature	Adult	TOTAL
Eastern	SEA	0	11	11
Western	EGOA	19	0	19
	CGOA	26	0	26
	WGOA	0	0	0
	EAI	14	0	14
	CAI	15	0	15
	WAI	3	0	3
	TOTAL	77	11	88

summaries herein these animals have been grouped with the immature (YOY and juvenile) age class since all but one falls into the juvenile age class as typically defined (1-3 years of age) and data were not provided separately for the one 45-month old individual. In addition Rehberg and Burns (2008) did not find significant differences in diving metrics between their juvenile and subadult animals.

Of the 262 units deployed by ADFG and NMFS, analyses from 214 (81.7%) have been published in peer-reviewed scientific literature (Call *et al.* 2007; Fadely *et al.* 2005; Loughlin *et al.* 1998; Loughlin *et al.* 2003; Merrick and Loughlin 1997; Pitcher *et al.* 2005; Raum-Suryan *et al.* 2004; Sigler *et al.* 2009). The 58 units for which no published analyses are available consist of 25 excluded due to equipment failure, malfunction, and/or sparse or missing data; and 23 units deployed in recent years (2003-2005) that may eventually result in published accounts. Data from early deployments on adult females were the most likely to be excluded from analysis due to inadequate data, thus further reducing the sample size from adult animals.

All together analyses have been published from a total of 302 telemetry units (Table 3-3). Slightly under 10% (n=29) of the reported summaries come from adult animals, all of which are female. Approximately two thirds of the published data comes from western DPS (declining population) animals, including those from Russian waters (Figure 3-1). Of any single sub-region, southeast Alaska has produced the most individuals from which published data were derived (n=95). The central Gulf of Alaska sub-region has had the second most published deployments (n=47) overall and the most in the western DPS, while the western Gulf of Alaska and western Aleutians have had the fewest, with 4 and 3 respectively.

Reported Metrics. Mean and maximum dive depth, mean and maximum dive duration, as well as foraging trip metrics such as mean trip duration and distance, and mean percent time at sea and on land are the metrics most often reported in published

Table 3-3. Summary of satellite telemetry units deployed by Alaska Department of Fish and Game, the National Marine Fisheries Service, and other entities, from which published data were derived, 1992-2005.

		Age Class		
DPS	Region	Immature	Adult	TOTAL
Eastern	WA	6	0	6
	SEA	84	11	95
Western	EGOA	43	0	43
	CGOA	71	6	77
	WGOA	2	2	4
	EAI	45	2	47
	CAI	19	0	19
	WAI	3	0	3
	Russia	0	8	8
	TOTAL	273	29	302

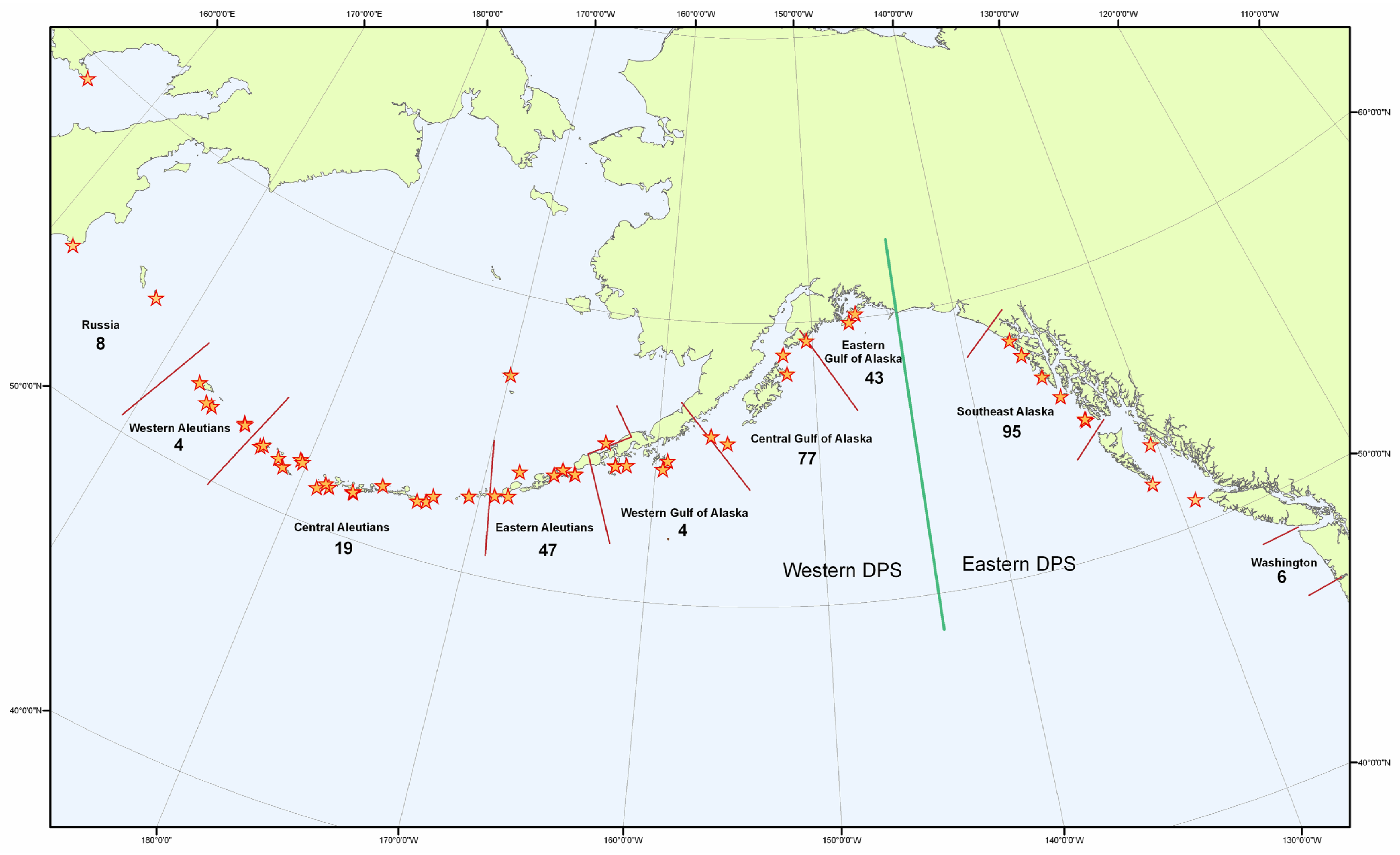

Figure 3-1. The number of satellite telemetry units deployed by Alaska Fish and Game, National Marine Fisheries Service, and other entities between 1991 and 2002. These numbers represent only those units from which analyses have been published in the scientific literature.

analyses. Three studies also reported some measure of foraging effort (Lander *et al.* 2010; Merrick and Loughlin 1997; Rehberg *et al.* 2009). Two studies reported mean home range size (Merrick and Loughlin 1997; Rehberg *et al.* 2009), while a third reported a study area size for each animal which consisted of a rectangle covering the minimum convex polygon home range plus a 15km buffer (Lander *et al.* 2010). In the last several years, a few studies have also begun to relate sea lion use areas with habitat characteristics (Fadely *et al.* 2005; Lander *et al.* 2009; Lander *et al.* 2010). These three are the only studies that utilize the location data from satellite telemetry deployments in a spatially explicit manner.

Tables 3-4 and 3-5 summarize the findings of all published peer-reviewed papers in which Steller sea lion satellite telemetry data have been analyzed and reported. Dive data are presented in Table 3-4, and foraging trip metrics and links between foraging location and habitat information are the focus of Table 3-5. Data from 10 adult females to which VHF radio telemetry units were attached are also included in Table 3-5 since some trip metrics similar to those derived from satellite telemetry data were calculated for these units as well. The data outlined in the tables are also summarized and synthesized in the following section.

At-Sea Movement and Habitat Use Findings

General Patterns for Adults. From telemetry studies, on-shore observations, and diet studies we are beginning to gain insight into how, and to a certain extent where, Steller sea lions forage. Although sample sizes are small, it is clear from the few studies

Table 3-4. Summary of published analyses on diving metrics using data from satellite telemetry units deployed on Steller sea lions from 1992 to 2005. Values represent means ± standard deviations (when available) in the units noted in the column heading. Values in parentheses represent confidence intervals unless noted otherwise.

Source	Age Class/Group	Season	DPS	Location	n	Mean Dive Depth (m)	Mean Daily Max Depth	Max Depth	Mean Dive Duration (minutes)	Max Dive Duration (minutes)
Merrick & Loughlin 1997	Adult F	Summer	Western	EAI, WGOA, CGOA	5	21		150-250	1.3	>8
	Adult F	Winter	Western	EAI to CGOA	5	24		>250	2	8
	YOY	Winter	Western	EAI to CGOA	5	9		72	1	>6
Loughlin et al 1998	Adult F	Summer	Western	Kuril Islands, Russia	8	53		250	1.87	8
Loughlin et al. 2003	YOY	all	Western	CAI, EAI, EGOA, CGOA	13	7.7 ± 1.7	25.7 ± 16.9	252	0.85 ± 0.1	
	Juvenile (>10 mo)	all	Western	EAI, EGOA, CGOA	5	16.6 ± 10.9	63.4 ± 37.7	288	1.1 ± 0.4	
	Alaska Pooled	all	Western	CAI, EAI, EGOA, CGOA	18	10.3	33.8 ± 7.2			
	Juvenile	all	Eastern	WA	7	39.4 ± 14.9	144.5 ± 32.6	328	1.75 ± 0.6	
	All Pooled	all	Both	CAI, EAI, EGOA, CGOA, WA	25	18.42 ± 16.23	62.42	135.36	1.1	
Pitcher et al. 2005	YOY	all	Both	EAI, EGOA, CGOA, SEAK	75			252		>12
	Juvenile	all	Both	EAI, EGOA, CGOA, SEAK	36			452		>12
	All Pooled	all	Both	EAI, EGOA, CGOA, SEAK	111	86.9% <10m		452	82.3% <2	>12
Fadely et al. 2005	YOY	all	Western	CAI, EAI, CGOA	26	10.3				
	Juvenile	all	Western	CAI, EAI, CGOA	4	13				
Rehberg and Burns 2008	YOY	all	Western	CAI, CGOA	11	13 (10.2-16.5)		325	0.9 (0.8-1.1)	4.9
	Juveniles (12-24mo)	all	Western	CAI, EGOA	17	29 (23.9-34.0)		>361	1.7 (1.5-1.9)	13.2
	Sub-adult (>30mo)	all	Western	EGOA	4	38 (25.8-56.5)		>361	2.0 (1.5-2.7)	18-32.9
	All Pooled	all	Western	CAI, EGOA, CGOA	32	31 ± 17		>361	1.7 ± 0.6	
Sigler et al. 2009[a]	Juvenile	Summer	Eastern	SEAK	6		99 ± 29	244		
	Juvenile	Winter	Eastern	SEAK	4		85 ± 42	420		
Rehberg et al. 2009	Adult F	Summer	Eastern	SEAK	11	29.6 ± 9.5	190.5	236	1.8 ± 0.3	>16
Lander et al. 2010[b]	YOY & Juveniles	all	Western	WAI, CAI, EAI, CGOA	21					68.4 ± 47.8

Abbreviations: WA=Washington state, SEAK=Southeast Alaska, EGOA=Eastern Gulf of Alaska, CGOA=Central Gulf of Alaska, WGOA=West Gulf of Alaska, EAI=Eastern Aleutian Islands, CAI=Central Aleutian Islands, WCAI=Western Aleutian Islands.

Note: Data from many of the deployed units have been used in multiple published analyses. See footnotes:

[a] Animals used in this analysis are a subset of the animals used in Pitcher *et al.* 2005

[b] Animals used in this analysis are a subset of the animals used in Lander *et al.* 2009

Table 3-5. Summary of published analyses using data from satellite and radio telemetry units deployed on Steller sea lions from 1992 to 2005. Values represent means ± standard deviations (when available) in the units noted in the column heading. Values in parentheses represent confidence intervals unless noted otherwise.

Source	Age Class/Group	Season	DPS	Location	n	Mean Trip Duration (h)	Mean Trip distance	Mean % Time at Sea	Mean % Time Spent Diving	Foraging Effort (hrs/day)	Mean Home Range Size (90% MCP)(km²)	or Linked to Habitat?
Merrick & Loughlin 1997	Adult F[1]	Summer	Western	EAI, CGOA	10	23 ± 2.8		52.5 - 58.1				
	Adult F	Summer	Western	EAI, WGOA, CGOA	5	18 ± 3.1	17 ± 4.6	50		4.7 ± 0.6	319 ± 61.9	
	Adult F	Winter	Western	EAI to CGOA	5	204 ± 104.6	133 ± 59.9	89.9		5.3 ± 1.3	47,579 ± 26,704	
	YOY	Winter	Western	EAI to CGOA	5	15 ± 2.2	30.0 ± 14.5	37.5		1.9 ± 0.9	9,196 ± 6,799.3	
Loughlin et al 1998	Adult F	Summer	Western	Kuril Islands, Russia	8		20					some
Loughlin et al. 2003	YOY	all	Western	CAI, EAI, EGOA, CGOA	13	7.5 ± 7.5	7.0 ± 19.0					
	Juveniles	all	Both	CAI, EAI, EGOA, CGOA, WA	12	18.1 ± 34.2	24.6 ± 57.2					
	All Pooled	all	Both	CAI, EAI, EGOA, CGOA, WA	25	12.1 ± 23.8	16.6 ± 44.9					
Raum-Suryan et al. 2004[a]	YOY & Juv	all	Western	EAI, CGOA, EGOA	29		6.5 (5.08-8.26)					
	YOY & Juv	all	Eastern	SEAK	74		4.7 (3.92-5.53)					
	All Pooled	all	Both	EAI, CGOA, EGOA, SEAK	103	84% trips ≤ 20	90% trips ≤ 15					
Fadely et al. 2005	YOY and Juveniles	Feb-Apr	Western	CAI, EAI, CGOA	30	8.9 (8.4-9.4)	0.56 (0.56-0.74)[2]					Y
	YOY and Juveniles	May-July	Western	CAI, EAI, CGOA	30	12.5 (11.3-13.9)	1.3 (0.93-1.49)[2]					
	YOY and Juveniles	Nov-Jan	Western	CAI, EAI, CGOA	30	10.1 (8.2-12.5)	1.11 (0.74-1.67)[2]					
Call et al. 2007[b]	YOY & Juveniles	all	Both	EAI	?	9.8 ± 11.7						
	YOY & Juveniles	all	Both	CGOA	?	10.2 ± 12.2						
	YOY & Juveniles	all	Both	EGOA	?	8.9 ± 10.2						
	YOY & Juveniles	all	Both	SEAK	?	8.2 ± 9.0						
	All Pooled	all	Both	EAI, CGOA, EGOA, SEAK	109	9.2 ± 12.0		44				
Rehberg and Burns 2008	YOY	all	Western	CAI, CGOA	11			41 (33-50)	10 (5-17)			
	Juveniles (12-24mo)	all	Western	CAI, EGOA	17			56 (50-62)	27 (20-34)			
	Sub-adult (>30mo)	all	Western	EGOA	4			69 (55-80)	32 (16-50)			
	All Pooled	all	Western	CAI, EGOA, CGOA	32			48 ± 12				
Sigler et al. 2009[a]	Juvenile	Summer	Eastern	SEAK	6				27.4			some
Rehberg et al. 2009	Adult F	Summer	Eastern	SEAK	11	20.8 ± 8.1	17.8 ± 3.0	48	22.1 ± 4.3	3.3 ± 2.2	190.0 ± 67.2	some
Lander et al. 2009	YOY & Juveniles	Summer	Western	WAI, CAI, EAI, CGOA	45							Y
Lander et al. 2010[c]	YOY & Juveniles	all	Western	WAI	3			52.9[3]	7.3 ± 3.4[4]		10,834.2 - 35,248.2[5]	Y
	YOY & Juveniles	all	Western	CAI	6			43[3]	13.0 ± 5.4[4]		4,634.8 - 154,125.8[5]	
	YOY & Juveniles	all	Western	EAI	7			35.6[3]	8.3 ± 5.7[4]		1,808.4 - 44,530.7[5]	
	YOY & Juveniles	all	Western	CGOA	5			50.1[3]	12.3 ± 8.4[4]		2,154.8 - 24,891.5[5]	
	All Pooled	all	Western	WAI, CAI, EAI, CGOA	21	8.6 ± 14.8		44.3 ± 18.3	11.2 ± 6.8[4]		1,808.4 - 154,125.8[5]	

Abbreviations: WA=Washington state, SEAK=Southeast Alaska, EGOA=Eastern Gulf of Alaska, CGOA=Central Gulf of Alaska, WGOA=West Gulf of Alaska, EAI=Eastern Aleutian Islands, CAI=Central Aleutian Islands, WCAI=Western Aleutian Islands.

Note: Data from many of the deployed units have been used in multiple published analyses. See footnotes:

[a] Animals used in this analysis are a subset of the animals used in Pitcher *et al.* 2005

[b] About 95% of the animals used in this analysis were also used in Pitcher *et al.* 2006, Fadely *et al.* 2005, and Loughlin *et al.* 2003.

[c] Animals used in this analysis are a subset of the animals used in Lander *et al.* 2009.

[1] These animals were equipped with VHF telemetry units

[2] These distances represent the distance to shore from the furthest point in a trip not the actual trip distance as measured in other studies

[3] These values are the sum of the % time at sea <6m deep and the % time spent diving(>6m)

[4] These values are the% out of the entire time budget spent diving (including time on shore), whereas the other values in this column represent the % of time at sea that was spent diving

[5] These values are the ranges of values representing the size of a standard rectangle covering the minimum convex polygon plus a 15km buffer

on adult animals that summer and winter foraging patterns are markedly different. Estimates of mean trip distances for adults range between 17 and 20 km in the summer (n=24) (Loughlin *et al.* 2003; Merrick and Loughlin 1997; Rehberg *et al.* 2009) and 133 km in the winter (n=5) (Merrick and Loughlin 1997). The longest summer trips observed for adult animals in each study was 263 km, 49 km, and 55 km respectively (Loughlin *et al.* 2003; Merrick and Loughlin 1997; Rehberg *et al.* 2009), whereas the longest winter trip recorded was 543 km (Merrick and Loughlin 1997). Rehberg *et al.* (2009) noted that all foraging locations for the 11 adults in their study were landward of the continental shelf break (<200 m deep) but some foraging trips traversed deeper nearshore canyons. During their long winter foraging trips two adults in the Merrick and Loughlin (1997) study were tracked out to seamounts in the middle of the Gulf of Alaska, foraging in waters greater than 2 km deep. These animals stayed out in that region for long periods before returning to shore.

Summer home range size estimates (based on 90% minimum convex polygon, MCP, methodology) for adults range from 190 ± 67.2 km^2 in the eastern DPS (Rehberg *et al.* 2009) to 319 ± 61.9 km^2 in the western DPS (Merrick and Loughlin 1997). The 5 adults observed in the winter in the western DPS exhibited a mean home range size of 45,579 ± 26,704 km^2 (Merrick and Loughlin 1997).

On-shore observations as well as telemetry data confirm that adults spend more time foraging in the winter than in the summer. Adult females spend about 20 hours at sea per trip in summer months (Maniscalco *et al.* 2006; Merrick and Loughlin 1997; Milette and Trites 2003; Rehberg *et al.* 2009; Sandegren 1970). Estimates of winter trip duration vary considerably between studies, with 204 hours per trip estimated from 5 animals equipped with telemetry units (Merrick and Loughlin 1997), and between 50 and 60 hours from on-shore observations (Maniscalco *et al.* 2006; Trites and Porter 2002). The percent time spent at sea for adults ranges between 40% and 50% in the summer (Maniscalco *et al.* 2006; Merrick and Loughlin 1997; Milette and Trites 2003; Rehberg *et al.* 2009), and between 60% and 90% in the winter (Maniscalco *et al.* 2006; Merrick and Loughlin 1997; Trites and Porter 2002). Trip distances and time at sea have both been shown to be greater for animals in the western (declining) population than for the eastern population (Pitcher *et al.* 2005; Raum-Suryan *et al.* 2004), although one study found mean trip durations longer in the eastern population (Milette and Trites 2003).

Patterns of use at rookeries and haul-outs can also inform our understanding of how Steller sea lions forage. Sea lions from southeast Alaska demonstrate more complex patterns of haul-out use than those from the western DPS, using 29% more haul-outs on average per individual (Raum-Suryan *et al.* 2004). This pattern is supported by the many studies conducted in southeast Alaska that demonstrate that sea lions move between haul-outs and vary their diet in response to ephemeral concentrations of prey (Sigler *et al.* 2004; Sigler *et al.* 2009; Womble *et al.* 2005; Womble and Sigler 2006; Womble *et al.* 2009).

<u>General Patterns for Immature Animals</u>. Foraging patterns in immature animals tends to vary considerably between individuals and regions but a few patterns have emerged. As with diving ability, trip durations and distances for immature animals increase with age, and may reach the level of adult development by age 2 or 3 (Call *et al.*

2007; Loughlin *et al.* 2003; Pitcher *et al.* 2005; Raum-Suryan *et al.* 2004). Juveniles have been found to spend 26% to 43% more time at sea than YOY, and 12.5% more time diving while at sea than YOY (Rehberg and Burns 2008; Trites and Porter 2002). Overall, estimated percent time spent at sea for immature animals ranges between 44% and 48% (Lander *et al.* 2010; Rehberg and Burns 2008). Call *et al.* (2007) found that time on shore did not increase with age.

Loughlin *et al.* (2003) categorized trips to sea by immature animals into three types: short foraging trips (<15 km and <20 h), longer foraging trips (>15 km and >20 h), and transit trips (6.5 - 454 km). Both foraging trip types include departure and return to the same starting haul-out or rookery, whereas transit trips have different starting and ending locations. Short-range foraging trips have been found to compose between 88 and 90% of all trips to sea by immature animals, with long range and transit trips making up the other 10 to 12% (Loughlin *et al.* 2003; Raum-Suryan *et al.* 2004). Similarly, in another study, most telemetry location associated with diving activity were found to be between 9 and 18 km straight-line distance from shore in on-shelf waters less than 100 meters deep (Fadely *et al.* 2005). The majority of trips by immature animals appear to last less than 20 hours, with per study means ranging between 8 and 18 hours (Call *et al.* 2007; Fadely *et al.* 2005; Lander *et al.* 2010; Loughlin *et al.* 2003; Merrick and Loughlin 1997; Raum-Suryan *et al.* 2004).

Immature animals do, however, travel long distances starting at about 7 to 9 months of age (Loughlin *et al.* 2003; Raum-Suryan *et al.* 2004). Maximum trip distances for some young individuals far exceed maximum distances recorded for the few adults that have been telemetered. One 9 month old animal traveled more than 500 km, another moved 840 km, and a 19 month old was recorded to have moved 1,300 km over the course of 48 days (Raum-Suryan *et al.* 2004). In the study by Loughlin *et al.* (2003) the maximum trip distance for animals under 10 months of age was 261 km, and for those over 10 months, 447 km. In one mark-resight study on Steller sea lions, YOY and adult individuals generally stayed within 500 km of their natal rookeries, while juvenile animals dispersed more widely and were recorded as far away as 1,785 km from the rookery where they were initially observed and branded (Raum-Suryan *et al.* 2002). It should be noted that all the trips recorded for immature animals in both the mark-resight study as well as the telemetry study that exceeded 500 km were undertaken by males (Raum-Suryan *et al.* 2002; Raum-Suryan *et al.* 2004).

Although Fadely *et al.* (2005) did not report trips as long as the ones above, they did note that the animals in their study tended to make longer trips in May, a month in which 23% of animals made offshore trips upwards of 37 km from shore. Longer trips to the Bering sea were in off-shelf waters beyond 55 km from shore, while foraging trips into the north Pacific remained over the continental shelf within 55 km of shore. Other studies have also reported increases in trip length by juveniles in the period from April to June (Raum-Suryan *et al*. 2004; Rehberg and Burns 2008).

Linking Foraging to Habitats. In addition to the studies providing the generalized patterns of use described above, a few studies have attempted to identify spatially explicit Steller sea lion foraging areas, and to link the areas used by Steller sea lions to the habitat features located there. Habitat features in the ocean can include unchanging physical features such as water depth and ocean floor slope as well as features that change over various time scales such sea surface temperature (SST) and chlorophyll *a* (chl *a*).

In one study, diving activity by immature animals was found to be associated with certain water depths (<100 m), but monthly averages of SST and chl *a* in the vicinity of dive locations were not found to strongly or consistently explain variability in diving activity for all immature animals (Fadely *et al.* 2005). Increases in SST were found to correlate with increases in dive rate and median dive depth, but these changes were also coincident with sea lion maturation and dive development (Fadely *et al.* 2005).

Two other studies that used SST and chl *a* heterogeneity or various patch characteristics related to these habitat variables, however, were more successful in relating Steller sea lion foraging to habitat characteristics. Within each of four sub-regions in the western DPS, Lander *et al.* (2009) defined a study area that encompassed all filtered telemetry data from that sub-region, and found that SST spatial heterogeneity and temporal homogeneity was most beneficial to local populations. In other words, local populations grew where there was higher diversity of sea surface temperature patches that persisted through time. The temporal homogeneity finding is similar to that of Gende and Sigler (2006) who found that inter-annual persistence of prey hotspots was more important in attracting Steller sea lions than prey density. Although the Gende and Sigler (2006) and Lander *et al.* (2009) studies relate to different temporal time scales, they both suggest that consistency in the location of resources may be of primary importance in minimizing search effort for foraging sea lions. The patterns of spatial SST diversity between sub-regions found in the Lander *et al.* (2009) study was generally consistent with patterns of diet diversity in those sub-regions, and like diet diversity was inversely related to population trends (Lander *et al.* 2009; Sinclair and Zeppelin 2002). The same patterns were not, however, found for chl *a*. These results indicate that habitat diversity as measured by SST diversity may attract or concentrate a more diverse array of prey species, which in turn benefits Steller sea lion populations. Interestingly, trips by immature animals tracked in the Fadely *et al.* (2005) study were found to be significantly oriented toward the Unimak Pass area during May and June when SST and chl *a* are rapidly changing. The rapidly changing habitat features may have in fact exhibited a high level of diversity, thus supporting a diverse array of prey species and providing ideal foraging habitat to young sea lions.

Lander *et al.* (2010) used an even more complex suite of metrics related to SST to identify how foraging Steller sea lions utilize oceanic frontal features. In general, sea lion foraging efficiency increased with decreasing shape complexity of SST frontal features and higher density of these habitats (Lander *et al.* 2010). The size of the frontal features, however, did not appear to influence sea lion behavior (Lander *et al.* 2010).

Habitat Use Summary. Based on telemetry data and on-shore behavioral observations that support the findings of telemetry studies, female adult Steller sea lions appear to require nearshore habitat within about 20 km of rookeries and haul-outs for summer foraging. Immature animals also tend to spend much of their time at sea within these areas. Most often these nearshore habitats are located in on-shelf waters less than 100 or 200 m deep. In winter, however, adult animals spend much longer periods at sea and swim much further distances to find sufficient prey resources. Although the area used by wintering adult females is unclear, at least some animals travel to deep offshore waters; a home range greater than 45,000 km^2 may be necessary for some animals. Young animals are also capable of long distance movements, but how these longer distance movements relate to habitat use is unclear.

Habitat diversity but not necessarily frontal shape complexity appears to be beneficial to Steller sea lions both at the population level and for individual foraging sea lions. Habitats that are temporally predictable may aid sea lions foraging efficiency. Further exploration of the relationship of SST and perhaps chl *a* to Steller sea lion foraging will certainly be necessary to further elucidate these patterns.

Designated Critical Habitat

Under the United States Endangered Species Act (Act or ESA) (1972) the managing agency is required to designate critical habitat for threatened and endangered species and to establish regulations related to those habitats to ensure the survival of the species. Within the Act however, no specific methodologies are stipulated to aid in determining a species' critical habitat. In 1993, Steller sea lion critical habitat for the endangered western DPS was defined to include a 20 nautical mile (nm) (37 km) buffer around all major rookeries and haul-outs as well as the air and terrestrial zones associated with those sites (U.S. Federal Register 50 CFR 226.202)(Figure 3-2). An additional three critical habitat foraging areas were also designated in the area of Shelikof Strait north of Kodiak Island, in the vicinity of Seguam Pass, and in an area including Unimak Pass and Bogoslof Island in the southwest portion of the Bering Sea (Figure 3-2). Critical habitat for the threatened eastern DPS includes a 3,000 feet (0.9 km) buffer around all major

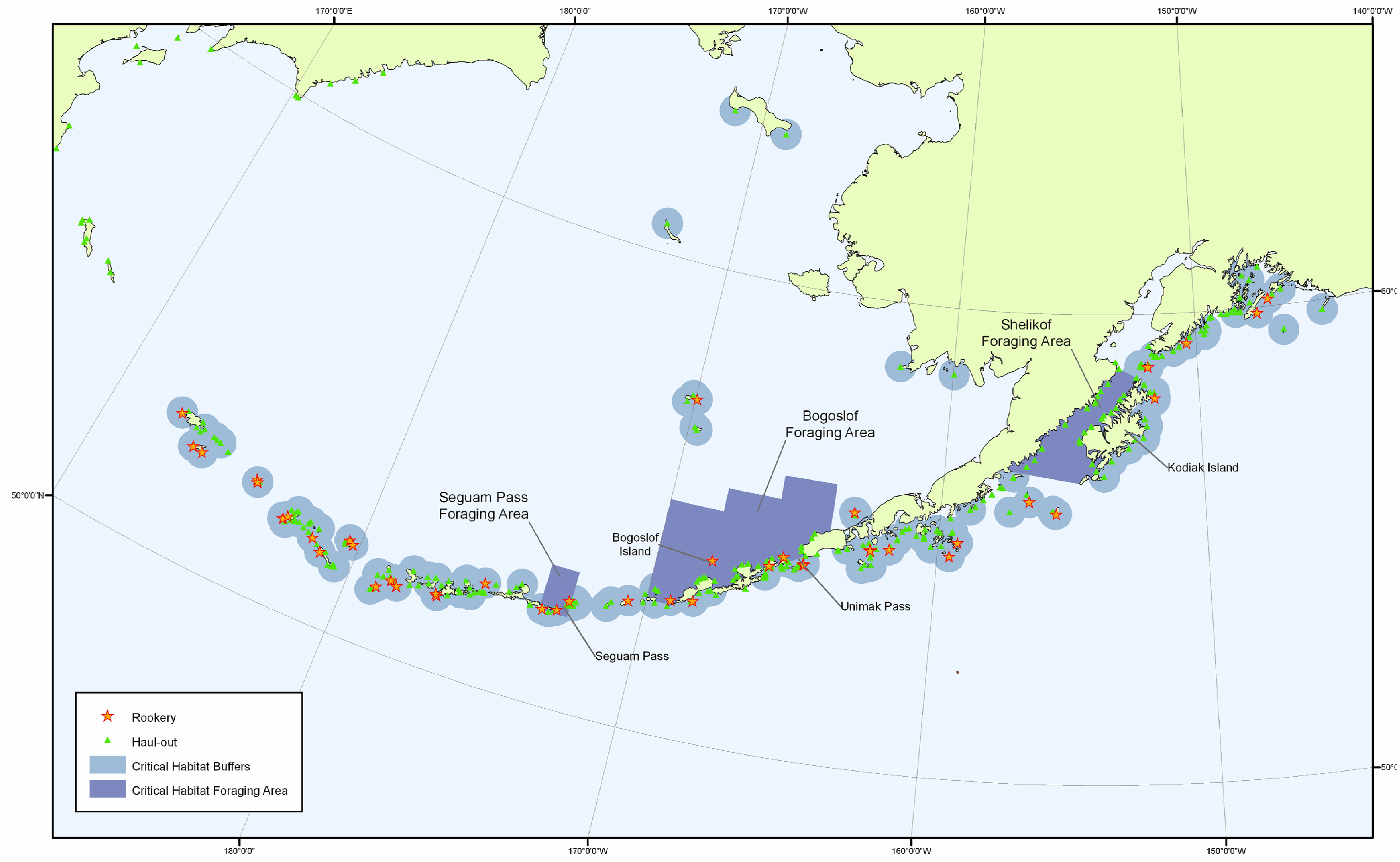

Figure 3-2. Designated Steller sea lion critical habitat areas for the western DPS, including a 20 nautical mile buffer around all major rookeries and haul-outs and three foraging areas.

rookeries and haul-outs (U.S. Federal Register 50 CFR 226.202). A complex suite of fishing regulations related to these areas and designed to protect the foraging habitat of Steller sea lions has been subsequently established. These critical habitat areas have been based on the studies of at-sea use patterns of Steller sea lions summarized above in addition to knowledge about prey concentrations and patterns of historic incidental take of Steller sea lions in fisheries (Loughlin and Nelson 1986; NMFS 2008).

Predictive Habitat Modeling

One attempt has been made to use predictive habitat modeling to identify areas of importance to Steller sea lions. Gregr and Trites (2008) developed four models predicting Steller sea lion presence based on habitat characteristics, and then assessed how well their areas of predicted Steller sea lion habitat corresponded to opportunistic Steller sea lion sighting locations. Their model that best predicted the sightings data used the following assumed Steller sea lions preferences: water depths of 150 to 200 m, steeply sloped bottom topography, and high sea surface height variability (used as a proxy for frontal activity). This best model was able to capture 43.7% of the opportunistic sightings within its highest quality habitat. Comparing this performance with the proportion of opportunistic sightings captured within designated critical habitat areas (36.1%), their model outperformed the currently defined critical habitat for Steller sea lions.

If their model assumptions are true, Steller sea lions are more likely to be found in areas of substantial frontal activity, with an ideal depth of 150 to 200 m, and a steeply sloping ocean floor. However, the accuracy of their predictions will only be as accurate as the relationships postulated between sea lions and their habitats. Although these relationships are intuitively appealing and have some basis in observations of Steller sea lions and other pinnipeds, they are not strictly empirical and therefore we have no measure of their reliability. In addition, as with other taxa, sea lion response to habitat features is unlikely uniform across their entire range, and assuming spatial stationarity (or equilibrium) over large geographic regions has been cautioned against (Guisan and Zimmermann 2000; Osborne *et al.* 2001; Osborne and Suarez-Seoane 2002; also see next section). Finally, the tests used to validate the models simply provided relative measures of performance without any absolute assessment of accuracy.

How Is This Current Knowledge Inadequate?

From the studies that have thus far been produced on Steller sea lion at-sea movements and habitat use, we now have a broad outline of how far sea lions go when they leave the rookery or haul-out, how much time they spend at sea, and for a small number of individuals we have an estimate of home range size. These metrics tell us generally where sea lions are foraging but may be insufficient for adequately managing a species which continues to decline. The slowing of the population decline in the western DPS coincided with the implementation of protective measures including critical habitat designations and tighter commercial fishing restrictions. These measures may have slowed or perhaps arrested the decline, but the population has failed to recover and the most recent surveys indicate a recurrence of declines in parts of the western DPS that had previously been stable (Fritz *et al*. 2008a ; Fritz *et al*. 2008b).

The most recent Steller sea lion Recovery Plan (NMFS 2008) stated that potential modifications to “critical habitat designations should also consider spatial and temporal variation of essential habitat characteristics.” In addition, one of the stated goals for the NMFS in relation to Steller sea lion management and recovery is to “evaluate all information on sea lion foraging areas and develop a description of foraging needs” (NMFS 2008). To this end, spatially explicit information on Steller sea lion habitat will be required. Below I outline why the data we have obtained thus far and the reported metrics are inadequate to fully understand Steller sea lion habitat use, and by extension inadequate for managing and protecting the species. The most recent studies connecting sea lion foraging behavior to spatially explicit habitat features hold the most promise in helping us understand the habitat needs of Steller sea lions, but further work is needed.

Sample Size and Uneven Sampling

Overall sample sizes for assessing at-sea movement patterns are low relative to the range and population size of the species. In addition, sampling has occurred unevenly in age- and sex-classes as well as spatially. A total of 302 tagged individuals have produced useable foraging pattern information, and of those only 29 are adults; of those adults, all are female. Although low juvenile survival had been implicated as one of the drivers of the precipitous declines of Steller sea lion populations in 1980s (York 1994; Pascual and Adkison 1994), recent population modeling suggests that low birth rates may be preventing population recovery and that the relative stability in the western population is dependent upon and sensitive to high adult survivorship (Holmes *et al.* 2007). Understanding the foraging patterns and habitat needs of all age- and sex-classes will be important for long-term management and growth of the population.

The geographic distribution of data is spatially uneven as well (Figure 3-1). Only 4 telemetry units have been deployed in the western Aleutians; 8 in Russian waters; 19 in the central Aleutians, the largest sub-region in the western DPS; and 4 in the western Gulf of Alaska. The western Aleutians is arguably one of the most critical areas for which we need habitat use information since its population has continued to decline even while other regions have stabilized. The central Aleutians are one of the sub-regions that showed declining numbers in the last survey despite several years of stable or increasing numbers (Fritz *et al*. 2008b). Based on the analysis of O'Corry-Crowe *et al.* (2006), animals in the central Aleutians and westward may exhibit substantially different foraging ecology than animals from rookeries in the continental shelf region, therefore obtaining data specific to the central and western Aleutian sub-regions is critical.

Locational Error and Bias

In addition to the number of telemetered individuals being small and unevenly distributed, the location data derived from telemetry units is often also sparse and error prone. The location data must be filtered for accuracy, thus further reducing the quantity of useable data for individual sea lions. Various filtering algorithms have been used in different studies and have resulted in reported retention of between 19% and 68% of location data points (Fadely *et al.* 2005; Raum-Suryan *et al.* 2004). In one study of adult animals in Russian waters, a total of 73 acceptable at-sea locations were obtained for 8 animals (Loughlin *et al.* 1998). These 8 animals made 63 foraging trips, which means that each trip was represented on average by only 1.2 at-sea locations. Rehberg *et al.* (2009) also reported that reliable at-sea location data were sparse. Of 71 trips they could adequately identify, only 54% had location data associated with the central portion of the trip (0.25-0.75 of trip duration), and of those, 28% were represented by only 1 location.

Given the above statistics it is obvious that we are missing a lot of location information when sea lions may be most actively foraging. Telemetry location data are often clustered very close to rookeries and haul-outs. This pattern certainly reflects some level of truth, but the data also likely contain a nearshore bias. Since onshore observational studies reinforce the findings from telemetry data that indicate Steller sea lions make shorter trips in summer and longer trips in winter, the telemetry data are not misrepresenting gross patterns of use. The telemetry may not however, be presenting a fully accurate picture of how far away from shore sea lions are traveling and how frequently.

Although the telemetry data are inherently spatial, the limited number of reliable location fixes makes spatially-explicit analysis tenuous. Most of the studies that have provided maps of home ranges or direct measures of habitat characteristics associated with SSL at-sea locations are confined to relatively small geographic regions and very small sample sizes (e.g. Merrick and Loughlin 1997; Fadely *et al.* 2005; Rehberg *et al.* 2009). Most often, location data have been utilized only to quantify summarized at-sea trip characteristics such as distance from shore and total trip distance, without specific reference to geographic locations or habitat features utilized (e.g. Merrick and Loughlin 1997; Loughlin *et al.* 2003; Raum-Suryan *et al.* 2004; Rehberg *et al.* 2009).

Even the more spatially explicit studies that have associated at-sea use patterns with habitat characteristics were only able to use broad definitions of sea lion foraging areas in attempting to connect foraging to habitat characteristics. It is unclear whether foraging activity was truly associated with the habitat characteristics being measured (e.g. Lander *et al.* 2009). Fadely *et al.* (2005) did not find strong associations between specific diving metrics and habitat variables but surmised that the lack of association may have been due in part to locational error in conjunction with the de-coupling of dive metric measurements from location data. Lander *et al.* (2010) used minimum convex polygons around telemetry locations (that were also buffered) to define a sea lion area of influence, measured habitat variables in those areas, and associated them with temporally correlated dive activity. Although this approach circumvents the issue of locational accuracy, one cannot be sure the recorded dive activity corresponded to the environmental features being measured.

Figures 3-3 and 3-4 offer a trivial but perhaps helpful visual demonstration of both the error-prone nature of the telemetry location data and the relative scarcity of data over the Steller sea lion range. Figure 3-3 shows unfiltered telemetry location data from 238 individuals for which I have data. Filtering those data using an unsophisticated but not overly conservative algorithm of excluding location quality (LQ) class A, B, and Z locations as well as those falling on land, results in 37% fewer locations total and substantially fewer off-shore locations (Figure 3-4). Although most studies utilize a more sophisticated iterative filtering algorithm using swim speeds and turning angles to cull erroneous data, these figures illustrate the limited nature of the telemetry location data.

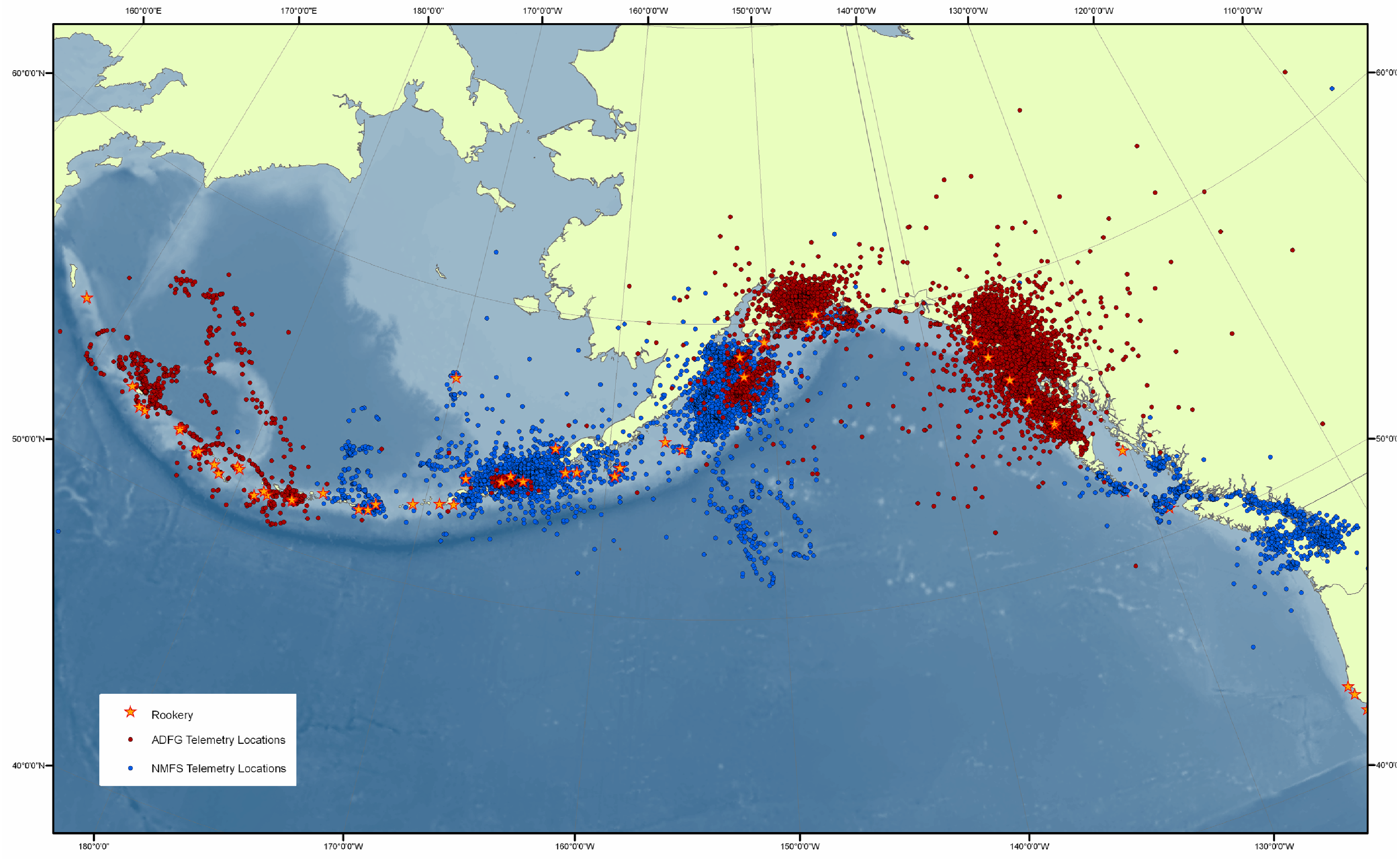

Figure 3-3. Unfiltered satellite telemetry locations from telemetry units deployed on Steller sea lions by the Alaska Department of Fish and Game (ADFG) and the National Marine Fisheries Service (NMFS) between 1992 and 2002. The telemetry data are overlaid on a map of bathymetric features.

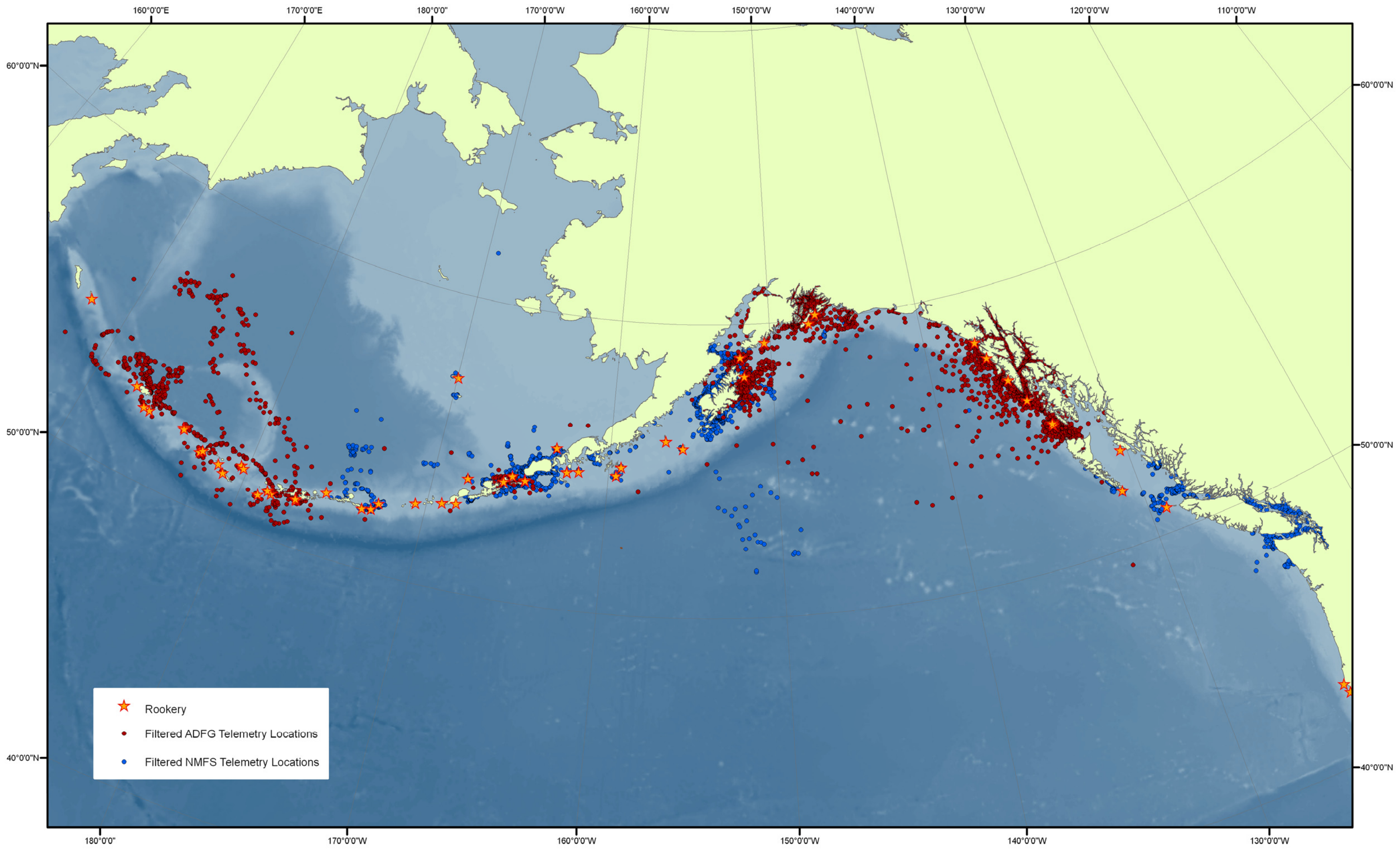

Figure 3-4. Filtered satellite telemetry locations from telemetry units deployed on Steller sea lions by the Alaska Department of Fish and Game (ADFG) and the National Marine Fisheries Service (NMFS) between 1992 and 2002. The telemetry data are overlaid on a map of bathymetric features. The filter excluded locations within the quality categories LQ A, B, and Z, and those on land.

Individual and Regional Foraging Differences

To characterized and define where Steller sea lions forage and what areas are important, average foraging trip metrics have been applied across the entire range, whenin fact these metrics have been shown to vary considerably between regions, rookeries, and even individuals from the same rookery.

As discussed in chapter 2, diet composition and diet diversity differ between sub-regions (Merrick *et al.* 1997; Sinclair and Zeppelin 2002; Sinclair *et al.* 2005; Trites *et al.* 2007). Based on prey consumption patterns and bioenergetic models, per capita food requirements can differ by as much as 24% between regions (Winship and Trites 2003). Even within a sub-region, diet composition has been shown to vary. Trites *et al.* (2007) found that diets of animals from three different rookeries within the southeast Alaska sub-region differed significantly from one another. In another study, diets of females at three separate locations in the same rookery complex were found to have similar diets, but males occupying a separate bachelor haul-out in the same rookery complex had significantly different diets from the females (Trites and Calkins 2008).

If diet composition is different, then one would expect foraging patterns to differ between populations, sub-regions and rookeries as well. Animals from the western DPS have been shown to exhibit greater trip distances and time at sea, and lower dive duration, maximum daily depth, and dive rate than animals from the eastern DPS (Pitcher *et al.* 2005; Raum-Suryan *et al.* 2004). Different haul-out use patterns between populations has also been demonstrated (Raum-Suryan *et al.* 2004). Even within the same DPS, many between sub-region differences have also been documented in foraging patterns, including diel haul-out patterns (Call *et al.* 2007; Lander *et al.* 2009; Lander *et al.* 2010; Loughlin *et al.* 2003; Rehberg and Burns 2008; Sigler *et al.* 2009). Loughlin *et al.* (1998) found substantial variation in foraging patterns and locations between animals from different islands of the Kuril Island chain in Russia. Animals from two different rookeries within southeast Alaska were also found to forage in different areas near their respective rookeries (Rehberg *et al.* 2009).

Seasonal changes in diet and foraging patterns have also been well documented. Telemetry studies have provided different metrics for summer and winter foraging patterns, but actual sea lion foraging patterns may be much more complex than this simple dichotomy would suggest. In some regions diet composition remains relatively constant between seasons, while in other areas, the species composition or proportions consumed in summer are different than in winter (Sinclair and Zeppelin 2002). Trites *et al.* (2007) found that diet diversity is highest in summer and lowest in the fall for animals in southeast Alaska. Early spring appears to be period of shifting patterns for juvenile animals. Based on bioenergetic models, Steller sea lions require 45-60% more food per day in early spring compared to late summer (Winship and Trites 2003). April through June has been characterized in several studies by increased foraging activity and longer trips (Fadely *et al.* 2005; Raum-Suryan *et al.* 2004; Rehberg and Burns 2008). Raum-Suryan *et al.* (2004) found that trip distances increased in October as well. Sea lions in southeast Alaska were found to track various prey concentrations, shifting their haul-out use patterns in December, May, July, and September (Womble *et al.* 2009).

Evidence has been found that Steller sea lion diets and foraging patterns also change over time within the same region. Merrick *et al.* (1997) found differences in prey diversity and prey composition between time periods for animals within the eastern Aleutian sub-region. Significant year to year differences in the amount of time spent at sea (Maniscalco *et al.* 2006; Milette and Trites 2003) is also indicative that foraging patterns change inter-annually depending on prey availability and location. Milette and Trites (2003) suggest that similarity in inter-annual trends in attendance cycles among populations may be indicative of changes in oceanic conditions in the entire North Pacific that affected prey patterns and thus foraging basin-wide. Such inter-annual differences may be common but as yet undetected with current data.

A large amount of individual variability in foraging patterns among animals from the same haul-out or region has been demonstrated in most Steller sea lion telemetry studies (e.g. Fadely *et al.* 2005; Loughlin *et al.* 2003; Merrick and Loughlin 1997; Raum-Suryan *et al.* 2004; Rehberg *et al.* 2009; Sandegren 1970). Diets among male and female Steller sea lions within the same rookery complex have also been shown to differ, which also indicates different foraging patterns and locations between the sexes (Trites and Calkins 2008). At-sea use patterns in other pinniped species have also been shown to differ significantly between males and females (Beck *et al.* 2005), adults and juveniles (Sterling and Ream 2004), individuals from nearby rookeries (Robson *et al.* 2004), and seasons (Burns *et al.* 2004).

These examples of differences in foraging patterns at different temporal and spatial scales, and between individual animals do not invalidate the general patterns of use that have been gleaned from telemetry studies thus far. They do however, demonstrate that our relatively small sample of telemetered animals may not provide us with a complete picture of Steller sea lion foraging patterns, and current critical habitat designations that are uniform across all sub-regions may not be sufficient.

Conclusions

Although satellite telemetry data have improved our understanding of Steller sea lion diving habits and movements at sea, especially for young-of-the-year and juvenile animals, the available telemetry are not sufficient for assessing broad-scale habitat use patterns for the entire species or for the endangered population in the western DPS. The overall sample size (number of tagged individuals) is small, and is even smaller for adult animals. The geographic distribution of data is limited and spatially uneven. The telemetry location data also have large associated error that make them difficult to use and interpret, and likely contain a near-shore bias.

The summarized metrics derived primarily from telemetry data have been extrapolated across regions and age-classes in order to define important habitat for the entire SSL population. Based on the evidence for spatial, temporal, and individual differences in foraging patterns, the wisdom of doing so is questionable.

Although the exercise can be revealing, predictive habitat modeling suffers similarly from applying generalized patterns across the entire species range, when in fact, habitat use appears to be, at minimum, regionally specific. The predictive habitat modeling that has been completed thus far for Steller sea lions may provide fodder for future investigations, but before it can be used as a reliable source of information about

Steller sea lion use patterns, more substantial validation with empirical data will be necessary.

To truly understand the habitat needs of Steller sea lions, we need spatially explicit at-sea information from all areas of their range. The Platforms of Opportunity (POP) Steller sea lion sighting data hold promise in this respect. In the following chapter I will outline how the difficulties of the POP data can be overcome, and how the data can be used to provide information about Steller sea lion at-sea use patterns that to this point has not been available from telemetry or other sources of data.

CHAPTER 4:

BAYESIAN ESTIMATION OF STELLER SEA LION ENCOUNTER RATES

Introduction

Identifying the spatial use patterns and habitat needs of a species is essential to understanding its ecology, and critical for its management and protection. Accurately delineating habitat for an entire species requires knowledge of range-wide foraging patterns by all classes of individuals. The time-scale over which habitat use is assessed should also be broad enough to encompass the natural variability of the species of interest as well as the natural variability of the resources upon which it relies (Bjørge 2001). Unfortunately, for many species of conservation concern, movement and habitat use data meeting these high standards are not available; such has been the case for Steller sea lions (SSL). In this chapter I outline an approach to using opportunistic sightings of Steller sea lions recorded over nearly a half-century throughout their entire range and over all seasons to remedy the current paucity of spatially explicit information on Steller sea lion at-sea use.

To date, information about Steller sea lion at-sea spatial use has been derived primarily from satellite telemetry data, but these data have mostly provided summarized metrics of at-sea movement from a relatively small sample of individuals. As outlined in the previous chapter, these limited data are not sufficient to adequately address questions of range-wide habitat use. An alternative source of information that has thus far been underutilized as a source for habitat use information for Steller sea lions is the Platforms of Opportunity (POP) data collected by the National Marine Fisheries Service (NMFS).

The POP dataset contains nearly 50 year's worth of opportunistic marine mammal observations from across the entire Pacific basin.

The POP data have not be used previously because of the difficulties associated with analyzing sighting data that are not associated with quantified observation effort. To overcome this obstacle I developed a novel methodology for deriving an effort index from observations of non-SSL marine mammals in the POP dataset. Using the effort index, I created a Bayesian model to estimate Steller sea lion encounter rates at a resolution of 15 km^2 throughout the north Pacific and Bering Sea. These encounter rates reveal spatially-explicit patterns of Steller sea lion use across their entire range, something that has previously never been possible. The data were also parsed into breeding and non-breeding seasons to estimate seasonal patterns of use.

Methods and Materials

Platforms of Opportunity Data

The Platforms of Opportunity (POP) dataset is a collection of marine mammal sightings that were made from ships and other platforms, and that were made outside the framework of a formal sampling design. The dataset used for this analysis spans 43 years from 1958 to 2000, includes 91,824 marine mammal observation records, and contains sightings between 30°N and 70°N latitude, and from 115°W to 120°E longitude (Figure 4-1). The platforms from which observations were made include National Oceanic and Atmospheric Administration (NOAA), U.S. Coast Guard, Navy, fishing, research, and a small number of tourist vessels, as well as aircraft (n=614) and “shore stations” (n=230).

Participants recorded marine mammal observations on standard reporting forms

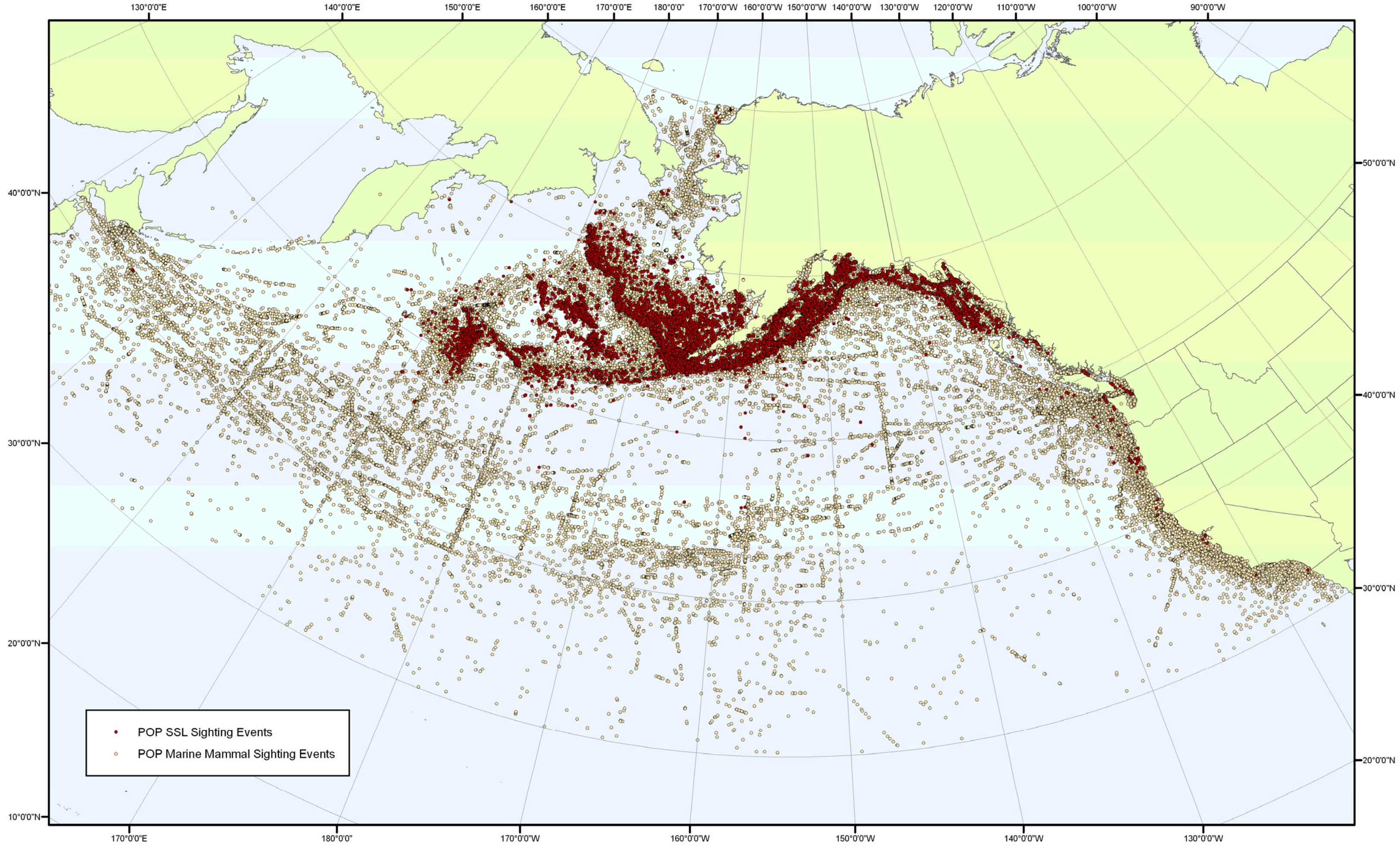

Figure 4-1. Platforms of Opportunity (POP) sighting events in the North Pacific and Bering Sea. Steller sea lion sighting events are shown in red and all other marine mammals sighting events are shown in tan.

provided by the National Marine Fisheries Service. Observers had varying degrees of marine mammal identification experience but most were provided at minimum with a manual and short training session and slide show by NMFS personnel. The observation form has changed over the years, but was designed to accommodate less experienced observers and still result in quality species identification data. Latitude and longitude coordinates were recorded to one tenth of a minute (<0.2 km) if the vessel was using a satellite navigation system or LORAN, or to the nearest minute (<2 km) if dead reckoning navigation was used. Observers were encouraged to identify an animal to lowest taxonomic group possible in addition to sketching a picture and indicating as many specifics about the animal as possible via the provided note section, behavior codes, and/or silhouettes. Quality control has also changed over the years but in general was achieved both through automated computer methods as well as manual checks. Manual quality control was conducted by experienced marine mammal scientists and included species identification or confirmation from descriptions, behaviors, sketches, and/or silhouettes, but also included deleting or flagging questionable records.

Each record in the dataset documents one marine mammal sighting event. I define a sighting event as the observation of one or more individuals of a single species of marine mammal on a single occasion. Each record contains at minimum the species (or closest taxon), date, latitude and longitude, estimated number of animals present, platform type, platform name, and animal behavior and sighting codes. In addition, some records also contain time of day, observer name, cruise number, vessel code, a measure of visibility, and a confidence interval on the number of animals observed.

Nearly 69% of sighting events were multiple animal sightings, i.e. the number of individual animals recorded for that sighting event was greater than 1. The 91,824 sighting events in the dataset resulted in a total of 685,480 individual marine mammal observations. Of these, Steller sea lions comprised 13,037 (14.2%) of the sighting events and 109,323 (15.9%) of the individual animals observed. Steller sea lions were sighted in all years within the range of the dataset except 1959, 1964-1967, and 1969. Observations of Steller sea lions occurred as far south as southern California (32.62°N, 117.32°E), as far west as Japan (147.55°W, 41.42°N), and as far north as the northern Chukchi Sea north of the Bering Strait (69.5°N, 166.5°E) (Figure 4-1).

Effort Index

In order to utilize the POP data, the observations must be effort-corrected. No records were kept as part of the POP data collection process to indicate how much time was spent or how much area was surveyed while searching for marine mammals. The consequence of the absence of effort data is that true measures of marine mammal density cannot be calculated, and raw counts of observations are confounded by unknown variability in observation intensity and the frequency of ship paths. For example, if an observer is scanning out to 500 m from a ship trackline looking for marine mammals as the ship covers 80 kilometers, and in that time makes only one sighting of 10 Steller sea lions, the observed sea lion density in that case would be relatively low, 0.20 SSL/km^2. Whereas, if another observer records a sighting of 10 Steller sea lions but only scanned a total of 500 m^2, the observed sea lion density in this case would be quite high, 20 SSL/km^2. Based on the raw POP Steller sea lion observation data these two sighting events would be indistinguishable from one another despite the fact that they represent very different situations in terms of the sea lion density. To extract accurate animal densities from the POP data, a denominator that reflects some measure of effort must be derived.

Various indices that estimate the effort expended to obtain the POP observations can be produced from the sighting records, although any effort index will only be an approximation of true effort. In particular, an effort index cannot fully compensate for null data, when observers were looking but no sightings were made, since there is no information in the database to reflect this. However, since this analysis is focused exclusively on Steller sea lions, and the POP data contain records from all marine mammal observations, some sea lion "absence" data is available in the dataset when observers recorded other marine mammals but no Steller sea lions.

One approach to defining an effort index is to use the number of marine mammals observed in an area, and estimate the density as the number of Steller sea lions observed per marine mammal. This approach, however, underestimates Steller sea lion use in areas where other marine mammals are particularly dense, and overestimates sea lion densities in areas used solely by them. To address these limitations, I developed an effort index, referred to as a "platform-day" that utilizes other marine mammal observations but does not make sea lion density a function of the number of other marine mammals observed except in as much as they allow for identification of days and places where sighting effort occurred.

Grid and Scale. To begin the process of defining the effort index, a grid of 15 km by 15 km cells was drawn over on the entire north Pacific Ocean and Bering Sea from 29°N, 119°E to 72°N, 115°W using ArcGIS Desktop 9.3.1 (ESRI Inc., Redlands, California, USA). The outcome of any model will depend upon the scale at which data are analyzed (Wiens 1989). Oceanic processes have been categorized into three hierarchical scale classes. At the small scale, high density prey patches are concentrated by species' spawning or anti-predator behavior or turbulent diffusion and mixing for planktonic and weakly swimming organisms (Redfern *et al*. 2006). Meso-scale prey patches of approximately 10 km to 100s of kilometers form from aggregation of these small-scale patches by oceanic processes such as fronts and eddies (Moser and Smith 1993; Redfern *et al*. 2006). Migration, spawning, and broad-scale feeding behavior fall under the category of large-scale processes and are influenced by current systems and water mass movement at the basin-wide scale of 1000s of kilometers (Redfern *et al*. 2006). In this analysis we are interested in meso-scale processes and have chosen the grid-size accordingly.

Previous research on Steller sea lion movement patterns showed foraging trips by immature and reproductively active females in summer on the order of 10s of kilometers, thus analysis within 15 km^2 grid cells allows such patterns to be further explored. Since the POP data span almost 50 years, it was also important to try to capture temporally homogeneous oceanic and prey processes. Temporal rates of change are expected to decrease, and predictability is expected to increase, at increasing spatial scales (Redfern *et al*. 2006). Choice of the 15 km^2 grid cell size may be too small to capture the desired temporal invariance, but looking for contiguous areas of similarly valued Steller sea lion densities may address this issue.

Platform-Day. Within each grid cell the number of “platform-days” was tallied. A “platform-day” is defined by the presence of one or more marine mammal observation from a single platform on a single day within one 15 km^2 grid cell. If marine mammal observations were recorded from multiple platforms in the same cell on the same day, the number of platform-days equaled the number of different observation platforms present in that cell on that day.

Although every sighting event in the POP database has an associated ship name, in some cases this name is a generic reference such as “Misc. Catcherboat” or “Unidentified Troller”. If multiple sighting events occurred under the same generic platform name in the same cell on the same day, all sighting events under that generic name were considered the same platform, and thus only one platform-day was counted for any given generic ship name. If, however, sighting events from two different generically named platforms were recorded in the same cell on the same day they were counted separately in the platform-day tally.

It should be emphasized that a platform-day is not a direct measure of time spent looking for marine mammals or area surveyed. A platform-day is an indication that some level of effort was expended observing and recording marine mammals in that cell. With this approach I assume that *on average* the platform-day index corresponds to a fairly consistent quantity of true effort, and variations in this proportionality term are themselves random and will tend to cancel out in the analyses. The platform-day index arguably has the lowest potential for bias compared to other derived effort indices, especially in cells in which many platform-days were logged.

If there were no platform-days, i.e. no marine mammals observed, in a given cell, that cell was considered a non-surveyed cell. A non-surveyed cell does not contribute data to the analysis, nor does it provide any information about presence or absence of Steller sea lions. As a result, all non-surveyed cells were excluded from further analysis.

Encounter Rate Point Estimate

To calculate the number of Steller sea lions observed per platform-day, the number of Steller sea lions observed in each grid cell was tallied from the POP data. The counts in each cell include Steller sea lion observations made during sighting events from all platforms over all years (1958-2002); however, only Steller sea lion sighting events for which the observer and/or quality control technician was certain of the species identification ("confirmed" sighting) and for which the behavior codes did not indicate the sea lion was dead or on land were used for this analysis. A total of 11,451 Steller sea lion sighting events met these criteria, for a total of 59,016 live, confirmed, at-sea sea lions.

Using the counts of Steller sea lion observations and the platform-days in each grid cell, a simple point estimate of the Steller sea lion encounter rate in a cell can be obtained by dividing the number of sea lions observed by the number of platform-days. Making this calculation for each cell and summarizing over all cells yields a mean Steller sea lion observation rate of 0.3243 and a standard deviation of 2.843. The mode for the distribution of sea lions per platform-day across the entire study area was zero, reflecting the fact that Steller sea lion observations were never recorded in the majority (82.4%) of surveyed cells.

Although this metric of Steller sea lions per platform-day is a reasonable start in assessing which areas were used by Steller sea lions, it suffers from several limitations. First, sparse sampling of some cells makes some of the point estimates statistically questionable. The law of large numbers states that as the number of sampling occasions (platform-days in this case) increases in a cell, the per platform-day encounter rate calculated for that cell will become a more precise estimator of the true encounter rate. A point estimate based on only one sampling occasion may or may not be a reasonable estimate of the true encounter rate. Worse yet, we have no measure of how confident we should be in the point estimate because we have no measure of the uncertainty introduced under variable sampling intensity.

Frequentist statistical procedures do offer methods for placing confidence limits around a point estimate, but a frequentist confidence interval is not a true measure of uncertainty in the estimate. A Bayesian estimation approach offers an alternative to frequentist procedures, and explicit in the Bayesian approach is incorporation of the various sources of uncertainty contained within the estimate.

Bayesian Encounter Rate Estimation

The posterior distributions obtained from a Bayesian analysis reveal both the probable Steller sea lion platform-day encounter rate as well as the uncertainty surrounding that rate in each cell. The spread or variance of the posterior distribution embodies the associated uncertainty. For cells in which many platform-days were logged, the uncertainty around the encounter rate estimate will be lower, but for cells in which only a few platform-days occurred the posterior distribution will be broad, reflecting the higher uncertainty in the encounter rate estimate.

Likelihood Function. A negative binomial likelihood function was chosen to model the Steller sea lion encounter rate. The negative binomial can be parameterized in a variety of ways, each of which lends itself to convenient description of different aspects of the distribution. The one most readily adaptable to this analysis follows:

$$p(y_{ij} \mid m_j, k_j) = \frac{(y_{ij} + k_j - 1)!}{y_{ij}!(k_j - 1)!} \left(\frac{k_j}{m_j + k_j} \right)^{k_j} \left(\frac{m_j}{m_j + k_j} \right)^{y_{ij}},$$

where y_{ij} is the count of sea lions on platform-day i in cell j, m_j is the expected value of y_j or the estimated mean Steller sea lion encounter rate in cell j, and k_j is the shape parameter of the distribution, which also represents a measure of dispersion or aggregation in cell j (Al-Saleh and Al-Batainah 2003). The moments of the negative binomial distribution are as follows:

$$\text{mean} = m$$

$$\text{variance} = \frac{m(m+k)}{k}$$

$$\text{mode} = \begin{cases} \dfrac{m(k-1)}{k} & \text{for k>1} \\ 0 & \text{for k} \leq 1 \;. \end{cases}$$

The following is the full joint likelihood function for all Steller sea lions observed over all platform-days in cell j:

$$p(y_j \mid m_j, k_j) = \prod_{i=1}^{n} \frac{(y_{ij} + k_j - 1)!}{y_{ij}!(k_j - 1)!} \left(\frac{k_j}{m_j + k_j} \right)^{k_j} \left(\frac{m_j}{m_j + k_j} \right)^{y_{ij}},$$

where *n* is the number of platform-days for cell *j*, and all other parameters are the same as in the marginal likelihood equation above. Both m_j and $\mathrm{k_j}$ are the unknown parameters being estimated in this process. To a certain extent, k_j is a nuisance parameter and will not be discussed extensively in the results section, but it can be informative (see next section below).

Choosing a Likelihood Function: Negative Binomial vs. Poisson. The negative binomial is a flexible distribution that can accommodate a wide variety of patterns in count data from highly “clumped” to randomly distributed observations (White and Bennets 1996). Although both the negative binomial and Poisson distributions are commonly used to model count data, the negative binomial distribution can model data fitting a Poisson distribution as well as data that are over-dispersed or under-dispersed with respect to a Poisson model. Under a Poisson model, the expected mean and variance of the data are assumed be equal to one another; if the variance is larger than the mean, the data are said to be over-dispersed with respect to the Poisson; if the variance is smaller then the mean, the data are said to be under-dispersed. Unlike the Poisson, the negative binomial distribution is not restricted to mean and variance equality assumption.

With respect to the Poisson distribution, the additional parameter *k* in the negative binomial distribution allows for this flexibility. As *k* approaches infinity, the distribution approaches a Poisson distribution and as *k* goes to zero, the distribution approaches a logarithmic series (White and Bennets 1996). In terms of the POP data, the value of *k* will tend to be higher in cells where the number of sea lion observations is more uniformly distributed across platform-days, and will tend to be closer to zero in cells where observations are clumped in a few platform-days with no sea lion observations in the remaining platform-days.

In assessing the empirical data, the actual counts of POP sea lion observations per platform-day in individual cells tend to have variances that are much larger than the mean. Only a few cells exhibit under-dispersion (variance less than the mean), or nearly equal mean and variance. The negative binomial is appropriate in any of these cases, whereas the Poisson would be an inappropriate model for the majority of POP Steller sea lion observation data.

Prior Distributions. An informative empirically-based gamma distribution was used for the prior on m. The gamma distribution is a relatively flexible distribution bound between 0 and positive infinity:

$$p(m) = \frac{\beta e^{-\beta\lambda}(\beta\lambda)^{\alpha-1}}{\Gamma(\alpha)} .$$

The m in the equation, as in the likelihood equation, represents the expected number of Steller sea lions per platform-day (estimated encounter rate), β is the scale parameter for the distribution, α is the shape parameter for the distribution, and Γ is the gamma function where $\Gamma(\alpha) = \int_0^\infty t^{\alpha-1} e^{-t} dt$. The moments of the gamma distribution as parameterized are as follows:

$$\text{mean} = \frac{\alpha}{\beta}$$

$$\text{variance} = \frac{\alpha}{\beta^2}$$

$$\text{mode} = \frac{\alpha - 1}{\beta} \quad \text{for } \alpha \geq 1 \text{ .}$$

Hyper-parameters for the gamma distribution on *m* (α and β) were based on summary statistics of the POP data. A histogram of the Steller sea lion observation rate point estimates from all cells was constructed, and the overall mean and variance of these point estimates was calculated (see first paragraph of Encounter Rate Point Estimate section). The resulting histogram had a very high mode at zero, a mean of 0.324 and a standard deviation of 2.843. The gamma prior on *m* was modeled after this histogram, with a mode of zero, and a shape (α) and scale (β) parameter of 0.0216 and 0.0396 respectively. These parameters yield a prior distribution weighted heavily toward zero, consistent with the preponderance of surveyed cells in which no sea lions were observed, and with a very long tail, also consistent with the empirical data. This prior is "conservative" in that it corresponds to a default of uniform distribution of Steller sea lion encounter rates across space.

An empirically-based gamma prior was also used for the dispersion parameter, *k*, of the negative binomial distribution. Just as a mean observation rate can be calculated from the empirical POP observation data across all cells, an estimate of data dispersion, *k*, can also be derived. Using a method of moments estimator (MME) for *k*,

$$\hat{k} = \frac{\overline{X}^2}{S^2 - \overline{X}},$$

where

$$\bar{X} = \frac{1}{n}\sum_{i=1}^{n} X_i \quad \text{and} \quad S^2 = \frac{1}{n}\sum_{i=1}^{n}\left(X_i - \bar{X}\right)^2 ,$$

and where X represents the number of Steller sea lions observed per platform-day over all cells and all days, an overall dispersion (k) estimate of 0.01558 was derived from the POP data. This MME of k was the backbone around which the gamma prior was built. Explorations of the mean and variance of the per cell observation rate that were conducted to determine if the Poisson or negative binomial was the more appropriate likelihood function, revealed that while most cells had variances that far exceeded the mean (a sign of over-dispersion), data from some cells had nearly equal mean and variance (resembling data derived from a Poisson distribution), and others showed signs of under-dispersion. In order to accommodate this broad range of potential dispersion values a wide distribution on k was desired. As a result, a gamma prior distribution was constructed with a mode equal to the empirical MME of k at 0.01558, but also expressing a large variance. The resulting gamma prior distribution had a mean of 10 and a variance of 100. The gamma shape (α) and scale (β) parameters for this prior distribution on k were 1.001558 and 0.1 respectively.

Estimation Procedures. To obtain Bayesian posterior distributions on both m and k, a sample-weighted likelihood (SWL) simulation technique was used that is similar to the sampling-importance resampling, or SIR, technique commonly used in numerical Bayesian esimation. The SWL technique developed by Dr. Dan Goodman (http://www.esg.montana.edu/) directly samples values from the prior distributions using random number generators, then weights the values by their likelihood. The likelihood of any given set of values results from calculating the joint likelihood function using those values in the equation. The posterior histograms and summary statistics are produced from the cumulated likelihood-weighted values of the sampled priors.

An SWL simulation was performed for each cell in the grid containing one or more platform days, and histograms and summary statistics of the posterior distributions for each unknown parameter (*k* and *m*) were derived. To obtain each posterior simulation, a Monte Carlo sample size of 250 million was used. This large number of samples was necessary to achieve results that were stable under different initial seed values.

Since the full two dimensional posterior distribution for each cell cannot be displayed on a map, one-dimensional representations of the posterior distribution must be chosen to illustrate the results of the Bayesian inference on *m* and *k*. In this case, the mode and lower 5th percentile were chosen to characterize the full distribution. The mode is an indication of the central tendency of the posterior, while the 5th percentile represents the lower bound of a two-sided 90% credible interval and can be interpreted as a minimum likely value for the parameter being estimated. Specifically, we can say that based on our model and the POP data, we are 95% certain that the encounter rate in any given cell is higher than the 5th percentile value. Note that this interpretation of the posterior distributions and credible intervals assumes that observations in each cell is independent from surrounding cells. Due to the variability of sea lion observations and the long-tailed prior distribution, the majority of the posterior distributions are positively skewed (long right tail) resulting in modes lower than the means. Under this scenario, the mode is a more conservative representative of the posterior distribution than the mean and is less influenced by high variance values.

Several examples of full posterior distributions are also presented. Seeing the full posterior distributions can be helpful in understanding how the number of platform-days and the variability in the number of SSL observed per platform-day influence the variance and general shape of the posterior distribution. Although the production of a full posterior distribution instead of a simple point estimate is one of the primary benefits of utilizing a Bayesian approach, the number of posteriors produced in this analysis precludes the display of all posteriors. The examples presented were chosen for their capacity to be representative of the full array of posteriors for all cells.

Seasonal Patterns of Use. Because at-sea Steller sea lion use is not uniform over seasons, it is also of interest to understand how encounter rates differ at different times of year. In addition to calculating encounter rates over all years and all seasons, a separate rate was obtained for the breeding season (May through August) and non-breeding season (September through April). The same negative binomial Bayesian model used for the overall analysis was used to calculate breeding and non-breeding season encounter rate estimates. Similarly, gamma priors on the unknown parameters k and m were used and were parameterized with the following empirically-based hyper-parameters:

m gamma shape hyperparameter (α_m) = 0.028

m gamma scale hyperparameter (β_m) = 0.056

k gamma shape hyperparameter (α_k) = 1.000658

k gamma scale hyperparameter (β_k) = 0.1 .

As in the overall analysis, a mean, mode, and variance of the distribution of the per cell observation rate point estimates and an MME of the overall k were calculated separately for each season. These values were used to determine the above hyper-parameters for the gamma priors.

Standardized definitions of “breeding” and “non-breeding” seasons are lacking in the scientific literature on Steller sea lions. Classification of the breeding season from May to August has been used in at least two studies (Gregr and Trites 2008; Milette and Trites 2003), but other definitions of “summer” and “breeding season” have also been used. Depending on the aim of the study and the available data the following definitions have been use for summer or breeding season: June to July (Merrick and Loughlin 1997), April to September (Call *et al*. 2007), May to September (Sinclair and Zeppelin 2002), and June to August (Lander *et al*. 2009). From various studies, we know that males tend to congregate and begin establishing rookeries in May, and females arrive at rookeries in May and June, giving birth from mid-May to mid-July (Hoover 1988; Loughlin *et al*. 1987; Pitcher and Calkins 1981). Males maintain rookeries up to 68 days, indicating that they might leave the rookeries sometime in July (Hoover 1988). Females with pups have been found to disperse from natal rookeries between August and October (Calkins and Pitcher 1982; Raum-Suryan *et al*. 2002). Although no arbitrary cutoff dates will perfectly align with Steller sea lion foraging patterns across their entire range, I chose to use May to August to correspond in general with the rookery-residence period for the breeding population and in line with the definition used by at least two other studies (Gregr and Trites 2008; Milette and Trites 2003). This seasonal definition is primarily focused on the reproductive population and may not accurately reflect seasonal patterns of other classes of individuals. For example, spring and early summer may be a period of increased activity and longer trips by juvenile animals (Fadely *et al*. 2005; Raum-Suryan *et al*. 2004; Rehberg and Burns 2008), which contrasts to the restricted or non-existent at-sea use of reproductively active individuals.

Model Assumptions and Potential Biases. The validity of this analysis is of course subject to its assumptions. The primary assumption, which could potentially have the most influence on the results of the study, is that the platform-day effort index is a reasonable measure of true effort. It is likely that the true effort expended within each cell varies between days and platforms and that the true level of effort per platform-day is random across platforms, cells, and time. If this is true, the platform-day index is not subject to systematic bias. In addition, the higher the number of platform-days in a cell, the more likely the platform-day index approaches a measure of the average true effort both within that cell and across all cells. Although not biased when averaged over all cells, the platform-day index is most subject to inaccurate representation of true effort in cells with few recorded platform-days.

Uncertainty inherent in the platform-day index is not explicitly accounted for in the model, however, if survey effort is fairly random across platforms and days, and if variation in survey effort results in variability in the number of sea lions observed, the negative binomial model accounts for this in the width of the posterior distribution on the encounter rate estimate. For example, if a total of 100 sea lions were observed over the course of 10 platform-days, but the per platform-day count was highly variable among those 10 days, the posterior distribution will have a wider distribution than if 10 sea lions were observed on each of the 10 platform-days. Such variation in sightings can result from variability in sea lion presence, measurement error, as well as from variability in survey effort. Under any scenario, the posterior distribution will reflect the uncertainty in the estimate of the true encounter rate but the sources of the uncertainty are confounded and cannot be disentangle from one another. As a result, the width of the posterior distribution will be more of a reflection of our uncertainty in the estimate than a measure of true variability in the number of sea lions that occur in that area.

If survey effort is strongly biased and not random in individual cells, then encounter rate estimates will be biased. If certain platforms usually survey certain cells AND the duration or intensity of observation is specific to those platforms then systematic bias may result. To offer a specific example, say observers on fishing vessels are most likely to make observations while near the continental shelf break and they return to the same area repeatedly, few other vessel-types occur in the same area, and the fishing-vessel observers tend to only record animals that interfere with fishing operations (thus exhibiting relatively low sampling effort). The SSL estimated encounter rates for those continental shelf cells will tend to be biased low in relation to other cell estimates with higher or more randomly distributed effort levels.

Other observation issues might also bias the sample. If surveyors are more likely to observe and record large whales than Steller sea lions, for example, and large whales are more likely to be encountered in certain areas, then Steller sea lion encounter rate estimates may be biased low in these cells if they are present but remain unobserved.

Similarly, if Steller sea lions that occur in large groups are more likely to be observed and recorded, then encounter rate estimates could be biased high.

Because the POP data observations are made by individuals with a wide range of marine mammal experience, species identification errors may also be present. Although steps were taken to reduce the possibility of including erroneous observations of Steller sea lions in the encounter rate estimate (see POP data section above), some non-SSL observations may have been included. Unless, however, large numbers of individuals were misidentified, this source of error is unlikely to cause widespread bias in the results. In addition, both false-positive (identifying non-SSL as SSL) and false-negative (failing to correctly identify a SSL) species identification errors are likely to have occurred. Although this will bias the results within the cell containing the misidentification, this source of error will not systematically bias the results across the entire range and the few errors are likely to be swamped by accurate data.

Results

POP Steller Sea Lion Observations

A total of 18,321 of the 15 km by 15 km grid cells overlaid on the North Pacific and Bering Sea contained marine mammal survey data from the POP database. Of those surveyed cells, 3,217 (17.6%) contained records of Steller sea lion observations. The number of Steller sea lions observed in each grid cell ranged from 0 to 1644 (Figure 4-2). The minimum, and most common, number of sea lions observed across all 18,321 surveyed cells was zero. The maximum number of SSL observed in any one cell was 1644 individuals, which were observed over the course of 157 separate sighting events.

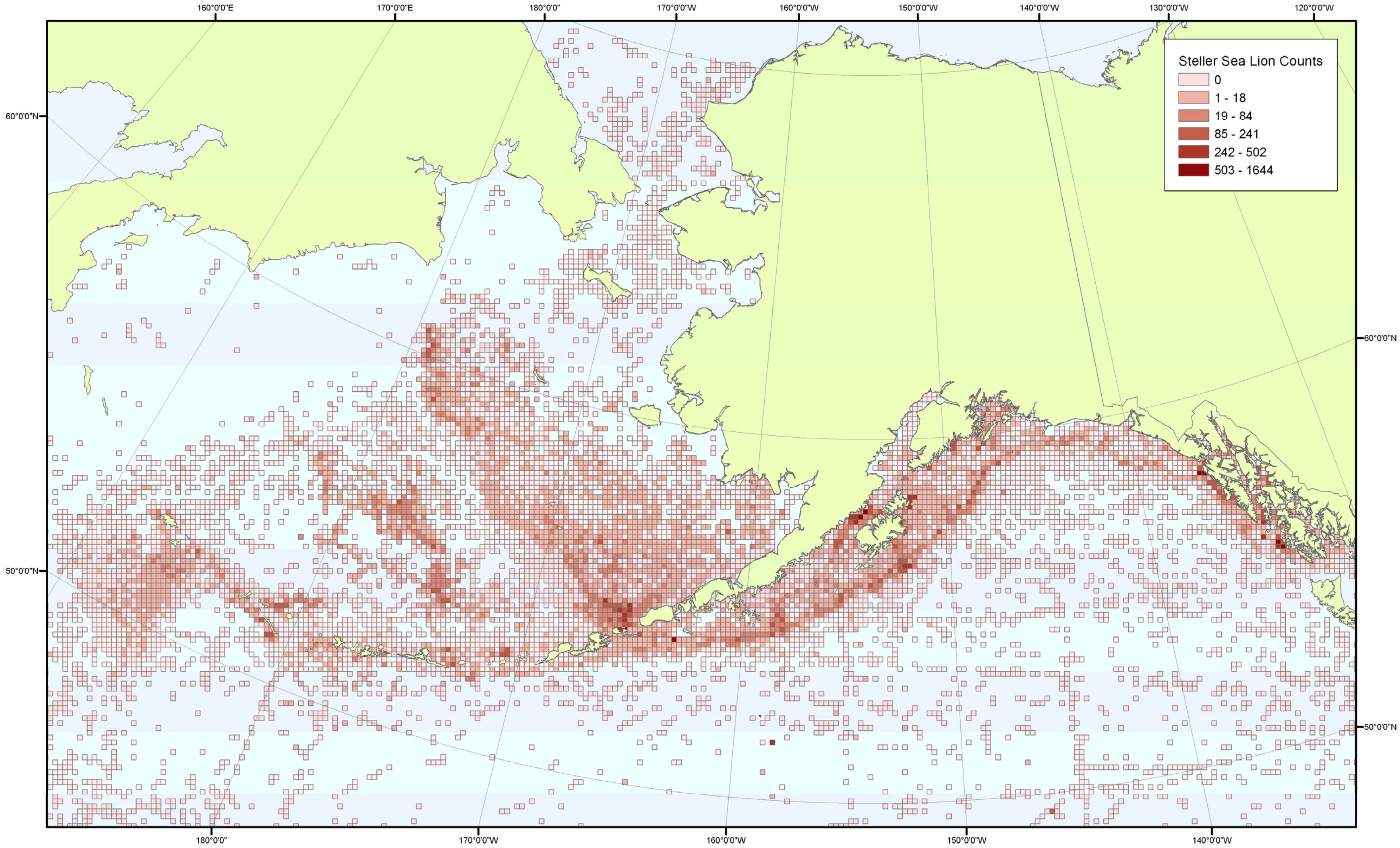

Figure 4-2. The number of Steller sea lions observed in each 15 kilometer by 15 kilometer grid cell from Platforms of Opportunity. Counts included live confirmed at-sea Steller sea lion observations from all sighting events across all platforms and all years from 1958 to 2002.

Effort Index

Within surveyed cells the number of platform-days (effort index) ranged from 1 to 236, with 1 being the most frequent (Figure 4-3). The areas of highest effort were north of Unimak Pass, scattered locations in Southeast Alaska, around Kodiak Island, portions of the Bering Sea continental shelf break, and in the Seguam Pass area (Figure 4-4). POP observation effort is sparse throughout most of the oceanic waters of the Gulf of Alaska, but the neritic zone out to the continental shelf break has been relatively well surveyed. Most areas along the shelf break in both the Bering Sea and north Pacific contained at least 7 recorded platform-days. The most notable exceptions to the good coverage over the shelf and shelf break are a few areas along the Aleutian island arc and in a few isolated areas south of the western portion of the Alaska Peninsula east of Unimak Pass.

Bayesian Inference

Overview of Results.

The Bayesian negative binomial analysis over all seasons and all years resulted in a minimum encounter rate estimate (posterior mode on *m*) of 0.0025 Steller sea lions per platform-day, which was found in a total of 15,104 cells, and a maximum encounter rate estimate of 49.15 SSL per platform-day (n=1; cell #237424)(Figure 4-5). The standard deviation in the cells with an encounter rate mode of 0.0025 ranged from 0.657 for cells with 1 platform-day and no Steller sea lion observations, to 0.056 for cells with 57 platform-days and no Steller sea lions.

Cell #237424 with the maximum estimated encounter rate (49.15 SSL/platform-

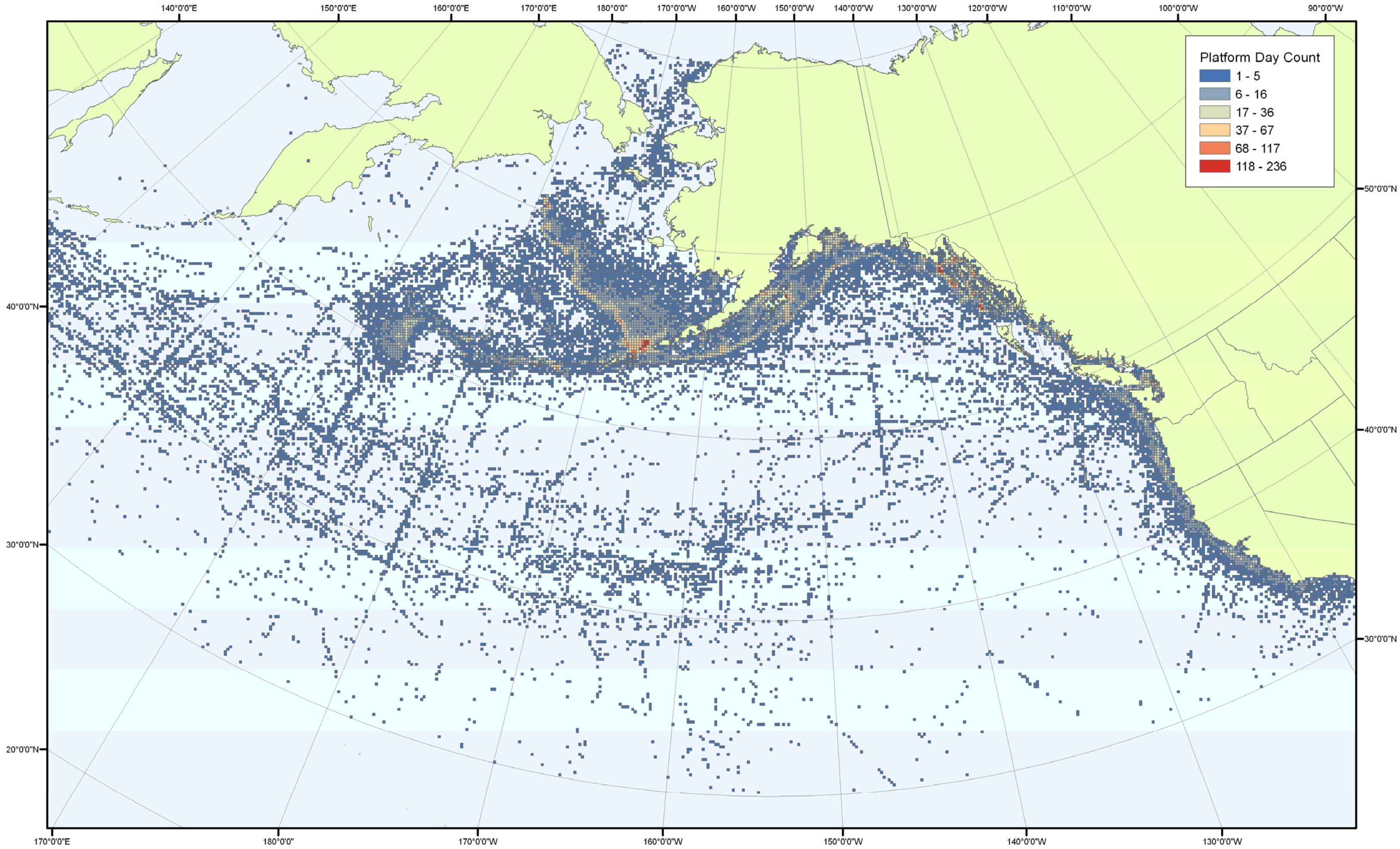

Figure 4-3. POP observation effort as measured by the number of platform-days per cell. Platform-days are an index of effort and are defined as the presence of at least one marine mammal sighting event from one ship on one day in a cell.

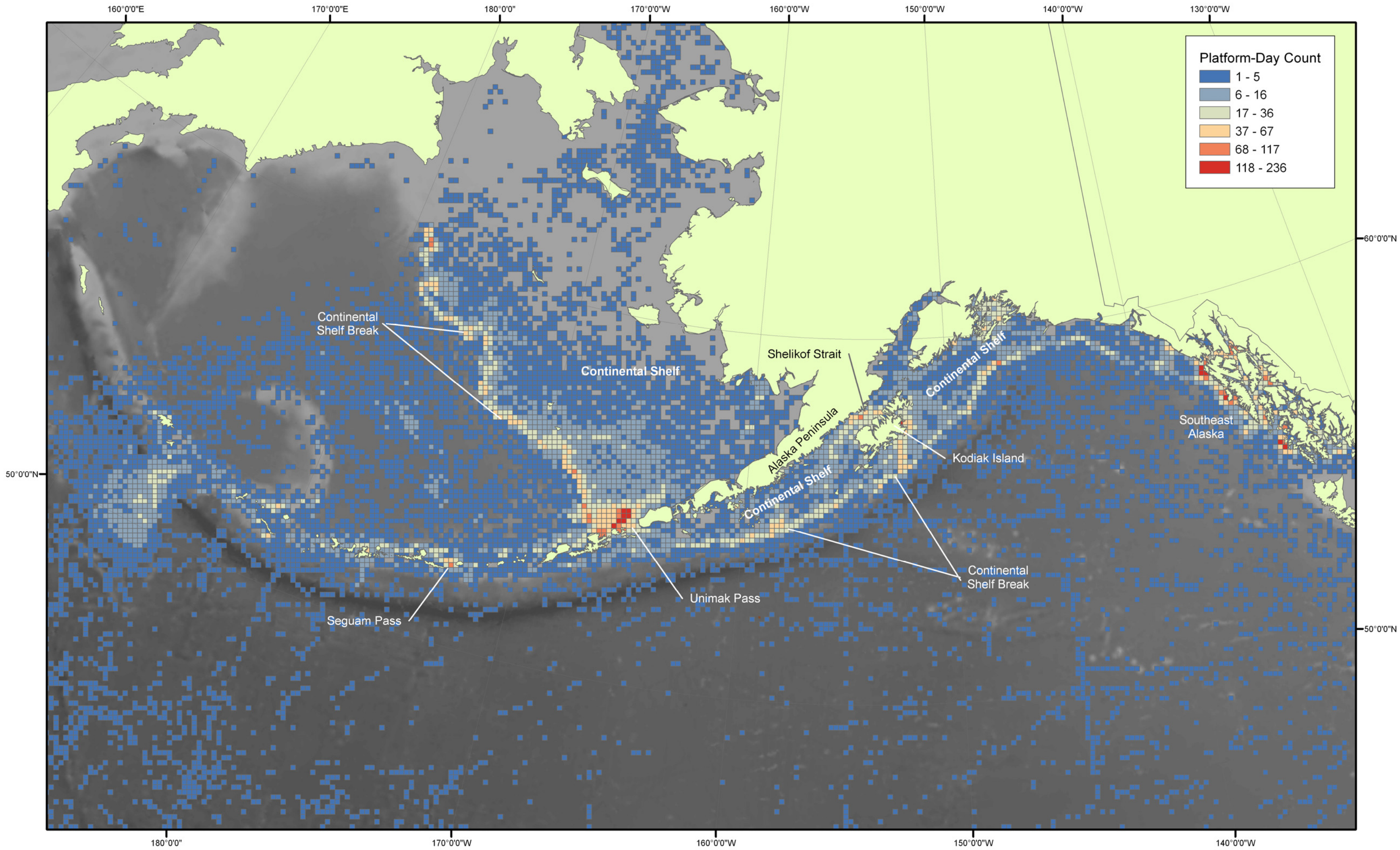

Figure 4-4. A closer view of the POP observation effort as measured by the number of platform-days per cell in Alaska waters.

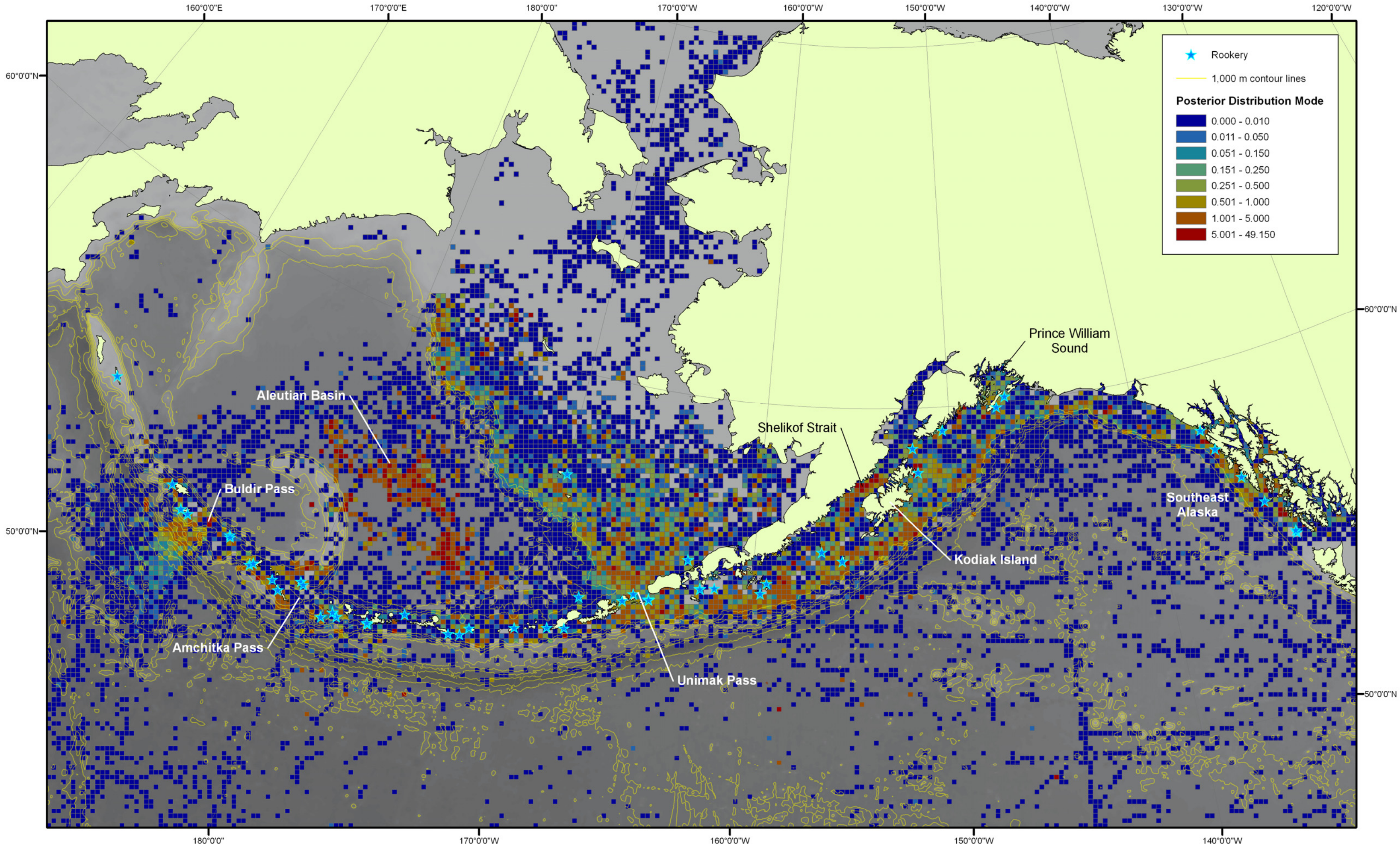

Figure 4-5. Encounter rate posterior distribution modes resulting from the Bayesian inference on Steller sea lion observations per platform-day.

day) had the second highest posterior standard deviation, 22.266. A total of 75 sea lions were observed on 1 platform-day in this cell, which resulted in a mode for the posterior distribution on *k*, the dispersion parameter, of 0.325. Recall that the closer to zero the *k* estimate is, the more clumped the sea lion observations are. For comparison, the cell with the highest standard deviation, 48.39 (cell #185919), for the encounter rate (*m*) posterior contained 300 sea lion observations which were observed on one platform day; this produced an encounter rate (*m*) posterior mode of 37.95, and a dispersion (*k*) posterior mode of 0.075. The observations in cell #185919 were more clumped than in cell #237424, thus the lower estimate on *k*; and the encounter rate posterior exhibiting more uncertainty (higher standard deviation). Figures 4-6 and 4-7 show posterior distributions on *m* and *k* from these two cells as well as a sample of other cells with platform-day counts ranging from 1 to 224, and Steller sea lion counts ranging from 0 to 1644.

Spatial Patterns. Except for a few notable exceptions, most of the cells with high encounter rate estimates were found over the continental shelf, landward of the 1,000 m isobath (Figures 4-8 and 4-9). Throughout southeast Alaska and the Gulf of Alaska, this pattern holds true. The shelf is relatively narrow in southeast Alaska, and Steller sea lions used most of the area over the shelf in the central portion of the region between Hazy and Graves rookeries. South of Hazy to the Forrester Island rookery complex, use was focused closer to shore, with less use out along the shelf break. High-use areas were scattered throughout the interior waters of the region as well.

Encounter rate estimates in the eastern Gulf of Alaska tended to be focused near

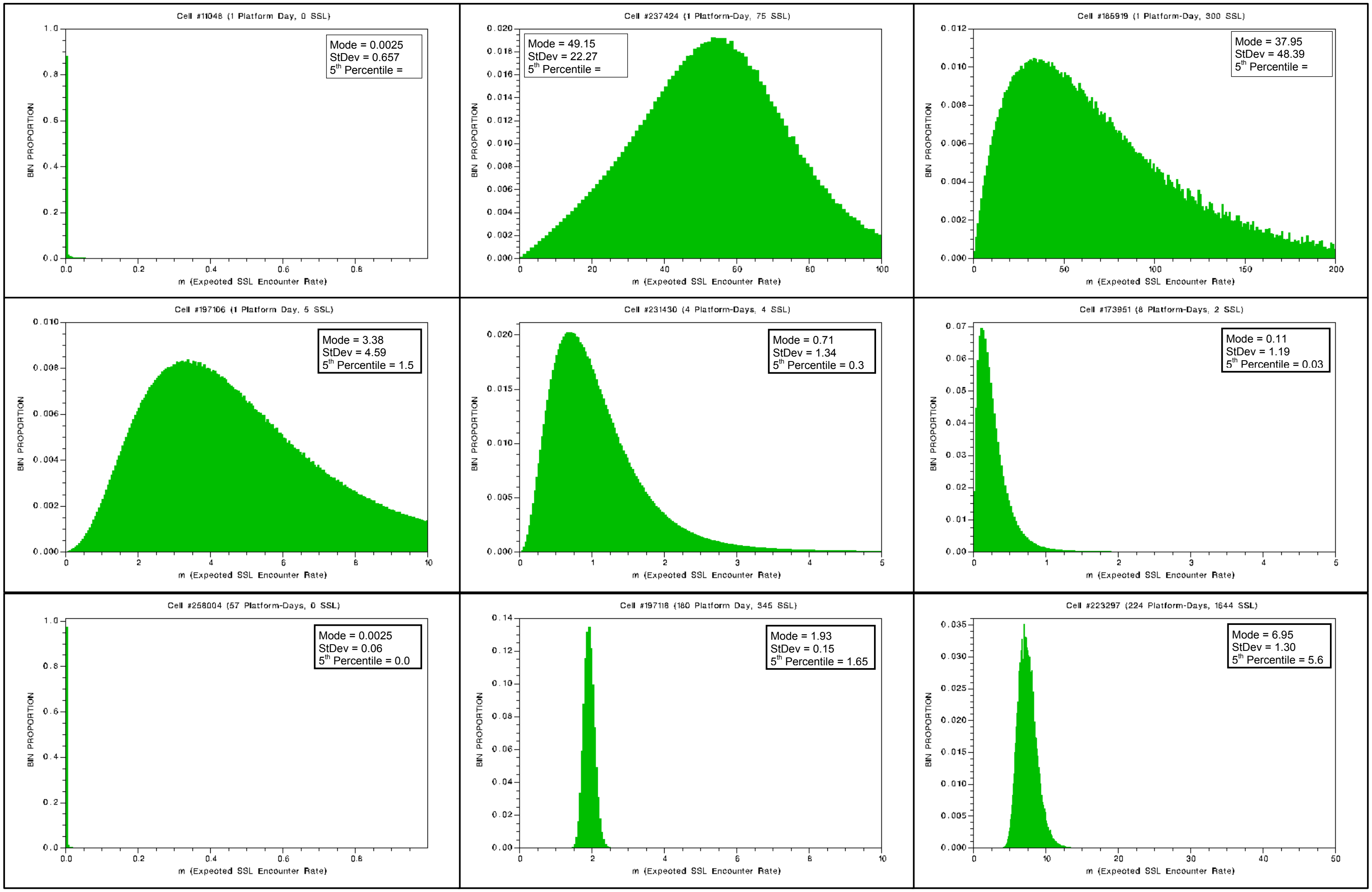

Figure 4-6. Steller sea lion encounter rate (parameter *m*) posterior distributions from a sample of cells.

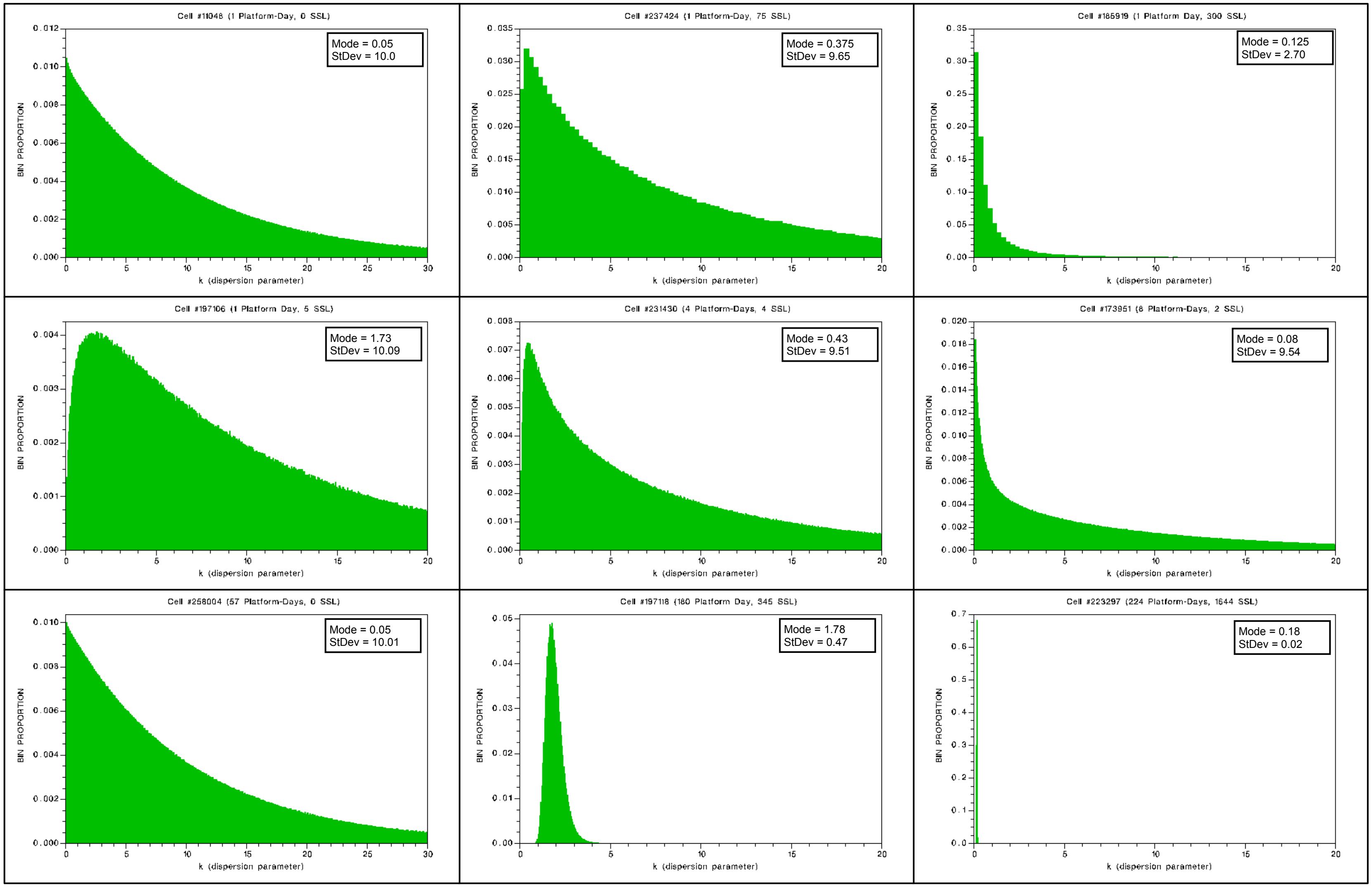

Figure 4-7. Dispersion parameter (*k*) posterior distributions from the same sample of cells as in Figure 4-6.

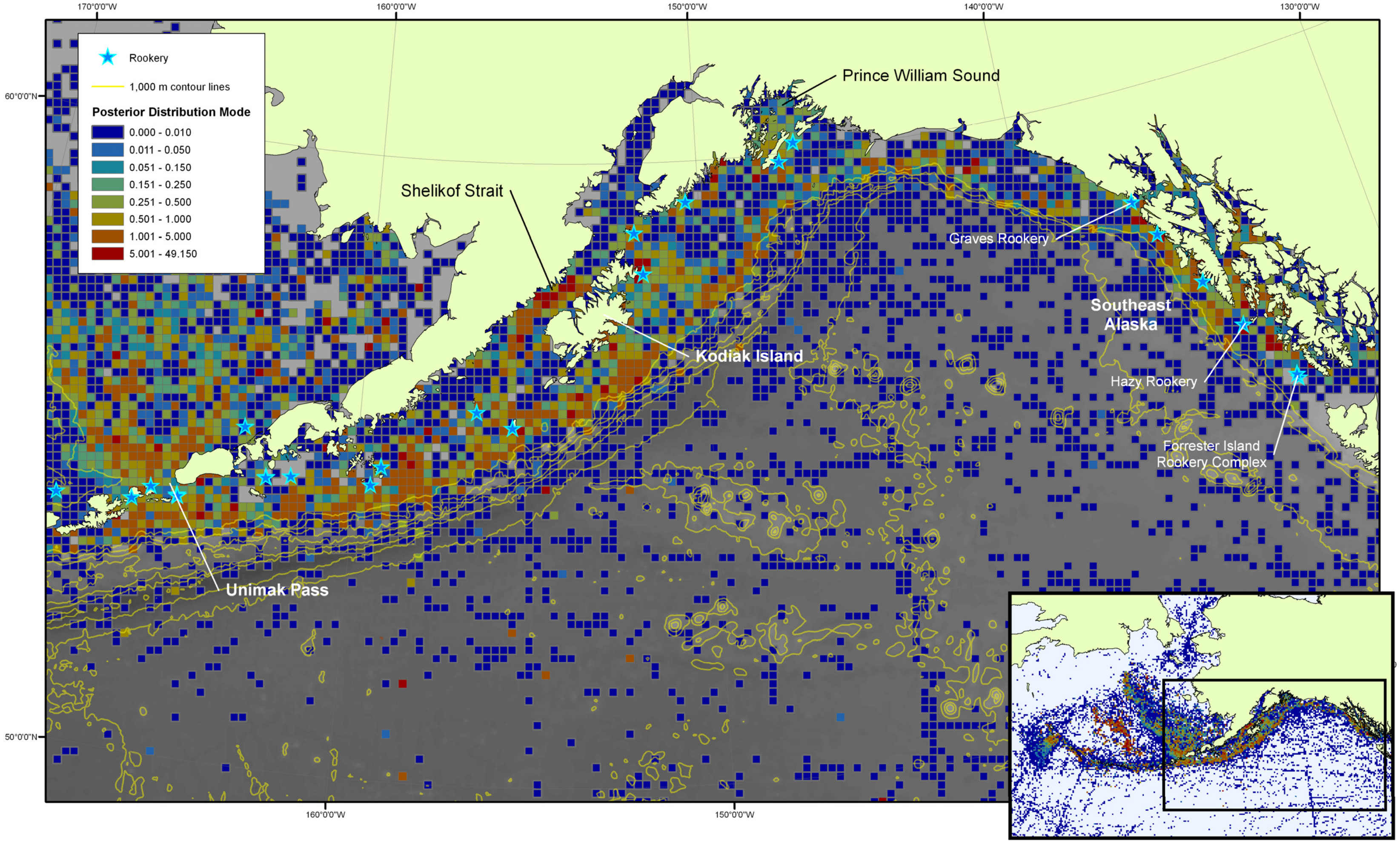

Figure 4-8. A close-up of encounter rate posterior distribution modes resulting from the Bayesian inference on POP Steller sea lion observations per platform-day in the Gulf of Alaska and Southeast Alaska.

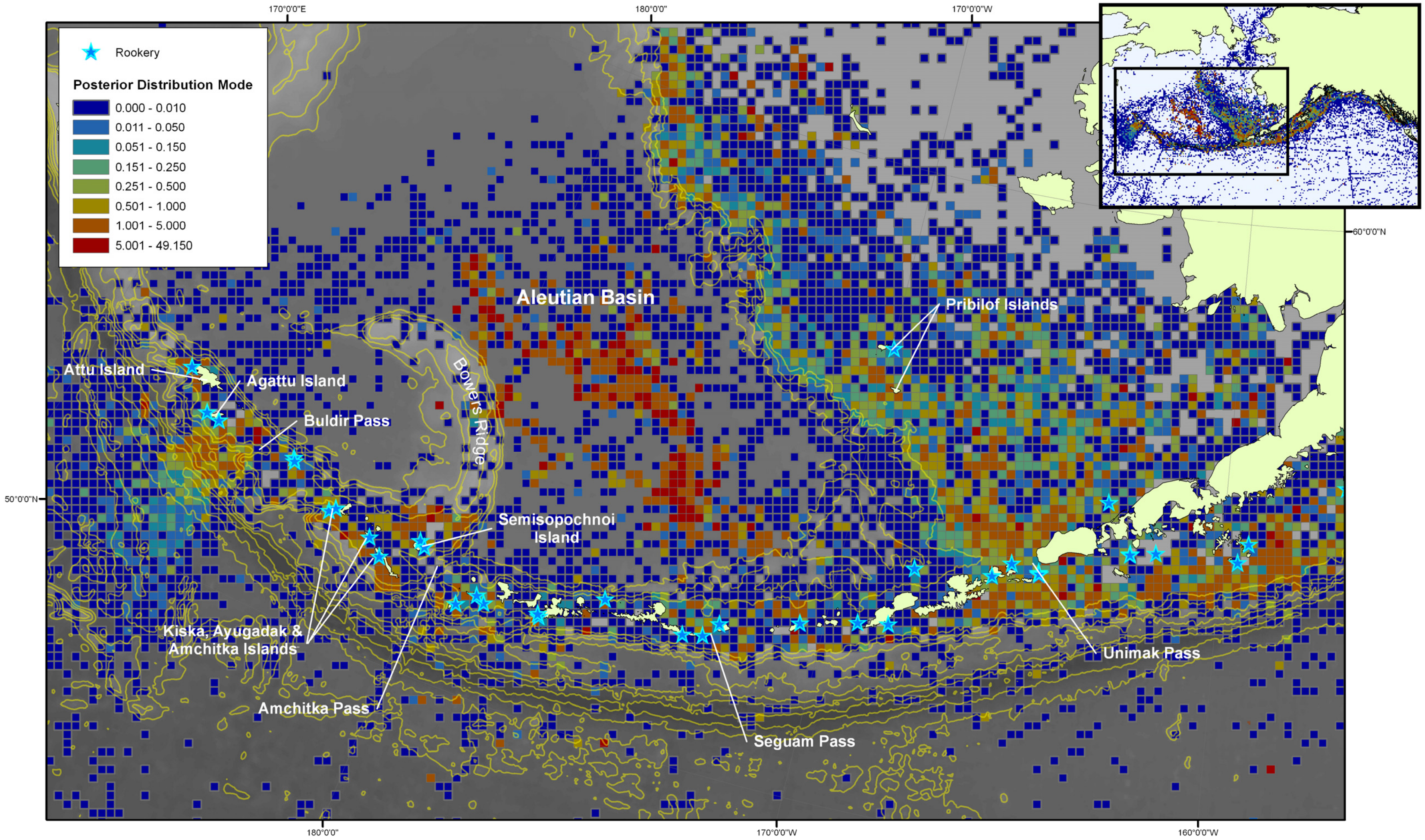

Figure 4-9. A close-up of encounter rate posterior distribution modes resulting from the Bayesian inference on POP Steller sea lion observations per platform-day in the Bering Sea and along the Aleutian Chain.

the shelf break (1000 m isobath) or nearer shore in the region of Prince William Sound, with less use between these two extremes. In contrast, in the central Gulf of Alaska Steller sea lion encounter rates were more consistent over most areas of the continental shelf from nearshore waters out to the 1,000 m isobath. Shelikof Strait was a very high-use area with several encounter rate modes exceeding 6 sea lions per platform-day and one cell exceeding 13 SSL/platform-day. The lower 5th percentile values for the highest use areas ranged from 3 to 9 Steller sea lions per platform-day (Figure 4-10). Based on both the encounter rate mode values and the lower 5th percentile values, one relatively large area south of Kodiak Island exhibited high estimated Steller sea lion use. The area extends from about 50 to 60 km off the coast of the island out to the 1,000 m isobath, and in some areas to the 2,000 and 3,000 m isobaths where the continental shelf slope is steep. The cells containing the highest use in this area had encounter rate estimates ranging from 1 to 13.45 SSL/platform-day, and 5th percentile values from 0.6 to 6.2.

In the western Gulf of Alaska, the areas used by Steller sea lions were concentrated about half-way between the mainland shore and the continental shelf break. Most of the higher use areas were seaward of the off-shore islands and Steller sea lion rookeries. Encounter rate modes in the high-use areas of this sub-region generally ranged between 0.5 and 3 SSL/platform-day, although in several cells the posterior modes exceeded 3 SSL/platform-day. Similar to the area south of Kodiak Island the continental shelf slope beyond the shelf break is relatively steep, and some Steller sea lion high-use areas in this sub-region extended out to the 3,000 m isobath, but none were found beyond that.

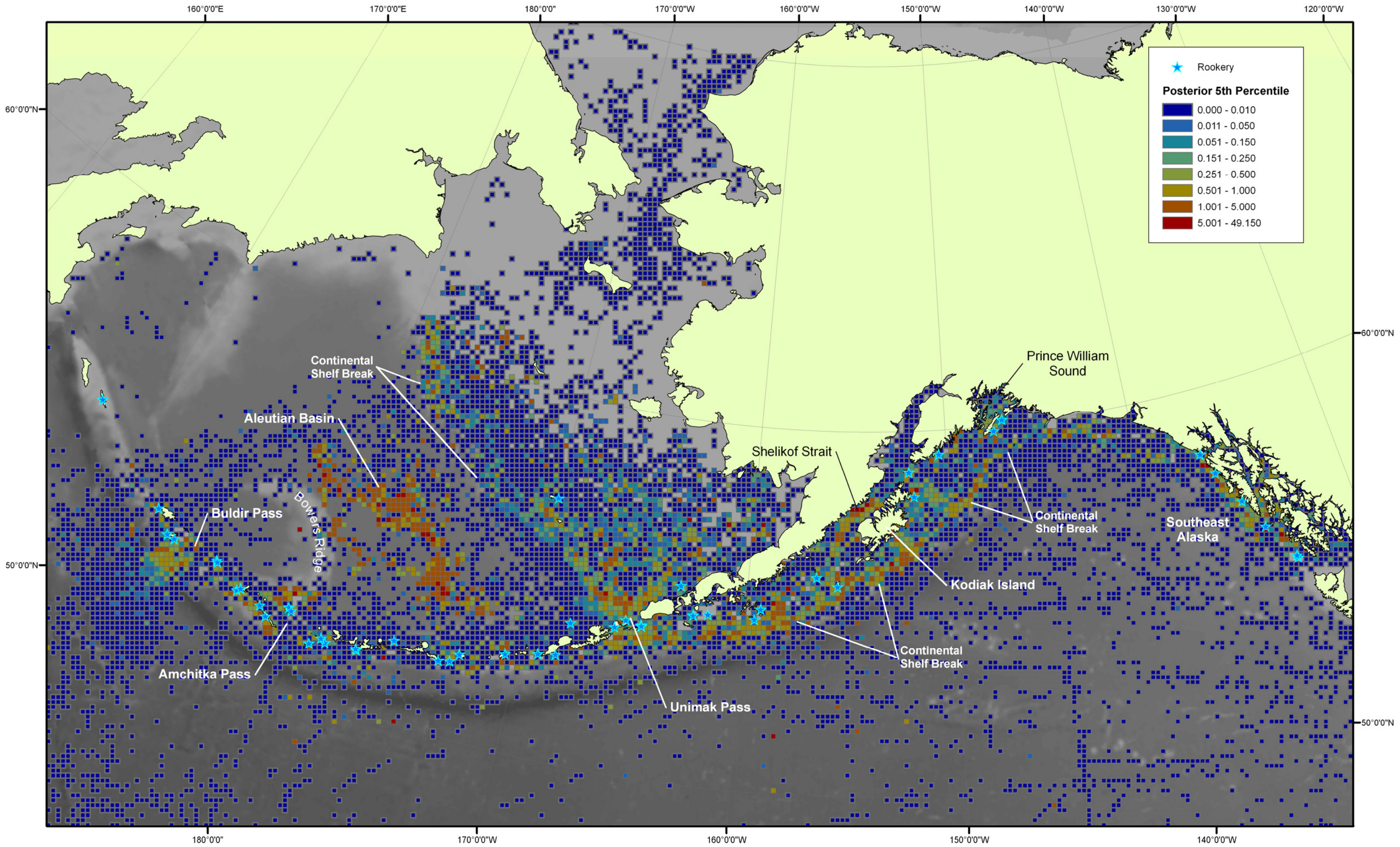

Figure 4-10. The value at the 5th percentile of the Steller sea lion encounter rate (*m*) posterior distribution for each surveyed 15 km^2 grid cell. Based on the POP data, we have 95% certainty that the true encounter rate is greater than or equal to this value.

The eastern Aleutian sub-region contains Unimak Pass, which appears to be the dominant feature dictating Steller sea lion spatial use in this area since most of the high encounter rates occur in the eastern half of the region in the area surrounding the pass. Steller sea lions use the areas both north and south of Unimak Pass but less so over the middle of the pass itself. Encounter rates were relatively high over the whole continental shelf area to the south out to the shelf break but rarely beyond the 1,000 m isobath. From the center of the pass, high-use areas extended to about 140 km west and about 100 km to the east on the Pacific side. North and east of the pass, encounter rates were high along the north coast of Unimak Island to about 40 km offshore. A relatively contiguous area of elevated encounter rate estimates extended north and west of the pass about 140 km. The high-use cells north of the pass were all landward of the continental shelf break, but did not follow the contour of the 1,000 m isobath as in other areas.

Aside from the area just north of Unimak Pass, Steller sea lion use appears to be fairly diffuse across much of the Bering Sea continental shelf. Although many cells exhibiting high encounter rates occur throughout the shelf region, few large contiguous areas of high use were found. Steller sea lions do not appear to be focusing their use along the break itself; some low level use occurs up to the 1,000 m isobath then generally declines to near zero along the shelf slope.

In deeper waters of the Bering Sea, however, encounter rates were found to be very high in the central portion of the Aleutian Basin. A total of 246 cells in the Basin had an estimated encounter rate distribution mode greater than 1. The highest encounter rate mode in this area was 19.15 Steller sea lions per platform-day with an associated standard deviation of 11.85. In this cell, 159 sea lions were observed over the course of 6 platform-days. Many of the highest encounter rates in the Aleutian Basin were found in a contiguous area extending through the central portion of the lower half of the basin covering approximately 80,000 square kilometers, but high-use areas were also found just north and east of Bowers Ridge and scattered between the core high-use area and the continental shelf. Although the encounter rate posterior distributions for some of these cells are rather broad, the lower 5th percentile values in the highest use areas of the Basin were in excess of 1 SSL per platform-day (Figure 4-10).

The central and western Aleutians exhibit use-patterns different from the sub-regions to the east. In the eastern-most third of the central Aleutians, cells with high encounter rate modes are scattered between the 1,000 m isobaths on either side of the Aleutian chain, but further to the west, use patterns do not appear to be as closely linked to bathymetry. West of Atka Island the bathymetry and Steller sea lion use-patterns were more complex. Cells with high encounter rate estimates were scattered throughout the area both on- and off-shore including several out beyond the Aleutian trench, the deepest waters of the north Pacific at the base of the continental shelf slope. Despite sparse sampling effort offshore, at least six cells between 175 and 325 km offshore and in water depths of approximately 5,000 m had encounter rate estimates greater than 1 SSL/platform-day and 5th percentile values greater than 0.5.

West of Amchitka Pass Steller sea lions appear to use two regions most consistently. North of Semisopochnoi Island at the southern terminus of Bowers Ridge was a relatively large high-use area. Most of the cells with high encounter rate modes were located in waters shallower than 1,000 m but a few extended out to the 2,000 m isobath. Steller sea lion use was also high along the south side of Amchitka, Ayugadak, and Kiska Islands, but was sparse in the area between these island to the south and Semisopochnoi to the north. The high-use area to the south of the islands occurred over a range of depths from nearshore to 3,000 m.

Further to the west, a very distinct use pattern was present in the vicinity of Buldir Pass. The highest use areas were centered around the pass and extended south as far as 120 km offshore where encounter rates declined prior to reaching waters over the deepest portion of the Aleutian trench at the toe of the continental shelf slope. However, encounter rate estimates did not decline to zero at the trench, but instead exhibited a generally decreasing pattern with distance from the pass out to about 300 km and beyond.

Seasonal Patterns. As revealed by Figures 4-11 and 4-12, which show encounter rates in breeding (May through August) and non-breeding (September through April) seasons, encounter rates were generally lower throughout the entire study area in the breeding season. On a broad scale, the continental shelf break in the Gulf of Alaska tended to exhibit high encounter rates year-round, although the non-breeding season appears to have somewhat higher and more consistent widespread use. In the Bering Sea encounter rates tended to be much higher on the shelf and along the shelf break during the non-breeding season.

The high encounter rates in the vicinity of Buldir Pass were based solely on observations made during the breeding season. No platform-days were recorded during non-breeding months so it is unclear whether Steller sea lion use was high year-round or

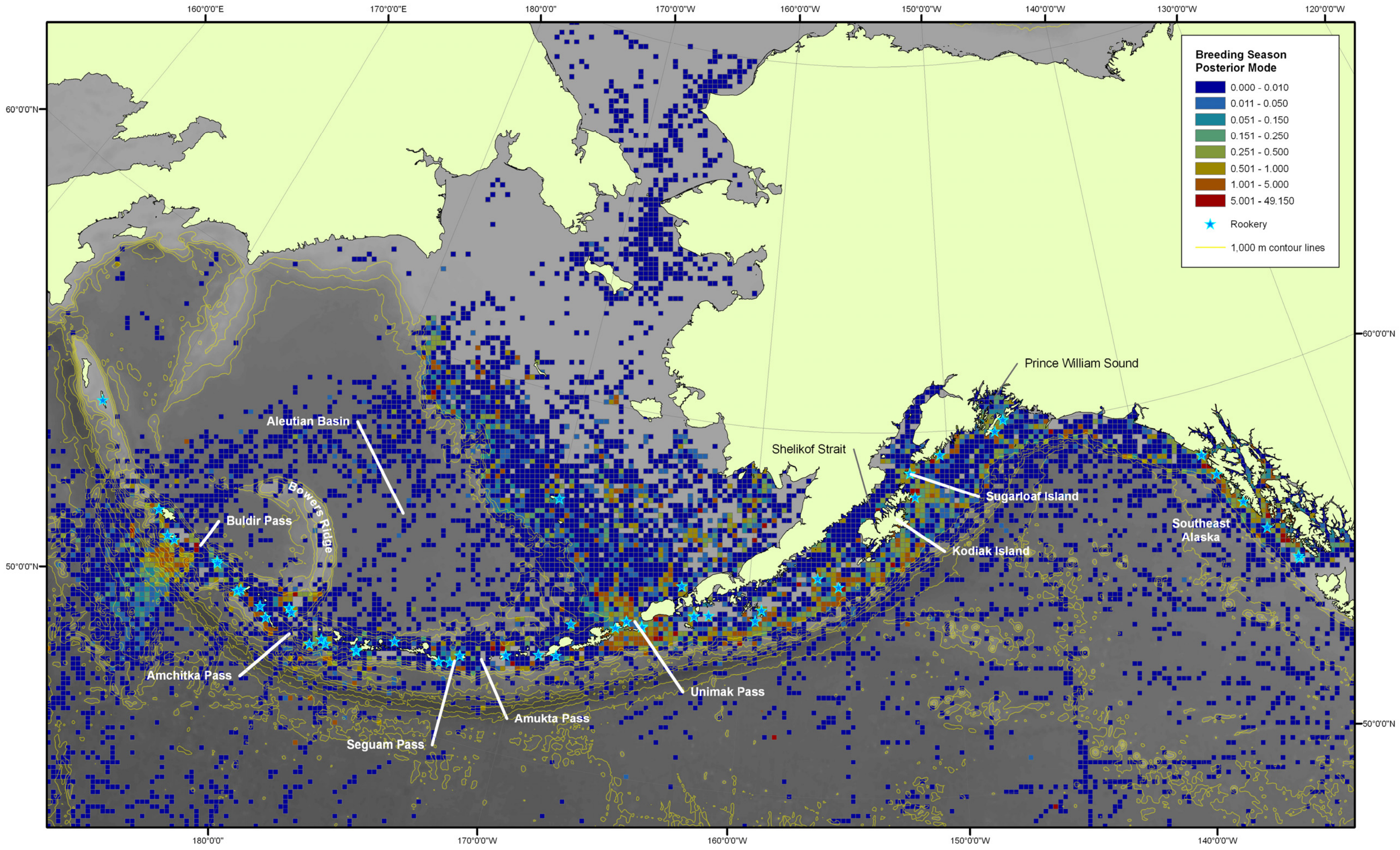

Figure 4-11. Breeding season (May through August) encounter rate posterior distribution modes resulting from the Bayesian inference on POP Steller sea lion observations per platform-day.

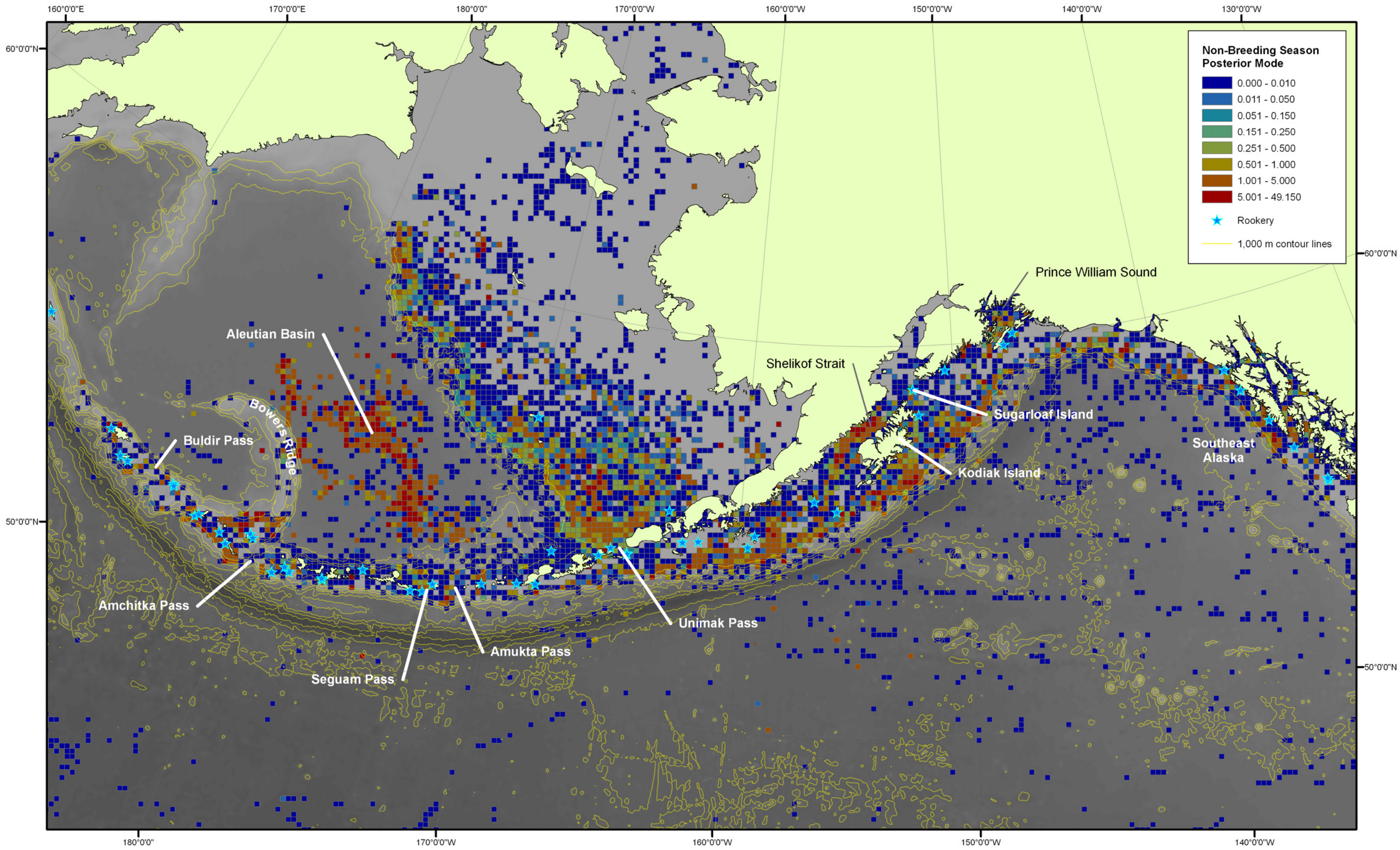

Figure 4-12. Non-breeding season (September through April) encounter rate posterior distribution modes resulting from the Bayesian inference on POP Steller sea lion observations per platform-day.

during the breeding season only. In contrast, the area of high encounter rates in the Aleutian Basin was high mostly during the non-breeding season. Observer effort in this area was much more sparse in the breeding season than the non-breeding season, but the cells that did contain platform-day effort show low encounter rates. Of the approximately 400 cells surveyed in the breeding season 95% had an encounter rate posterior mode of 0.005, and a 95th percentile value (a maximum estimated encounter rate) of 0.1 or lower. Based on the POP data, the Aleutian Basin appears to be used primarily in winter months.

The area north of Amchitka Pass at the southern end of Bowers Ridge was found to be utilized year round. The same holds true for the area north of Unimak Pass, although sea lion use of the area to the south of the pass appears to have been most prevalent during the breeding season. Little Steller sea lion use was recorded in the vicinity of Amukta Pass in the breeding season, but the pass appears to attract high numbers of sea lions in the non-breeding season. Steller sea lions utilized Shelikof Strait almost exclusively during the non-breeding season. Just to the north and east of Kodiak Island and southwest of Sugarloaf, Steller sea lions used these shelf waters more consistently during the breeding season, but appear to move closer to the shelf break during non-breeding season. Prince William Sound received higher use in the non-breeding season. Other areas in the eastern Gulf of Alaska also received higher and more widespread use in the non-breeding season compared to the breeding season. High-use areas occurred in southeast Alaska in both the breeding and non-breeding seasons, but the patterns are somewhat different.

<u>Critical Habitat</u>. If we classify high-use areas to included cells with estimated

encounter rate modes greater than 0.5 Steller sea lions per platform-day, then officially-designated critical habitat areas encompass approximately 37% of all high-use areas within the western DPS. The remaining 63% of high-use cells in the western DPS lie outside of designated critical habitat (Figure 4-13). About half of the high-use cells occurred within the Aleutian Basin, none of which fell inside any regions of critical habitat. Much of the high-use area north of Unimak Pass lies within the Bogoslov Foraging critical habitat area. The Bogoslov Foraging Area, however also encompassed a large area to the west of Unimak Pass beyond the 1,000 isobath in which the POP data showed very low use. Much of the area used most heavily by Steller sea lions on the Pacific side of Unimak Pass was captured within the 20 nm buffered critical habitat areas. The diffuse use over the Bering Sea continental shelf fell outside critical habitat boundaries except within 20 nm of the Pribilof Islands.

The cells with the highest encounter rate estimates in the Buldir Pass area were not within critical habitat boundaries, although the highest use areas around Attu Island were all within protected habitat. Further east, critical habitat areas captured all of the most heavily used areas lying on the south side of Amchitka, Ayugadak, and Kiska Islands, but missed the Steller sea lion hotspots north of Semisopochnoi Island at the southern end of Bowers Ridge. Aside from a few scattered offshore areas to the east of Amchitka Pass, most of Steller sea lion use in the central Aleutians occurred within critical habitat zones. Despite high effort levels in the Seguam Pass area, the POP data did not show the Seguam Pass Foraging area to contain very many high-use cells.

Throughout the Gulf of Alaska, many of the highest use areas fell outside of

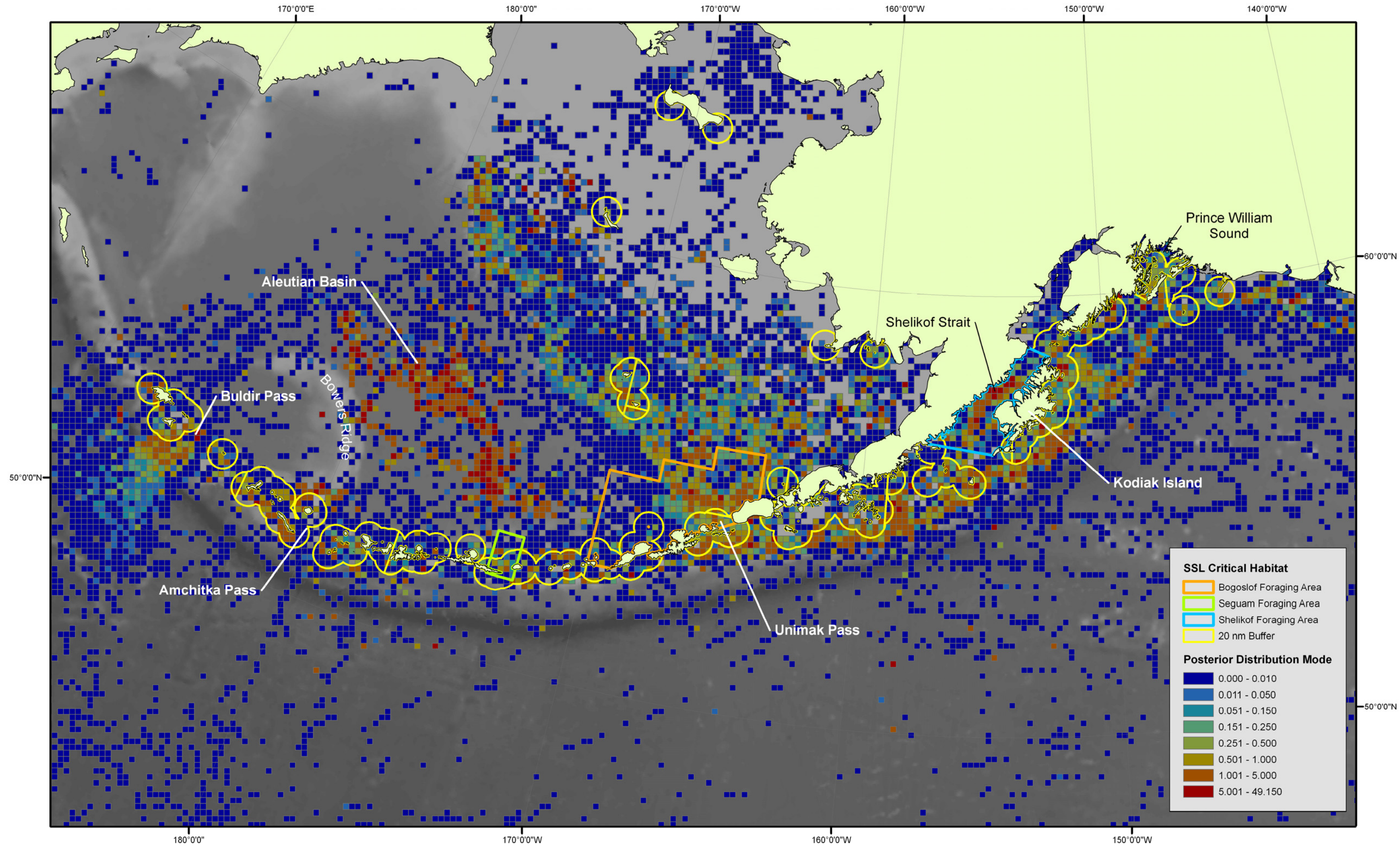

Figure 4-13. Steller sea lion critical habitat buffers and foraging areas in the western DPS overlaid on encounter rate posterior distribution modes resulting from the Bayesian inference on Steller sea lion observations per platform-day.

designated critical habitat. The one exception to this was within the Shelikof Strait Foraging area, which captured all of the high-use cells between Kodiak and the mainland. South of Kodiak Island, however, the highest estimated use was found near the shelf break outside designated critical habitat. Similarly in the western Gulf of Alaska, east of Unimak Pass, the majority of high-use cells fell outside the protected buffers. High-use areas along the shelf break in the eastern Gulf of Alaska, east and north of Kodiak, mostly fall outside critical habitat areas as well.

Discussion

Buldir Pass Area

While it is generally thought that sea lions in the central and western Aleutian sub-regions forage in oceanic waters rather than over the shelf (O'Corry-Crowe *et al.* 2006), few specifics about their foraging habits are known. The area east and south of Agattu rookery had a high level of sampling effort and showed a very clear pattern of high use closest to Buldir Pass and Agattu, with consistent but steadily decreasing use out to 300 km and beyond. The highest use in this area occurred landward of the Aleutian trench within about 120 km of the pass. The pattern of use south of Buldir Pass appears to be quite discrete with consistent boundaries both to the east and west despite relatively high observation effort outside these areas. Such a pattern suggests that this area south of Buldir Pass contains distinct habitat of importance to Steller sea lions. In one of the few telemetry studies targeting western Aleutian animals, at least one animal appears to have utilized this Buldir foraging area (Lander *et al*. 2009). The habitat may be related to circulation patterns created by the pass that concentrate or attract prey. Little is known about the flow dynamics around Buldir Pass but a southern flow at the rate of less than 10^6 m^3s^{-1} has been estimated (Stabeno and Reed 1992; Stabeno et al. 1999). It is possible that water flowing south from the pass collides with waters from the Alaska Stream flowing westward creating a front that may concentrates productivity and prey, providing Steller sea lions with increased foraging opportunities.

Since data is more sparse in other offshore areas south of the central and western Aleutian Islands, it might be tempting to assume this decreasing pattern of use out to the Aleutian trench is representative of a general pattern south of the Aleutian island arc into the north Pacific. However, the distinct boundaries present around the Buldir Pass foraging area suggests that it is particular to this area. Animals from this region (western Aleutians) have longer trip durations but spend less time diving than sea lions from other parts of the Aleutians and the central Gulf of Alaska, suggesting longer travel distances during foraging trips (Lander *et al*. 2010). These diving and trip characteristics are consistent with the pattern of use observed in the POP data in the Buldir foraging area especially since the western Aleutian animals in the Lander *et al*. (2010) study were tagged at Attu and Buldir which are further from the Buldir foraging area than Agattu.

It is certainly possible that this pattern of high use to the Aleutian trench then steadily decreasing beyond that repeats itself south of other Aleutian passes that consist of southern flow from the Bering sea. More POP or other sources of Steller sea lion use data in conjunction with more in-depth analysis of oceanic circulation patterns throughout the Aleutian archipelago would be required to explore this idea further.

It should be noted that the pattern of encounter rates south of Buldir Pass are based primarily on sea lion observations and platform days from the 1980s. Despite relatively sparse effort before and after the 1980s, Steller sea lions were observed both in the 1970's and the 1990's, as recently as 1995. The pattern of observation effort in the 1990's, however, was very different than in the 1980's, with very little effort directly south of the pass in the area shown to be used most intensively by Steller sea lions. Most of the recent effort has occurred along the continental shelf break on the north side of the Aleutians, but Steller sea lion presence in this area does not appear to be substantial. Approximately 300 sea lion observations have been made in this region of the western Aleutians since 1990; sea lion use patterns in this area appear to have been high historically and may continue to be high in the current period, although it is unclear whether the pattern of use continues to be the same.

Aleutian Basin

The highest encounter rates estimated and the largest contiguous area of high Steller sea lion use were found in the Aleutian Basin of the Bering sea. The Aleutian Basin comprises the deepest portion of the Bering sea, and is bounded by the Aleutian Islands to the southeast and south, Bowers Ridge to the southwest and west, Shershov Ridge to the northwest, and the Bering Sea continental shelf to the north and east. Depths in the Basin are generally between 3,000 and 4,000 m. The cells exhibiting the highest Steller sea lion use (>1 SSL/platform-day) had a maximum median depth of 3,950 m, a minimum median depth of 3,100 m, and a mean median depth of 3,715 m.

The southern- and southeast-most portion of the Aleutian Basin high-use area corresponds with at-sea locations of juveniles identified by Fadely *et al* (2005) and

Lander *et al*. (2009). All of the telemetry locations were recorded in summer months from May to August, while the majority of POP sightings in this area occurred in the non-breeding season.

The southeastern portion of the Aleutian Basin is a spawning area for walleye pollock from January through March (Mito *et al*. 1999) . Pacific herring (*Clupea pallasi*) are also distributed throughout the Aleutian Basin in the summer (Mito *et al*. 1999). Based on midwater trawl surveys, in 1988, the Aleutian Basin contained 2.5 million tons of walleye pollock biomass (Mito *et al*. 1999). Approximately 97% of the Steller sea lion sighting events that occurred in the Aleutian Basin were recorded from December through March, although a majority of the survey effort also occurred during this time period. Of the remaining 3% of Steller sea lion sightings, the majority were recorded in July. Steller sea lions using this area during the non-breeding season may be targeting large spawning aggregations of walleye pollock, and Steller sea lions foraging in summer months may be feeding on Pacific herring.

Similar to the Buldir Pass area, effort in the Aleutian Basin was not uniform across years, nor were Steller sea lion observations. About three-quarters of the marine mammal sighting events in this area were recorded between 1982 and 1987 (78.0%). In contrast, 98.7% of the Steller sighting events occurred in that same 6-year period, while only a few SSL were recorded in the area before or after that period despite moderate observation effort. This Aleutian Basin area appears to have been an important area to Steller sea lions in the mid-1980s; whether it is currently used to the extent that it was in the 1980's is unclear. Prior to this analysis, little focus had been placed on the Bering sea as an important foraging area for Steller sea lions of the Aleutians, but sea lions, at least historically, have used the Aleutian Basin extensively. Gaining a clearer understanding of current uses of the Basin by Steller sea lions may be an important step in understanding the foraging habits of Aleutian animals.

Critical Habitat and Regional Differences

The areas in the vicinity of Unimak Pass and Shelikof Strait were both areas previously identified as important Steller habitat and protected as designated critical habitat. The patterns of encounter rate estimates derived from the POP data are in complete agreement with previous assessments of these areas as high-use, important Steller sea lion foraging habitat. The POP data did not, however, show extensive Steller sea lion use in the Seguam Pass area, with the exception of a few small areas directly over the Pass and just to the north. The highest encounter rate posterior modes in this area were just over 1 Steller sea lion per platform-day, despite very high survey effort in this area. Similarly, the western third of the Bogoslof Foraging Area was not found in this analysis to be important Steller sea lion foraging grounds. Encounter rate estimates in this area declined to low levels in waters shallower than the 1,000 m isobath, and beyond the shelf slope encounter rates were negligible.

In most areas, the POP data confirmed that Steller sea lion use is primarily concentrated landward of the continental shelf, but regional differences exist both in this pattern as well as in how far from shore sea lions are foraging. Although results from telemetry studies have focused on general patterns of use, and their finding have been embodied within designated critical habitat areas, as discussed in Chapter 3, Steller sea lion use-patterns vary across their range. Many studies have demonstrated this non-uniformity of foraging behavior (e.g. Merrick *et al*. 1997; Lander *et al*. 2009; Sinclair and Zeppelin 2002), but acknowledgement of regional differences has yet to be incorporated into protection measures. The findings of this POP data analysis confirms that use patterns are not uniform across the entire range, but that that within regions generalized patterns do exist and could be used to modify existing habitat designations.

Animals from the eastern Aleutians, where the population has continued to decline even while other sub-region populations of the western DPS have grown or remained static, may be using the area south of Buldir Pass as well as the Aleutian Basin area. If prey depletions or competition with fisheries in these areas are reducing foraging opportunities for Steller sea lions then this may help explain declining numbers. Similarly, in the central Aleutians, where recent growth in the population appears to have ceased in the most recent years, if the Aleutian Basin or offshore areas to the south or the area around Bowers Ridge were important foraging areas but the resources in these regions are depleted or access is limited, then this may contribute to lack of full recovery in this subregion.

Since about 1990, the eastern Aleutian sub-region population has remained relatively stable (Fritz *et al*. 2008a). Adequate protection of important foraging areas may be responsible. The POP data confirm the importance of the Unimak Pass area and indicate that much of the highest use areas do fall within the Bogoslof Foraging area. A few areas south of the Pass fall outside the critical habitat buffer, but the remainder of high-use areas are protected in this region.

Despite these correlations, it is unclear whether population trajectories can be attributed to inadequate protection of important foraging areas. The population in the western Gulf of Alaska has exhibited some of the most consistent growth since 2000 (Fritz *et al*. 2008a), yet the majority of cells with the highest estimated encounter rates fall outside of designated critical habitat. The central Gulf of Alaska subregion contains the Shelikof Strait Foraging area that protects at least half of the highest use cells in the regions, yet the population has mostly been declining. There is a relatively large area in this sub-region to the south of Kodiak Island that shows consistently high estimated encounter rates that falls outside of protected habitat. Whether this omission is responsible for declines cannot be determined with the current analysis. In the eastern Gulf of Alaska, the POP data show relatively diffuse use, much of which is focused near the shelf break, far beyond designated critical habitat zones. This subregion experienced moderate growth between 2000 and 2006, but appears to have declined in the last couple of years. Again, it is unclear if inadequate protection of foraging areas is partially to blame.

Seasonal Patterns

The broad-scale seasonal patterns found using the POP data generally confirm the finding of the telemetry data as well as what we know about the biology of the animals, namely that Steller sea lions make longer foraging trips to sea in the non-breeding season and tend to stick closer to rookeries during the breeding season. The lower encounter rates overall during the breeding season are most likely a reflection of the reduction in the number of foraging animals in the early summer, and a reduction in the time spent at sea once reproductively active animals resume foraging trips. The much reduced encounter rates on the Bering sea continental shelf in the breeding season compared to the non-breeding season also likely reflects the shortened trip length in the summer. However, consistent high-use patterns along the continental shelf break in the central and western Gulf of Alaska in the breeding season is counter to findings from telemetry studies. The high encounter rate estimates associated with the shelf break are found between 30 km and 100 km from nearby rookeries. In addition, the high-use patterns found south of Buldir Pass occurred solely in the breeding season but extend far offshore, beyond what would be predicted based exclusively on the 20 km breeding season range estimated from telemetry studies.

Sparse or Missing Data

There are some areas where POP observation data are consistently so sparse that our knowledge of Steller sea lion at-sea use is incomplete. Although the vast majority of presumed Steller sea lion habitat has undergone some level of POP observation and many of the areas of highest interest to us (probable SSL use areas) received some of the highest number of platform-days, a few important areas were not surveyed or not surveyed more than once or twice. In particular, oceanic waters of the Gulf of Alaska and north Pacific south of the Aleutians received only scattered survey effort. While we might not expect these offshore waters to be used extensively by Steller sea lions, telemetry data reveal at least two individuals (one adult female in 1991, and one pup in 2002, most likely accompanying his mother) making one or more foraging trips into the oceanic waters of the Gulf (unpublished data). The extent to which such trips are typical for Steller sea lions cannot be adequately ascertained from the POP dataset.

Two relatively large areas of approximately 1,100 km^2 and 2,700 km^2 over the continental shelf east of Unimak Pass in the western Gulf of Alaska were completely lacking in survey effort. Scattered areas in nearshore waters around the Aleutians also lacked survey information, including seven non-contiguous grid cells in the Amchitka Pass area. Although most other areas over the continental shelf in the Aleutians were surveyed, little effort occurred beyond that. Data are sparse or missing for much of the area over the continental shelf slope and Aleutian trench on the Pacific side of the Aleutians, with the exception of the area south of Buldir Pass and Amchitka Pass. While much of the continental shelf break in this region contains adequate POP observation effort for relatively precise estimation, some of the areas landward of the break contain few POP observations. Since these areas have the potential to be used with some frequency by Steller sea lions, the paucity of data in these areas may reduce the precision of encounter rate estimates made in these areas.

The area north of the western-most US portion of the Aleutian Chain in the area of Bowers Basin and Bowers Ridge, and north of Attu Island and Buldir Pass also lacks full POP coverage. Very few POP observations were recorded along Bowers Ridge and within Bowers Basin, and the data that do exist for the area further to the west and north are somewhat sparse. The telemetry data show multiple at-sea trips in this area by at least 1 animal in the summer of 2002 (unpublished data). Another telemetered individual with an exceptional record of at-sea locations took one long foraging trip passing over Bowers Ridge heading north to Shirshov Ridge (over 500 km north of Buldir Pass) then swimming through the waters over Bowers Basin on his way back to Kiska Island. Although this was only one individual, it demonstrates that at least some level of use occurs in this area. The POP data contain a few scattered observations of Steller sea lions in this area but they were all made in the 1980s, and little POP effort was recorded outside this period. Whether these areas are utilized by more than the occasional sea lion is impossible to know without more POP data or other sources of information regarding sea lion use patterns.

Other Considerations

As discussed in Chapter 3, Steller sea lion seasonal use is much more complex than breeding versus non-breeding season. As presented, the POP data do not address finer scale seasonal patterns, and it is unlikely that they are sufficient to allow for parsing by month. This analysis also does not address how Steller sea lion use patterns may have changed over time. Some portions of the study area were more or less prone to be surveyed in different time periods. As a result, in some areas parsing the data temporally tends to also parse the data spatially so that information from a certain era yields information about a particular area, but data from other time periods may be absent in that same area. Thus, assessing temporal changes in overall patterns across the entire range is difficult with the current dataset.

The validity of this POP data analysis, however, does not hinge on the assumption that Steller sea lion use patterns have remained static over the course of the nearly 50 years spanned by the POP observations. Evidence suggests that Steller sea lions are at least in part social foragers that rely on previously gained knowledge of prey concentrations to minimize search effort and maximize energy gain (Gende and Sigler 2006). And although they are central-place foragers, they are able to use multiple central-places in order to maximize seasonally available prey in different areas (Gende *et al*. 2001; Sigler *et al*. 2004; Sigler *et al*. 2009; Womble *et al*. 2005; Womble and Sigler 2006; Womble *et al*. 2009). Based on these patterns it is likely that pups and juveniles learn about foraging hot-spots from their mothers and/or other sea lions at their rookery or haulout, or what Bonadonna *et al*. (2001) refers to as "colony memory". If this is true, and if general oceanographic patterns have not changed substantially or have fluctuated between predictable patterns, then it is reasonable to assume that in the absence of long-term prey depletions, areas of historic importance to Steller sea lions will continue to be important to the species now and/or in the future. In addition, if foraging habitat has contracted over the last 30 years as a result of declining populations, then understanding where important foraging areas have occurred historically may allow us to be proactive with protective measures that will allow a growing Steller sea lion population to reclaim historic foraging habitat.

Conclusions

Despite missing data in some areas and low survey effort in others, this analysis of the Platforms of Opportunity data using the platform-day effort index and the Bayesian negative binomial model has provided substantial new insight into foraging patterns of Steller sea lions. The results of this analysis may be used in a variety of applications to continue to further our understanding of the habitat needs of Steller sea lions. Chapter 5 provides a final summary of the findings of this work and explores how these findings might be further expanded upon in the future.

CHAPTER 5:

CONCLUSIONS AND FUTURE WORK

Assessment of Steller sea lion at-sea use from spatially explicit data for all age- and sex-classes, range-wide, and on a broad temporal scale is vital to understanding Steller sea lion foraging ecology and successfully managing for their continued survival. The Steller sea lion observations in the POP database are the only available source of data that meet all these criteria, and this analysis of sea lion encounter rates is the only empirically-based assessment of spatially-explicit at-sea use available on those broad temporal and spatial scales.

This novel analysis has revealed some new, previously unrecognized high-use areas. Most notable among these are the Aleutian Basin and Buldir Pass. Two other areas that may also warrant additional attention are the area north of Amchitka Pass at the south end of Bowers Ridge and the continental shelf break in the Gulf of Alaska. Although Steller sea lion use was found to be diffuse over the continental shelf in the Bering Sea, this region appears to provide important foraging areas for the species. In addition, the POP analysis indicates low use of the area in the western-most portion of the ESA-designated Bogoslof Foraging Area and in much of the Seguam Pass area.

Future Work

Missing Data and Habitat Modeling

A number of approaches could be taken to address poor data coverage in areas where Steller sea lion use is likely but for which little POP data exist. First, extending this analysis to include more recent POP observation data beyond 2002 may fill in some of these gaps. Where it does not, predictive modeling could be utilized. Development of generalized linear or generalized additive models to identify the relationship between Steller sea lion spatial patterns and habitat characteristics is an essential next step in furthering our understanding of Steller sea lion foraging patterns. In addition, such models could be used to predict levels of use in areas where POP data are sparse or missing.

Prey and Fisheries Data.

Prior to this analysis, comparisons between Steller sea lion use patterns and areas of prey concentrations were limited to very small areas where surveys of Steller sea lions and prey species could be performed in conjunction with one another or where sea lion presence at haul-outs could be associated with nearby prey concentrations. Using the results of this analysis, correspondence between temporally persistent or recurring prey species hotspots and Steller sea lion high-use area can be assessed across much of the Steller sea lion range. Such comparisons could yield substantial new information about what species Steller sea lions are targeting and what drives sea lion foraging patterns.

In addition, both historic and current fisheries catch data could be combined with the model results to further our understanding of Steller sea lion foraging in the past and present. Since many of the observations contained in the POP dataset were recorded by observers on fishing vessels, it may be possible to link Steller sea lion use to specific prey species and concentrations. Such comparisons for data obtained prior to and during the major population declines may reveal new information about foraging patterns, changes in prey densities, and/or fisheries competition.

Management Decision Support

Not only does the Bayesian POP analysis described herein provide substantially broader temporal and spatial coverage of Steller sea lion at-sea use than has been previously available from telemetry and other sources, it also provides a measure of the uncertainty associated with calculated encounter rates. It is possible to put these encounter rate estimates in a decision theoretical framework to identify areas for which the posterior probability that the encounter rate exceeds some threshold, T, exceeds some critical probability, C. For example, if we want to identify areas with encounter rates greater than 1 SSL/platform-day and we want to be 95% certain that they are over that threshold, then the areas in which the posterior distribution 5th percentile value exceeds 1 SSL/platform-day would be identified. These areas can readily be identified in Figure 4-10 but any threshold and any critical probability can be used. Such an analysis provides quantifiable justification for designation of important habitat.

Conclusion

The Bayesian analysis of the POP data have revealed previously unknown patterns of Steller sea lion use, provided greater insight into region-specific foraging patterns, and may be used as a tool to assess the appropriateness of current protection measures. Further development of this and other models utilizing the POP data and the platform-day effort index holds the potential to further enhance our knowledge, and provide information and tools for better management of the species in the future.

REFERENCES CITED

Allen, B.M. and R.P. Angliss. 2009. Alaska Marine Mammal Stock Assessments, Steller sea lion (*Eumetopias jubatus*): Western U.S. stock. U. S. Dep. Commer., NOAA Technical Memo. NMFS-AFSC-206.

Al-Saleh and Al-Batainah. 2003. Estimation of the shape parameter k of the negative binomial distribution. Applied Mathematics and Computation 143: 431-441.

Baker, A.R., T.R. Loughlin, V. Burkanov, C.W. Matson, R.G. Trujillo, D.G. Calkins, J.K. Wickliffe, and J.W. Bickham. 2005. Variation of mitochondrial control region sequences of Steller sea lions: the three-stock hypothesis. Journal of Mammalogy 86(6): 1075-1084.

Beck, C.A., S.J. Iverson, and W.D. Bowen. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. Canadian Journal of Zoology 83: 377-388.

Berta, A. 2002. Pinnipedia, overview. In W.F. Perrin, B. Wursig, and J.G.M. Thewissen (ed.), *Encyclopedia of Marine Mammals*, 903-911. Academic Press.

Berta, A. and Sumich, J.L. 2003. *Marine Mammals: Evolutionary Biology*. Academic Press.

Bickham, J.W., J.C. Patton, and T.R. Loughlin. 1996. High variability for control-region sequences in a marine mammal: Implications for conservation and biogeography of Steller sea lions (*Eumetopias jubatus*). Journal of Mammalogy 77(1):95-108

Bjørge, A. 2001. How persistent are marine mammal habitats in an ocean of variability? Habitat use, home range and site fidelity in marine mammals. In P.G.H. Evans and J.A. Raga (eds.) *Marine mammals: Biology and conservation*, 63-91. Klewer Adademic/Plenum Publishers. New York.

Bonadonna, F., M. Lea, O. Dehorter, and C. Guinet. 2001. Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazelle*. Marine Ecology Progress Series 223: 287-297.

Boness, D.J. 2002. Sea lions, overview. In W.F. Perrin, B. Wursig, and J.G.M. Thewissen (eds.), *Encyclopedia of Marine Mammals*, 1066-1068. Academic Press.

Braham, H.W., R.D. Everitt, and D.J. Rugh. 1980. Northern sea lion decline in the eastern Aleutian Islands. Journal of Wildlife Management 44: 25-33.

Burkanov, V. 2009. Russian Steller sea lion research update. Pages 6-11 in Alaska Fishereis Science Center Quarterly Report, January-February-March 2009. National Marine Fisheries Service. 27pp. http://www.afsc.noaa.gov/Quarterly/jfm2009/JFM09divrpts.pdf#NMML

Burns, J.M., D.P. costa, M.A. Fedak, M.A. Hindell, C.J.A. Bradshaw, N.J. Gales, B. McDonald, S.J. Trumble, and D.E. Crocker. 2004. Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. Deep-Sea Research II 51: 2279-2303.

Calkins, D.G. and K.W. Pitcher. 1982. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Pages 447-546 *in* Environmental Assessment of the Alaskan Continental Shelf. Final Report, U.S. Department of Commerce and U.S. Department of Interior. Principal Investigators 19:1-565.

Call, K.A., B.S. Fadely, A. Greig, and M.J. Rehberg. 2007. At-sea and on-shore cycles of juvenile Steller sea lions (*Eumetopias jubatus*) derived from satellite dive recorders: A comparison between declining and increasing populations. Deep Sea Research Part II: Topical Studies in Oceanography 54(3-4): 298-310.

Costa, D.P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. Symposia of the Zoological Society of London 66:293-314.

DeMaster, D. and S. Atkinson. 2002. Steller sea lion decline: Is it food? II. University of Alaska Sea Grant, AK-SG-0202, Fairbanks, AK.

Fadely, B.S., B.W. Robson, J.T. Sterling, A. Greig, and K.A. Call. 2005. Immature Steller sea lion (*Eumetopias jubatus*) dive activity in relation to habitat features of the eastern Aleutian Islands. Fisheries Oceanography 14 (Suppl. 1): 243-258.

Feldhamer, G.A., Drickamer, L.C., Vessey S.H., Merritt J.F., and Krajewski C. 2007. *Mammalogy: Adaptation, diversity, ecology*. Johns Hopkins University Press.

Fiscus, C.H. and G.A. Baines. 1966. Food and feeding behavior of Steller and California sea lions. Journal of Mammalogy 47(2): 195-200.

Frid, A., M.R. Heithaus, and L.M. Dill. 2007. Dangerous dive cycles and the proverbial ostrich. Oikos 116: 893-902.

Fritz, L., M. Lynn, E. Kunisch, and K. Sweeney. 2008a. Aerial, ship, and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 2005-2007. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-183, 70 p.

Fritz, L. W., K. Sweeney, C. Gudmundson, T. Gelatt, M. Lynn and W. Perryman. 2008b. Survey of Adult and Juvenile Steller Sea Lions, June-July 2008. Memorandum to the Record, NMFS Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle WA 98115. http://www.afsc.noaa.gov/nmml/pdf/SSLNon-Pups2008memo.pdf

Gende, S.M. and M.F. Sigler. 2006. Persistence of forage fish 'hot spots' and its association with foraging Steller sea lions (*Eumetopias jubatus*) in southeast Alaska. Deep-Sea Research II 53: 432-441.

Gende, S.M., J.N. Womble, M.F. Willson, and B.H. Marston. 2001. Cooperative foraging by Steller sea lions, *Eumetopias jubatus*. The Canadian Field-Naturalist 115: 355-356.

Gentry, R.L. 1970. Social Behavior of the Steller Sea Lion. Ph.D. thesis, University of California-Santa Cruz. 113pp.

Gentry, R.L. 2002. Eared seals, *Otariidae*. In W.F. Perrin, B. Wursig, and J.G.M. Thewissen (ed.), *Encyclopedia of Marine Mammals*, 348-351. Academic Press.

Gregr, E.J. and A.W. Trites. 2008. A novel presence-only validation technique for improved Steller sea lion *Eumetopias jubatus* critical habitat descriptions. Marine Ecology Progress Series 365: 247-261.

Guisan, A. and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147-186.

Heithaus, M.R. and L.M. Dill. 2002. Feeding strategies and tactics. In W.F. Perrin, B. Wursig, and J.G.M. Thewissen (ed.), *Encyclopedia of Marine Mammals*, pp. 412-422. Academic Press.

Hoffman, J.I., C.W. Matson, W. Amos, T.R. Loughlin, and J.W. Bickham. 2006. Deep genetic subdivision within a continuously distributed and highly vagile marine mammal, the Steller's sea lion (*Eumetoopias jubatus*). Molecular Ecology 15: 2821-2832.

Holmes, E.E., L.W. Fritz, A.E. York, and K. Sweeney. Age-structured modeling reveals long-term declines in the natality of western Steller sea lions. Ecological Applications 17(8): 2214-2232.

Hoover, A.A. 1988. Steller Sea Lion, *Eumetopias jubatus*. In J.W. Lentfer (ed.), *Selected Marine Mammals of Alaska: Species accounts with research and management recommendations*, 159-193. Marine Mammal Commission.

Kenyon, K.W. and Rice, D.W. 1961. Abundance and distribution of the Steller sea lion. Journal of Mammalogy 42(2): 223-234.

Lander, M.E., T.R. Loughlin, M.G. Logsdon, G.R. VanBlaricom, B.S. Fadely, and L.W. Fritz. 2009. Regional differences in the spatial and temporal heterogeneity of oceanographic habitat used by Steller sea lions. Ecological Applications 19(6): 1645-1659.

Lander, M.E., T.R. Loughlin, M.G. Logsdon, G.R. VanBlaricom, and B.S. Fadely. 2010. Foraging effort of juvenile Steller sea lions *Eumetopias jubatus* with respect to heterogeneity of sea surface temperature. Endangered species research 10: 145-158.

Loughlin, T.R. 1998. The Steller sea lion: a declining species. Biosphere Conservation 1: 91–98.

Loughlin, T.R. 2002. Steller's Sea Lion, *Eumetopias jubatus*. In W.F. Perrin, B. Wursig, and J.G.M. Thewissen (ed.), *Encyclopedia of Marine Mammals*, pp. 1181-1185. Academic Press.

Loughlin, T.R. and R. Nelson Jr. 1986. Incidental mortality of northern sea lion in Shelikof Strait, Alaska. Marine Mammals Science 2(1): 14-33.

Loughlin, T.R., M.A. Perez, and R.L. Merrick. 1987. *Eumetopias jubatus*. Mammalian Species 283:1-7.

Loughlin, T.R., A.S. Perlov, J.D. Baker, S.A. Blokhin, and A.G. Makhnyr. 1998. Diving behavior of adult female Steller se alions in the Kuril Islands, Russia. Biosphere Conservation 1(1): 21-31.

Loughlin, T.R., Perlov, A.S., and Vladimirov, V.A. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Marine Mammal Science 8(3):220-239.

Loughlin, T.R., Rugh, D.J., and Fiscus, D.J. 1984. Northern sea lion distribution and abundance: 1956-80. Journal of Wildlife Management 48(3):729-740.

Loughlin, T.R., J.T. Sterling, R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fishery Bulletin 101: 566-582.

Loughlin, T.R. and A.E. York. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. Marine Fisheries Review 62: 40–45.

Maniscalco, J., P. Parker, and S. Atkinson. 2006. Interseasonal and interannual measures of maternal care among individual Steller sea lions (*Eumetopias jubatus*). Journal of Mammalogy 87: 304-311.

Marston B.H., Willson M.F., Gende S.M. 2002. Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. Marine Ecology Progress Series 231: 229–236.

McAllister, D.C., D.G. Calkins, and K.W. Pitcher. 2001. Underwater capture of juvenile Steller sea lions with SCUBA: a narrated video presentation. In S.J. Jewett (ed.) *Cold Water Diving for Science.* University of Alaska Sea Grant Program, Rep. 01-06, pp. 53-55. Fairbanks, Alaska.

Merrick, R.L. 1995. The relationship of the foraging ecology of Steller sea lions (*Eumetopias jubatus*) to their population decline in Alaska. PhD dissertation, University of Washington. Seattle, WA.

Merrick, R. L., and D. G. Calkins. 1996. Importance of juvenile walleye pollock, *Theragra chalcogramma*, in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus*. Pages 153-166 in U.S. Dep. Commer. NOAA Tech. Rep. NMFS 126.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (Eumetopias jubatus) and their population decline in Alaska; a potential relationship. Canadian Journal of Fisheries and Aquatic Science 54: 1342-1348.

Merrick, R.L., T.R. Loughlin, A. Antonelis, and R. Hill. 1994. Use of satellite-linked telemetry to study Steller sea lion and northern fur seal foraging. Polar research 13: 105-114.

Merrick, R.L. and T.R. Loughlin. 1997. foraging behavior of adult female and young-of-the-year Steller sea lions in Alaska waters. Canadian Journal of Zoology 75: 776-786.

Milette, L.L. and A.W. Trites. 2003. Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska. Canadian Journal of Zoology 81: 340-348.

Mito, K., A. Nishimura, and T. Yanagimoto. 1999. Ecology of groundfishes in the eastern Bering Sea, with emphasis on food habits. In T.R. Loughlin and K. Ohtani (eds), *Dynamics of the Bering Sea*, 537-580. University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska. 838 pp.

Moser H.G. and P.E. Smith. 1993. Larval fish assemblages and oceanic boundaries. Bulletin of Marine Science 53: 283-289.

National Marine Fisheries Service (NMFS). 2008. Recovery Plan for the Steller Sea Lion (*Eumetopias jubatus*). Revision. National Marine Fisheries Service, Silver Spring, MD. 325 pages.

O'Corry-Crowe, G., B.L. Taylor, T. Gelatt, T.R. Loughlin, J. Bickham, M. Basterretche, K.W. Pitcher, and D.P. DeMaster. 2006. Demographic independence along ecosystem boundaries in Steller sea lions revealed by mtDNA analysis: implications for management of an endangered species. Canadian Journal of Zoology 84: 1796-1809.

Orr, R.T. and T.C. Poulter. 1967. Some observations on reproduction, growth, and social behavior in the Steller sea lion. Proceedings of the California Academy of Sciences 35(10): 193-226.

Osborne, P.E., J.C. Alonso, and R.G. Bryant. 2001. Modeling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. Journal of Applied Ecology 38: 458-471.

Pascual, M.A. and M.D. Adkison. 1994. The decline of the Steller sea lion in northeast Pacific: Demography, harvest or environment? Ecological Applications 4: 393–403.

Pitcher, K.W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fishery Bulletin 79(3): 467-472.

Pitcher, K.W. and D.G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. Journal of Mammalogy 62(3): 599-605.

Pitcher, K.W., P.F. Olesiuk, R.F. Brown, M.S. Lowry, S.J. Jeffries, J.L. Sease, W.L. Perryman, C.E. Stinchcomb, and L.F. Lowry. 2007. Abundance and distribution of the eastern North Pacific Steller sea lion (Eumetopias jubatus) population. Fishery Bulletin 105:102-115.

Pitcher K.W., M.J. Rehberg, G.W. Pendleton, K.L. Raum-Suryan, T.S. Gelatt, U.G. Swain, and M.F. Sigler. 2005. Ontogeny of dive performance in pup and juvenile Steller sea lions in Alaska. Canadian Journal of Zoology 83:1214–1231.

Raum-Suryan, K.L., K.W. Pitcher, D.G. Calkins, J.L. Sease, and T.R. Loughlin. 2002. Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. Marine Mammal Science 18(3): 746-764.

Raum-Suryan, K.L., M.J. Rehberg, G.W. Pendleton, K.W. Pitcher, and T.S. Gelatt. 2004. Development of dispersal, movement patterns, and haul-out use by pup and juveniles Steller sea lions (*Eumetopias jubatus*) in Alaska. Marine Mammal Science 20(4): 823-850.

Redfern, J.V., M.C. Ferguson, E.A. Becker, K.D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M.F. Baumgartner, K.A. Forney, L.T. Balance, P. Fauchald, P. Halpin, T. Hamazaki, A.J. Pershing, S.S. Qian, A. Read, S.B. Reilly, L. Torres, and F.

Werner. 2006. Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310: 271-295.

Rehberg, M.J., R.D. Andrews, U.G. Swain, and D.G. Calkins. 2009. Foraging behavior of adult female Steller sea lions during the breeding season in Southeast Alaska. Marine Mammal Science 25(3): 588-604.

Rehberg, M.J. and J.M. Burns. 2008. Differences in diving and swimming behavior of pup and juvenile Steller sea lions (Eumetopias jubatus) in Alaska. Canadian Journal of Zoology 86: 539-553.

Riedman, M. 1990. The Pinnipeds: Seals, sea lions, and walruses. University of California Press, Berkeley, CA. 439 pp.

Robson, B.W., M.E. Goebel, J.D. Baker, R.R. Ream, T.R. Loughlin, R.C. Francis, G.A. Antonelis, and D.P. Costa. 2004. Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). Canadian Journal of Zoology 82: 20-29.

Rodgers, A.R. 2001. Recent telemetry technology. In, J.J. Millspaugh and J.M. Marzluff (eds), *Radio tracking and Animal Populations*. p. 79-121. Academic Press. San Diego, CA. 474 pp.

Sandegren, F.E. 1970. Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubata*) in Alaska. Master's thesis, University of Alaska-Fairbanks.

Sease, J. L., and C. J. Gudmundson. 2002. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) from the western stock in Alaska, June and July 2001 and 2002. U. S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-131, 45 pp.

Sease, J.L. and T.R. Loughlin. 1999. Aerieal and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1997 and 1998. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-100. 61pp.

Sease, J.L., W.P. Taylor, T.R. Loughlin, and K.W. Pitcher. 2001. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1999 and 2000. U. S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-122, 52 pp.

Sigler, M.F., D.J. Tollit, J.J. Vollenweider, J.F. Thedinga, D.J. Csepp, J.N. Womble, M.A. Wong, M.J. Rehberg and A.W. Trites. 2009. Steller sea lion foraging response to seasonal changes in prey availability. Marine Ecology Progress Series 388: 243–261.

Sigler, M.F., J.N. Womble, and J.J. Vollenweider. 2004. Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a prespanwing aggregation of eulachon (*Thaleichthys pacificus*). Canadian Journal of Fisheries and Aquatic Science 61: 1475-1484.

Sinclair, E.H., S.E. Moore, N.A. Friday, T.K. Zeppelin, and J.M. Waite. 2005. Do patterns of Steller sea lion (*Eumetopias jubatus*) diet, population trend and cetacean occurrence reflect oceanographic domains from the Alaska Peninsula to the central Aleutian Islands? Fisheries Oceanography. 14(0): 223−242.

Sinclair, E.H. and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). Journal of Mammalogy 83(4): 973-990.

Stabeno, P.J. and R.K. Reed. 1992. A major circulation anomaly in the western Bering Sea. Geophysical Research Letters 19: 1671-1674.

Stabeno, P.J., J.D. Schumacher, and K.Ohtani. 1999. The physical oceanography of the Bering sea. In T.R. Loughlin and K. Ohtani (eds), *Dynamics of the Bering Sea*, 1-28. University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska. 838 pp.

Sterling, J.T. and R.R. Ream. 2004. At-sea behavior of juvenile male northern fur seals (*Callorhinus ursinus*). Canadian Journal of Zoology 82: 1621-1637.

Trites, A.W. and D.G. Calkins. 2008. Diets of mature male and female Steller sea lions (*Eumetopias jubatus*) differ and cannot be used as proxies for each other. Aquatic Mammals 34(1): 25-34.

Trites, A.W., D.G. Calkins, and A.J. Winship. 2007. Diets of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, 1993-1999. Fishery Bulletin 105: 234-248.

Trites, A.W. and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? Aquatic Mammals 22: 153–166.

Trites, A.W. and B.T. Porter. 2002. Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. Journal of Zoology 256: 547-556.

Vincent, C., B.J. McConnell, V. Ridoux, and M.A. Fedak. 2002. Assessment of Argos location accuracy from satellite tages deployed on captive gray seals. Marine Mammal Science 18(1):156-166.

White, G.C. and R.E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77(8): 2549-2557.

White, G.C. and R.A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press. San Diego, CA., 383 pp.

White, N.A. and M. Sjöberg. 2002. Accuracy of satellite positions from free-ranging grey seals using ARGOS. Polar Biology 25: 629-631.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.

Winship, A.J. and A.W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fisheries Bulletin 101: 147-167.

Womble J.N. and M.F. Sigler. 2006. Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Marine Ecology Progress Series 325: 281–293.

Womble, J.N., M.F. Sigler, and M.F. Willson. 2009. Linking seasonal distribution patterns with prey availability in a central-place forager, the Steller sea lion. Journal of Biogeography 36: 439-451.

Womble, J.N., M.F. Willson, M.F. Sigler, B.P. Kelly, and G.R. VanBlaricom. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska. Marine Ecology Progress Series 294: 271-282.

York, A.E. 1994. The population dynamics of northern sea lions, 1975–1985. Marine Mammal Science 10: 38–51.

York, A.E., R.L. Merrick, and T.R. Loughlin. 1996. An analysis of the Steller sea lion metapopulation in Alaska. In D.R. McCullough (ed), *Metapopulation and wildlife conservation*, pp. 259–292. Island Press, Washington, D.C.