

AN ABSTRACT OF THE DISSERTATION OF

Sheanna Marie Steingass for the degree of Doctor of Philosophy in Wildlife Science presented on June 13, 2018.

Title: HABITAT USE, SPATIAL ECOLOGY, AND STABLE ISOTOPE VARIABILITY OF THE PACIFIC HARBOR SEAL (*PHOCA VITULINA RICHARDII*) ALONG THE OREGON COAST

Abstract approved:

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Markus Horning

Pacific harbor seals (*Phoca vitulina richardii*) are one of Oregon's most common coastal predators, numbering between 10,000 and 12,000 individuals (Brown et al. 2005b). They consume more than 149 species or types of marine prey within the Pacific Northwest, which include a large variety of commercially important fisheries species. Despite their potential economic impacts and ecological role, little quantitative data are available regarding individual harbor seal spatial foraging behaviors and dietary habits along the Oregon coast, particularly outside of their estuarine habitat.

In order to examine the movement and dietary ecology of Pacific harbor seals in Oregon, I used satellite telemetry to track 24 adult harbor seals captured in two locations on the Oregon coast from September 2014 to September 2015. I also collected a whisker from each animal for dietary estimation via stable isotope analysis, namely the quantification of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  enrichment as proxies for trophic level and

spatial habitat use. These data were examined from three separate perspectives to highlight the ecological role of harbor seals along the Oregon coast.

Chapter 1 is a quantitative assessment of spatial habitat utilization of Pacific harbor seals. I quantified individual and population-level home range area, core area, foraging trip distance and duration, percent presence within eleven inland waters including bays and rivers, proximity to two wave energy test sites, use of Oregon's five marine reserves as well as marine protected areas and comparison areas, and percent use of inshore vs. at-sea habitats for all study animals.

Chapter 2 is a multi-level examination of variability and assessment of behavioral repeatability for harbor seals. It included an examination of differences and predictability in spatial behavior and diet for seals at the levels of individual, capture site, and whole sample population. This was accomplished by measuring 'repeatability' of specific behaviors. Repeatability and spatial use were compared to stable isotopes in generalized linear and linear mixed effects models to highlight strategies in foraging.

Chapter 3 investigates how local oceanography, dietary composition, and spatial movement were related for seals. I utilized generalized linear mixed models and linear mixed effects models to examine which environmental and site-related variables were most associated with movement and dietary patterns of the study animals. This was examined from a series of models of individually summarized parameters ( $n = 24$ ), and from three models examining the point-by-point parameters of haulout status, in bay vs. at sea, and distance from shore ( $n = 57,220$ ).

Overall, this dissertation demonstrates associations between stable isotope-derived diet and patterns in spatial habitat use, suggesting that stable isotope analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  can inform two-dimensional satellite telemetry, but also may provide post-hoc information regarding drivers of spatial movement of harbor seals. Results revealed a high degree of between-individual variability in diet and spatial behavior, a limited use of Oregon's newly established marine reserves and wave energy sites, and extensive utilization of Oregon's continental shelf. This dissertation represents the first in-depth description of spatial habitat use for Pacific harbor seals, a common marine mammal and upper trophic-level predator, along the Oregon coast.

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HABITAT USE, SPATIAL ECOLOGY, AND STABLE ISOTOPE VARIABILITY  
OF THE PACIFIC HARBOR SEAL (*PHOCA VITULINA RICHARDII*) ALONG THE  
OREGON COAST

by  
Sheanna Marie Steingass

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degree of

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Doctor of Philosophy dissertation of Sheanna Marie Steingass presented on June 13, 2018.

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Dean of the Graduate School

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

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Sheanna Marie Steingass, Author

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## INTRODUCTION

The Northern California Current System refers to the section of the California Current System (CCS) that extends north from Cape Mendocino ( $40.4401^{\circ}$  N) to northern Washington State (approximately  $50.0000^{\circ}$  N) on the western coast of North America. The California Current System is one of four global eastern boundary currents systems which supply approximately 20% of global fishery landings, making them especially important for biodiversity and fisheries production (Pauly and Christensen 1995). The CCS is a particularly dynamic ecosystem, being subject to strong seasonal and inter-annual variability in coastal processes, with a recent trend in warming and increased stratification due to climatological shifts (Casey et al. 1989; Lluch-Belda et al. 2001; Bograd and Lynn 2003; Lluch-Belda et al. 2003). The northern portion of the CCS is especially economically and biologically productive (Hickey and Banas 2008), and the diversity of species found within the CCS are important for commercial fisheries (Field et al. 2006; McClatchie 2014), cultural value (Miller 2000; Close et al. 2002; Campbell and Butler 2010) and tourism (Christensen et al. 2007), as well as ecosystem services (Worm et al. 2006; Barbier et al. 2011; van den Belt et al. 2012; Beaumont et al. 2014; Barbier 2015).

One group of species within the CCS that demonstrate particular cultural and ecological value are marine mammals. Due to their relatively high position in the food web, marine mammals can also be perceived as sentinels of ocean health (McCafferty et al. 1999; Reddy et al. 2001; Gulland and Hall 2007; Moore and Gulland 2014). Pinnipeds as a group are particularly relevant ecosystem indicators as they tend to be populous, often pursue the same resources as commercial or recreational fisheries (Wickens 1995; Baraff and Loughlin 2000; Scordino 2010), and share the shoreline with human inhabitants (Stevens and Boness 2003; Orsini 2005; Orsini et al. 2006; Stewart et al. 2008; Defeo et al. 2009). As marine megafauna, pinnipeds play an

ecological role as transporters of biomass and nutrients (Greig et al. 2005; Bejarano et al. 2008; Bargu et al. 2012; Doughty et al. 2016), and are subject to bottom-up ecological impacts of anthropogenic and natural contributions to the marine ecosystem (Anas 1974; Greig et al. 2005; Bejarano et al. 2008; Brookens et al. 2008; Bargu et al. 2012; Van Hooymissen et al. 2015).

Pinnipeds are abundant in the Northern CCS. Despite this, recent ecological data for several species is limited for at least one stretch of this region, the Oregon coast. The Oregon coast is a 363 mile (583 km) stretch of the Northern CCS that supported more than \$205 million dollars of fisheries landings 2015, totaling more than 209.9 million pounds of fish delivered to ports in the state in 2015 (The Research Group 2016). There are more than 29 species of marine mammals in Oregon, many of which are highly visible through direct observations, human-wildlife interactions, and through strandings (Warlick et al. 2018). The Pacific harbor seal (*Phoca vitulina richardii*) is one such species, numbering between 10,000-12,000 individuals hauling out at 91 surveyed locations within the boundaries of the Oregon Territorial Sea (Brown et al. 2005) (Figure I.1). Prior to the Marine Mammal Protection Act in 1973 harbor seals were nearly hunted to extinction within the state. Population estimates taken in 1967 and 1968 revealed approximately 500 individuals along the entirety of the Oregon coast (Pearson and Verts 1970). This was largely due to the bounty placed upon harbor seals, which encouraged harvesting of animals that were seen as ‘pests’ to fisheries. The \$5-25 bounty payment resulted in hundreds of animals being harvested annually in the 1930s and 40s, until that number dropped drastically in the 1960’s. In comparison to today’s 91 described haulouts, Harvey et al. (1990) conducted a harbor seal census in Oregon from 1975-1983 and observed seals at 32 haulout locations along the Oregon coast. Harbor seals are one of the few pinniped species within Oregon that do not undertake annual migrations throughout the CCS (Carretta et al. 2009).

Additionally, harbor seals are nearshore and continental shelf foragers whereas other local species spend more time offshore in the pelagic environment (Lance and Jeffries 2007; Steingass 2017).

The Oregon coast is subject to a number of alterations in ecosystem function, spatial planning, and marine resource management in recent years. The first of these is the development of five new marine reserves (Cascade Head, Cape Falcon, Otter Rock, Cape Perpetua, Redfish Rocks), as of 2012 (Kulongoski 2008), including associated marine protected areas and comparison areas (Table I.1). The second is the development of two wave energy test sites (North Energy Test Site, South Energy Test Site) offshore north and south of Newport, Oregon beginning in 2012. These features are relevant for marine mammal ecology as pinnipeds have been shown to heavily utilize anthropogenic structures, including alternative energy sites (Norman et al. 2010; Moore et al. 2013; Russell et al. 2014; Arnould et al. 2015). Marine mammals should be considered during the establishment of marine management areas, as they have the capacity to benefit from the biological effects of marine reserves (Reeves 2000), act as ecological indicators of success (Hooker and Gerber 2004; Cronin and McConnell 2008), or exert top-down pressure in reserve functioning (Fanshawe et al. 2003). The Oregon coast is also subject to the anthropogenic activities of increased shipping, boat traffic, and the potential for future offshore drilling. The assessment of the effects of these activities on marine mammal behavior requires data that demonstrate distribution and habitat use prior to, during, and after installation of these features. (Hastie et al. 2016; Russell et al. 2016; Chen et al. 2017; Hastie et al. 2018).

The general abundance and behavioral traits of harbor seals make them an ideal species for examining the effects of spatial management, as well as studying nearshore, estuarine and

neritic ecology from the aspect of a marine predator. The Pacific harbor seal is considered a generalist, consuming both benthic and neritic gilled fishes(Steingass 2017). However, the contribution of individuals to this population-wide diversity of diet is less well known.

Particularly, an understanding of whether the Oregon coastal stock of harbor seals is composed of a series of specialists that contribute to a wide overall dietary niche, whether the population is composed of opportunistic generalists, or a combination of these, is unclear, and could have implications for the effective management and understanding of populations or stocks. For example, there is evidence that seals respond to seasonal resource pulses such as salmonid runs (Wright et al. 2007), but there is also contrary evidence that seals do not always respond to such pulses (Thomas et al. 2011). One potential method for determining dietary variability over time and space is the utilization of stable isotope analysis. Stable isotope analysis has been well-demonstrated in marine mammal science to estimate dietary characteristics of individual animals, including trophic niche and geographic origin of food items (Newsome et al. 2010).

This dissertation represents the first in-depth assessment of at-sea movement, diet, and habitat associations of the Pacific harbor seal along the Oregon coast. I assessed patterns of habitat utilization, behavioral associations with the oceanographic environment, and stable-isotope derived dietary composition for 24 individual adult seals captured at two haulout locations (Netarts Bay, 45.4028° N, 123.9484° W and Alsea Bay, 44.4279° N, 124.0679° W) in Oregon. Animals were temporarily captured in September 2014-September 2015 in order to attach external Wildlife Computers SPOT5© Argos satellite tags. Seals were tracked as long as tags continued to provide locations (20-324 days). Additionally, one whisker was collected from each seal at the time of capture for stable isotope analysis of diet. Spatial data were preliminarily filtered using the speed-distance-angle method (Freitas et al. 2008) and then modeled using a

correlated random walk method (R package *crawl*) to generate regularly-spaced tracklines for further analysis (Johnson 2017). This dataset was used to calculate seals' use of marine reserves, marine protected areas, comparison areas, and wave energy sites. Utilization of bay and riverine habitats was also assessed. As satellite telemetry requires spatial interpolation, consideration of error, and precludes fine-scale (<1km) assessment of behavioral states (Costa et al. 2010), there is a necessity to rely upon alternative methods of analysis if at-sea behavior is to be further examined beyond general movement. In order to create a fuller picture of harbor seal ecology in Oregon, I used the method of stable isotope analysis to determine dietary patterns within and between individuals. Ten samples from each individual whisker were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and this information was used to estimate trophic level and trophic niche over time.

For further context, environmental datasets were also examined in the context of animal movement and diet, and these included bathymetry (depth), lithography (bottom type), solar zenith angle, calculated upwelling index, and tidal height. Generalized linear and linear mixed effects models were used to examine seal behavior and isotopic composition in relation to these features on a seasonal basis. Additionally, animals were assessed in terms of behavioral repeatability, or the predictability in behavior between foraging trips (Nakagawa and Schielzeth 2010). Data revealed a variety of potential strategies for individual animals, including differences in dietary composition and trophic niche, movement patterns, and associations with marine habitat. The data presented in this dissertation is a current assessment of the behavioral ecology of adult harbor seals in the State of Oregon, and lends itself to future comparison for applied questions regarding the movement and dietary composition of seals in this region.

## TABLES AND FIGURES

Table I.1. List of all marine reserves, protected areas, and comparison areas in Oregon.

|           | <b>Name</b>             | <b>Type</b>             | <b>Area (km<sup>2</sup>)</b> |
|-----------|-------------------------|-------------------------|------------------------------|
| <b>1</b>  | Cape Falcon             | Marine Reserve          | 32.02                        |
| <b>2</b>  | Cape Falcon Shoreside   | Marine Protected Area   | 0.61                         |
| <b>3</b>  | Cape Falcon West        | Marine Protected Area   | 19.01                        |
| <b>4</b>  | Moolack                 | Comparison Area         | 2.61                         |
| <b>5</b>  | Cascade Head            | Marine Reserve          | 24.97                        |
| <b>6</b>  | Cascade Head North      | Marine Protected Area   | 31.63                        |
| <b>7</b>  | Cascade Head South      | Marine Protected Area   | 24.85                        |
| <b>8</b>  | Cascade Head West       | Marine Protected Area   | 3.34                         |
| <b>9</b>  | Schooner Creek          | Comparison Area         | 27.60                        |
| <b>10</b> | Otter Rock              | Marine Reserve          | 2.99                         |
| <b>11</b> | Cape Foulweather        | Comparison Area         | 4.62                         |
| <b>12</b> | Cape Perpetua           | Marine Reserve          | 36.45                        |
| <b>13</b> | Cape Perpetua North     | Marine Protected Area   | 29.30                        |
| <b>14</b> | Cape Perpetua           | Seabird Protection Area | 57.56                        |
| <b>15</b> | Cape Perpetua Southeast | Marine Protected Area   | 19.42                        |
| <b>17</b> | Postage Stamp           | Comparison Area         | 37.94                        |
| <b>18</b> | Redfish Rocks           | Marine Reserve          | 6.81                         |
| <b>19</b> | Redfish Rocks           | Marine Protected Area   | 13.21                        |
| <b>20</b> | Humbug                  | Comparison Area         | 22.92                        |
| <b>22</b> | Orford Reef             | Comparison Area         | 18.36                        |
| <b>23</b> | Cavalier                | Comparison Area         | 30.79                        |

|                               | <b>Number of Sites</b> | <b>Area (km<sup>2</sup>)</b> | <b>% Territorial Sea</b> |
|-------------------------------|------------------------|------------------------------|--------------------------|
| <b>Marine Reserves Total</b>  | 5                      | 103.24                       | 3.18%                    |
| <b>Protected Areas Total</b>  | 9                      | 198.93                       | 6.12%                    |
| <b>Comparison Areas Total</b> | 7                      | 144.84                       | 4.46%                    |
| <b>TOTAL</b>                  | <b>21</b>              | <b>482.23</b>                | <b>13.75%</b>            |

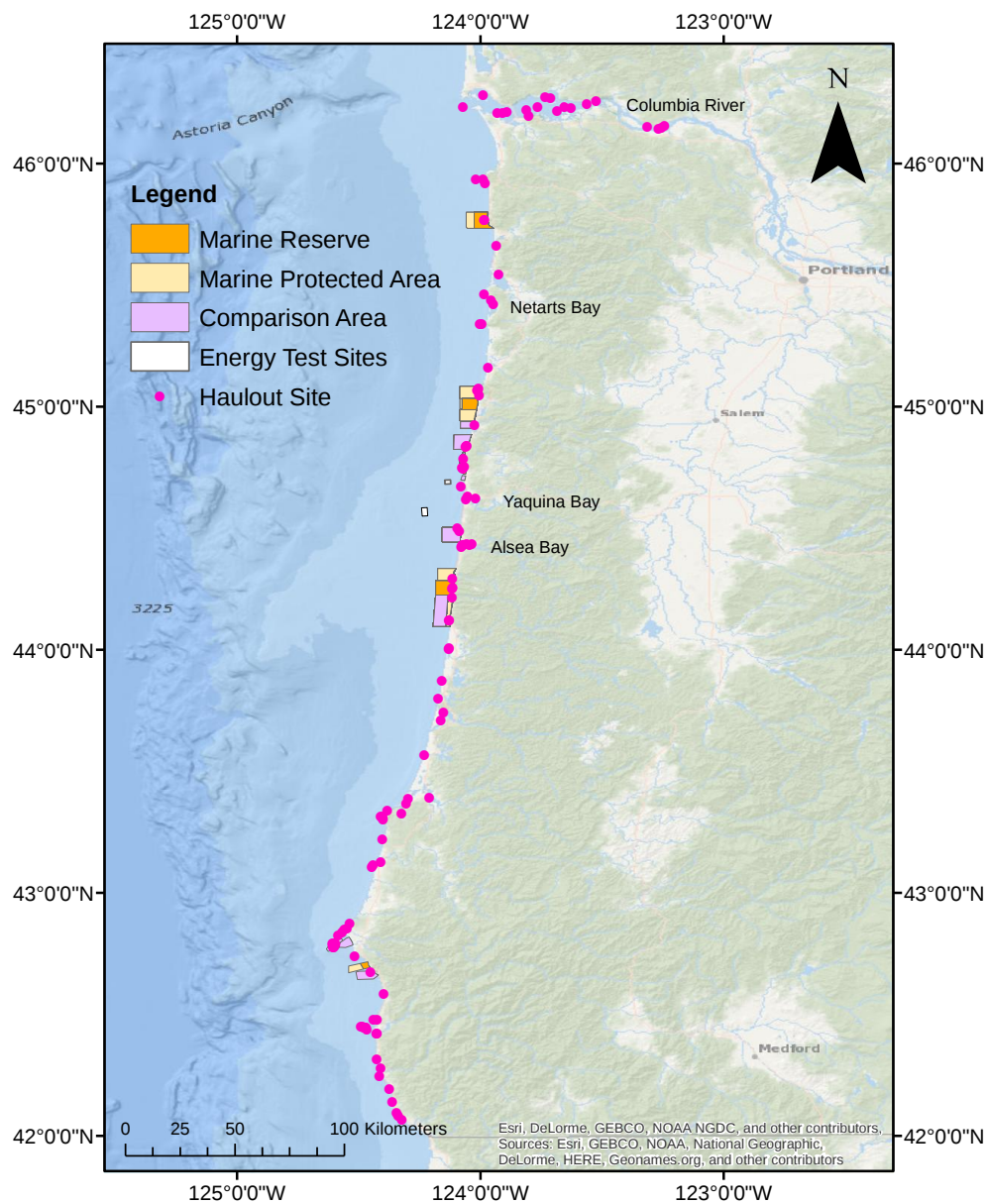


Figure I.1. Map of the Oregon Coast, including surveyed harbor seal haulout sites (2008) from Oregon Department of Fisheries and Wildlife Marine Mammal Program, marine reserves ( $n = 5$ ), marine protected areas ( $n = 8$ ), comparison areas ( $n = 10$ ), and Wave Energy Test Sites ( $n = 2$ ).

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CHAPTER 1 – SPATIAL HABITAT USE AND UTILIZATION OF MARINE  
RESERVES BY PACIFIC HARBOR SEALS (*PHOCA VITULINA RICHARDII*) IN  
THE NORTHERN CALIFORNIA CURRENT SYSTEM

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## ABSTRACT

Predator-prey interactions are an important aspect of marine reserve development in an ecosystem-based management framework. Pacific harbor seals (*Phoca vitulina richardii*) are a common marine predator off the Oregon coast, and unlike other species of pinnipeds, are reliably present year-round without undertaking annual migration. Their use of marine protected areas (MPAs) and energy development sites may thus influence community structure via top-down forcing. Beginning in 2012, five marine reserves have been established within the Oregon Territorial Sea.

Currently, the relative utilization of these areas by marine mammals is not well known. Using satellite telemetry, I examined how Pacific harbor seals (n=24) used these marine reserves relative to other areas of the Oregon coast. Data revealed widespread use of the continental shelf area (3,040km<sup>2</sup>, mean individual home range =  $364.47 \pm 382.87\text{km}^2$ ), but tagged animals did not travel north of the Columbia River or further south than Florence, Oregon (43.7788°N to 46.2682°N). Despite marine reserves representing a potentially food-rich, nearshore habitat for seals without fisheries competition, animals only spent a collective total of 1.33% of their time within marine reserves. Animals also did not demonstrate significant utilization of two planned or newly established fixed and moored wave energy platforms at the time of study.

This study represents the first comprehensive analysis of at-sea space use and home range extent for Pacific harbor seals in Oregon. Our results provide a baseline for marine mammal use of newly developed anthropogenic and management-oriented spatial development the Oregon coast; notably, limited use of reserves and wave energy sites. This research represents the first major documentation of the spatial ecology of harbor seals in the state for nearly three decades.

*Keywords: Pacific harbor seal, marine mammal, spatial habitat use, northern California Current System, satellite telemetry, marine reserves, Oregon coast*

## INTRODUCTION

The geomorphology of the Oregon coastal marine habitat lends itself to dynamic biological processes, including strong annual upwelling events (Checkley & Barth, 2009; Connolly et al., 2010), a continental shelf with a high degree of variability in longitudinal extent from the shoreline (Byrne, 1962), and strong seasonal and inter-annual productivity (Checkley and Barth 2009). The California Current System is one of four major Eastern Boundary Current Systems on the planet. Eastern Boundary Current Systems supply approximately 20% of global fishery landings, making them especially important for biodiversity and fisheries production (Pauly & Christensen, 1995). Since 2012, five marine reserves have been established in this system off the Oregon coast, along with eight marine protected areas, one seabird protection area, and nine associated comparison areas (Figure 1.1). These reserves and protected areas are subject to varying levels of management, the most stringent being within marine reserves, which are no-take areas reserved as ‘living laboratories’ for conservation and research. Oregon’s marine reserves, protected areas, and comparison areas occupy approximately 9.3% of the Oregon territorial sea (ODFW, *unpub. data*). Comparison areas are regions near reserves open to fishing which act as control sites for designated reserve areas.

The use of these reserves in Oregon by marine mammals is not well-documented, but may have implications for ecological functioning of these areas (Pinnegar & Polunin, 1999). For example, directed red abalone (*Haliotis rufescens*)

conservation goals for marine reserves in California were negated due to the fact that more abalone were consumed by sea otters (*Enhydra lutris*) than would have been harvested under previous fishing pressure (Fanshawe, Vanblaricom & Shelly, 2003). Additionally, trophic cascades and increased predator abundance have been noted for several established reserve networks globally (Graham, Evans & Russ, 2003; Shears & Babcock, 2003; Guidetti, 2006). Marine mammals also have the capacity to act as ecological indicators of functioning and priority species for effective establishment of marine protected areas, depending on conservation goals (Bailey & Thompson, 2009; Cordes et al., 2011).

An additional emerging spatial use issue in the northern California Current System is the development of renewable, alternative energy platforms including wave energy. There are currently two wave energy platform testing areas off the Oregon coast, the North Energy Test Site (NETS) and the South Energy Test Site (SETS). The NETS is located northwest of Newport, Oregon at 45-55m depth, and encompasses an area of approximately 1 nm<sup>2</sup> at 44.6899 °N and 124.1346 °W (Dallman & Neary, 2014). The SETS site was first used in 2017 and is located approximately 12.8km offshore, southwest of Newport, OR. The development of wave energy arrays is of biological significance as it has been shown that marine mammals, specifically harbor seals (*Phoca vitulina richardii*), can utilize anthropogenic structures at sea as foraging grounds due to their potential to act as ‘fish aggregators’ (Russell et al., 2014a). Understanding the effects of installing and developing these devices necessitates the

collection of baseline data prior to installation, as well as long-term monitoring along the Oregon coast.

Pacific harbor seal haulouts can be found throughout the entirety of the Oregon coast in more than 90 locations (Brown et al., 2005a; ODFW, 2017). These areas include bays, spits, abandoned anthropogenic structures, mud flats and rocky intertidal zones. Harbor seals are small phocid seals that generally dive within their relatively small aerobic dive limit (Bigg, 1981; Boyd & Croxall, 1996). They tend to forage nearshore on the continental shelf on a wide variety of potential prey items with strong inter-individual variability in prey resource emphasis, use of benthic habitat, and spatial use (Temte & Wiig, 1991; Lance & Jeffries, 2007; Blanchet et al., 2014; Steingass, 2017a). While in some cases they utilize multiple haulouts, harbor seals generally demonstrate a high degree of regional fidelity as documented in previous studies (Pitcher and McAllister 1981; Yochem Stewart et al. 1987; Thompson and Miller 1990; Suryan 1995; Watts 1996).

Pacific harbor seals are a prevalent generalist and upper trophic marine predator in the Northern California Current System. Unlike other species of pinnipeds, they are reliably present in the region year-round and do not undertake annual migrations. The most current population estimates suggest approximately 11,565 harbor seals inhabiting the Oregon coast (B. Wright ODFW 2017, *pers. comm*, and approximately 13,692 are present within Washington State (Huber et al., 2001). Despite rebounded populations, at-sea habitat use of Pacific harbor seals has not been

recently been examined south of the Columbia River and North of Cape Mendocino, particularly within the State of Oregon. While the population distribution (Newby, 1971, 1973; Dishman, 2011), foraging ecology (Bowen, Boness & Iverson, 1999; London, Lance & Jeffries, 2002; Austin et al., 2006a) and dietary composition (Bowen et al., 2002a; Lance et al., 2012) for harbor seals have been well-studied in the highly diverse Washington, California (Eguchi & Harvey, 2005; Grigg et al., 2009; Scordino, 2010; Germain et al., 2012) and Alaska (Bishop 1967; Pitcher & Calkins, 1979; Laake et al., 2002; Zhao & Schell, 2004; Mathews & Pendleton, 2006; Womble, Gende & Blundell, 2007), the only current existing data for harbor seals in Oregon relates to scatological dietary studies (Graybill, 1981; Brown & Mate, 1983; Roffe & Mate, 1984; Beach et al., 1985; Riemer et al., 1997; Orr et al., 2004a; Wright et al., 2007), or visual and radio telemetry observations (Brown et al., 2005a; Wright et al., 2007). One satellite telemetry study is available (Brown, Jeffries & Wright, 2013), but was restricted to tagging within, and movements proximal to the Columbia River basin. With a lack of existing information regarding at-sea habitat utilization in Oregon and the new development of management areas and nearshore anthropogenic structures, a clear need exists for current data regarding harbor seal habitat use and ecology in the North Pacific, particularly for the Oregon coast in order to inform effective management of the coastal ocean and oceanographic resources in this region.

Here, I aim to 1) define and describe individual home range and core areas along the Oregon coast for Pacific harbor seals, 2) quantify harbor seal utilization of

key areas of management interest, including marine reserves and wave energy test sites, and 3) to describe general spatial use for harbor seals in this poorly described region of their range.

## MATERIALS AND METHODS

### *Capture and tagging*

Adult Pacific harbor seals (23 males, one female) were captured in Alsea (44.4279°N, 124.0679°W, n=16) and Netarts (45.4028°N, 123.9484°W, n=8) Bays on the coast of Oregon, in September 2014, 2015 and April 2015 (Table 1.1). The female was included in data analysis as her total deployment days, home range area, and trip metrics fell well within the range of other sampled animals. Adult seals >50 kg were targeted as ideal study animals to reduce variability in behavior related to growth, reproductive energetic allocation, and sex-specific foraging behaviors, and male seals were targeted in spring to avoid interacting with pregnant or nursing females. Seals were captured with skiff-based purse seine or beach rush methods by teams of 5-13 biologists including veterinary staff (Jeffries, Brown & Harvey, 1993). Seals were individually weighed in hoop nets suspended from a tripod with a 0 – 200 x 1.0 kg hanging scale in all but two cases, then restrained on a v-board during tag attachment. All seals were given a numbered tag in each hind-flipper (Deflux sheep and goat ear tags, 2.25x7/8inch, 5g.) punched through the interdigital skin for visual identification. An external Wildlife Computers Satellite SPOT5© tag was attached to the post-cranial

dorsal pelage with Devcon© 5-minute epoxy or Loctite© 422 adhesive (Thomton et al., 2008). SPOT5 tags are Argos transmitters that allow the satellite service provider (CLS America Inc.) to estimate locations via the Doppler shift in sequential transmissions. Locational data are provided with associated classes for an estimated accuracy ranging from 150m (LC3) to >1.5km (LCB), or with an unspecified error (LC Z) (Hebblewhite & Haydon, 2010).

### *Tag Programming*

During the first two deployment periods (fall 2014, spring 2015), tags were duty cycled on an on-off monthly cycle to provide a longer period of data, and promote data overlap between tag deployments (Table 1.2). Tags were sequentially set to ‘ON’ during April through May and September through October to coincide with the spring and fall transitions of upwelling (Chan et al., 2008). Tags deployed in fall 2015 were programmed to transmit continuously to maximize total data overlap with previous deployments. Tags were programmed to begin transmission to the Argos satellite array when at the surface following initial immersion in salt water. To extend battery life and to avoid over-representation of haulout periods, tags were programmed to reduce transmission rate after 10 consecutive ‘dry’ transmissions, and to suspend transmitting after two hours of being dry.

### *Parameter Estimation*

After tags ceased transmitting, all data collected by the Argos satellite service provider CLS America, Inc. during deployment were downloaded via the Wildlife Computers Data Portal (© Wildlife Computers). Locations with a quality of LC 0-3, A and B were first manually filtered to remove duplicate locations. LC-Z locations were discarded due to lack of a measurable error estimate. Maximum swim speed for Pacific harbor seals is not widely documented; however minimum cost of transport occurs at approximately 1.0-1.4m/s (Davis, Williams & Kooyman, 1985). Therefore, a coarse speed-distance-angle filter was applied to the data in order to remove locations which required a biologically unlikely travel speed of >8m/s. The remaining data were used to create regularized tracks for each animal using the R package *crawl* (Johnson et al., 2008; Johnson, 2017). To create a roughly equal ratio of estimated to observed locations, time steps were calculated as the average time between consecutive ‘wet’ locations, as determined by the Argos 20-minute timeline. On-land points were not considered for this calculation. The resultant mean inter-location period was  $1.52 \pm 9.83$  hours. Therefore, a temporal resolution of one hour was used for the generation of regularized SSM points for analysis. SSM output locations were further adjusted by utilizing the Fix-Path function in the R package *crawl* (Johnson et al., 2008). Fix-Path utilizes a transition matrix to correct animal tracks to restrict travel through identified restricted areas, in this case over land. Once the state-space modeled and the filtered dataset was generated, the resultant SSM-derived locations were used for all further analyses.

### *Kernel Density Analysis*

Kernel analysis was used to estimate individual utilization distributions (UD) for each animal at the 95% isopleth, and subsequently every tenth isopleth from 10-90% using the Geospatial Modeling Environment (Beyer, 2015). Home range was quantified as the 95% utilization isopleth (Worton, 1989). Home range area was calculated for the population as a whole, and for individuals. Core area was calculated using methods from Vander Wal and Rodgers (2012) in order to determine a core area therein where area size continues to increase, but intensity of use (IU) reaches an asymptote., rather than using the standard 50% utilization distribution by default (Anderson, 1982). To generate this threshold, I utilized an exponential equation to identify the isopleth at which home range area, defined as the 95% utilization distribution began to increase at a greater rate than probability of use (Vander Wal & Rodgers, 2012). Core isopleths and area of core spaces were calculated for the population as a whole and separately for individuals. Core area was rounded down to be slightly conservative and encompass the nearest calculated 10% isopleth. Additionally, a relative intensity of use ( $I$ ) value was calculated which referred to the isopleth value associated with the boundary of the core area. An  $I$  value of  $>1$  indicates that the core area is being used more intensely than the remaining home range, but if this value was  $<1$ , there was assumed to be no distinct core area for an individual (Vander Wal & Rodgers, 2012). To determine how calculated home range

size (95% UD) was affected by the number of locations and deployment duration, a linear model of  $\log(95\% \text{ UD (km}^2\text{)})$  as a function of these two factors was created.

#### *Use of Marine Reserves, Riverine, and Estuarine Locations*

The use of potentially biologically important habitat characteristics was examined, including use of marine reserves, marine protected areas (MPAs), seabird protection areas, and comparison areas. The coordinates of all marine reserves, protected areas, and comparison areas were provided by the Oregon Department of Fisheries and Wildlife. The coordinates for the NETS and SETS (north and south wave energy test sites) south and north of Newport, Oregon, were also used to determine utilization of these sites by seals. In order to determine whether the use of marine reserves was more likely relative to 1) distance from haulout, 2) reserve area size, or 3) management category, a generalized linear model was created with individual percent presence within marine reserves as a function of area size, distance from haulout, and management designation. This was examined strictly for Alsea Bay seals' SSM-derived locations as all Netarts Bay animals only cumulatively demonstrated two locations (<0.10%) within reserves.

Inland waters (estuaries, bays or rivers) were defined as the area within the two farthest points of shore for each bay or river, including jetties. All points within these areas were considered 'inland' while all other points were considered 'at sea', regardless of wet or dry status. Utilization of inland waters was divided into

presence/absence and presence was further divided into wet/dry status, indicating time in water or hauled out. Excluded from this analysis were the final two trips from seal #61779, which spent winter within the Columbia River region, resulting in a lack of data for this period due to lack of salt water to activate the tag. Area use for bays, rivers, and management areas was calculated using the spatial join feature in ArcGIS, and calculated as percentage of total points per individual inside a feature. Total hours spent within these locations was also calculated. Trips within and outside of areas of interest were identified by two different criteria. First, foraging trips after leaving the haulout were calculated by identifying the first ‘wet’ SSM-derived location within a transmission period, and the last consecutive SSM-derived location with a ‘wet’ status before a ‘dry’ status was the trip end. Secondly, trips between inland waters were also calculated to quantify wet vs. dry (hauling out) utilization of bays, rivers and estuarine habitats. For all trips, trip duration (hours) and total distance traveled (km) were calculated as was mean and range in latitude (decimal degrees), and mean distance from shore (km).

Points were categorized as ‘present’ or ‘absent’ within four marine reserve areas (Cape Falcon, Cascade Head, Otter Rock, Cape Perpetua) and 11 inland water areas, including the Columbia River, Nehalem Bay, Tillamook Bay, Netarts Bay, Sandlake, Nestucca Bay, Siletz Bay, Depoe Bay, Yaquina Bay, Alsea Bay, and the Siuslaw River. Maximum and average distance from shore, total latitudinal travel distance, and the total distance traveled for each animal was calculated using ArcGIS.

## RESULTS

Tags transmitted for a mean  $\pm$  SD of  $130.25 \pm 82.16$  days. The minimum period of data collection for one tag was 20 days and the maximum period of data collected was 324 days on an alternating duty cycle which excluded the months of January, March, June, August and November for 2014 and 2015 (Table 1.2). 14% of raw locations were removed by applying a speed-distance-angle filter with a burnout (discard) of two locations at inception and end of transmission periods for each animal. Crawl was then applied to the remaining points, and a resultant 57,220 SSM hourly points were generated and corrected with FixPath. The average number of state-space modeled locations per animal totaled  $2385.17 \pm 1182.56$ .

In total, the cumulative 95% utilization distribution of all animals was 3,040km<sup>2</sup>, with a latitudinal range of (43.78 °N, 46.27°N) and a longitudinal range of (-124.96 °W, -123.83°W) (Figure 1.2). Utilization of the continental shelf was nearly exclusive, with only 0.24% of modeled locations occurring at depths greater than 200 meters. 85.34% of locations were within 10km of shore, 44.99% were within one km from shore, and 70.51% of modeled locations were within 10 kilometers of the 50 meter isobath.

### *Kernel Density Estimation*

Kernel density analysis revealed highly individualistic characteristics of habitat use by seals (Table 1.3). The mean individual home range area (95% UD) was  $364.47 \pm 382.87 \text{ km}^2$ . Animals tagged in Alsea Bay had a significantly larger home range than animals tagged in Netarts Bay (t-test  $p$  value = 0.028) (Figures 1.3, 1.4). Core area on average represented  $29.41 \pm 29.23 \text{ km}^2$  or  $11.2\% \pm 19.3\%$  of home range area for each site respectively. On average, the core area represented the 53% utilization distribution. One seal, #61773, had such a small overall home range ( $3.20 \text{ km}^2$ ) that no core area could be calculated. For all animals except for #61773, the relative intensity of use, or  $I$  value was  $>1$ , suggesting intensive use. This varied from a value of 2.41 to 59.51, and was on average  $12.8 \pm 14.9$ . Home range area was not related to total deployment days and number of locations ( $p$  value = 0.6079) (Table 1.4).

### *Intersite Differences*

Average point distance from shore in kilometers varied significantly for individuals from different tagging locations in a Welch's two-sample t-test ( $p$  value = 0.004, 95% CI = 1.91-8.74), whereas median distance did not ( $p$  value = 0.1638). Animals captured in Alsea Bay were more variable, but on average spent more time farther from shore ( $6.84 \pm 6.31$ ) than Netarts Bay animals ( $1.51 \pm 0.95$ ). Only 143 (0.25%) of the SSM locations were located beyond the 200m isobath, correlated with the continental shelf. Additionally, the farthest south any animal ventured was  $44.78^\circ\text{N}$ , and the farthest north any animal traveled was  $46.27^\circ \text{N}$  at the Columbia

River. Alsea Bay seals traveled farther during the deployment period than seals tagged in Netarts Bay ( $3189.34 \pm 1110.47\text{km}$  vs.  $1735.04 \pm 1121.55\text{km}$ , Welch's t-test  $p$  value = 0.0095). Alsea Bay seals did not travel significantly more kilometers per 24-hour period than seals tagged in Netarts Bay ( $27.73 \pm 11.68$  vs.  $19.90 \pm 14.17$ , Welch's t-test  $p$  value = 0.2015).

#### *Utilization of Inland Waters*

In total, 46.70% of all locations were within one of eleven inland waters. More specifically, 23.44% of all locations were present within Alsea Bay. Three animals tagged in Alsea Bay also visited Netarts Bay. Netarts Bay accounted for 6.01% of all locations, and points within Tillamook Bay directly north of Netarts Bay accounted for 7.5% of all locations. These three bays accounted for 36.95% of all data.

Within bay and riverine environments, seals spent an average of 70.88% of their time in the water, and the remainder of that period on land (dry). Seals spent an average of  $26.96 \pm 15.91$  hours per 'wet' trip (in the water), returning to haul out for an average of  $9.43 \pm 28.41$  hours.

Examining use of inland waters vs. open ocean, animals made 1,618 trips (individual average =  $67.42 \pm 42.35$ ) within the boundaries of inland waters during the tag deployment period, spending an average duration of  $17.24 \pm 80.95$  hours within these areas, followed by  $22.00 \pm 24.66$  hours in open water. In total, seals spent an

average of  $73.11 \pm 10.70\%$  of their time ‘wet’ within bay, riverine, and estuarine sites. The large amount of variation for inland trips was largely driven by animal #44611.

### *Utilization of Marine Reserves and Alternative Energy Sites*

The most commonly used marine reserve was Cape Perpetua, approximately 15km south of Alsea Bay, where 1.17% of total locations occurred. This presence is accounted for primarily by two individuals, PTT #44611 and #61771, which spent 28.65% and 18.16% of their time, respectively within this area. Both animals were initially tagged in Alsea Bay. All other animals that utilized Cape Perpetua spent less than 3.00% of their time within the boundaries of the reserve (Table 1.5).

In total, 1.33% of all state space modeled locations occurred within designated reserves. All northern management areas (excluding Redfish Rocks Marine Reserve and Marine Protected Area, McKenzie Comparison Area, Orford Reef Comparison Areas, and Humbug Comparison Area) fell within the home range of Alsea Bay seals; however, Cape Falcon Marine Reserve and West Marine Protected Area only fell within the home range of one Netarts Bay animal, #61774. On average, each animal visited marine reserves  $5.08 \pm 10.02$  times, and spent an average of  $6.36 \pm 10.73$  hours per trip in these areas. In examining the significance of management area size, distance to haulout, and area type in a series of generalized linear models, backwards AIC model selection via the *stepAIC* function resulted in the null model being selected (Table 1.6). As of the time of data collection, there was only one modeled location

from an animal (#44614, Alsea Bay) present within the South Energy Test Site, and no locations within the North Energy Test Site (Figure 1.1).

## DISCUSSION

This data set highlighted respective regions of high use by animals from both Netarts and Alsea Bays, Oregon, including marine reserve areas, open ocean, and inland waters. In this examination of the utilization of marine reserves, protected areas, and comparison areas by Pacific harbor seals in Oregon, only 2 of 24 animals in this sample were present in marine reserves more than 10% of the time. This was contrary to expectations as marine reserves represent a potentially food-rich nearshore foraging environment (Polunin & Roberts, 1993; Halpern & Warner, 2002; Willis, Millar & Babcock, 2003).

Our data, while based on a limited sample size of 24 animals, did not provide any evidence of preferential or intensified use of protected areas. This could be due to multiple factors. First, there may be no effective differences in ecological functioning for new reserves that are biologically relevant for harbor seals. For example, any potentially significant effects of marine reserve establishment may not have been statistically detectable due to a small sample size relative to the high degree of inter-individual variability masking a measurable response.

Low marine protected areas and reserve utilization by harbor seals may also reflect a lack of abundance of prey in sizes preferred by seals (Lester et al., 2009).

Harbor seals are generally benthic foragers, consuming prey on an average of 10-16cm (Tollit, Greenstreet & Thompson, 1997). Conversely, fish collected in hook and line surveys within management areas by the Oregon Department of Fish and Wildlife in fall 2016 were an average of 40.53cm (ODFW, *unpub. data*), roughly 2.5 to 4 times the size of preferred prey. This could be due to the nature of the survey method, but could also represent why Oregon's marine reserves may not be ideal foraging grounds for harbor seals. Whether this is due to effects of marine reserve establishment or just the hydrology and biology of the area remains to be examined. Lastly, effects of marine reserves may not be quantifiable until after a time lag that has not yet been completed. For example, in a review of 31 tropical and temperate marine reserves, Micheli et al. (2004) found that marine reserves established for  $\geq 10$  years demonstrated community responses four times greater than those reserves  $< 10$  years post-designation. Additionally, community responses to reserve establishment were strongly divergent, and sometimes demonstrated negative effects, potentially due to shifts in predation pressure. Babcock et al. (2010) also noted that direct effects of reserves on marine communities took an average of 5.13 years to be measurable; however indirect effects, potentially related to trophic cascades, took much longer (13.1 years on average) (Babcock et al., 2010). On a decadal timescale, Oregon's marine reserves first established in 2012 may not have demonstrable effects in this regard until at least 2022.

Two animals used marine reserves more than 10% of the time; #44611, tagged in Alsea Bay in Spring 2015; and #61771, tagged in Alsea Bay in Spring 2015. The other animals used these areas cumulatively 5.69% of the time. The majority of marine reserve use was within Cape Perpetua Marine Reserve, suggesting this may be due to both geographic proximity to haulout and the highly productive nature of Heceta Bank on which it is located. Cape Perpetua Marine Reserve is approximately 11.09 km from Alsea Bay, making it reachable within a daily foraging trip. However, it should be noted that distance was not selected as a significant driving factor for marine reserve use, nor was area size in the backwards generalized linear model selection. Therefore, the mechanisms for individual use of reserves are yet undefined for this area. Additionally, this study focused on primarily adult male animals, leaving a resultant lack of data for females, including pregnant or nursing females, or juvenile animals. Only one animal in this study utilized or visited either the North Energy Test Site (NETS) or South Energy Test Site (SETS) wave energy platforms, providing a baseline of limited use that can be re-examined in the future in terms of use of anthropogenic structures by marine mammals. Installation of these and additional structures in the long-term may increase marine mammal use of the nearby area as a result of increased abundance of prey near artificial fish aggregating devices, resulting in potential conflicts (Russell et al., 2014a).

The spatial habitat utilization of animals in this study fell within the general expectations of spatial behavior for Pacific harbor seals, as well as other subspecies

(Bjørge et al., 1995; Womble, 2012; Dietz et al., 2013). In Alaska, regional harbor seal MCP areas ranged from as little as 66.2 km<sup>2</sup> in the Icy Strait to 7885.1 km<sup>2</sup> in the Gulf of Alaska (Womble, 2012). Throughout their range, harbor seals are generally observed in nearshore areas and are associated with estuarine habitats (Brown & Mate, 1983; Orr et al., 2004b; Wright et al., 2007; Steingass & Horning, 2017a). Our results suggest that seals along the OR coast allotted similar amounts of time to hauling out as southern conspecifics in California (Yochem et al., 1987), subject to the same tidal cycles as Oregon.

While migration and potential multi-day use of open sea areas was documented for harbor seals in Glacier Bay National Park (Womble & Gende, 2013), animals in this and other studies did not display long-distance migration behavior (Thompson et al., 1996). The majority of existing data regarding Pacific harbor seal movement is present within Alaska and Glacier Bay's dynamic coastal geography, making inter-regional comparison difficult. Additionally, examination of harbor seal use of marine reserves was conducted by Womble and Gende (Womble & Gende, 2013), within one of the world's largest marine mammal protection areas. In contrast to Glacier Bay, the Oregon marine reserve system is composed of a series of small reserves, protected areas, and comparison areas that are ecologically focused on protection of fish species, rather than marine mammals.

Harbor seals in this study utilized a large proportion of the continental shelf region north of Cape Blanco, OR and south of the Columbia River. Animals in this

study were confirmed as nearshore foragers, with the majority of all locations within 10km of shore. Furthermore, nearly half this time was within bay, river and estuarine environments, including in-water and land use. Animals did not appear to migrate during the study period, but one animal (#61779) wintered in the Columbia River in 2015-16.

Animals were somewhat individually variable in behavior, but significant behavioral differences were measurable between the two tagging locations of Alsea Bay and Netarts Bay, including latitudinal range, distance from shore, home range and core area. The geomorphology of the narrow continental shelf near Netarts Bay (approximately 20km) and wider Heceta Bank (approximately 55km) directly southwest of Alsea Bay was likely a contributing factor. The home range and core areas between individuals had a high standard deviation, suggesting inter-individual differences that have also been demonstrated in previous studies of harbor seals (Small et al., 2005).

Open ocean trips lasted approximately 22 hours, revealing a pattern of foraging that matched roughly with the 24.83hr tidal cycle in the eastern North Pacific (Bruce, 1959). Variance was likely driven by differences in use of offshore waters, seasonality, and foraging strategy. Considering the size of the harbor seal population in the Northern California Current System, as well as in Oregon alone, the sample size of this study was relatively small (0.2% of the total estimated Oregon coastal stock). However, while the total travel distance increased with the total number of locations

gathered, as would be expected, the home range area did not increase with sample size. Therefore, it appears that the sample deployment period was adequate for capturing individual variability in behavior, as well as the overall home range for individuals.

Overall, this multi-annual study revealed a wide range of previously undocumented habitat use for a single species of generalist marine mammal in the northern California Current System, and a baseline for marine mammal use of wave energy sites and marine reserves off the Oregon coast. Animals were demonstrated as continental shelf foragers, and utilization of marine reserves by harbor seals was limited and not driven by the factors of distance to haulout, area size, or management type (reserve, protected area, and comparison area). Although not designed specifically as such, lack of travel to other states rendered this an in-depth examination of the utilization of the Oregon coast by Pacific harbor seals. The data presented here lends itself to future comparative analysis of marine mammal telemetry data in Oregon and the Pacific Northwest, and highlights the need for mechanistic understanding of behavioral diversity in a common marine predator in the northern California Current System.

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#### ETHICS APPROVALS

This study was carried out in strict compliance with all applicable animal care and use guidelines under the U.S. Animal Welfare Act and was approved as required under the U.S. Marine Mammal Protection Act by the National Marine Fisheries Service (NMFS #16991) and by the Institutional Animal Care and Use Committees of San Jose State University (AUP #1010) and Oregon State University (ACUP #4616).

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## TABLES AND FIGURES

Table 1.1. Individual animal ID, capture location and season, total period of transmission, and resultant locations after applying a regularized state space model.

| PTT (ID#) | Body Mass (kg) | Capture Location | Capture Season | Capture Year | Deployment Period (Days) | SSM Locations |
|-----------|----------------|------------------|----------------|--------------|--------------------------|---------------|
| 61694     | 84             | Alsea            | Fall           | 2014         | 111                      | 1927          |
| 61695     | 82             | Alsea            | Fall           | 2014         | 212                      | 2848          |
| 61764     | 66             | Alsea            | Fall           | 2014         | 172                      | 2661          |
| 61765     | 77             | Alsea            | Fall           | 2014         | 231                      | 3288          |
| 61766     | 55             | Alsea            | Fall           | 2014         | 264                      | 4114          |
| 61767     | 57             | Alsea            | Fall           | 2014         | 250                      | 3759          |
| 61768     | 90             | Netarts          | Fall           | 2014         | 112                      | 1956          |
| 61769     | 70             | Netarts          | Fall           | 2014         | 159                      | 2332          |
| 61774     | 87             | Netarts          | Fall           | 2014         | 112                      | 1967          |
| 61775     | 82             | Netarts          | Fall           | 2014         | 324                      | 4208          |
| 61776     | 68             | Netarts          | Fall           | 2014         | 51                       | 1227          |
| 44611     | 108            | Alsea            | Spring         | 2015         | 56                       | 1330          |
| 44613     | 71             | Alsea            | Spring         | 2015         | 143                      | 3425          |
| 44614     | 69             | Alsea            | Spring         | 2015         | 116                      | 2786          |
| 44615     | 53             | Alsea            | Spring         | 2015         | 44                       | 1039          |
| 61698     | 116            | Alsea            | Spring         | 2015         | 56                       | 1339          |
| 61754     | 98             | Alsea            | Spring         | 2015         | 112                      | 2679          |
| 61770     | 86             | Alsea            | Spring         | 2015         | 96                       | 2292          |
| 61771     | 105            | Alsea            | Spring         | 2015         | 42                       | 991           |
| 61772     | 104            | Netarts          | Spring         | 2015         | 66                       | 1587          |
| 61773     | 112            | Netarts          | Spring         | 2015         | 65                       | 1543          |
| 61777     | 98             | Netarts          | Spring         | 2015         | 20                       | 474           |
| 61778     | NA             | Alsea            | Fall           | 2015         | 89                       | 2133          |
| 61779     | NA             | Alsea            | Fall           | 2015         | 222                      | 5315          |

[illegible]

Table 1.3. Table of home range (95% isopleth), core area (Eq. 3), core isopleth (0.1-0.95), proportion core (core area (km<sup>2</sup>) / home range area (km<sup>2</sup>) \* 100), isopleth volume (rounded down to achieve core isopleth), and intensity of use (Eq. 4) for each animal.

| PTT   | Home Range Area (km <sup>2</sup> ) | Core Area (km <sup>2</sup> ) | Core Isopleth | Proportion Core (%) | Isopleth Vol. (%) | Intensity of Use |
|-------|------------------------------------|------------------------------|---------------|---------------------|-------------------|------------------|
| 44611 | 582.62                             | 30.40                        | 0.50          | 0.05                | 0.53              | 10.15            |
| 44613 | 112.87                             | 1.28                         | 0.40          | 0.02                | 0.48              | 42.57            |
| 44614 | 318.22                             | 70.04                        | 0.60          | 0.13                | 0.66              | 2.98             |
| 44615 | 164.12                             | 1.33                         | 0.40          | 0.03                | 0.48              | 59.51            |
| 61694 | 287.04                             | 17.90                        | 0.50          | 0.06                | 0.57              | 9.14             |
| 61695 | 1647.93                            | 87.01                        | 0.50          | 0.05                | 0.54              | 10.27            |
| 61698 | 363.41                             | 18.95                        | 0.50          | 0.05                | 0.58              | 11.22            |
| 61754 | 1198.02                            | 96.89                        | 0.50          | 0.08                | 0.58              | 7.20             |
| 61764 | 519.53                             | 79.78                        | 0.60          | 0.08                | 0.62              | 4.01             |
| 61765 | 385.58                             | 3.15                         | 0.30          | 0.02                | 0.36              | 43.87            |
| 61766 | 526.24                             | 23.62                        | 0.50          | 0.04                | 0.56              | 12.52            |
| 61767 | 187.33                             | 12.80                        | 0.50          | 0.07                | 0.53              | 7.80             |
| 61768 | 45.23                              | 2.26                         | 0.50          | 0.05                | 0.58              | 11.61            |
| 61769 | 179.10                             | 35.88                        | 0.60          | 0.11                | 0.64              | 3.22             |
| 61770 | 430.09                             | 31.48                        | 0.50          | 0.07                | 0.58              | 7.90             |
| 61771 | 229.97                             | 66.33                        | 0.60          | 0.19                | 0.69              | 2.41             |
| 61772 | 96.75                              | 5.67                         | 0.50          | 0.06                | 0.55              | 9.47             |
| 61773 | 3.20                               | 3.20                         | 0.95          | 100.00              | 1.00              | 1.00             |
| 61774 | 713.83                             | 42.98                        | 0.50          | 0.06                | 0.54              | 8.92             |
| 61775 | 50.83                              | 9.26                         | 0.60          | 0.07                | 0.62              | 3.40             |
| 61776 | 65.87                              | 9.69                         | 0.60          | 0.10                | 0.61              | 4.16             |
| 61777 | 124.15                             | 21.62                        | 0.60          | 0.10                | 0.64              | 3.68             |
| 61778 | 121.03                             | 21.71                        | 0.60          | 0.14                | 0.63              | 3.49             |
| 61779 | 394.26                             | 12.73                        | 0.40          | 0.06                | 0.46              | 14.13            |

Table 1.4. Linear model of log home range area (km<sup>2</sup>) for an individual animal versus total individual days of tag deployment and total individual modeled locations. Home range was not significantly correlated with these factors, suggesting that the deployment period was adequate to capture individual variability in space use.

|   | Response Variate               | Model                         | Intercept $\pm$ SE | Rsq   | Adj Rsq | <i>p</i> -value |
|---|--------------------------------|-------------------------------|--------------------|-------|---------|-----------------|
| 1 | log(95% UD (km <sup>2</sup> )) | TotalDays + TotalSSMLocations | 4.781 $\pm$ 0.630  | 0.047 | -0.437  | 0.6079          |

Table 1.5. Relative percent of time present within four marine reserves in Oregon. There was no presence within or near the Redfish Rocks Marine Reserve, which was subsequently excluded from analyses. Bold text represents animals tagged in Alsea Bay, standard text represents animals tagged in Netarts Bay.

| <i>Ptt</i>   | <i>Total #<br/>Locations</i> | <i>Cape<br/>Falcon</i> | <i>Cape<br/>Perpetua</i> | <i>Cascade<br/>Head</i> | <i>Otter<br/>Rock</i>     | <i>Total<br/>Reserve Use</i> |
|--------------|------------------------------|------------------------|--------------------------|-------------------------|---------------------------|------------------------------|
| <b>44611</b> | <b>1330</b>                  |                        | <b>32.63<br/>(n=434)</b> |                         |                           | <b>32.63<br/>(n=434)</b>     |
| <b>44613</b> | <b>3425</b>                  |                        |                          |                         |                           |                              |
| <b>44614</b> | <b>2786</b>                  |                        |                          |                         |                           |                              |
| <b>44615</b> | <b>1039</b>                  |                        |                          |                         |                           |                              |
| <b>61694</b> | <b>1927</b>                  |                        | <b>1.61 (n=31)</b>       |                         |                           | <b>1.61 (n=31)</b>           |
| <b>61695</b> | <b>2848</b>                  | <b>0.42<br/>(n=12)</b> |                          | <b>0.35<br/>(n=10)</b>  |                           | <b>0.77 (n=22)</b>           |
| <b>61698</b> | <b>1339</b>                  |                        | <b>0.15 (n=2)</b>        |                         |                           | <b>0.15 (n=2)</b>            |
| <b>61754</b> | <b>2679</b>                  |                        |                          |                         | <b>0.11<br/>(n=3)</b>     | <b>0.11 (n=3)</b>            |
| <b>61764</b> | <b>2661</b>                  |                        | <b>2.52 (n=67)</b>       |                         |                           | <b>2.52 (n=67)</b>           |
| <b>61765</b> | <b>3288</b>                  |                        | <b>0.06 (n=2)</b>        |                         |                           | <b>0.06 (n=2)</b>            |
| <b>61766</b> | <b>4114</b>                  |                        |                          |                         |                           |                              |
| <b>61767</b> | <b>3759</b>                  |                        | <b>0.24 (n=9)</b>        |                         |                           | <b>0.24 (n=9)</b>            |
| <b>61768</b> | <b>1956</b>                  |                        |                          |                         |                           |                              |
| <b>61769</b> | <b>2332</b>                  |                        |                          |                         |                           |                              |
| <b>61770</b> | <b>2292</b>                  |                        |                          |                         |                           |                              |
| <b>61771</b> | <b>991</b>                   |                        | <b>18.57<br/>(n=184)</b> |                         |                           | <b>18.57<br/>(n=184)</b>     |
| <b>61772</b> | <b>1587</b>                  |                        |                          |                         |                           |                              |
| <b>61773</b> | <b>1543</b>                  |                        |                          |                         |                           |                              |
| <b>61774</b> | <b>1967</b>                  | <b>0.10 (n=2)</b>      |                          |                         |                           | <b>0.10 (n=2)</b>            |
| <b>61775</b> | <b>4208</b>                  |                        |                          |                         |                           |                              |
| <b>61776</b> | <b>1227</b>                  |                        |                          |                         |                           |                              |
| <b>61777</b> | <b>474</b>                   |                        |                          |                         |                           |                              |
| <b>61778</b> | <b>2133</b>                  |                        |                          |                         |                           |                              |
| <b>61779</b> | <b>5315</b>                  | <b>0.09 (n=5)</b>      |                          | <b>0.04 (n=2)</b>       |                           | <b>0.13 (n=7)</b>            |
| <b>SUM</b>   | <b>57220</b>                 | <b>0.33<br/>(n=19)</b> | <b>1.27<br/>(n=729)</b>  | <b>0.02<br/>(n=12)</b>  | <b>&lt;0.01<br/>(n=3)</b> | <b>1.33<br/>(n=763)</b>      |

Table 1.6. Generalized linear models of individual percent utilization (binomial, 0 to 1) of marine reserves for Alsea Bay animals, vs. three predictor variables: total management area size in km<sup>2</sup> (MgmtArea\_SqKM), distance from Alsea Bay in km (Dist\_From\_AlseaKM), and management area type (MgmtArea\_Type). Categorical: marine reserve, protected area, comparison area). The null model (Model 0) was suggested as the optimal model with backwards selection in the R *stepAIC* function.

|          | Response Variable    | Model Predictors                                                     | AIC         |
|----------|----------------------|----------------------------------------------------------------------|-------------|
| <b>0</b> | <b>MRPercent_Use</b> | <b>1</b>                                                             | <b>9.49</b> |
| 1        | MRPercent_Use        | MgmtArea_SqKM, family="binomial"                                     | 10.08       |
| 2        | MRPercent_Use        | MgmtArea_SqKM + Dist_From_AlseaKM, family="binomial"                 | 11.88       |
| 3        | MRPercent_Use        | MgmtArea_SqKM + Dist_From_AlseaKM + MgmtArea_Type, family="binomial" | 14.89       |

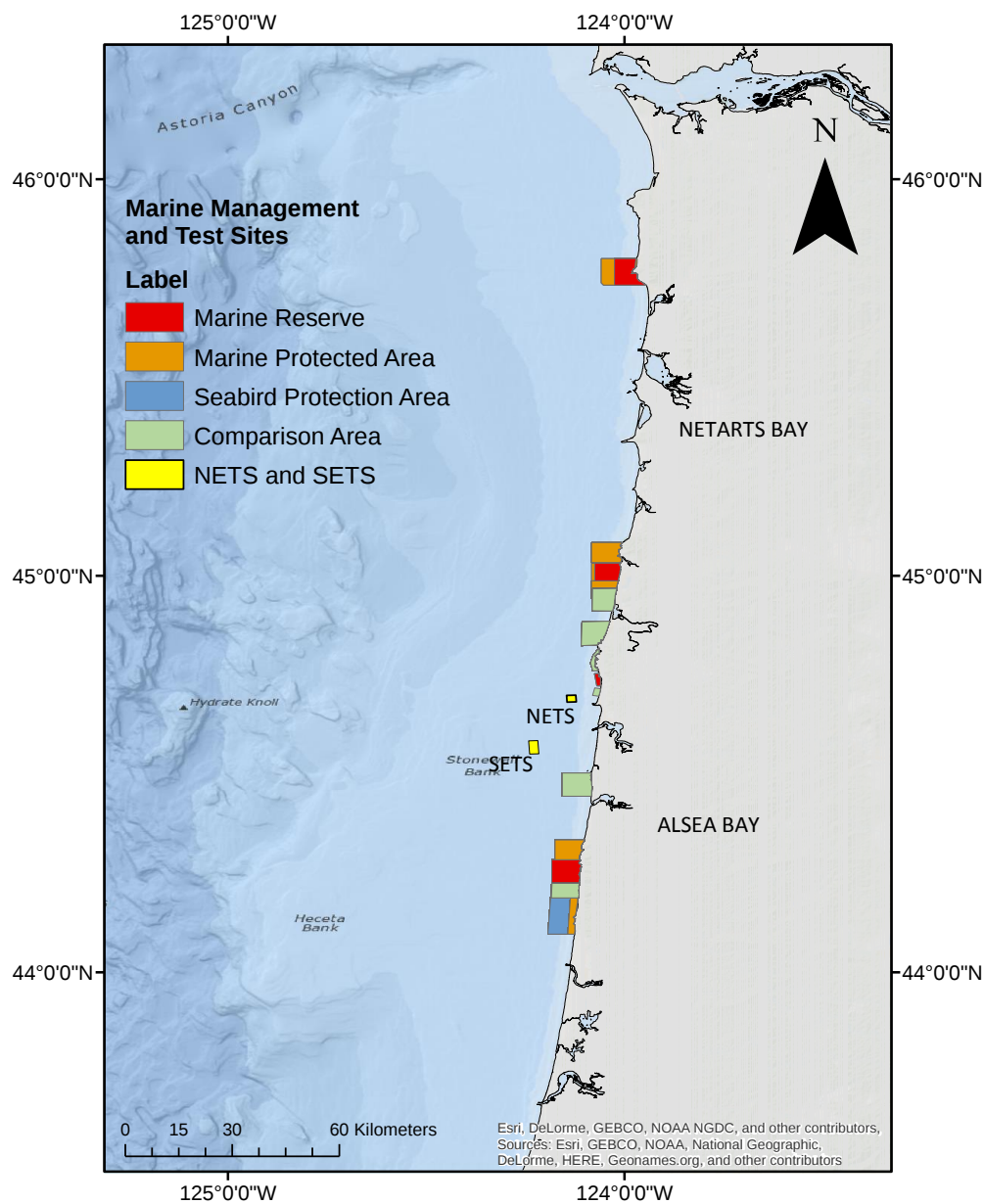


Figure 1.1. Management areas (marine reserves, protected areas, comparison areas, north and south energy test sites (NETS and SETS) within the region of study. Capture sites are labeled in capital letters. Redfish Rocks Marine Reserve is located south of the range of animals in this study (GCS\_WGS\_1984; D\_WGS\_1984).

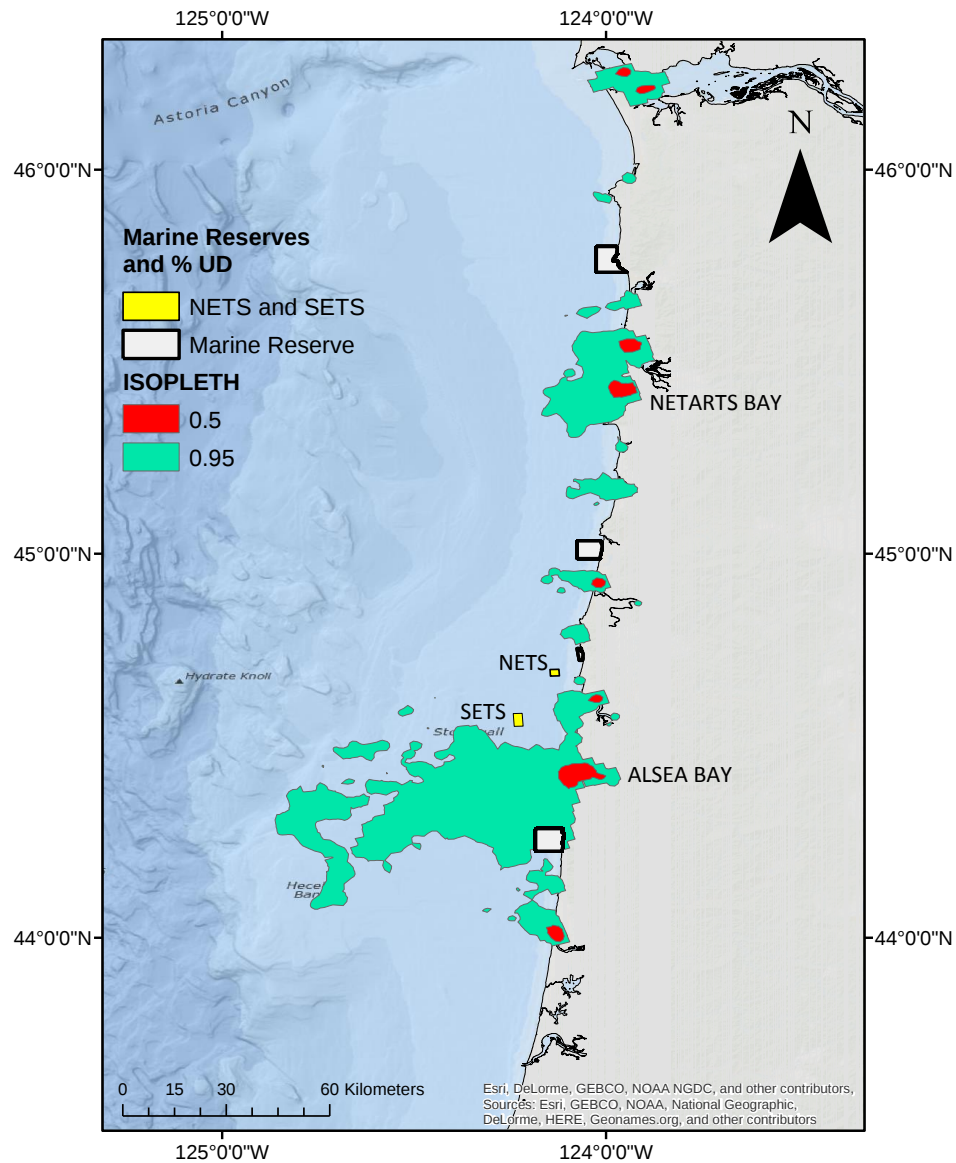


Figure 1.2. Map of high to 50% (average core area) to 0.95% utilization distributions (home range) for all 24 tagged harbor seals at a 2km x 2km (CVh) resolution. Marine reserves are depicted with black outlines, and wave energy test sites as yellow polygons. Neither north nor south ETS were within the 95% UD of any sampled animal (Coordinate system: GCS\_WGS\_1984; D\_WGS\_1984).

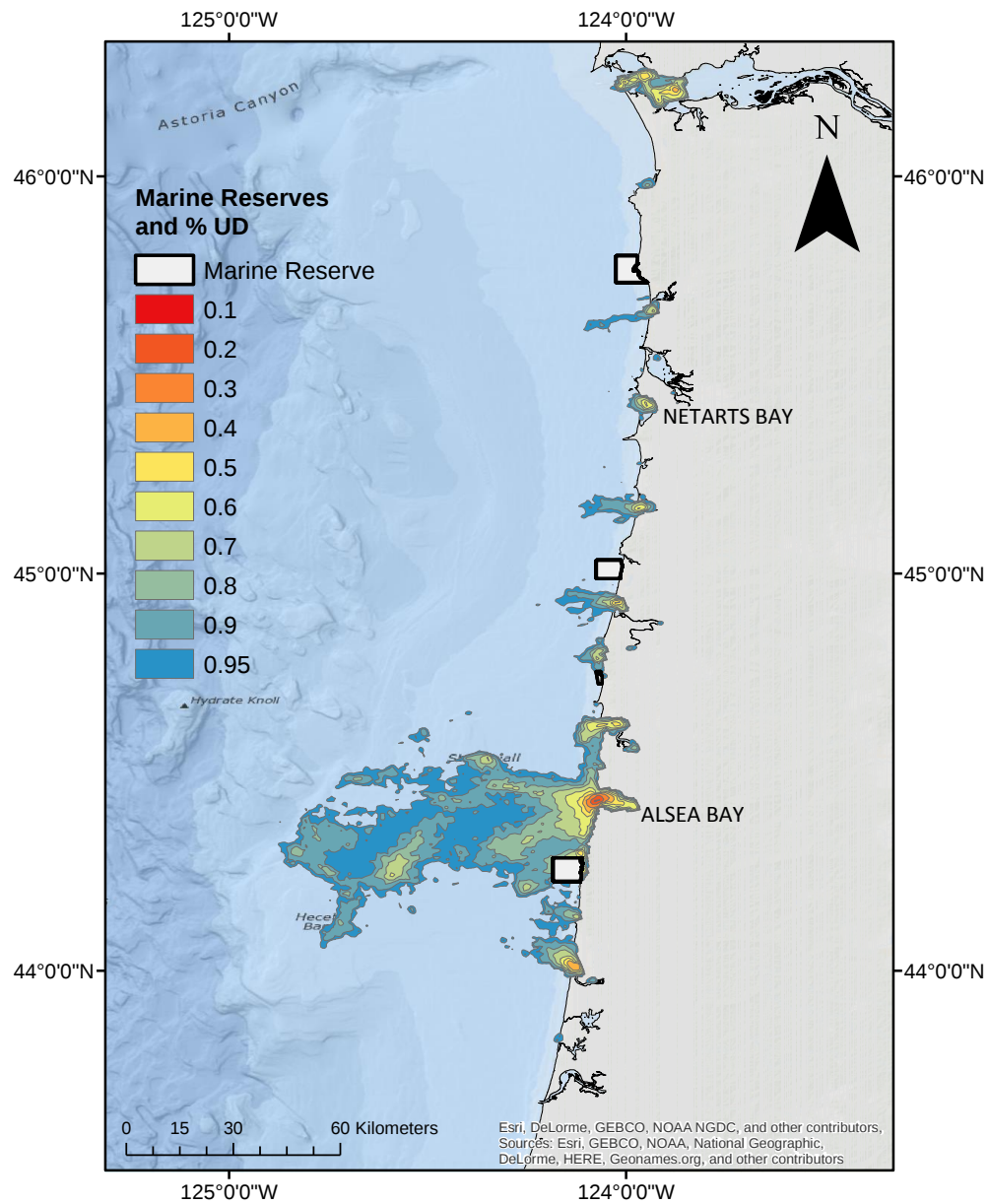


Figure 1.3. Utilization distribution isopleths (95% to 10%) at a 2km x 2km (CVh) resolution for seals ( $n=16$ ) captured in Alsea Bay, with labels indicating two capture sites in capital letters, and four marine reserves outlined in black. (Coordinate system: GCS\_WGS\_1984; D\_WGS\_1984).

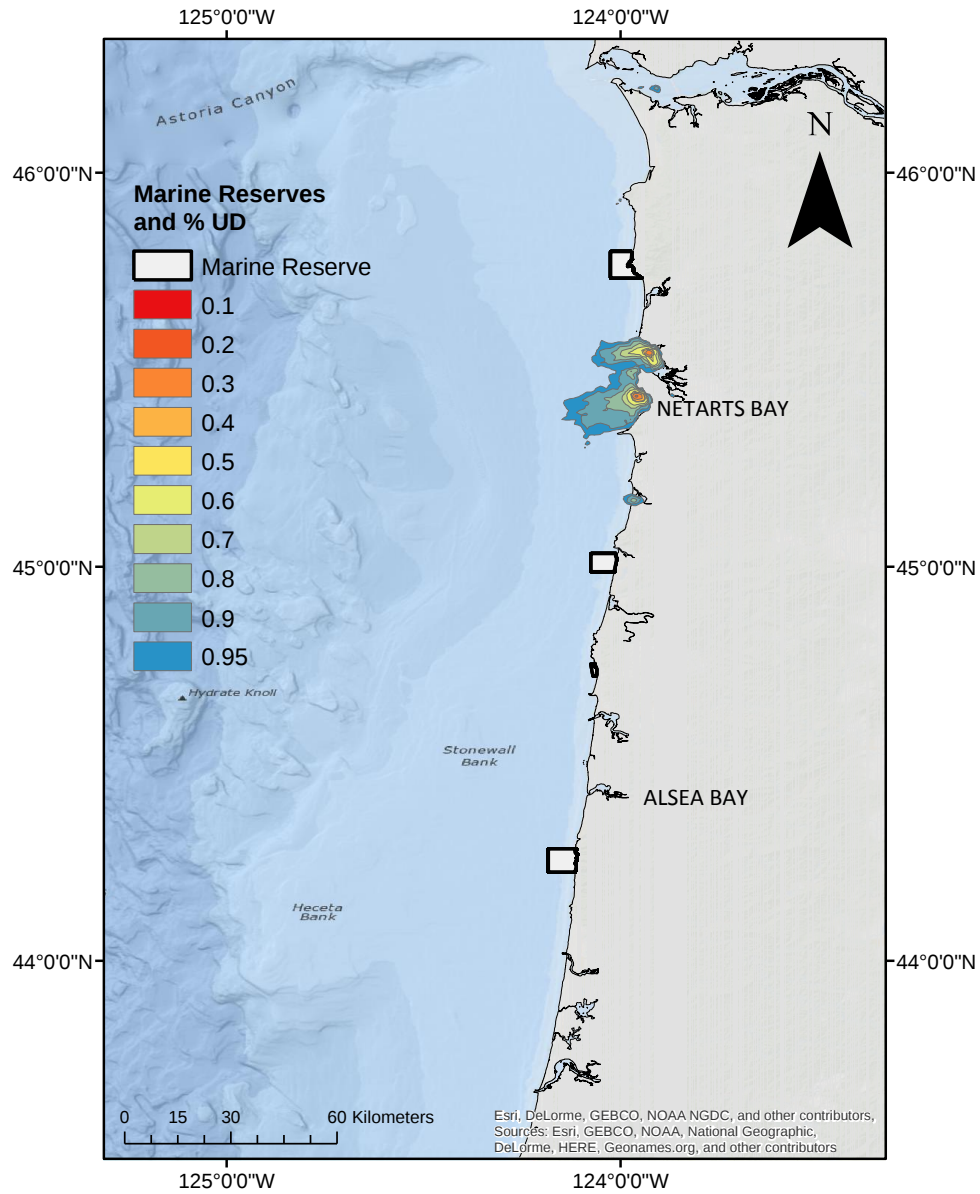


Figure 1.4. Utilization distribution isopleths (95% to 10%) at a 2km x 2km (CVh) resolution for seals (n=8) captured in Netarts Bay, with labels indicating two capture sites in capital letters, and four marine reserves outlined in black. (Coordinate system: GCS\_WGS\_1984; D\_WGS\_1984).

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CHAPTER 2 – ASSOCIATIONS OF SPATIAL BEHAVIOR, DIET, AND  
ENVIRONMENT IN A COMMON PINNIPED OF THE NORTHERN  
CALIFORNIA CURRENT SYSTEM

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## ABSTRACT

Associations between spatial habitat use, dietary niche, and use of oceanographic habitat in the Pacific harbor seal (*Phoca vitulina richardii*) in Oregon are not particularly well-known. Therefore, we examined these associations using satellite telemetry, stable isotope analysis and both directly- and remotely-measured oceanographic datasets for 24 adult (>50kg) seals captured at two haulout locations along the Oregon coast. Whiskers from each animal were collected at time of tagging and subsampled longitudinally. Harbor seal tracks were refined utilizing correlated-random walk analysis. Characteristics of spatial behavior, including bathymetry, bottom type (lithography), distance from shore, home range, and core area were summarized for each individual seal at the completion of tag deployment (n = 24). Use of four different isobaths and three types of substrate were examined using generalized linear and linear mixed effect modeling and isotopic composition of individuals, including mean and range  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Isotope values were compared against spatial habitat use to determine which, if any, isotopic variables might be associated with these factors. Lastly, point-by-point generalized linear models were run for distance from shore, haul out status, and presence in bays and rivers as functions of solar zenith angle, season, daily calculated upwelling index, and tidal height (n = 57,220). The best-fitting representative models for all parameters were selected by automated model selection.

A variety of site-specific differences became apparent, with the factors of (log) mean distance from shore (km), use of the 50- and 100-meter isobaths, mean  $\delta^{15}\text{N}$ , hauling-out time, and use of bays and rivers differing significantly between populations of animals captured in Netarts Bay and Alsea Bay. Differences in season were also apparent in use of sandy substrate and range of  $\delta^{15}\text{N}$ , suggesting the potential for inter-seasonal dietary shifts. Hauling out behaviors was tied to tidal cycle and solar zenith, reaffirming that seals time foraging trips based on both daylight and tidal phase. This study highlights correlations between movement, use of different types of neritic habitat, and dietary patterns for animals from two haulout locations in Oregon.

*Keywords: Pacific harbor seal, Northern California Current System, spatial habitat use, generalized linear models, environmental drivers of habitat use, stable isotopes, satellite telemetry*

## INTRODUCTION

The Oregon coast represents a dynamic stretch of the Northern California Current System, with seasonally variable coastal processes and a widely undulating continental shelf stretching from less than 20km to more than 55km wide in a distance of 363 miles. The northern CCS is also a portion of one of four eastern boundary current systems (EBCs), which represent ~20% of fisheries production (Pauly & Christensen, 1995). The northern CCS supports a wide diversity of sea mammals and birds, whose behaviors and foraging success are impacted by oceanographic variables, strong seasonal variability, and prey distribution (Checkley and Barth, 2009). Pacific harbor seals (*Phoca vitulina richardii*) are a common marine mammal species in the Northern California Current System (CCS), with an estimated 11,565 individuals within the territorial sea of the State of Oregon (B. Wright, *pers. comm.*). Although experiencing sustained population increases since the 1970s and being estimated as near carrying capacity (Brown et al., 2005b), there is little known about the at-sea behavior of Pacific harbor seals in the state, including basic drivers of foraging ecology. Effective management approaches for topics of interest must also be informed by a strong understanding of the general ecology and behavior of the individuals that compose a population such as the potential for site-specific depredation of salmonids (Brown & Mate, 1983; Orr et al., 2004b; Wright et al., 2007; Scordino, 2010) and pinniped responses to seasonal resource pulses (Scordino, 2010; Thomas et al., 2011). Pacific harbor seals are populous species considered to be a

generalist nearshore predator of several species of commercial and recreational interest, including salmonids, rockfish, forage fish and flatfish species (Orr et al., 2004b; Brown et al., 2005a; Thomas et al., 2011; Lance et al., 2012; Luxa & Acevedo-Gutiérrez, 2013; Steingass, 2017a). Knowledge of the at-sea ecology of Pacific harbor seals requires information regarding the movement ecology, habitat use, and associations between these animals and their coastal habitat.

For marine predators in other eastern boundary current systems, environmental predictors such as sea surface temperature (SST) and primary productivity (Chlorophyll *a* concentration) (Grémillet et al., 2008), upwelling index (Sydeman & Allen, 1999), bathymetry (Sjöberg & Ball, 2000) and lithography (Tollit et al., 1998) have been correlated with spatial habitat use of a variety of marine mammal species. However, within the Oregon region of the Northern CCS, there are no published findings describing the at-sea habitat use of marine mammals in association with oceanographic features. As Pacific harbor seals are continental shelf foragers, they represent an optimal species to examine associations of marine mammal spatial habitat use in relation to the nearshore environment, including bathymetry, lithography, seasonal effects, upwelling, site-related differences, and tidal patterns in order to discern environmental associations of movement patterns.

Satellite telemetry via ARGOS has been used to quantify spatial habitat utilization of harbor seals and other pinnipeds in many instances (Stewart et al., 1989; Lowry et al., 2001; Small et al., 2005; Johnson et al., 2008; Cunningham et al., 2009;

Sharples et al., 2012). However, the large error ellipse generated around most locations makes discernment of behavioral states, such as foraging vs. transit, particularly difficult to accurately discern and assess (Hart, Irving & Mackenzie, 1959; Merrick et al., 1994; Lydersen, Aars & Kovacs, 2008; Andrews-Goff et al., 2010; Costa et al., 2010; Hart & Hyrenbach, 2010). Therefore, alternative methods that provide context for what animals are doing while not directly observable are particularly valuable. One such method is stable isotope analysis, which can be used to assess trophic level, trophic niche, and source of diet (Newsome, Clementz & Koch, 2010a) and therefore discern foraging behavior without the benefit of behavioral state analysis or dive data. In other species of pinnipeds, stable isotope analysis, particularly of vibrissae, has been shown useful for describing seasonal or annual dietary patterns (Seymour, Horstmann-Dehn & Wooller, 2014a,b). A potential caveat is that, unlike otariids (McHuron et al. 2016), growth rates of phocid vibrissae are variable and not well-known, so temporal patterns in diet over time may not be directly linkable to temporally explicit seasonal effects. However, they still provide a chronologically ordered record of diet that can be subsampled and assessed in terms of range and variability over time, with the whisker root representing the most current point in time, radiating outwards toward the whisker tip. The methodologies of linking isotopes to spatial habitat use has been well-represented in studies of marine megafauna (Newsome, Clementz & Koch, 2010a), including but not limited to otariids (Lowther & Goldsworthy, 2011; Hückstädt et al., 2012; McHuron, 2016), elasmobranchs, sea

turtles (Ceriani et al., 2012; Seminoff et al., 2012), and cetaceans (Bentaleb et al., 2011).

Stable isotopes are generally measured as the ratio between non-enriched and stable enriched versions of elements in units of per mil (‰). Two of the most common of these are carbon and nitrogen; the ratio of  $\delta^{15}\text{N}$ :  $\delta^{14}\text{N}$  (‰) is indicative of trophic level (Miller, Brodeur & Rau, 2008; Newsome, Clementz & Koch, 2010b), while the ratio of  $\delta^{13}\text{C}$ :  $\delta^{12}\text{C}$  (‰) is robust to trophic effects and is generally indicative of spatial habitat utilization including nearshore vs. offshore resource selection and benthic vs. pelagic foraging (Germain et al., 2012). Isotope data collected from pinniped vibrissae generally represent an annual or multi-year dataset of dietary tendencies for an individual (Hirons, Schell & St Aubin, 2001; Seymour, Horstmann-Dehn & Wooller, 2014b). Despite potential caveats of mismatch in retrospective isotopic data gathered at the time of satellite tag deployment, significant correlations with spatial behavior, utilization of specific oceanographic features, and isotopic may represent a potentially less-invasive way to assess at-sea behavior of harbor seals and other marine mammals where direct spatial measurement is difficult or not available, and may additionally inform ecology when only broad satellite data are available. I aimed to determine potential correlations between spatial habitat use, external environmental variables, and dietary patterns of harbor seals in Oregon. With the assistance of a team of biologists and veterinary staff, I deployed satellite tags on 24 adult Pacific harbor seals and collected whiskers from animals at two sites in Oregon in order to determine at-

sea habitat use of harbor seals within the Northern CCS. These spatial habitat use patterns in addition to whisker-derived isotope values of sampled animals were compared against two sets of variables. First, they were correlated with dynamic and oceanographic parameters including season, year, solar zenith, upwelling index, and tidal height. Secondly, they were correlated with behavioral characteristics including capture site, capture year, capture season, home range and core area. Associations between movement, diet, and environmental variables were estimated using generalized linear and linear mixed effects models.

## METHODS

### *Field Methods*

Adult Pacific harbor seals (53-116kg, 23M/1F) were captured in Alsea (44.4279°N, 124.0679°W, n=16) and Netarts (45.4028°N, 123.9484°W, n=8) Bays on the coast of Oregon in September 2014, 2015 and April 2015. The female was included in data analysis as her total deployment days, home range area, and trip metrics fell well within the range of other sampled animals. Adult seals >50 kg were targeted as ideal study animals to reduce variability in behavior related to growth, reproductive energetic allocation, and sex-specific foraging behaviors. Male seals were particularly targeted in spring to avoid interacting with pregnant or nursing females. Seals were captured with skiff-based purse seine or beach rush methods by

teams of 5-13 biologists including veterinary staff (Jeffries, Brown & Harvey, 1993). Seals were individually weighed in hoop nets suspended from a tripod with a 0 – 200 x 1.0 kg hanging scale in all but two cases, then restrained on a v-board during tag attachment. All seals were given a numbered tag in each hind-flipper (Deflux sheep and goat ear tags, 2.25x7/8inch, 5g.) punched through the interdigital skin for visual identification. An external Wildlife Computers Satellite SPOT5© tag was attached to the post-cranial dorsal pelage with Devcon© 5-minute epoxy or Loctite© 422 adhesive. SPOT5 tags are Argos transmitters that allow the satellite service provider (CLS America Inc.) to estimate locations via the Doppler shift in sequential transmissions. Locational data are provided with associated classes of locations ranging in accuracy from 150m (LC3) to >1.5km (LCB) or unspecified error (LC Z) (Hebblewhite & Haydon, 2010).

### *Tag Programming*

During the first two deployment periods (fall 2014, spring 2015), tags were duty cycled on an on-off monthly cycle to provide a longer period of data, and promote data overlap between tag deployments. Tags were sequentially set to ‘ON’ during April through May and September through October to coincide with the spring and fall transitions of upwelling (Chan et al., 2008). Tags deployed in fall 2015 were programmed to transmit continuously to maximize total data overlap with previous deployments. All tags were programmed to begin transmission to the Argos satellite

array upon sensing immersion in salt water. To extend battery life and to avoid over-representation of haulout periods, tags were programmed to reduce transmission rate after 10 consecutive ‘dry’ transmissions, and to stop transmitting after two hours of being dry.

### *Location Refinement*

After tags ceased transmitting, all data collected by the Argos satellite service provider CLS America, Inc. during deployment were downloaded via the Wildlife Computers Data Portal (© Wildlife Computers). Locations with a quality of LC 0-3, A and B were first manually filtered to remove duplicate locations. LC-Z locations were discarded due to lack of a measurable error estimate. Maximum swim speed for Pacific harbor seals is not widely-documented; however minimum cost of transport occurs at approximately 1.0-1.4m/s (Davis, Williams & Kooyman, 1985). Therefore, a coarse speed-distance-angle (SDA) filter was applied to the data in order to remove locations which required a biologically unlikely travel speed of >8m/s. The remaining data were used to create regularized state space models (SSM's) for each animal using the R package *crawl* (Johnson et al., 2008; Johnson, 2017). To create a roughly equal ratio of estimated to observed locations, time steps were calculated as the average time between consecutive ‘wet’ locations, as determined by the Argos 20-minute timeline. On-land points were not considered for this calculation. The resultant mean inter-location period was  $1.52 \pm 9.83$  hours. Therefore, a temporal resolution of one hour was

used for the generation of regularized SSM points for analysis. SSM output locations were further adjusted by utilizing the Fix-Path function in the R package *crawl* (Johnson et al., 2008). Fix-Path utilizes a transition matrix to correct animal tracks to restrict travel through identified restricted areas, in this case over land. Once the state-space modeled and the filtered dataset was generated, the resultant SSM-derived locations were used for all further analyses.

### *Behavioral Estimation*

Presence or absence for each individual location within inland waters (classified as estuaries, bays or rivers) was categorized as a binomial variable where '0' meant absent, or at sea, and '1' mean present. Presence within a bay, river, or estuary was defined as being within the area inside (proximal to land) of the two farthest points of shore for each bay or river, including jetties, regardless of wet or dry status. Presence within inland waters was further categorized into presence within individually identified bays and rivers. As being within a bay or river was not necessarily indicative of haulout status, individual locations were further categorized as 'on land' or 'in water' based on the 20-minute percent wet/dry timeline provided by the SPOT5 tag. Timeline bins were categorized as  $>$  or  $\leq 50\%$  'wet'. Any points within a bin categorized as  $> 50\%$  'wet' were considered to be in water 'wet'. Any points within a  $\leq 50\%$  'wet' bin were considered to be on land (hauled out or 'dry').

### *Kernel Density Estimation for Home Range and Core Area*

Kernel analysis was used to estimate individual utilization distributions (UD) for each animal at the 95% isopleth, and subsequently every tenth isopleth from 10-90% using the Geospatial Modeling Environment (Beyer, 2015). Home range was quantified as the 95% utilization isopleth (Worton, 1989). Home range area was calculated for individuals and the sample population as a whole. Core area was calculated using methods from Vander Wal and Rodgers (2012) (Vander Wal & Rodgers, 2012) in order to estimate a biologically-relevant threshold. To generate this threshold, I utilized an exponential equation to identify the isopleth at which home range area, defined as the 95% utilization distribution began to increase at a greater rate than probability of use (Vander Wal & Rodgers, 2012). Core area was rounded down to the nearest calculated 10% isopleth.

### *Stable Isotope Analysis*

Seal vibrissae were collected at time of capture, with an effort to collect the longest caudal whisker on the left side of the head for all animals. Whiskers were measured for total and sheath length and sonicated to remove debris. The sheath and whisker plug were removed, and the whisker was cleaned with  $\text{CHCl}_3:\text{CH}_4\text{O}$  solution and prepared on a sterile table.

Whiskers were sectioned and weighed every 0.5cm, and the first ten samples beginning at the root were analyzed. 0.20-0.55mg of sample were cut using a chisel

and packed in tin boats. In total, ten samples were prepared from each individual to generate a total of 240 samples for analysis. Prepared samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility using continuous-flow isotope ratio mass spectrometry (CFIRMS) employing a Thermo Scientific Flash 2000 elemental analyzer and Thermo Scientific ConFlo IV interfaced with a Thermo Scientific DeltaV<sup>Plus</sup> Mass Spectrometer. Results were reported as parts per thousand (‰) deviation from the international standards PDB (carbon) and Air (nitrogen) with a precision of <0.2 ‰.

### *Oceanographic Characteristics*

The dynamic oceanographic variable of hourly tidal height (m) was extracted for all data points from the NOAA Tides and Currents Data Server (<https://tidesandcurrents.noaa.gov/waterlevels.html?id=9435380>) for the South Beach, Oregon oceanographic mooring (Station #9435380, 45°N, 125°W) and matched to the nearest hour of each SSM-generated location. Daily upwelling index was obtained from the Pacific Fisheries Environmental Laboratory (PFEL) live access server for the South Beach, Oregon oceanographic mooring (Station #9435380, 45°N, 125°W) and matched to date for each point (<https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html>). PFEL generates coastal upwelling indices (CUI) using the magnitude of Ekman Transport (wind stress divided by the Coriolis parameter). Stronger equatorward

(northerly) wind stress, which drives upwelling, is denoted by higher positive values of the CUI. Stronger poleward (southerly) wind stress, which drives downwelling, is denoted by stronger negative values of the CUI. CUI values were additively- then log-transformed for generalized linear modeling, and resulting model summary coefficients for predictive variables were back-transformed for interpretation. Solar zenith was extracted for each point and further sorted into the categories of ‘day’ (zenith < 90°), ‘night’ (zenith > 102°) or ‘transitional’ (zenith  $\geq 90^\circ$  or  $\leq 102^\circ$ ) as per McHuron (2012).

Static oceanography including bathymetric isopath and three primary categories of bottom substrate (or ‘other’) were extracted for each point, as were presence within bay or riverine sites, distance from shore (km), and presence within marine reserve sites. For assessment of bathymetry, locations were categorized to either the 50m, 100m, 150m, 200m, and >200m (off shelf) isobaths using the ArcGIS Spatial Join tool. As harbor seals are generally benthic foragers and use of bottom substrate is likely dependent on foraging strategy and preferred prey, lithography was extracted for each modeled location using the Spatial Join tool in ArcGis for the the Goldfinger et al. OR-WAGeo-HapMaps dataset, which had a spatial resolution of 0.5m to 50-100’s of meters. Resolution differed based on whether lithography data was collected via side-scan sonar or direct sediment sampling, however the lowest resolution of this data is still below that of the ARGOS satellite data, making it

appropriate for comparison (Goldfinger et al., 2002). Presence on these substrates and depth ranges were also converted to total percent use by individuals.

### *Generalized Linear Modeling and Mixed Effects Modeling*

In order to determine which environmental and biological predictors were significantly associated with characteristics of spatial behavior, linear mixed effects models (LMEMs) and generalized linear models (GLMs) were fit using R Package *lme4* while designating ‘capture year’ as a random effect to account for inter-annual difference (Bolker & Bolker, 2007; Bates et al., 2015). Two sets of models were run; 1) a total of 17 models using individually summarized variables (n = 24) (Table 2.1) and 2) three models for haulout status, presence in bay and riverine areas, and distance from shore using point-by-point variables (n = 57,220) (Table 2.2). To determine whether isotopic variables correlated with spatial habitat use, range, mean and root values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the whiskers/vibrissae including the vibrissal root were modeled as a response to the spatial parameters of capture location, capture site, percent presence in bay and riverine sites, percent presence of sandy substrate, home range and core area, and distance from shore, while accounting for year of capture. In addition to the mean and range values for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , the vibrissal root value of these stable isotopes was individually modeled versus spatial parameters to determine whether the most current point in time, or the average of all values, were most strongly correlated with spatial habitat use. In all 20 models, both non-log transformed and log-

transformed versions of response variables were checked for adherence to normality using the Shapiro-Wilkes test (`shapiro.test` in R) (Bolker, 2008). Variables having a non-normal untransformed distribution ( $p < 0.05$ ) but a normally-distributed log-transformed variant ( $p > 0.05$ ) were log-transformed for analyses, and resulting model summary coefficients for predictive variables were back-transformed for interpretation. All possible model combinations including all input variables were generated and best-fitting models selected based on AICc value using R Package *MuMIn* (function ‘`dredge`’), and further subset with the nesting selection rule (function ‘`subset`’) to exclude overly-complex models in the final list (Barton, 2015).

## RESULTS

### *Individually Summarized Parameters*

Final models are listed in Tables 2.3 and 2.4, with final model estimates including AICc values in Tables 2.5 and 2.6. All model response estimates are presented with  $\pm$  standard error (SE).

**Trophic level (mean  $\delta^{15}\text{N}$ ) and niche (range  $\delta^{15}\text{N}$ ) were correlated with capture location and season, respectively.** Seals captured in Netarts Bay exhibited a significantly lower mean  $\delta^{15}\text{N}$  ( $0.51 \pm 0.24$ ,  $p$  value = 0.0482) value than seals tagged in Alsea Bay (Figures 2.1, 2.2). Range  $\delta^{15}\text{N}$  (‰) was higher for animals tagged in spring ( $0.73 \pm 0.26$ ,  $p$  value = 0.0092) than animals tagged in fall (Figure 2.3).

**Mean carbon  $\delta^{13}\text{C}$  (‰) was significantly associated with mean distance from shore.** Animals that demonstrated an overall higher mean in distance from shore had a lower mean  $\delta^{13}\text{C}$  (‰) once capture year was accounted for (value =  $-0.0569 \pm 0.02$ ,  $p$  value = 0.0211) (Figure 2.4). Range  $\delta^{13}\text{C}$  was not correlated with any significant predictor variables, with the null value being selected by stepwise AIC selection ( $p$  value = 0.00). Median distance from shore (km) was not linked to any predictive variables, but resulted in a significant null model ( $p$  value = 0.0175).

**The most ‘current’ whisker root  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were not significantly correlated with any examined environmental factors.** For  $\delta^{13}\text{C}$ , the final model included both capture location and capture season, but neither of these factors were significant ( $p$  value = 0.0711, 0.1166 respectively). For  $\delta^{15}\text{N}$ , the final model included capture season as a non-significant factor ( $p$  value = 0.135).

**Utilization of bathymetry and the offshore environment were associated with capture site.** Log mean distance from shore was significantly correlated with tagging locations, with seals tagged in Netarts Bay on average having a significantly smaller mean distance from shore than Alsea Bay animals ( $-1.38 \pm 0.44\text{km}$ ,  $p$  value = 0.0046) while accounting for capture year (Figure 2.5). Utilization of the 50-meter and the 100-meter isobath also differed between sites, with animals tagged in Netarts Bay spending more time within the 50-meter isobath ( $16.69 \pm 6.18$ ,  $p$  value =  $<<0.05$ ), and less time within the 100-meter isobath ( $-12.28 \pm 5.39$ ,  $p$  value = 0.0333) than animals tagged in Alsea Bay after accounting for capture year.

**Percent utilization of marine reserves and riverine and bay sites was not significantly associated with any other examined variables.** The final model chosen for percent utilization of marine reserves included the non-significant factor of season ( $p$  value = 0.169). The final model selected for percent utilization of bay/riverine sites included the factors of capture site and season, but neither of these predictors were significant ( $p$  value = 0.1386, 0.113 respectively).

**Utilization of sandy substrate significantly correlated with capture season, but use of mud and rock did not significantly link to any other examined variables.** Animals that were captured in spring had a higher use of sandy substrate than animals captured in fall ( $17.95 \pm 6.86$ ,  $p$  value = 0.0162) (Figure 2.6). The final model selected for use of rocky substrate was the null model. . Lastly, the final model selected to describe use of muddy substrate was non-significant and included capture location as a non-significant predictor ( $p$  value = 0.13796).

**Animal tagged in Netarts Bay spent the most time in the shallow 50-meter isobath, but there were no significant predictors for the deeper isobaths of 150-meters and greater.** Netarts Bay animals were associated with higher use of the shallowest isobath ( $16.67 \pm 6.18\%$ ,  $p$  value = 0.01) and lower use of the 100-meter isobath ( $-12.28 \pm 5.39$ ,  $p$  value = 0.0333) than animals captured in Alsea Bay. For both percent use of the 150-meter and 200-meter isobath, the null model was selected by AIC stepwise analysis.

*Generalized Linear and Linear Mixed Models for Point-by-Point Parameters*

**Seals were more likely to be hauled out during higher solar zenith angle, and during winter months, negative upwelling, and low tides.** For every 1% increase of solar zenith angle, the probability of being hauled out increased by  $1.20 \pm 1.02\%$  ( $p$  value  $<0.0001$ ), meaning that animals were more likely to be hauled out while the sun was lower in the sky than during peak daylight hours. Seals spent the most time hauled out during the winter (value =  $0.45 \pm 0.03$ ,  $p$  value  $<0.0001$ ). As the upwelling index increased, probability of being hauled out increased (a 1% increase of CUI resulted in a  $0.86 \pm 1.05\%$  increase in probability of being hauled out,  $p$  value =  $0.000945$ ). Additionally, seals were more likely to be hauled out during lower tides (value =  $-0.32 \pm 0.01$ ,  $p$  value  $<0.0001$ ).

**Netarts Bay animals, on average, spent less time hauled out than Alsea Bay animals.** Hauling out was significantly correlated with capture location, with Netarts Bay animals being more likely to have a ‘dry’ status than Alsea Bay animals (value =  $0.12 \pm 0.02$ ,  $p$  value =  $6.70e-08$ ).

**Study animals were less likely to be present within bays or rivers during summer months, lower tides, and during low upwelling periods, but inland water use was associated with capture location.** Presence within inland waters, but not necessarily being hauled out, was most negatively associated with summer months (value =  $-0.82 \pm 0.04$ ,  $p$  value =  $<2e-16$ ). Probability of being within inland waters

increased with increased tidal height (value =  $0.05 \pm 0.01$ ,  $p$  value =  $1.45e-05$ ) and with increased upwelling (value =  $0.50 \pm 1.05$ ,  $p$  value =  $<2e-16$ )

Animals captured in Netarts Bay were  $29.25 \pm 2.00\%$  more likely to be present within inland waters than animals captured in Alsea Bay.

**Distance from shore changed seasonally, with upwelling, and differed between capture locations.** Average distance from shore increased during summer months (value =  $2.22 \pm 0.17$ ,  $p$  value =  $<0.0001$ ) and during higher upwelling periods (value =  $25.70 \pm 1.27$ ,  $p$  value  $<0.0001$ ). Animals captured in Netarts Bay had a significantly smaller average nearshore distance than Alsea Bay animals (value =  $-4.97 \pm 0.11$ ,  $p$  value =  $<0.0001$ ).

## DISCUSSION

This study examined the spatial habitat use and stable isotope-derived dietary characteristics of 24 adult ( $>50\text{kg}$ ) harbor seals, and revealed general associations between spatial habitat use characteristics of seals in Oregon with patterns in dietary composition and oceanographic characteristics. Stable isotope analysis revealed  $\delta^{13}\text{C}$  as a potential proxy for spatial associations in prey selection and trophic level.

In many cases of the individually summarized models, the null model was the best-fitted explanatory model for behavioral patterns. This included median distance from shore, utilization of rocky substrate and the deeper 150- and 200-meter isobaths. This indicates that measured behavioral responses were driven by or influenced by

predictors that were not included in these models. However, site-specific differences in behavior emerged for several parameters including mean distance from shore and use of the shallow 50-meter isobath. This is likely due to the biogeography of the Oregon continental shelf. Seals extensively utilized the continental shelf north of Cape Blanco (42.8376°N). The continental shelf directly south of Waldport Oregon extends into 55-meter wide, highly productive region of Heceta Bank, whereas the shelf surrounding Netarts Bay extends only approximately 20 meters. Therefore, the wider continental shelf south of Alsea Bay represents a larger area of available habitat. In an examination of seasonal differences in habitat characteristics, utilization of sandy substrate was the only significantly correlated factor, with lower use of sandy substrate by seals captured in spring. This could have been driven by seasonal differences in prey availability, changes in use of bay and riverine vs. neritic habitat, or due to bias from small sample size.

Utilization of inland waters, regardless of hauling out status, was lower during night and transitional dusk and dawn periods. Time spent in inland waters also decreased the most in summer, during high upwelling periods and during higher tides. Submergence in water accrues two possible costs of thermal energy loss and increased predation risk (Watts, 1992), so it should be a consideration that animals may benefit from returning to haulout locations when not actively foraging. However, this is not always the case for pinnipeds. While at sea, if food is not a limiting resource and body lipid stores are optimal, there may be less pressure to increase foraging success by

devoting a higher proportion of time to diving (Austin et al., 2006b), and energetic efficiency of prey may additionally dictate foraging strategy in a generalist predator such as the Pacific harbor seal (Bowen et al., 2002b). Additionally, constraints on hauling out include hyperthermia during warmer months which may further explain decreased proportion of time spent ‘dry’ during summer months (Watts, 1992).

Dietary composition itself has been found to be an associated factor of individual fitness in pinnipeds (Rosen & Trites, 2000; Gomez, Rosen & Trites, 2016). This study examined potential behavioral and environmental differences as correlates to diet as estimated by stable isotopes. There was a significant relationship between  $\delta^{13}\text{C}$  enrichment in seal vibrissae and average distance from shore as measured for SSM-derived locations. Mean  $\delta^{13}\text{C}$ :  $\delta^{12}\text{C}\text{‰}$  values increased (were more enriched) for animals who had a smaller average distance from shore. These findings align with previous findings of offshore vs. nearshore carbon sources in the Northern California Current System (Miller, Brodeur & Rau, 2008), meaning there may be potential to utilize stable isotopes as a relative proxy for foraging behavior and at-sea habitat use for seals in this system.

Site- and season-specific differences in mean trophic level and range became apparent for the sample population. That is, animals captured in Alsea Bay had an overall higher mean trophic signature than animals captured in Netarts Bay. However, this appears to be driven by Seal #61773, which had a particularly enriched nitrogen signature. It is difficult to discern the representative time period represented by

whiskers samples. For each individual approximately the first 4.15-4.35cm of the whisker was represented in analysis. The growth of phocid whiskers is non-linear and remains poorly defined. This issue, and differences in growth rates between captive and wild animals were highlighted in Hirons et al. (2001). Based on the rates described in Hirons et al, it could be estimated that a 4.20cm could represent anywhere between 525 days (1.44 year) period based on samples from wild harbor seals, to 127 days (4.24 months) or 113 days (3.78 months) based on samples from captive animals which is more representative of the previous one to two seasons.

In a strongly dynamic ecosystem, stable isotope analysis conducted on whiskers at the time of capture relies on a heavy assumption that behavior is consistent year to year, or between and within seasons, and thus can be prospectively predicted by existing isotope values within tissue. However, the presence of significant relationships between isotope patterns and spatial behavior, haulout location, and season were indicators that isotope analysis could be a less invasive, and retrospective method to study pinniped ecology without reliance on complex tracking datasets if adequate baseline data exists (Burton & Koch, 1999; Lowther & Goldsworthy, 2011). In consideration of the caveat of retrospective isotope vs. prospective tracking data, I also modeled the most recent isotope value, the whisker root, against behavioral and oceanographic variables. There were no significant relationships for this value, demonstrating that longer-term, longitudinal sampling of isotopes in whiskers were better suited to describe foraging behavior than the most recent single-point value.

Stable isotope analysis can also predict prey type predominance in pinnipeds if comparative isotopic composition values of representative prey groups are available and discrimination ratios between predator tissue and prey are known (Hückstädt, Rojas & Antezana, 2007; Hückstädt et al., 2012; Beltran et al., 2016). Limited prey data were collected for this study, and stable isotope values seemed most reflective of a diet with a predominance of flatfish (Steingass, *unpub. data*) based on discrimination ratios of harbor seal whiskers (Hobson et al., 1996; Beltran et al., 2016). However, as harbor seals in the Northern California Current System have been shown to consume over 100 species and genera of prey (Steingass, 2017a), it was not possible to create a stable isotope mixing model robust enough to quantify dietary proportions. Rather, the rougher qualifications of higher versus lower trophic level were sufficient to describe general patterns in diet here.

As highlighted by these analyses, Pacific harbor seals are predominantly continental shelf foragers with seasonal- and site-related differences in spatial and foraging behavior. Animals utilized a large proportion of available continental shelf habitat, with seals from the relatively narrow continental shelf of Netarts Bay ranging less far from shore, on average, than their southerly counterparts. These differences in spatial range correlated with select stable isotope values. Behavior of the tagged animals was seasonally-dynamic and showed strong associations with diel patterns as demonstrated by London et al. (2012) for seals in Puget Sound.

Seasonal upwelling is likely a strong driver of foraging behavior as upwelling creates increased nearshore productivity (Checkley Jr & Barth, 2009). Extreme upwelling events may also lead to bouts of coastal hypoxia which has implications for distribution, mortality and morbidity of fish and invertebrates (Vaquer-Sunyer & Duarte, 2008). Events of severe nearshore hypoxia and anoxia have been recorded in recent years in the Northern CCS (Chan et al., 2008), and are increasing globally (Rabalais et al., 2009; Craig, 2012; Breitburg et al., 2018). Changes in prey distribution may temporarily benefit fisheries and marine predators, as long as thresholds for population sustainability of fish and invertebrates are not exceeded (Breitburg et al., 2009; Steingass & Horning, 2017b). Pacific harbor seals are perhaps an ideal species to study the bottom-up impacts of nearshore processes on air-breathing central place foragers as they remain regionally year-round without undertaking major migrations as with other species of pinnipeds within the northern CCS.

This study moved beyond sole examination of spatial behavior of a populous marine mammal, and instead incorporated stable isotope ecology and utilization of oceanographic characteristics via linear mixed effects and generalized linear modeling to form an integrated ecological picture of a common and understudied marine mammal in Oregon. This was also a proof-of-concept for the integration of oceanographic, dietary and spatial data for this species in Oregon. These methods could be expanded to other species or other regions, and results illuminated a variety

of relationships between harbor seal behavior and the coastal environment. I suggest the relationships highlighted here could be relevant for future, refined measures of behavioral analysis for harbor seals and other pinnipeds, and further as a method of validation of foraging characteristics of individuals.

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#### ETHICS APPROVALS

This study was carried out in strict compliance with all applicable animal care and use guidelines under the U.S. Animal Welfare Act and was approved as required under the U.S. Marine Mammal Protection Act by the National Marine Fisheries Service (NMFS

#16991) and by the Institutional Animal Care and Use Committees of San Jose State University (AUP #1010) and Oregon State University (ACUP #4616).

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## TABLES AND FIGURES

Table 2.1. Initial models run for variables summarized by individual animal (n = 24).

|           | <b>Response</b>    | <b>Predictor</b>                                                                                                                      |
|-----------|--------------------|---------------------------------------------------------------------------------------------------------------------------------------|
| <b>1</b>  | MeanDistShore.km   | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>2</b>  | MedianDistShore.km | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>3</b>  | SumReserve_PU      | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>4</b>  | Bay_PU             | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>5</b>  | MUD_PU             | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>6</b>  | ROCK_PU            | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>7</b>  | SAND_PU            | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>8</b>  | 50m_ISO_PU         | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>9</b>  | 100m_ISO_PU        | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>10</b> | 150m_ISO_PU        | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>11</b> | 200m_ISO_PU        | ~ Location + Season + (1   CaptureYear)                                                                                               |
| <b>12</b> | Mean_d13C          | ~ Location + Season + Bay_PU + SAND_PU + HomeRange.km2 + CoreArea.km2 + MeanDistShore.km + HomeRange.km2*Location + (1   CaptureYear) |
| <b>13</b> | Mean_d15N          | ~ Location + Season + Bay_PU + SAND_PU + HomeRange.km2 + CoreArea.km2 + MeanDistShore.km + HomeRange.km2*Location + (1   CaptureYear) |
| <b>14</b> | Range_d13C         | ~ Location + Season + HomeRange.km2 + CoreArea.km2 + HomeRange.km2*CaptureSite + (1   CaptureYear)                                    |
| <b>15</b> | Range_d15N         | ~ Location + Season + HomeRange.km2 + CoreArea.km2 + HomeRange.km2*CaptureSite + (1   CaptureYear)                                    |
| <b>16</b> | Root_d13C          | ~ Location + Season + Bay_PU + SAND_PU + (1   CaptureYear)                                                                            |
| <b>17</b> | Root_d15N          | ~ Location + Season + Bay_PU + SAND_PU + (1   CaptureYear)                                                                            |

Table 2.2 Initial models run for variables with individual values for each point (n = 57,220).

|          | <b>Response</b>  |   | <b>Predictor</b>                                                                                                                                                                               |
|----------|------------------|---|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>1</b> | Hauled           | ~ | logZenith + DayNight + Season + UpwellingIndex.Scaled + TidalHeight.m + CaptureLocation + (1   CaptureYear), data=alldata, family=binomial, control=glmerControl(optimizer="bobyqa"), nAGQ=10) |
| <b>2</b> | Bay/Ocean        | ~ | logZenith + DayNight + Season + UpwellingIndex.Scaled + TidalHeight.m + CaptureLocation + (1   CaptureYear), data=alldata, family=binomial, control=glmerControl(optimizer="bobyqa"), nAGQ=10) |
| <b>3</b> | DistFromShore.km | ~ | logZenith + DayNight + Season + UpwellingIndex.Scaled + TidalHeight.m + CaptureLocation + (1   CaptureYear), data=alldata, family=gaussian(link="identity"))                                   |

Table 2.3. Final dredged models for summarized generalized linear or linear mixed-effects models. Significant (<0.05) *p*-values denoted by a \*.

|           |                                                                                                                    |                                                         |                                                      |
|-----------|--------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------|------------------------------------------------------|
| <b>1</b>  | <b>lme(LogDist ~ Season + Location, random= 1 Year, data = SumData, method="REML")</b>                             | LocationNetarts = -1.38                                 | <b><i>p</i> = 0.0046*</b>                            |
| <b>2</b>  | <b>lme(LogMedDist ~ 1, random= 1 Year, data = SumData, method="REML")</b>                                          | <b>Intercept = -0.54</b>                                | <b><i>p</i> = 0.0175*</b>                            |
| <b>3</b>  | <b>glm(SUM_ReservesPercent ~ Season + (1   Year), family = gaussian(link = "identity"), data=SumData))</b>         | SeasonSpring = 4.26                                     | <i>p</i> = 0.169                                     |
| <b>4</b>  | <b>lme(Bay_PU ~ Location + Season, random=1 Year, data = SumData, method="ML")</b>                                 | LocationNetarts = 11.67<br>SeasonSpring = 11.87         | <i>p</i> = 0.1386<br><i>p</i> = 0.113                |
| <b>5</b>  | <b>glm(MUD ~ Location + (1 Year), data=SumData, family=gaussian(link="identity"))</b>                              | LocationNetarts = -5.75                                 | <i>p</i> = 0.13796                                   |
| <b>6</b>  | <b>glm(ROCK ~ + (1 Year), data=SumData, family=gaussian(link="identity"))</b>                                      | <b>Intercept = 4.00</b>                                 | <b><i>p</i> = 0.0056*</b>                            |
| <b>7</b>  | <b>lme(SAND ~ Season, random= ~ 1 Year, data = SumData, method="REML")</b>                                         | <b>SeasonSpring = -17.94</b>                            | <b><i>p</i> = 0.0162*</b>                            |
| <b>8</b>  | <b>glm(50m_IsobathPU ~ Location + Season + (1 Year), data=SumData, family=gaussian(link="identity"))</b>           | <b>LocationNetarts = 16.69</b><br>SeasonSpring = 8.00   | <b><i>p</i> = &lt;&lt;0.05*</b><br><i>p</i> = 0.1853 |
| <b>9</b>  | <b>glm(100m_IsobathPU ~ Location + Season + (1 Year), data=SumData, family=gaussian(link="identity"))</b>          | <b>LocationNetarts = -12.28</b><br>SeasonSpring = -8.94 | <b><i>p</i> = 0.0333*</b><br><i>p</i> = 0.0943       |
| <b>10</b> | <b>glm(150m_IsobathPU ~ + (1 Year), data=SumData, family=gaussian(link="identity"))</b>                            | <b>Intercept = 3.06</b>                                 | <b><i>p</i> = 0.0178*</b>                            |
| <b>11</b> | <b>glm(200m_IsobathPU ~ (1 Year), data=SumData, family=gaussian(link="identity"))</b>                              | Intercept = -0.74                                       | <i>p</i> = 0.119                                     |
| <b>12</b> | <b>lme(Mean_d13C ~ MeanDistShore.km, random= ~ 1 Year, data = SumData, method="REML")</b>                          | <b>MeanDistShore.km = -0.06</b>                         | <b><i>p</i> = 0.0211*</b>                            |
| <b>13</b> | <b>lme(Mean_d15N ~ Location, random= ~ 1 Year, data = SumData, method="REML")</b>                                  | <b>LocationNetarts = 0.51</b>                           | <b><i>p</i> = 0.0482*</b>                            |
| <b>14</b> | <b>lme(Range_d13C ~ 1, random= ~ 1 Year, data = SumData, method="REML")</b>                                        | <b>Intercept = 1.82</b>                                 | <b><i>p</i> = &lt;&lt;0.05*</b>                      |
| <b>15</b> | <b>lme(Range_d15N ~ Season, random= ~ 1 Year, data = SumData, method="REML")</b>                                   | <b>SeasonSpring = 0.73</b>                              | <b><i>p</i> = 0.0092*</b>                            |
| <b>16</b> | <b>glm(formula = Root_d13C ~ Location + Season + (1   Year), family = gaussian(link="identity"), data=SumData)</b> | LocationNetarts = 0.66<br>SeasonSpring = -0.54          | <i>p</i> = 0.0711<br><i>p</i> = 0.1166               |
| <b>17</b> | <b>lme(Root_d15N ~ Season, random= ~ 1 Year, data = SumData, method="REML")</b>                                    | SeasonSpring = 0.43                                     | <i>p</i> = 0.135                                     |

Table 2.4. Final dredged generalized linear models for point-by-point associations of hauled-out status (HAULED), presence in inland waters (InlandWaters), and point distance from shore (DistFromShore.km). Significant ( $<0.05$ )  $p$ -values denoted by a \*.

|   | Final Model                                                                                                                                                                                                  | Coefficient Value                                                                                                                                                                                                        | Sig. Value                                                                                                                                                                                              |
|---|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1 | glmer(HAULED ~ logZenith + Season + UpwellingIndex.Scaled + TidalHeight.m + CaptureLocation + (1   CaptureYear), data = alldata, family = binomial, control = glmerControl(optimizer = "bobyqa"), nAGQ = 10) | Log(Zenith) = 0.18<br>SeasonSpring = -0.10<br>SeasonSummer = 0.20<br>SeasonWinter = 0.45<br>Upwelling.Scaled = -0.15<br>TidalHeight.m = -0.32<br>LocationNetarts = -0.12                                                 | $p = 2.50\text{e-}14^*$<br>$p = 0.000355^*$<br>$p = 8.98\text{e-}08^*$<br>$p = <2\text{e-}16^*$<br>$p = 0.000945$<br>$p = <2\text{e-}16^*$<br>$p = 6.70\text{e-}08^*$                                   |
| 2 | glmer(InlandWaters ~ logZenith + DayNight + Season + UpwellingIndex.Scaled + TidalHeight.m + CaptureLocation + (1   CaptureYear))                                                                            | Log(Zenith) = -0.07<br>DayNightNIGHT = -0.08<br>DayNightTRANS = -0.07<br>SeasonSpring = -0.46<br>SeasonSummer = -0.82<br>SeasonWinter = -0.28<br>Upwell.Scaled = -0.69<br>TidalHeight.m = 0.05<br>LocationNetarts = 0.29 | $p = 0.0728$<br>$p = 0.0341^*$<br>$p = 0.0117^*$<br>$p = <2\text{e-}16^*$<br>$p = <2\text{e-}16^*$<br>$p = <2\text{e-}16^*$<br>$p = <2\text{e-}16^*$<br>$p = 1.45\text{e-}05^*$<br>$p = 2\text{e-}16^*$ |
| 3 | glm(DistFromShore.km ~ Season + UpwellingIndex.Scaled + CaptureLocation + (1   CaptureYear))                                                                                                                 | SeasonSpring = 2.20<br>SeasonSummer = 2.22<br>SeasonWinter = 2.10<br>Upwell.Scaled = 3.25<br>LocationNetarts = -4.97                                                                                                     | $p = 2\text{e-}16^*$<br>$p = 2\text{e-}16^*$<br>$p = 2\text{e-}16^*$<br>$p = 2\text{e-}16^*$<br>$p = 2\text{e-}16^*$                                                                                    |

Table 2.5. Best explanatory generalized linear and linear mixed effects models for individually summarized parameters (n = 24) selected by the MuMIn ‘dredge’ function in R, including capture year as a random effect. Response variables best fit by the null model with random effect are denoted in bold text.

| #  | Fn  | Response        | Predictors                       | Intercept      | Df       | logLikelihood   | AICc         | weight       |
|----|-----|-----------------|----------------------------------|----------------|----------|-----------------|--------------|--------------|
| 1  | lme | log(meandist)   | ~ Location + (1   Year)          | 1.49           | 4        | -33.155         | 76.4         | 0.760        |
| 2  | lme | log(mediandist) | ~ <b>(1   Year)</b>              | <b>-0.5425</b> | <b>3</b> | <b>-34.348</b>  | <b>75.9</b>  | <b>0.566</b> |
| 3  | glm | Reserves_PU     | ~ <b>(1   Year)</b>              | <b>2.3710</b>  | <b>2</b> | <b>-81.814</b>  | <b>168.2</b> | <b>0.387</b> |
| 4  | lme | Bay_PU          | ~ <b>(1   Year)</b>              | <b>45.99</b>   | <b>3</b> | <b>-103.319</b> | <b>213.8</b> | <b>0.362</b> |
| 5  | glm | Mud_PU          | ~ <b>(1   Year)</b>              | <b>4.015</b>   | <b>2</b> | <b>-83.616</b>  | <b>171.8</b> | <b>0.342</b> |
| 6  | glm | Rock_PU         | ~ <b>(1   Year)</b>              | <b>3.993</b>   | <b>2</b> | <b>-78.078</b>  | <b>160.7</b> | <b>0.425</b> |
| 7  | lme | Sand_PU         | ~ Season + (1   Year)            | 54.09          | 4        | -100.654        | 211.4        | 0.681        |
| 8  | glm | 50m_Iso_PU      | ~ Location + (1   Year)          | 75.65          | 3        | -97.098         | 201.4        | 0.846        |
| 9  | glm | 100m_Iso_PU     | ~ Location + Season + (1   Year) | 23.23          | 4        | -92.796         | 195.7        | 0.444        |
| 10 | glm | 150m_Iso_PU     | ~ <b>(1   Year)</b>              | <b>3.055</b>   | <b>2</b> | <b>-75.990</b>  | <b>156.6</b> | <b>0.457</b> |
| 11 | glm | 200m_Iso_PU     | ~ <b>(1   Year)</b>              | <b>0.7438</b>  | <b>2</b> | <b>-52.995</b>  | <b>110.6</b> | <b>0.567</b> |
| 12 | lme | Mean_13C        | ~ MeanDistShore.km               | -13.86         | 4        | -21.853         | 53.8         | 0.818        |
| 13 | lme | Mean_15N        | ~ Location + (1   Year)          | 16.66          | 4        | -19.067         | 48.2         | 0.676        |
| 14 | lme | Range_13C       | ~ <b>(1   Year)</b>              | <b>1.0820</b>  | <b>3</b> | <b>-20.708</b>  | <b>48.6</b>  | <b>0.393</b> |
| 15 | lme | Range_15N       | ~ Season + (1   Year)            | 1.0270         | 4        | -21.665         | 53.4         | 0.421        |
| 16 | glm | Root_13C        | ~ Location + (1   Year)          | -15.25         | 3        | -28.351         | 63.9         | 0.476        |
| 17 | lme | Root_15N        | ~ <b>(1   Year)</b>              | <b>16.88</b>   | <b>3</b> | <b>-24.849</b>  | <b>56.9</b>  | <b>0.205</b> |

Table 2.6. Best explanatory generalized linear and linear mixed effects models for point-by-point parameters of hauling out status, presence in bays/rivers, and distance from shore (n = 57,220) selected by the MuMIn ‘dredge’ function in R, including capture year as a random effect.

| # | Fn  | Response     | Predictors                                                                                               | Intercept | Df | logLikelihood | AICc     | weight |
|---|-----|--------------|----------------------------------------------------------------------------------------------------------|-----------|----|---------------|----------|--------|
| 1 | glm | HAULED       | ~ logZenith + Season +<br>UpwellingIndex.Scaled + TidalHeight.m<br>+ CaptureLocation + (1   CaptureYear) | -0.32240  | 9  | -34113.50     | 68245.0  | 0.988  |
| 2 | glm | InlandWaters | ~ logZenith + DayNight + Season +<br>UpwellingIndex.Scaled + TidalHeight.m + (1<br>  CaptureYear)        | 5.11      | 10 | -39088.10     | 78196.2  | 0.517  |
| 3 | glm | DistShore    | ~ Season + UpwellingIndex.Scaled +<br>CaptureLocation + (1   CaptureYear)                                | -14.780   | 7  | -220393.3     | 440801.7 | 1      |

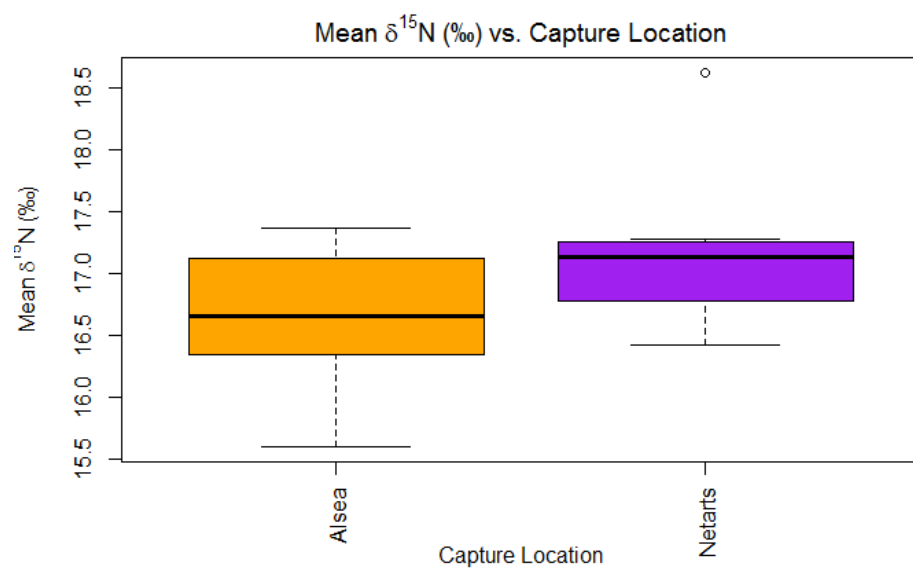


Figure 2.1. Boxplot of  $\delta^{15}\text{N}$  vs. capture site. Median values are represented by the black bar, and whiskers represent  $\pm 2$  confidence intervals.

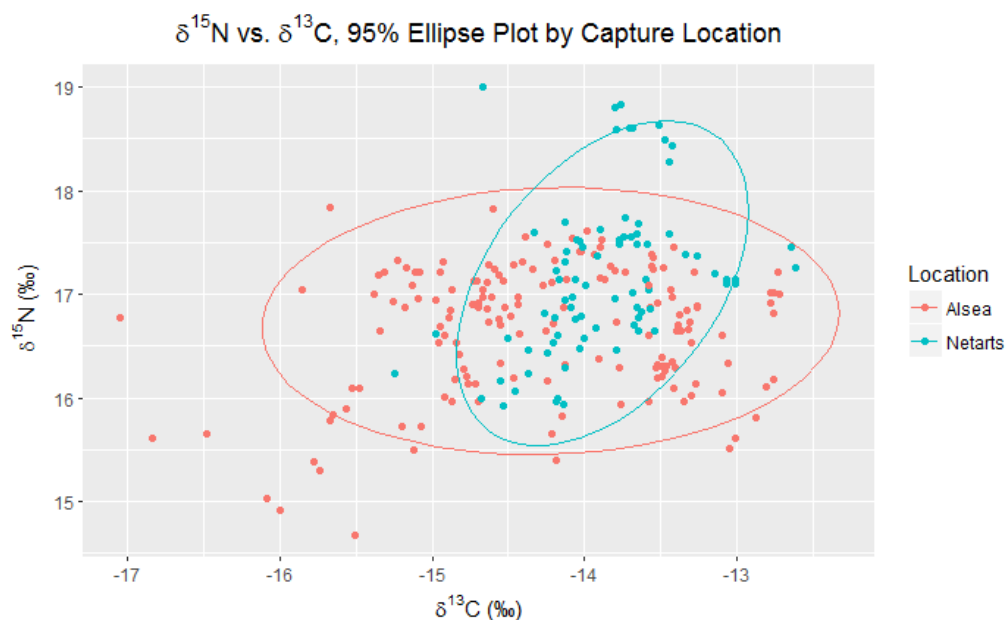


Figure 2.2. 95% ellipse plots for  $\delta^{15}\text{N}$  vs  $\delta^{13}\text{C}$  between sites. Alsea Bay animals are depicted in red, and Netarts Bay animals are depicted in blue. Netarts Bay animals had a wider 95% CI for trophic niche than Alsea animals, but Alsea bay animals had a wider range of  $\delta^{13}\text{C}$  signatures.

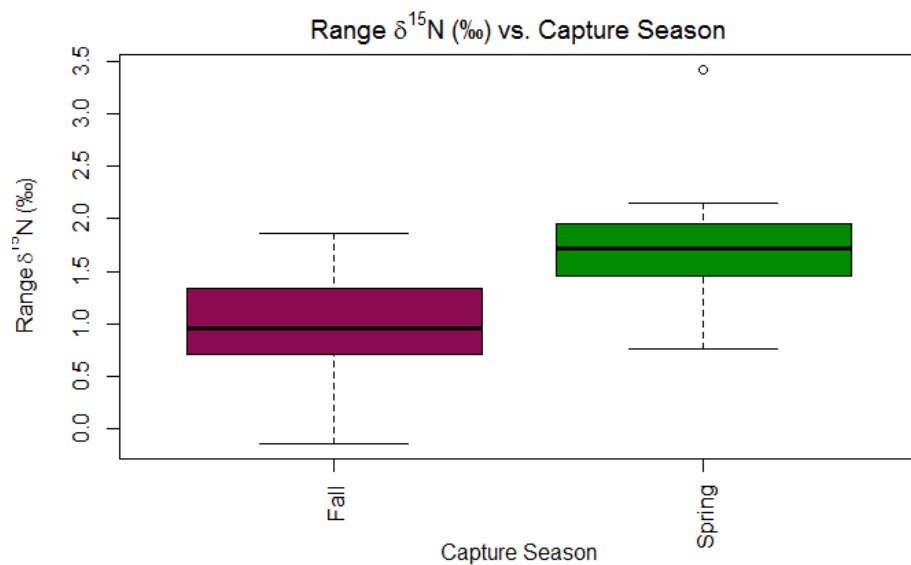


Figure 2.3. Range  $\delta^{15}\text{N}$  vs. capture site. Median values are represented by the black bar, and whiskers represent  $\pm 2$  confidence intervals.

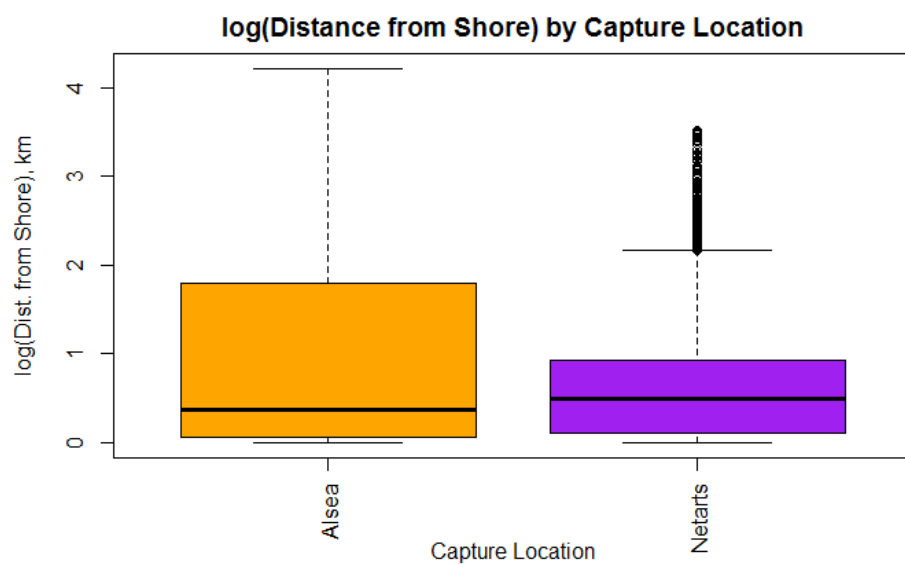


Figure 2.4. Boxplot of (log) distance from shore (km) vs. capture site. Median values are represented by the black bar, and whiskers represent  $\pm 2$  confidence intervals.

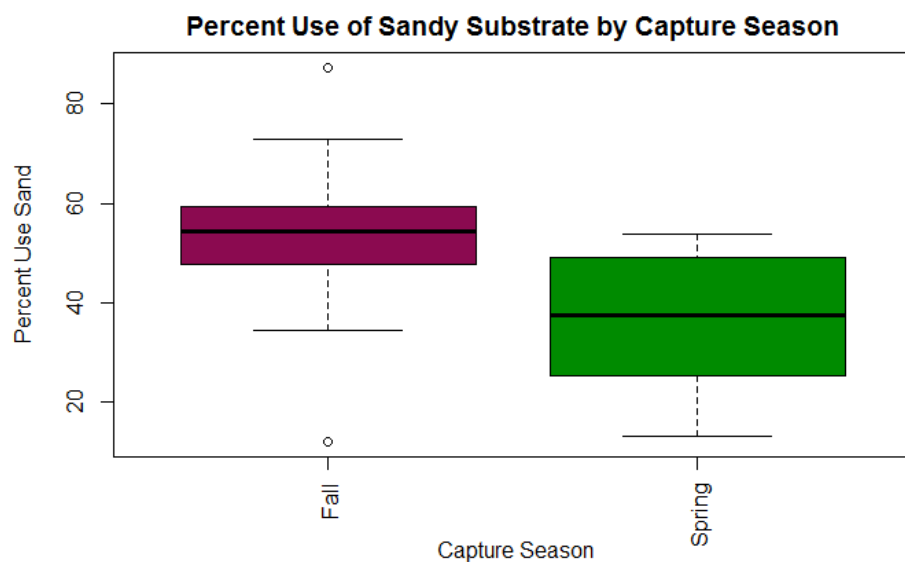


Figure 2.5. Boxplot of percent use of sandy substrate for animals tagged in fall vs. spring. Median values are represented by the black bar, and whiskers represent  $\pm 2$  confidence intervals.

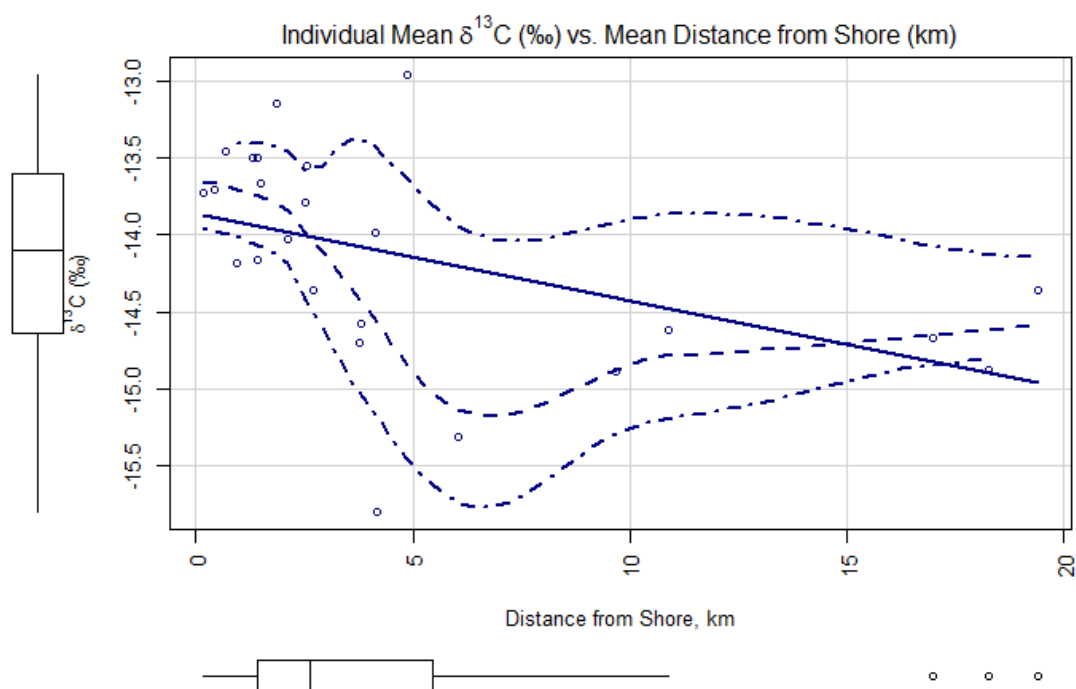


Figure 2.6. Mean  $\delta^{13}\text{C}$  vs. mean distance from shore. Shown is a scatterplot with 95% confidence intervals (2 standard errors), linear trendline, median and quartile box-and-whiskers and outliers (denoted by single points) on both axes.

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CHAPTER 3 – BEHAVIORAL AND DIETARY VARIABILITY OF A COMMON  
UPPER TROPHIC LEVEL PREDATOR IN THE NORTHERN CALIFORNIA  
CURRENT SYSTEM

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## ABSTRACT

Pacific harbor seals (*Phoca vitulina richardii*), are abundant upper-trophic level marine predators present throughout the Northern California Current System. They are distributed from Alaska to Baja California, and are continental shelf foragers that consume both neritic and benthic species. Harbor seals are abundant along the coast of Oregon, but the at-sea ecology of these animals, particularly of individuals, is not well described. This has implications for ecological management and spatial planning objectives including conservation areas and alternative energy development. To quantify the ecological role, individual variability, and associated foraging strategies of Pacific harbor seals in Oregon, I examined the spatial behavior of 24 adult Pacific harbor seals captured in Netarts and Alsea Bays, Oregon using satellite telemetry. Additionally, dietary composition within individuals was assessed with stable isotope analysis of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . The behavioral repeatability, or predictability over individual foraging trips, was calculated at the level of individual, capture site, and within individuals for the entire population. Generalized linear and linear mixed effects models were used to examine whether dietary composition, via stable isotopes, predicted spatial foraging behavior or behavioral repeatability.

Overall mean and range latitude were associated with  $\delta^{13}\text{C}$ . Harbor seals with a greater prevalence of higher latitudes had a higher  $\delta^{13}\text{C}$  value and seals with a higher mean  $\delta^{13}\text{C}$  had a lower range in use of latitudes, meaning they foraged further north but within a more specific latitudinal range.  $\delta^{15}\text{N}$  was not predictive of habitat use or

repeatability. However, in a comparison of spatial use vs. isotope values, (log) mean distance from shore (km) was positively correlated with range  $\delta^{13}\text{C}$  and negatively correlated with mean  $\delta^{13}\text{C}$  while accounting for year and capture site. Secondly, (log) median distance from shore (km) and median latitude were significantly positively correlated with range  $\delta^{13}\text{C}$ . Study results represent general patterns between spatial use and diet of Pacific harbor seals in the Northern California Current System, and more broadly provides a starting point for further consideration of the behavioral ecology of a large population of phocid seals that use the nearshore continental shelf area of Oregon.

*Keywords: Pacific harbor seal, Oregon, spatial habitat use, stable isotope analysis, cluster analysis, behavior, ecotypes*

## INTRODUCTION

The ecological concepts of the fundamental and realized niche were first introduced by Hutchinson (Hutchinson, 1965; Robert. H. Whittaker, Levin & Root, 1973; Roughgarden, 1974). Ecological niche is a multi-faceted term that can include: the ecological role of a species within a community including the food resource utilization by that species; the distributional relation of a species within the environment; or a combination of these factors (Whittaker et al, 1973). As stated in Newsome et al. (2009) in relation to diet, the realized niche of a population is the diversity of prey across all individuals. Conversely, the fundamental niche of a species is resource selection and utilization in the absence of interspecific competition, as determined by physiological constraints of individuals (Roughgarden, 1974). Populations, and individuals, can be categorized as specialists or generalists in their strategies. For example, specialization at the individual level can be identified by an individually realized ecological niche that is considerably narrower than the total realized niche width (TNW) of the population (Bolnick, 2002; Newsome et al., 2007). In the marine environment, individual specialization has been clearly demonstrated for predators, including sea otters (*Enhydra lutris*) (Estes et al., 2003; Tinker et al., 2007; Newsome et al., 2009), polar bears (Thiemann et al., 2011), bottlenose dolphins (Sargeant et al., 2005; Weiss, 2006), fur seals and penguins (Cherel et al., 2007; Villegas-Amtmann et al., 2008), sea lions (Villegas-Amtmann et al., 2008; Baylis et al., 2015) guillemots (Woo et al., 2008), great white sharks (Kim et al., 2012) and

southern elephant seals (*Mirounga leonina*) (Field et al., 2005; Hückstädt et al., 2012). Furthermore, divergent dietary specialization of whole populations of marine predators has also been demonstrated in multiple instances (Whitehead et al., 2003).

The comparison between population- and individual level-specialization is an important consideration when identifying the ecological role of species and populations (Connor, 2001; Bolnick, 2002; Cherel et al., 2009). One form of measurement of individual specialization is through the examination of behavioral consistency. This can include quantification of individual variance as compared to the total variance of the population (Matich, Heithaus & Layman, 2011; Snowberg, Hendrix & Bolnick, 2015); calculating plasticity in behavior (Van de Pol & Wright, 2009; Dingemanse et al., 2010); or measurement of behavioral predictability. One potential way to calculate this predictability at the level of individual, subpopulation, or population is to use an estimate of repeatability. Repeatability is the proportion of variation that is reproducible in repeated measurements of a study population or individual (Shrout & Fleiss, 1979; Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010). For example, in an examination of behavioral consistency in the northern gannet (*Morus bassanus*), Patrick et al. 2014 (Patrick et al., 2014) found that as central place foragers, gannets demonstrated low levels of repeatability in terms of trip duration and total distance traveled, but high repeatability in use of foraging locations, suggesting that animals adjusted their travel characteristics to arrive at preferred foraging sites using different routes based on environmental conditions.

The traits of behavioral plasticity and individual variability increase the likelihood of populations to continue to thrive in uncertain and variable environments, or to exploit newly available niches (Sexton, McKay & Sala, 2002; Pearman et al., 2008; Cockrem, 2012, Abrahms et al., 2018). Alternatively, environmental stressors and resource limitation can drive the diversification of populations (Killen et al., 2013) or specialization of individuals (Sargeant et al., 2005). The Oregon coast in the northern California Current System (CCS) is a relevant example of a seasonally and annually dynamic environment, being subject to drastic seasonal and inter-annual changes both predictable and unpredictable which affect the functioning of its ecological communities (Checkley & Barth, 2009). In summer, equatorward (northerly) winds create wind-driven upwelling of the nearshore environment, resulting in cold, nutrient-rich water being driven upwards in the water column. This results in an increase in seasonal productivity, and shifts in distribution of plankton, forage fish and their predators (Checkley & Barth, 2009). Conversely, winter months are characterized by southerly winds reversing the upwelling process with warmer nearshore waters. On a larger temporal scale, the CCS is also subject to the processes of the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), which also strongly influence productivity. Upper trophic level marine predators are subject to the bottom-up forcing represented by these environmental shifts and the resultant availability of prey.

Pacific harbor seals (*Phoca vitulina richardii*), are abundant upper-trophic level marine predators present throughout the Northern California Current System. They are distributed from Alaska to Baja, California, and are continental shelf foragers preying on both neritic and benthic species (Steingass, 2017b). As a species, harbor seals are generalists that occupy a rather large dietary niche in the northern CCS (Steingass, 2017b). However, it is unclear whether this large dietary niche is made up of a series of generalists, or individually specialized animals that contribute to a wide population niche composed of a series of specialist behaviors. Womble (2012) stated that in a conservation framework, populations that demonstrate a high degree of spatial and resource utilization may promote consideration of management by ecotypes, rather than stocks or the population as a whole (Bolnick, 2002; Lowther et al., 2012). Therefore, for considerations of management and predator population ecology, it is relevant to understand whether populations of animals are composed of individuals that demonstrate behaviors that can be categorized as specialized or generalized in the context of resource utilization.

In an effort to further quantify the ecological role, individual variability, and associated foraging strategies of Pacific harbor seals in Oregon, I examined the spatial behavior of 24 adult Pacific harbor seals captured in Netarts and Alsea Bays, Oregon with satellite telemetry methodology. I quantified behavior of individuals and the population as a whole in terms of spatial habitat use, particularly including measures of at-sea movement. To examine foraging patterns of individuals, one whisker was

taken from each animal for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. The ratio of  $^{13}\text{Carbon}:^{12}\text{Carbon}$  (‰) (hereafter  $\delta^{13}\text{C}$ ), is generally representative of spatial foraging behavior,  $\delta^{13}\text{C}$  is indicative of food web source and can highlight both nearshore or offshore utilization, or benthically or pelagically associated origin of prey. The ratio of  $^{15}\text{Nitrogen}:^{14}\text{Nitrogen}$  (‰) (hereafter  $\delta^{15}\text{N}$ ) in particular, is indicative of trophic level within the food web. Together,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  can broadly represent dietary composition, particularly when compared with representative prey values (Newsome, Clementz & Koch, 2010c).

I compared dietary and behavioral characteristics to illuminate potential ecological strategies. In order to determine whether individuals demonstrated strong behavioral consistency, I applied the measure of behavioral repeatability between and within individuals, capture locations and at the sample population level. Our primary objectives were to: (1) use repeatability index in foraging trip characteristics to determine if seals were predictable in spatial dietary behavior at the population, sites, or individual level; (2) to estimate the general dietary patterns within and among individual Pacific harbor seals captured in Oregon, and (3) to estimate the quantitative relationships between space use, repeatability, and isotope-derived dietary patterns with generalized linear and linear mixed effect modeling. Ultimately, these analyses were used to form a multi-tiered ecological picture of harbor seal ecology in the northern CCS.

## METHODS

### *Field Methods*

Adult Pacific harbor seals (23 males, one female) were captured and tagged with Wildlife Computers SPOT5© satellite tags in Alsea (44.4279°N, 124.0679°W) and Netarts (45.4028°N, 123.9484°W) Bays on the coast of Oregon, in September 2014, 2015 and April 2015. Adult male seals >50 kg were targeted as ideal study animals to reduce variability in behavior related to growth, reproductive energetic allocation, and sex-specific foraging behaviors, and to avoid interacting with pregnant or nursing females during the spring field season. Seals were captured individually with skiff-based beach rush methods by teams of 5-13 biologists including veterinary staff (Jeffries et al. 1993). Seals were weighed with a hanging scale in all but two cases, and then restrained on a v-board during tag attachment. All seals were given a numbered tag in each hind-flipper (Deflux sheep and goat ear tags, 2.25x7/8inch, 5g.) punched through the interdigital skin for visual identification. An external Wildlife Computers Satellite SPOT5© tag was attached to the post-cranial dorsal pelage with Devcon© 5-minute epoxy or Loctite© 422 adhesive (Horning et al., 2012). SPOT5 tags are Argos transmitters that allow the satellite service provider (CLS America Inc.) to estimate locations via the Doppler shift. Locational data are provided with associated classes based on locations with accuracy ranging in accuracy from 150m (LC3) to >1.5km (LCB) or unspecified error (LC Z) (Boyd & Brightsmith, 2013).

### *Tag Programming*

During the first two deployment periods (fall 2014, spring 2015), tags were duty cycled on an on-off bimonthly cycle to provide a longer period of data, and promote data overlap between tag deployments. Tags were sequentially set to 'ON' during April through May and September through October to coincide with the spring and fall transitions of upwelling. Tags deployed in fall 2015 were programmed to transmit continuously to maximize total data overlap with previous deployments. Time at Temperature and Percent Dry Timeline histograms were collected for all deployments.

### *Parameter Estimation*

After tags ceased transmitting, all data collected by the Argos satellite service provider CLS America, Inc. during deployment were downloaded via the Wildlife Computers Data Portal (© Wildlife Computers). Locations with a quality of LC 0-3, A and B were first manually filtered to remove duplicate locations. LC-Z locations were discarded due to lack of a measurable error estimate. Maximum swim speed for Pacific harbor seals is not widely-documented; however minimum cost of transport occurs at approximately 1.0-1.4m/s (Lesage, Hammill & Kovacs, 1999). Therefore, a coarse speed-distance-angle (SDA) filter was applied to the data to remove locations which required a biologically unlikely travel speed of  $>8\text{m/s}$ . The remaining data were used to create regularized state space models (SSM's) for each animal using the R

package *crawl* (Johnson et al., 2008; Johnson, 2017). To create a roughly equal ratio of estimated to observed locations, time steps were calculated as the average time between consecutive ‘wet’ locations, as determined by the Argos 20-minute timeline. On-land points were not considered for this calculation. The resultant mean inter-location period was  $1.52 \pm 9.83$  hours. Therefore, a temporal resolution of one hour was used for the generation of regularized SSM points for analysis. SSM output locations were further adjusted by utilizing the *Fix-Path* function in the R package *crawl* (Johnson, 2017). *Fix-Path* utilizes a transition matrix to correct animal tracks to restrict travel through identified restricted areas, in this case over land. Once the state-space modeled and the filtered dataset was generated, the resultant pseudolocations were used for all further analyses. The percent timeline collected by the tags was utilized to estimate whether seals were in water or hauled out on land. When an hour bin was identified as >50% ‘dry’, it was considered hauled out. If an hour bin was <50% dry, the animal was considered to be ‘wet’ or in the water and this was counted as an individual foraging trip until the percent timeline data once again indicated a status of ‘dry’. A trip was considered as the first ‘wet’ location followed by all consecutive locations with the same status until the tag returned to a ‘dry’ status.

#### *Stable Isotope Analysis*

To create an assessment of foraging preference, stable isotope analysis of seal vibrissae (whiskers) was conducted. Seal vibrissae were collected at time of capture, with an effort to collect the longest caudal whisker on the left side of the head for all

animals. Whiskers were measured for total and sheath length and individual sonicated to remove debris. The sheath and whisker plug were removed, and the whisker was cleaned with 2:1  $\text{CHCl}_3$ : $\text{CH}_4\text{O}$  solution and prepared on a sterile table as per Rea et al. (2015).

Whiskers were sectioned and weighed every 0.5cm, and the first ten samples beginning at the root were analyzed. 0.20-0.55mg of sample were cut using a chisel and packed in tin boats. Blood presence in the whisker shaft, as well as beading pattern was recorded in a qualitative value of 0 (absence of visible blood) or 1 (presence of visible blood). One sample, belonging to Seal #61769, consisted of a vascularized soft tissue plug that separated from the root during sonication. This sample was analyzed separately to provide a baseline for soft tissue/blood that may be present within whiskers. In total, ten samples were prepared from each individual plus the blood plug to generate a total of 240 samples for analysis. Prepared samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility using continuous-flow isotope ratio mass spectrometry (CFIRMS) employing a Thermo Scientific Flash 2000 elemental analyzer and Thermo Scientific ConFlo IV interfaced with a Thermo Scientific DeltaV<sup>Plus</sup> Mass Spectrometer. Results were reported as parts per thousand (‰) deviation from the international standards PDB (carbon) and Air (nitrogen) with a precision of <0.2 ‰. Welch's t-test for equal variance were run for whisker segments that included blood vs. no blood and beaded vs. smooth segments, in order to determine whether there were apparent effects of these characteristics on

isotopic estimates. However, quantification of the amount of blood in the whisker is difficult to assess, so results of this test were purely informative for a potential caveat of analysis.

### *Repeatability Analysis*

The quantitative method of repeatability (Nakagawa & Schielzeth, 2010) was used at the level of foraging trip to estimate consistency between and within individuals and capture sites (Alsea vs. Netarts Bay), and within the population. Repeatability was measured for the trip-summarized metrics of mean latitude, latitude range, mean and median distance from shore, and trip duration (hours). Because there was no dive data to indicate foraging status, foraging trips were identified utilizing wet-dry histogram data provided by the SPOT5 tags. The measure of repeatability of trips within the population, and between- and within-capture site was calculated with R package *rptR*. Package *rptR* fits a linear mixed-effect model (R package *lme4*) for a parameter of interest, and produces an estimate of repeatability with associated uncertainty. It utilizes the general equation (McHuron, 2016; Nakagawa and Schielzeth, 2010):

$$R = \frac{\sigma^2_{\alpha}}{\sigma^2_{\alpha} + \sigma^2_{\varepsilon}} \quad (\text{Eq. 1})$$

Where  $\sigma^2_{\alpha}$  is the between-individual variability, and  $\sigma^2_{\varepsilon}$  is the residual error for a parameter of interest. The resultant models were used within R Package *rptR* to

compute repeatability. Between-individual models were run as adjusted ( $r_{adj}$ ) models, accounting for capture site as a fixed effect.

For intra-individual variability, the repeatability of distance from shore and latitude was estimated using ‘trip’ as the grouping variable of interest. For this measure of repeatability, Eq 2 was used:

$$R = \frac{\sigma^2_{\alpha}}{\sigma^2_{\alpha} + \sigma^2_i} \quad (\text{Eq. 2})$$

Where  $\sigma^2_{\alpha}$  was the between-individual variability, and  $\sigma^2_i$  is the residual error for individual  $i$  (Eq.5). Similar comparisons of inter- versus intra-individual variabilities were made by McHuron (2016) for California sea lions. Repeatability values range from 0 to 1, where 1 represents perfectly repeatable values and 0 represents high variance with no repeatability (Harris et al., 2014; McHuron, 2016).

### *Linear Mixed Effects Modeling*

Repeatability of spatial behavior within individuals, as well as the original trip-based values of mean and median distance from shore, mean and median latitude, and trip duration (hrs) were modeled as response variables against isotopic values of mean and range  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in order to determine whether spatial behavior, and the consistency of such, was potentially associated with dietary characteristics. Both mean and median values were included in analysis, as mean values were more demonstrative

of the full range of habitat use, while median values represented a more accurate description of behavioral tendencies as they related to central place foragers returning to one haulout, foraging location, or latitude between trips. Resultantly, median values tended to be more skewed towards shore or haulout latitude while mean values were more variable in both regards. Comparison of spatial vs. isotopic values was achieved by fitting generalized-linear models (GLMs) and linear mixed-effects models (LMEMs) (R package *lme4*), and performing model selection using the function ‘*dredge*’ in R package *MuMIn* to choose the best-fitting, most parsimonious model based on AICc value. Response variables that were determined as normally distributed by a Shapiro-Wilkes test were run in LMEMs, and response variables that were determined not to have a normal distribution by the Shapiro-Wilkes test were run in GLMs to account for non-normality. Repeatability was fit as a continuous variable versus the continuous predictor variables of trip-based mean latitude, latitude range, mean and median distance from shore, and trip duration (hours).

Linear mixed-effects models were also examined for the continuous response variables of individual isotopic mean and range versus the continuous variables of individual overall (non trip-based) values for mean, median and range latitude, and mean and median distance from shore in order to determine whether there were general patterns between habitat use and isotopic composition, beyond the consideration of behavioral predictability estimated by repeatability.

## RESULTS

### *Stable Isotope Analysis*

For Seal #61769, a Grubb's Outlier Test (R package *outliers*) identified the blood plug as an outlier in  $\delta^{15}\text{N}$  ( $p$  value = 0.002) but not  $\delta^{13}\text{C}$  ( $p$  value = 0.195); it was not included in further analysis. Mean  $\delta^{15}\text{N}$  for all animals was  $16.83 \pm 0.41\text{‰}$  (2 S.D.), with a range of 4.32‰ (14.68, 19.00). Mean  $\delta^{13}\text{C}$  for all animals was  $-14.14 \pm 0.79\text{‰}$  with a total range of 4.43‰ (-17.05, -12.62) (Figure 3.1). No significant outliers for  $\delta^{13}\text{C}$  were detected ( $p$  value = 0.134) so all 240 segments were included in analysis.

The presence of blood in the shaft resulted in a significantly higher value of  $\delta^{15}\text{N}$  ( $p$  value = 0.0003635), but not  $\delta^{13}\text{C}$  ( $p$  value = 0.8333). Whisker texture of 'smooth' vs. 'beaded' did not significantly affect  $\delta^{13}\text{C}$  ( $p$  value = 0.1632) or  $\delta^{15}\text{N}$  ( $p$  value = 0.5699).

### *Repeatability Analysis*

At the between-individual level, the adjusted repeatability was less than 0.5 for all estimates of mean and range latitude, mean and median distance from shore, and total trip duration while accounting for capture location (Table 3.1). Mean latitude was strongly bimodal and was the most repeatable variable with a value of  $0.477 \pm 0.077$  (Figure 3.2). At the level of capture site, only mean latitude was repeatable to a high degree ( $R = 0.856 \pm 0.314$ ). Individual, between-trip repeatability was generally more

repeatable than between-individual and between-site behaviors. Netarts Bay animals were more repeatable than Alsea Bay animals (Tables 3.2, 3.3). This was particularly the case for Seal #61773, which displayed moderate to strong (0.63-1.00) repeatabilities in all behaviors.

#### *Repeatability vs. Stable Isotope Values*

The best-fitting generalized linear and linear mixed effects models for repeatability only highlighted repeatability in mean and median distance from shore as being reliably associated with stable isotope characteristics. The final GLM selected for trip-based repeatability in median distance from shore (km) included the variables of range  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Trip repeatability in median distance from shore was significantly positively correlated with mean  $\delta^{13}\text{C}$  (value =  $0.24 \pm 0.09$ ,  $p$  value = 0.017), but not significantly correlated with range  $\delta^{15}\text{N}$  (value =  $-0.19 \pm 0.09$ ,  $p$  value = 0.053). The final generalized linear model selected for trip-based repeatability in mean distance from shore (km) also included the variables of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Repeatability in trip mean distance from shore was significantly positively correlated with mean  $\delta^{13}\text{C}$  (value =  $0.24 \pm 0.09$ ,  $p$  value = 0.01771), but not significantly correlated with range  $\delta^{15}\text{N}$  even though it was included in the model (value = -0.18,  $p$  value = 0.05976).

#### *Spatial Use vs. Stable Isotope Analysis*

In the final dredged LMEM, (log) mean distance from shore (km) was positively correlated with range  $\delta^{13}\text{C}$  ( $0.68 \pm 0.30$ ,  $p$  value = 0.0329) and negatively correlated with mean  $\delta^{13}\text{C}$  (value =  $-0.84 \pm 0.26$ ,  $p$  value = 0.0042) while accounting for year and capture site. Secondly, (log) median distance from shore (km) was significantly positively correlated with range  $\delta^{13}\text{C}$  (value =  $0.78 \pm 0.34$ ,  $p$  value = 0.0316). Mean latitude was not found to correlate with any significant isotope factors. In the final selected generalized linear model for median latitude which included mean and range  $\delta^{13}\text{C}$ , median latitude was positively correlated with mean  $\delta^{13}\text{C}$  (value  $0.04 \pm 0.03$ ,  $p$  value = 0.0363). In the final LMEM for range latitude which accounted for capture site and year, range latitude was negatively associated with mean  $\delta^{13}\text{C}$  (value =  $-0.23 \pm 0.06$ ,  $p$  value = 0.0006).

## DISCUSSION

This paper highlighted the individual and site-level variability in spatial and foraging behavior of a populous and under examined phocid, the Pacific harbor seal, in Oregon. It also demonstrated associations between habitat use, behavioral consistency, and dietary composition for these animals. Harbor seals were captured at two tagging locations approximately 112 kilometers apart; animals captured at the two locations displayed differences in individual and site-level predictability. Seals from the northernmost site of Alsea Bay were on average more dynamic in their spatial behaviors, demonstrated by lower levels of repeatability for mean and median latitude,

mean distance from shore, median distance from shore, and trip duration. There was higher between-individual consistency in mean latitude for Alsea Bay seals, and higher between-individual repeatability in mean distance from shore, median distance from shore, trip duration (hours) and latitudinal range for Netarts Bay seals. This suggests that while Alsea Bay animals returned to a certain latitude predictably, they still utilized more diverse habitats and foraging locations than Netarts Bay animals. The most repeatable individual was seal #61773, who also had an overall higher trophic signature than all other seals. In addition, the home range area (95% KDE) for this individual was merely 3.00km<sup>2</sup> while for all individuals, the calculated mean home range area was 364.47km<sup>2</sup> (Steingass et al. 2018, *unpub. data*). Therefore, this individual is likely a specialist in a very specific food source within close range of the haulout site.

Some associations between repeatability in behavior and isotopic composition became apparent through generalized linear and linear mixed effect models. Between-trip repeatability in median and median distance from shore were the only two repeatability values that associated with isotopic composition. In both cases, mean and median distance were positively associated with mean  $\delta^{13}\text{C}$ , meaning that animals with higher repeatability in distance from shore site tended to have a higher mean  $\delta^{13}\text{C}$ . In addition to this, animals with a higher range in  $\delta^{13}\text{C}$  tended to have higher overall mean and median distance from shore. Therefore, it can be deduced that  $\delta^{13}\text{C}$  is indeed an indicator of spatial foraging behavior for this population. Seals that spent more time

further from shore overall demonstrated a more generalist diet than those that spent more time nearshore, and seals that spent more time inshore tended to have a higher overall  $\delta^{13}\text{C}$  enrichment value.

Although no further factors of repeatability were associated with isotope values, overall mean and range latitude were associated with  $\delta^{13}\text{C}$ . The positive association between median latitude and mean  $\delta^{13}\text{C}$  demonstrates that animals utilizing higher latitudes had an overall higher  $\delta^{13}\text{C}$  value. Additionally, animals with a higher mean  $\delta^{13}\text{C}$  (and, therefore, utilizing higher latitudes) had a lower range in use of latitudes overall, meaning they foraged further north but within a more specific latitudinal range. Neither behavioral repeatability nor spatial habitat use correlated significantly with  $\delta^{15}\text{N}$ . This may indicate that there are no significant determining factors of diet and spatial habitat use, including the potential caveat that isotopic data represents a retrospective archive of diet as compared to collected satellite data. However, there is also the possibility that animals visit a number of different foraging locations in order to target preferred, patchily distributed prey resources (Boyd, 1996; Thompson & Fedak, 2001; Field et al., 2005). Comparing behavioral repeatability and spatial habitat use makes the assumption that while foraging locations may differ on a temporal basis (which is why capture year was utilized as a fixed effect in LMEMs and GLMs); the general behavioral patterns of an individual animal are reliable over time within the context of foraging tactics. In general, Netarts Bay animals were more repeatable than animals captured in Alsea Bay. A potential explanatory factor for

differences in repeatability may be coastal geomorphology. Netarts Bay is located on a particularly narrow section of the continental shelf in Oregon. Alsea Bay is located directly north of Stonewall and Heceta Bank, a highly productive region of the continental shelf that extends up to 70 kilometers from shore.

Repeatability was strongest at the individual, between-trip level rather than between-individual or between-site, suggesting that overall the study population is composed of a series of diverse individuals demonstrating both specialization and more generalized strategies (Connor, 2001; Patrick et al., 2014; Layman, Newsome & Gancos Crawford, 2015) . However, this being the case, this level of repeatability varied between individuals. At the between-individual and between-site levels, the only strongly repeatable factor ( $\geq 0.75$ ) was mean latitude.

The use of isotopes to inform spatial behavior and foraging ecology in pinnipeds has been well-demonstrated (Burton & Koch, 1999; Zeppelin et al., 2015). The use of isotope analysis has further implications in behavioral estimation of both stranded animals and without more invasive tagging procedures. However, this could have been further verified in this study by the ability to recapture animals at the end of tag deployment. Based on correction factors by Hobson et al. (1997) and Beltran et al. (2016), the diet of seals in this study correlates with flatfish collected in Oregon in 2016 (Steingass, *unpub. data*), but the wide range of potential prey for these animals makes stable isotope mixing models difficult as a representative sample of the full spectrum of food sources is an important consideration for these models (Beltran et al., 2016).

Intra-population variation in diet, diving, and foraging behavior has been documented in several pinniped species (Lea et al., 2002; Villegas-Amtmann et al., 2008; Weise, Harvey & Costa, 2010; Lowther et al., 2012; Páez-Rosas et al., 2012; Páez-Rosas, Villegas-Amtmann & Costa, 2017). The data in this study demonstrated moderate to high repeatability on the individual, between-trip level for spatial foraging behavior and generally overlapping isotopic composition for 23 of 24 individuals. However, the range of trophic niche width was variable between individuals, suggesting that some animals are more general in their diet than others. There are an estimated 10,000-12,000 Pacific harbor seals in the state of Oregon (Brown et al., 2005c) and this study only represented 24 adult individuals. Therefore, before management considerations might be fully investigated, a larger and more demographically representative sample size should be achieved. There is a continued need to understand the foraging ecology of Pacific harbor seals as they represent a widely distributed and biologically relevant species to fisheries-pinniped interactions, ecological functioning of nearshore food webs, and seasonal and inter-annual changes in ecosystem function of a highly-productive eastern boundary current system. The data presented here provides a starting point for further consideration of the behavioral ecology of a large population of phocid seals that utilize the nearshore continental shelf area of Oregon.

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## ETHICS APPROVALS

This study was carried out in strict compliance with all applicable animal care and use guidelines under the U.S. Animal Welfare Act and was approved as required under the U.S. Marine Mammal Protection Act by the National Marine Fisheries Service (NMFS #16991) and by the Institutional Animal Care and Use Committees of San Jose State University (AUP #1010) and Oregon State University (ACUP #4616).

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## TABLES AND FIGURES

Table 3.1. Between-trip repeatabilities for individuals. Higher values are represented by green, lower values are represented by red.

| PTT                      | Mean Latitude      | Range Lat.         | Mean km from Shore | Median km from Shore | Trip Duration (hrs) |
|--------------------------|--------------------|--------------------|--------------------|----------------------|---------------------|
| 44611                    | 0.57               | 0.02               | 0.01               | 0.03                 | 0.57                |
| 44613                    | 0.39               | 0.22               | 0.01               | 0.06                 | 0.39                |
| 44614                    | 0.97               | 0.11               | 0.02               | 0.12                 | 0.97                |
| 44615                    | 0.96               | 0.12               | 0.19               | 0.38                 | 0.96                |
| 61694                    | 0.35               | 0.03               | 0.63               | 0.05                 | 0.35                |
| 61695                    | 0.05               | 0.02               | 0.09               | 0.03                 | 0.05                |
| 61698                    | 0.51               | 0.03               | 0.12               | 0.58                 | 0.51                |
| 61754                    | 0.38               | 0.05               | 0.01               | 0.35                 | 0.38                |
| 61764                    | 0.01               | 0.04               | 0.02               | 0.02                 | 0.01                |
| 61765                    | 0.81               | 0.07               | 0.06               | 0.03                 | 0.81                |
| 61766                    | 0.74               | 0.08               | 0.02               | 0.06                 | 0.74                |
| 61767                    | 0.4                | 0.16               | 0.72               | 0.08                 | 0.4                 |
| 61768                    | 0.91               | 0.27               | 0.93               | 0.06                 | 0.91                |
| 61769                    | 0.97               | 0.2                | 0.38               | 0.03                 | 0.97                |
| 61770                    | 0.85               | 0.05               | 0.07               | 0.37                 | 0.85                |
| 61771                    | 0.42               | 0.02               | 0.08               | 0.15                 | 0.42                |
| 61772                    | 0.99               | 0.36               | 0.56               | 0.56                 | 0.99                |
| 61773                    | 1                  | 0.99               | 0.99               | 0.63                 | 1                   |
| 61774                    | 0.18               | 0.03               | 0.31               | 0.06                 | 0.18                |
| 61775                    | 0.98               | 0.65               | 0.87               | 0.03                 | 0.98                |
| 61776                    | 0.81               | 0.07               | 0.94               | 0.28                 | 0.81                |
| 61777                    | 0.9                | 0.03               | 0.14               | 0.21                 | 0.9                 |
| 61778                    | 0.59               | 0.04               | 0.82               | 0.16                 | 0.59                |
| 61779                    | 0.05               | 0.01               | 0.06               | 0.01                 | 0.05                |
| <b>Mean Alsea ± SD</b>   | <b>0.50 ± 0.31</b> | <b>0.07 ± 0.06</b> | <b>0.18 ± 0.27</b> | <b>0.18 ± 0.28</b>   | <b>0.16 ± 0.17</b>  |
| <b>Mean Netarts ± SD</b> | <b>0.84 ± 0.28</b> | <b>0.33 ± 0.34</b> | <b>0.64 ± 0.33</b> | <b>0.64 ± 0.34</b>   | <b>0.23 ± 0.24</b>  |

Table 3.2. Between-individual and between-site repeatability in foraging trip characteristics for all animals. Repeatability was higher between individuals for mean and median distance from shore and trip duration, but higher between sites for mean and range latitude.

|                                     | <b>Repeatability Between Individuals</b> | <b>Repeatability Between Sites</b> |
|-------------------------------------|------------------------------------------|------------------------------------|
| <b>Mean Latitude</b>                | $0.477 \pm 0.077$                        | $0.856 \pm 0.314$                  |
| <b>Range Latitude</b>               | $0.022 \pm 0.009$                        | $0.026 \pm 0.036$                  |
| <b>Mean Dist. From Shore (km)</b>   | $0.107 \pm 0.031$                        | $0.057 \pm 0.072$                  |
| <b>Median Dist. From Shore (km)</b> | $0.106 \pm 0.03$                         | $0.056 \pm 0.066$                  |
| <b>Trip Duration (hrs)</b>          | $0.001 \pm 0.002$                        | $0.000 \pm 0.001$                  |

Table 3.3. Comparative between-animal repeatability for Alsea Bay vs. Netarts Bay-tagged animals. Results reveal higher between-individual consistency in mean latitude for Alsea Bay animals, and higher between-individual repeatability in mean distance from shore, median distance from shore, trip duration (hours) and latitudinal range for Netarts Bay animals.

| SITE    | Mean Latitude | Mean Dist. from Shore (km) | Median Dist. from shore (km) | Duration (hrs) | Lat. Range |
|---------|---------------|----------------------------|------------------------------|----------------|------------|
| Alsea   | 0.60          | 0.58                       | 0.58                         | 0.51           | 0.55       |
| Netarts | 0.46          | 0.95                       | 0.95                         | 0.90           | 0.86       |

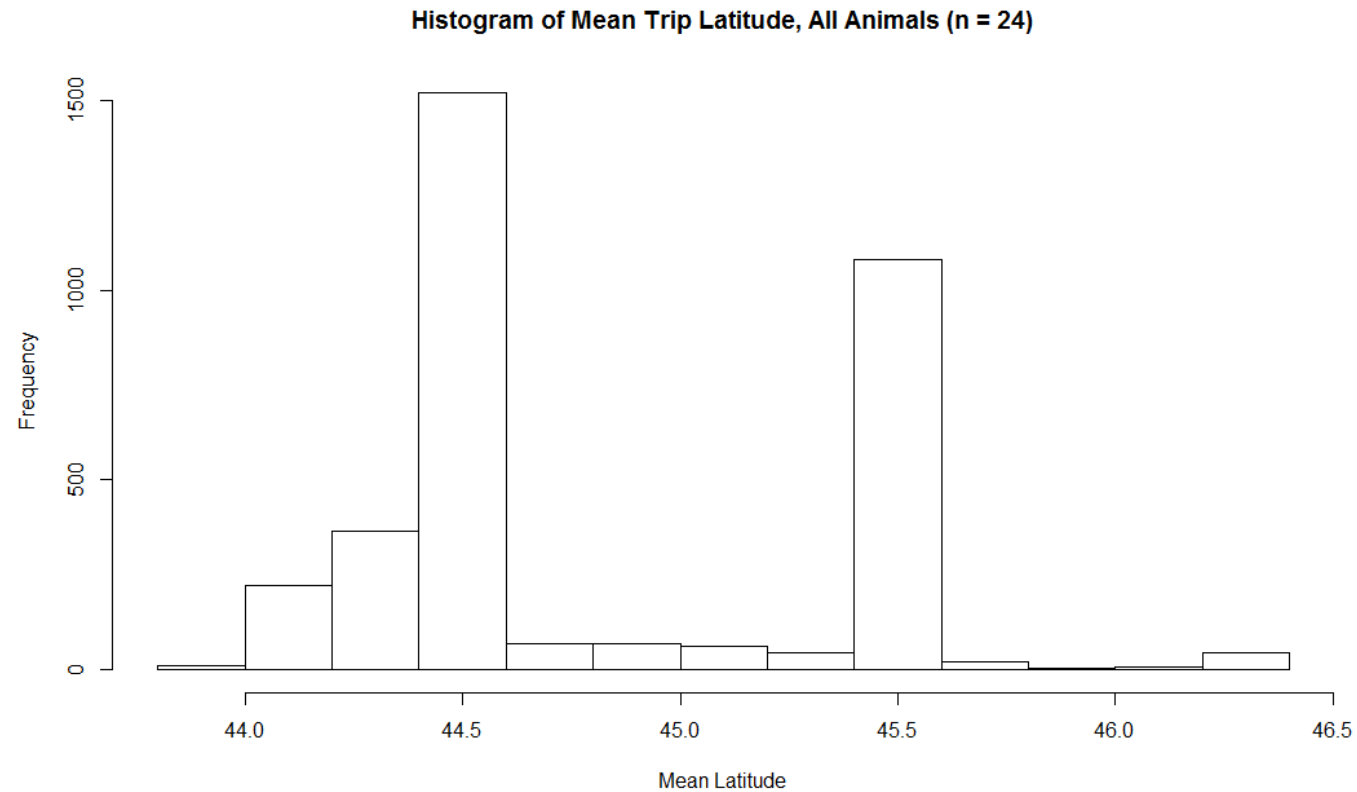


Figure 3.1. Histogram of mean trip latitude, averaged over all trips and all animals. Alsea Bay is located at  $44.44^{\circ}$  N, Netarts Bay is located at  $45.40^{\circ}$  N. High use of both of these areas (as well as Heceta Bank, south of Alsea Bay) is highlighted by relative location frequency. Desdemona Sands on the Columbia River, located at  $46.20^{\circ}$  N was also used by two individuals.

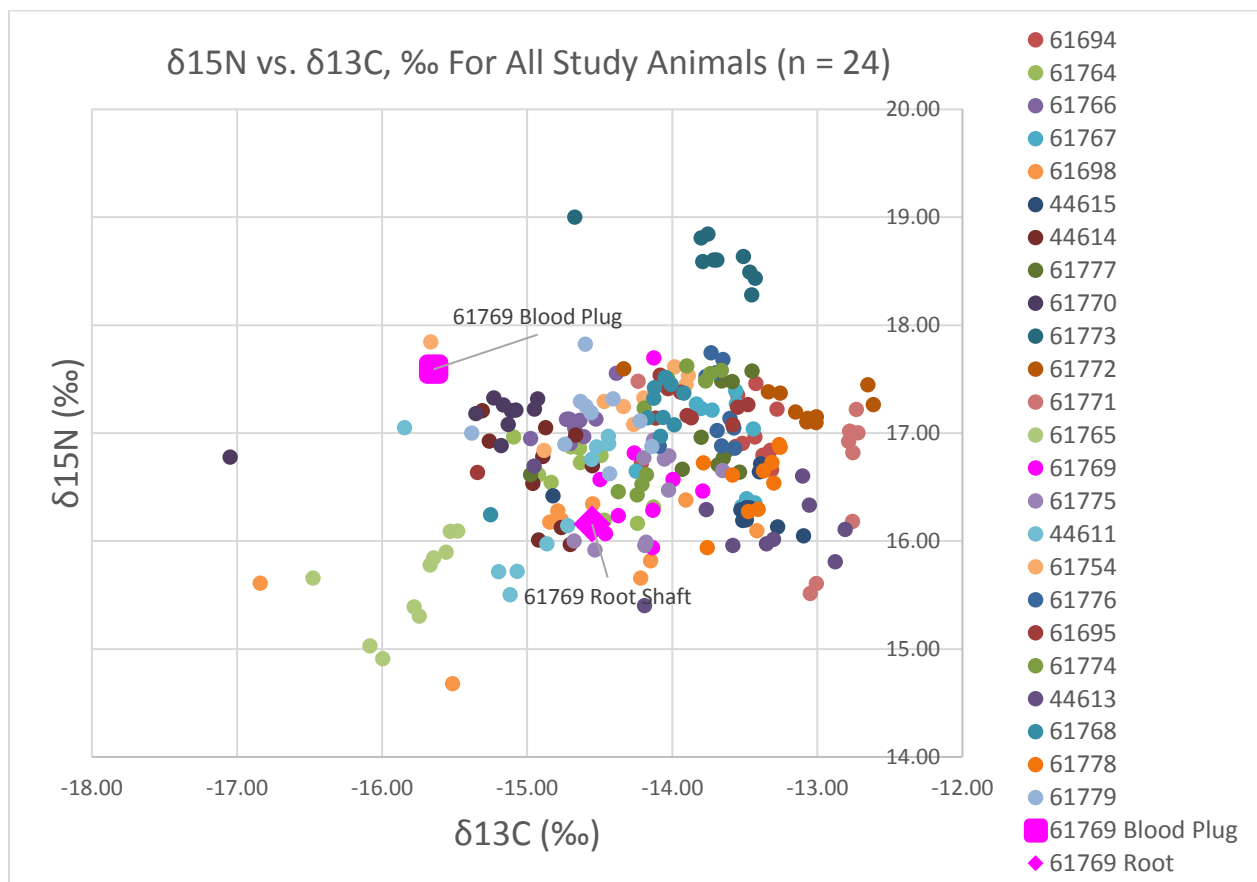


Figure 3.2. Scatterplot of isotope values for all individual, including blood plug and root segment. Individual #61773 displayed higher  $\delta^{15}\text{N}$  values than other animals and was demonstrated as an outlier by the Grubbs Outlier Test.

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## CONCLUSION

Pinnipeds, fisheries, and human activities in the coastal ocean will always overlap. Pinnipeds are a natural and native upper trophic level predator in many coastal ecosystems and play an important role as ecosystem sentinels, marine predators, and visible megafauna that allow the assessment of coastal ecosystem functioning. This dissertation examined the behavioral ecology of a common non-migratory pinniped on the Oregon coast, the Pacific harbor seal. I utilized a combination of satellite telemetry, stable isotope ecology, and oceanography to describe behavioral associations of 24 adult seals with the nearshore ocean, including seasonal effects. Beyond describing the utilization of coastal habitat by seals, this dissertation highlighted the apparently wide range of foraging strategies utilized by harbor seals in the state.  $\delta^{13}\text{C}$  obtained from whiskers of seals displayed associations with repeatability in behavior and spatial habitat use. Furthermore, site-specific differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  demonstrate that to some degree, haulout site fidelity and origin plays a role in foraging patterns. Efficient and effective management of marine mammals and their prey species as coastal resources requires sufficient knowledge of the population-wide and individual level distribution, ecology and behavioral patterns of these species.

The first data chapter of this dissertation examined the spatial habitat use of 24 animals on the Oregon coast, as well as utilization of marine reserves, bays and estuarine sites, and wave energy test sites. Results demonstrated limited utilization of

marine reserve and wave energy areas, but high use of bay and estuarine sites (~42% of locations). As Oregon's marine reserves were only established in 2012, the functional community responses to the exclusion of fisheries is likely to take a decade or more before clear trends become apparent. Additionally, the North and South Energy Test Sites represent the very beginning of offshore alternative energy exploration, and could additionally be preliminary to other future developments, including offshore wind energy, tidal energy, and the possibility of offshore drilling. Therefore, the limited information on use of these areas, or apparent lack of preferential use by animals, is useful for future comparison.

The second data chapter of this dissertation examined patterns in habitat use and harbor seal diet as they relate to both static and dynamic oceanographic characteristics. Harbor seal behavior was correlated with the variables of season, upwelling index, and tidal cycles. Seals utilized a foraging cycle of approximately 22 hours, which correlated with tidal cycles in the Pacific Northwest. Harbor seal diet, particularly  $\delta^{13}\text{C}$ , correlated with spatial habitat use patterns, and therefore may be a useful proxy for habitat use of animals. The utility of isotopic composition lends itself to estimation of at-sea behavioral patterns without being reliant on expensive and more invasive telemetry methods, and may also be useful for examination of the ecology of stranded animals.

The third and final data chapter of this dissertation examined the behavior of adult harbor seals in the context of behavioral repeatability and association between

stable isotopes and behavioral patterns. Again,  $\delta^{13}\text{C}$  was associated both with spatial foraging characteristics, as well as the degree of repeatability in foraging trip characteristics that animals displayed. On the whole, animals from Netarts Bay utilized the nearshore environment more than Alsea Bay animals, and were more predictable in their behavior. In general, animals from Netarts Bay consumed food from a higher trophic level than animals from Netarts Bay, further highlighting between-site differences that were apparent from telemetry methods.

This dissertation represents a relatively small, primarily male-biased portion of the Oregon coastal stock of Pacific harbor seals ( $\sim 0.2\%$ ), but it did demonstrate some clear patterns of diet and habitat use for the sample population. Overall, this dissertation represents the first ever in-depth assessment of at-sea habitat use of Pacific harbor seals along the Oregon coast, and provides a baseline for future studies, shifting ecosystem regimes, and ecological changes in a rapidly-warming North Pacific Ocean. The broader impact of this work lies not only in what was discerned from these analyses, but also in the highlighting of data gaps which must be informed to achieve adequate ecological assessment of a common upper trophic level predator in the Northern California Current System.

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## ETHICS STATEMENT

All work presented in this dissertation was carried out in strict compliance with all applicable animal care and use guidelines under the U.S. Animal Welfare Act and was approved as required under the U.S. Marine Mammal Protection Act by the National Marine Fisheries Service (NMFS #16991) and by the Institutional Animal Care and Use Committees of San Jose State University (AUP #1010) and Oregon State University (ACUP #4616).

## APPENDIX I: CHAPTER 1 SUPPLEMENTARY TABLES AND FIGURES

Supplementary Table 1.1. Percent of total State Space Modeled locations present within 11 coastal bodies of water in Oregon. Other bodies of water were excluded if there was no presence of seals nearby or within these areas. In total, 47.60% of data points (n = 27,235) were classified as present within one of these areas. Gray represents animals tagged in Alsea Bay, white represents animals tagged in Netarts Bay.

| <i>Ptt</i>   | <i>Total #<br/>Locations</i> | <i>Alsea Bay</i>  | <i>Columbia<br/>River</i> | <i>Depoe<br/>Bay</i> | <i>Nehalem<br/>Bay</i> | <i>Nestucca<br/>Bay</i> | <i>Netarts<br/>Bay</i> | <i>Sand<br/>Lake</i> | <i>Siletz<br/>Bay</i> | <i>Siuslaw<br/>River</i> | <i>Tillamook<br/>Bay</i> | <i>Yaquina<br/>Bay</i> | <i>Total</i>      |
|--------------|------------------------------|-------------------|---------------------------|----------------------|------------------------|-------------------------|------------------------|----------------------|-----------------------|--------------------------|--------------------------|------------------------|-------------------|
| <b>44611</b> | 1330                         | 15.34<br>(n=204)  |                           |                      |                        |                         |                        |                      |                       |                          |                          |                        | 15.34<br>(n=204)  |
| <b>44613</b> | 3425                         | 51.88<br>(n=1777) |                           |                      |                        |                         |                        |                      |                       |                          |                          |                        | 51.88<br>(n=1777) |
| <b>44614</b> | 2786                         | 18.59<br>(n=518)  |                           |                      |                        |                         |                        |                      |                       |                          |                          | 0.97<br>(n=27)         | 19.56<br>(n=545)  |
| <b>44615</b> | 1039                         | 53.80<br>(n=559)  |                           |                      |                        |                         |                        |                      |                       |                          |                          |                        | 53.80<br>(n=559)  |
| <b>61694</b> | 1927                         | 38.30<br>(n=738)  |                           |                      |                        |                         |                        |                      |                       | 3.84<br>(n=74)           |                          | 0.36<br>(n=7)          | 42.50<br>(n=819)  |
| <b>61695</b> | 2848                         | 4.60<br>(n=131)   | 10.04<br>(n=286)          | 0.04<br>(n=1)        | 3.69<br>(n=105)        | 13.65<br>(n=389)        | 1.58<br>(n=45)         | 0.11<br>(n=3)        | 13.66<br>(n=389)      |                          | 0.46<br>(n=13)           |                        | 47.82<br>(n=1362) |
| <b>61698</b> | 1339                         | 42.12<br>(n=564)  |                           |                      |                        |                         | 7.99<br>(n=107)        |                      |                       |                          |                          |                        | 50.11<br>(n=671)  |
| <b>61754</b> | 2679                         | 22.84<br>(n=612)  |                           | 1.38<br>(n=37)       |                        |                         |                        |                      |                       |                          |                          | 0.26<br>(n=7)          | 24.49<br>(n=656)  |
| <b>61764</b> | 2661                         | 29.20<br>(n=777)  |                           |                      |                        |                         |                        |                      |                       |                          |                          | 0.08<br>(n=2)          | 29.27<br>(n=779)  |
| <b>61765</b> | 3288                         | 79.68<br>(n=2620) |                           |                      |                        |                         |                        |                      |                       | 0.79<br>(n=26)           |                          |                        | 80.47<br>(n=2646) |
| <b>61766</b> | 4114                         | 40.62<br>(n=1671) |                           |                      |                        |                         |                        |                      |                       |                          |                          | 0.32<br>(n=13)         | 40.93<br>(n=1684) |
| <b>61767</b> | 3759                         | 16.73<br>(n=629)  |                           |                      |                        |                         |                        |                      |                       | 27.96<br>(n=1051)        |                          |                        | 44.69<br>(n=1680) |
| <b>61768</b> | 1956                         |                   |                           |                      |                        |                         |                        |                      |                       |                          | 77.97<br>(n=1525)        |                        | 77.97<br>(n=1525) |

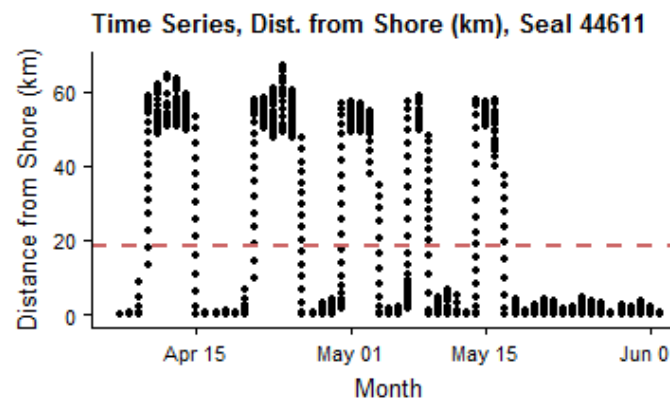
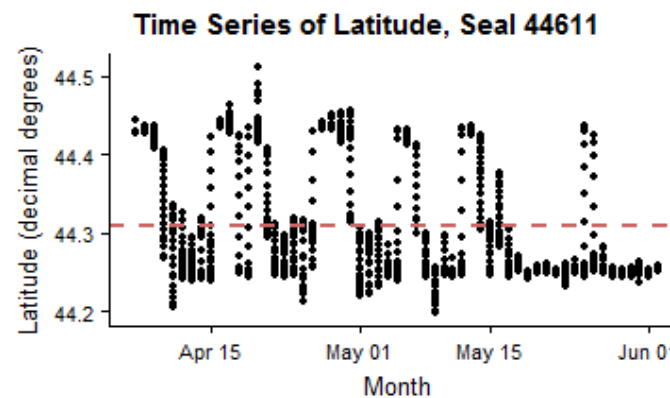
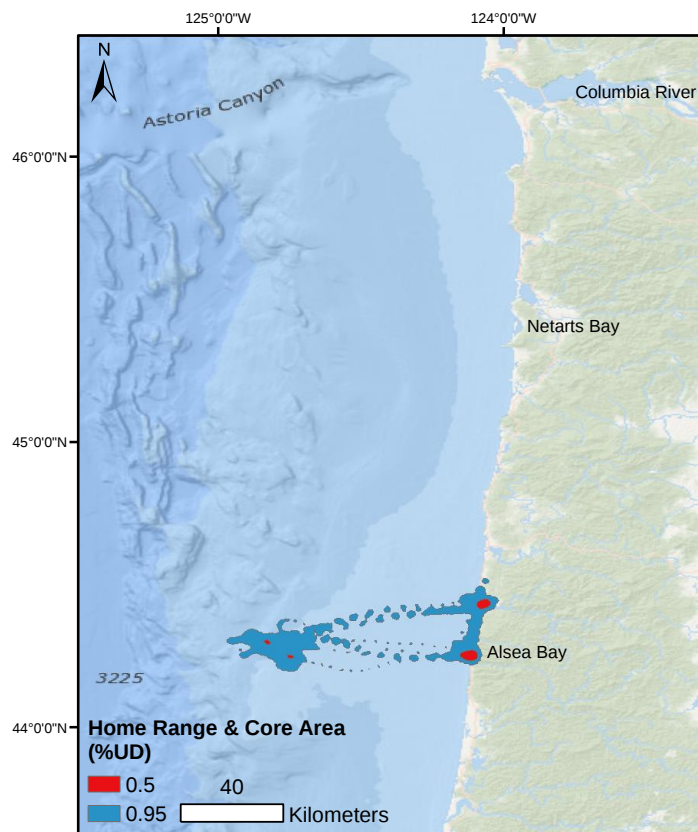
|              |              |                            |                          |                        |                         |                         |                          |                       |                         |                          |                          |                         |                   |
|--------------|--------------|----------------------------|--------------------------|------------------------|-------------------------|-------------------------|--------------------------|-----------------------|-------------------------|--------------------------|--------------------------|-------------------------|-------------------|
| <b>61769</b> | 2332         |                            |                          |                        |                         |                         |                          |                       |                         |                          | 0.99<br>(n=23)           | 0.04<br>(n=1)           | 1.03<br>(n=24)    |
| <b>61770</b> | 2292         | 41.67<br>(n=955)           |                          |                        |                         |                         |                          |                       |                         |                          |                          |                         | 41.67<br>(n=955)  |
| <b>61771</b> | 991          | 10.09<br>(n=100)           |                          |                        |                         |                         |                          |                       |                         |                          |                          |                         | 10.09<br>(n=100)  |
| <b>61772</b> | 1587         |                            |                          |                        |                         |                         | 43.23<br>(n=686)         |                       |                         |                          |                          |                         | 43.23<br>(n=686)  |
| <b>61773</b> | 1543         |                            |                          |                        |                         |                         | 73.36<br>(n=1132)        |                       |                         |                          |                          |                         | 73.36<br>(n=1132) |
| <b>61774</b> | 1967         |                            | 5.59<br>(n=110)          |                        | 0.56<br>(n=11)          |                         | 23.95<br>(n=471)         | 0.31<br>(n=6)         |                         |                          | 0.86<br>(n=17)           |                         | 31.27<br>(n=615)  |
| <b>61775</b> | 4208         |                            |                          |                        |                         |                         | 1.45<br>(n=61)           |                       |                         |                          | 60.27<br>(n=2536)        |                         | 61.72<br>(n=2597) |
| <b>61776</b> | 1227         |                            |                          |                        |                         |                         | 33.90<br>(n=416)         |                       |                         |                          | 11.82<br>(n=145)         |                         | 45.72<br>(n=561)  |
| <b>61777</b> | 474          |                            |                          |                        |                         |                         | 44.30<br>(n=210)         |                       |                         |                          | 3.16<br>(n=15)           |                         | 47.47<br>(n=225)  |
| <b>61778</b> | 2133         | 17.25<br>(n=368)           |                          |                        |                         |                         |                          |                       |                         |                          |                          | 36.19<br>(n=772)        | 53.45<br>(n=1140) |
| <b>61779</b> | 5315         | 22.37<br>(n=1189)          | 52.25<br>(n=2777)        |                        |                         |                         | 5.85<br>(n=311)          |                       |                         |                          | 0.30<br>(n=16)           | 0.02<br>(n = 1)         | 80.77<br>(n=4293) |
| <b>SUM</b>   | <b>57220</b> | <b>23.44<br/>(n=13412)</b> | <b>5.55<br/>(n=3173)</b> | <b>0.07<br/>(n=38)</b> | <b>0.20<br/>(n=116)</b> | <b>0.68<br/>(n=389)</b> | <b>6.01<br/>(n=3439)</b> | <b>0.02<br/>(n=9)</b> | <b>0.67<br/>(n=389)</b> | <b>2.01<br/>(n=1151)</b> | <b>7.50<br/>(n=4290)</b> | <b>1.45<br/>(n=829)</b> |                   |

Supplementary Table 1.2. Percent of total SSM locations within 7 MPAs or seabird PAs in Oregon. In total, 1.55% of data points (n = 886) were classified as present within one of these area.

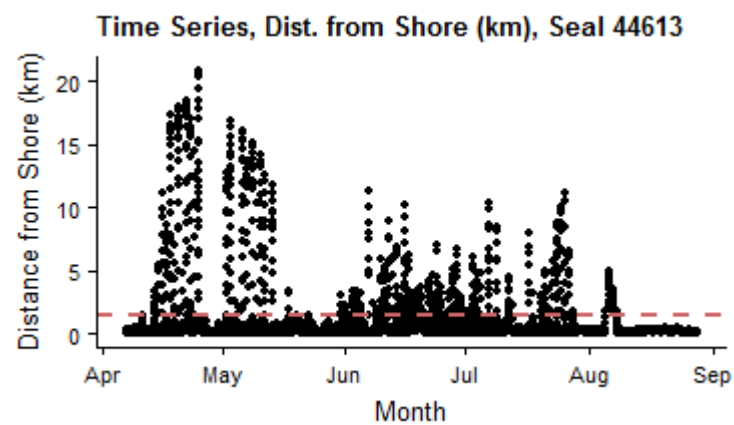
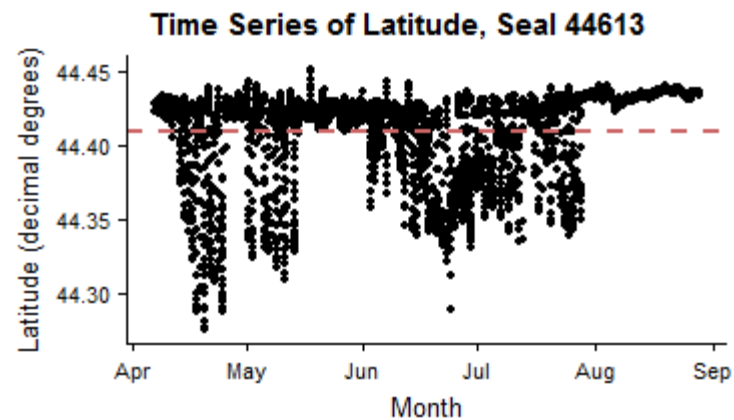
| <i>Ptt</i> | <i>Total #<br/>Locations</i> | <i>Cape Perpetua<br/>North MPA</i> | <i>Cape Perpetua<br/>Seabird<br/>Protection Area</i> | <i>Cape Perpetua<br/>SE MPA</i> | <i>Cape Falcon<br/>West MPA</i> | <i>Cascade Head<br/>North MPA</i> | <i>Cascade Head<br/>South MPA</i> | <i>Cascade Head<br/>West MPA</i> |
|------------|------------------------------|------------------------------------|------------------------------------------------------|---------------------------------|---------------------------------|-----------------------------------|-----------------------------------|----------------------------------|
| 44611      | 1330                         | 1.13 (n = 15)                      |                                                      |                                 |                                 |                                   |                                   |                                  |
| 44613      | 3425                         | 0.32 (n = 11)                      |                                                      |                                 |                                 |                                   |                                   |                                  |
| 44614      | 2786                         | 0.04 (n = 1)                       |                                                      |                                 |                                 |                                   |                                   |                                  |
| 44615      | 1039                         | 3.46 (n = 36)                      |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61694      | 1927                         |                                    | 6.80 (n = 131)                                       | 4.41 (n = 85)                   |                                 |                                   |                                   |                                  |
| 61695      | 2848                         |                                    |                                                      |                                 |                                 | 0.49 (n = 14)                     | 1.09 (n = 31)                     | 0.07 (n = 2)                     |
| 61698      | 1339                         | 0.22 (n = 3)                       | 0.22 (n = 3)                                         |                                 |                                 |                                   |                                   |                                  |
| 61754      | 2679                         | 0.15 (n = 4)                       |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61764      | 2661                         | 15.30 (n = 407)                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61765      | 3288                         | 0.06 (n = 2)                       |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61766      | 4114                         | 0.02 (n = 1)                       |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61767      | 3759                         | 0.19 (n = 7)                       | 0.56 (n = 21)                                        | 0.27 (n = 10)                   |                                 |                                   |                                   |                                  |
| 61768      | 1956                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61769      | 2332                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61770      | 2292                         | 0.57 (n = 13)                      |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61771      | 991                          | 7.47 (n = 74)                      | 1.11 (n = 11)                                        |                                 |                                 |                                   |                                   |                                  |
| 61772      | 1587                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61773      | 1543                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61774      | 1967                         |                                    |                                                      |                                 | 0.15 (n = 3)                    |                                   |                                   |                                  |
| 61775      | 4208                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61776      | 1227                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61777      | 474                          |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61778      | 2133                         |                                    |                                                      |                                 |                                 |                                   |                                   |                                  |
| 61779      | 531                          |                                    |                                                      |                                 |                                 |                                   | 0.19 (n = 1)                      |                                  |
| <b>SUM</b> | <b>57220</b>                 | <b>2.11<br/>(n = 574)</b>          | <b>0.29<br/>(n = 166)</b>                            | <b>0.17<br/>(n = 95)</b>        | <b>0.01<br/>(n = 3)</b>         | <b>0.02<br/>(n = 14)</b>          | <b>0.06<br/>(n = 32)</b>          | <b>&lt;0.01<br/>(n = 2)</b>      |

Supplementary Figures 1.1-1.24(a-c). *Crawled* locations and time series of distance from shore and latitude for all individual seals.

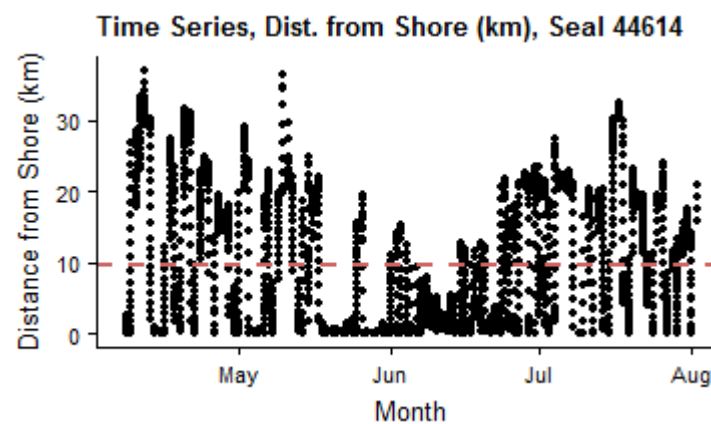
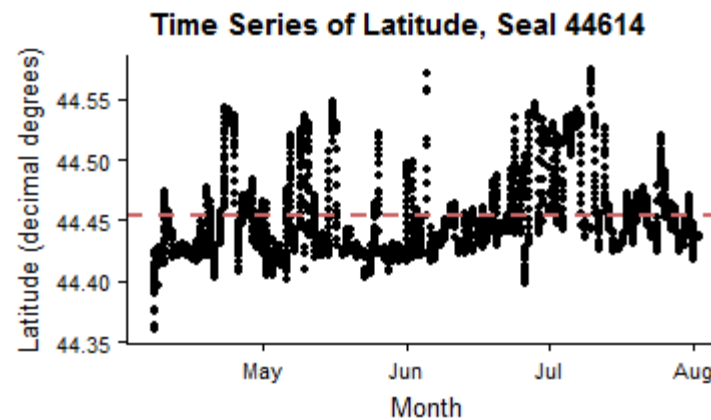
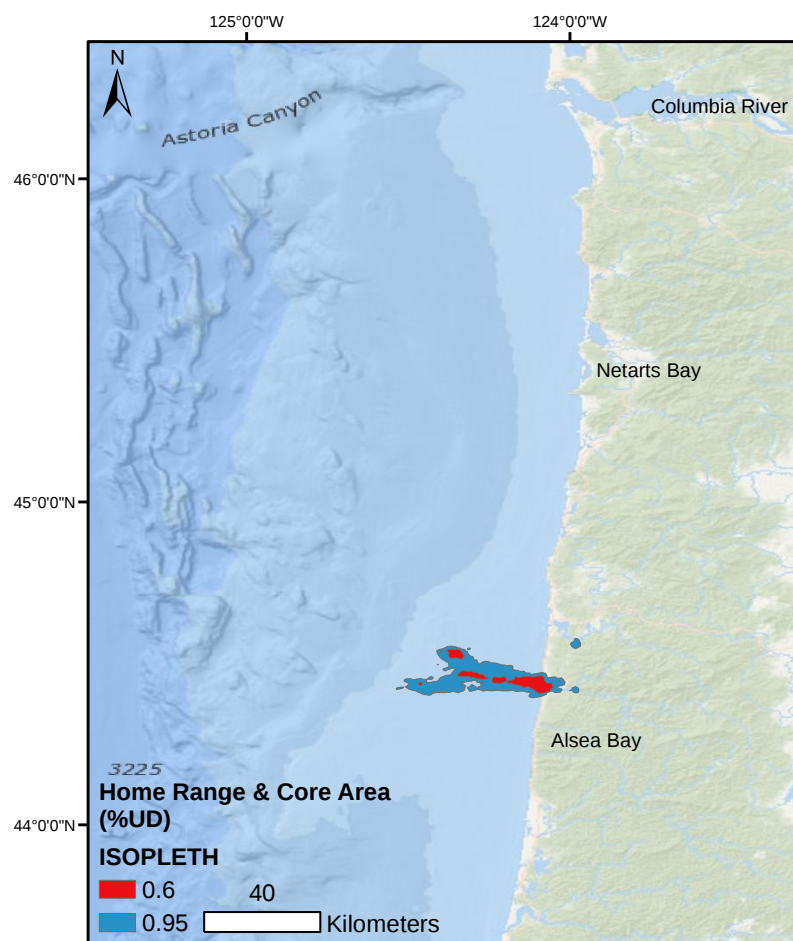
Seal 44611 Home Range and Core Area from 'crawled' Locations  
(n = 1330) 7 Apr. 2015 - 2 Jun. 2015



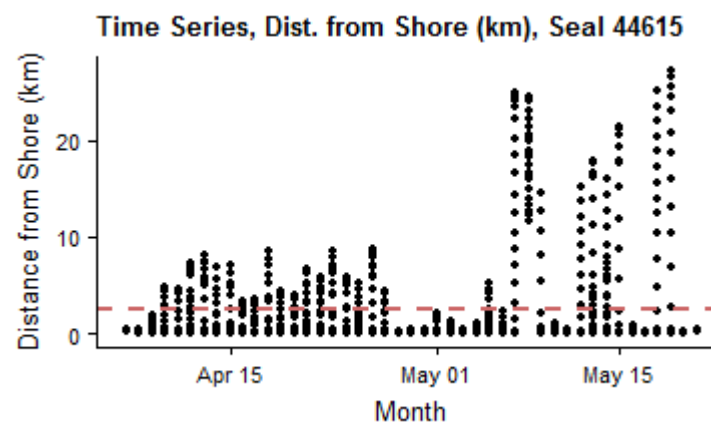
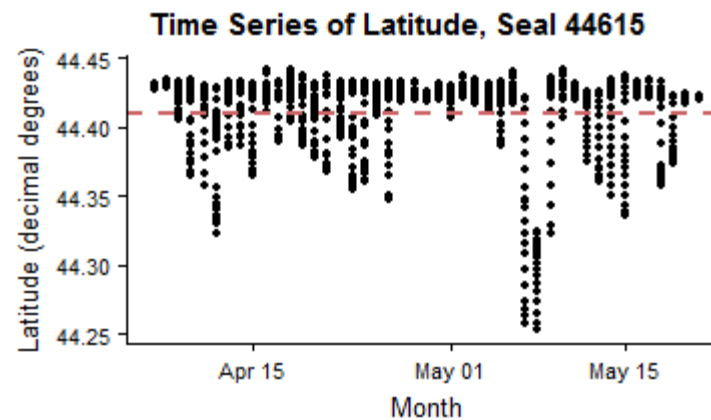
Seal 44613 Home Range and Core Area from 'crawled' Locations  
(n = 3425) 7 Apr. 2015 - 28 Aug. 2015



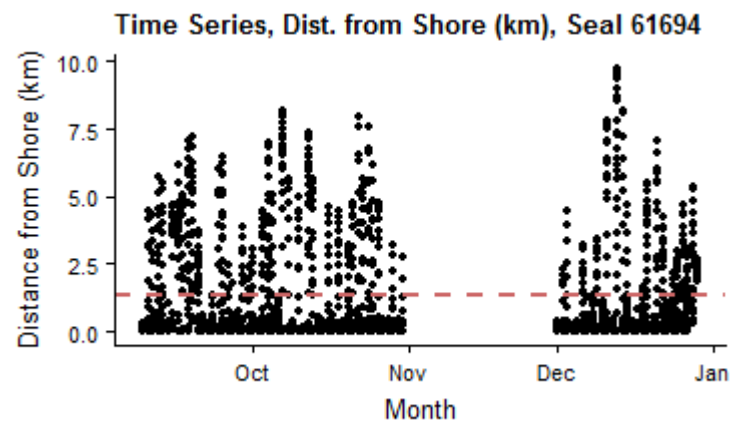
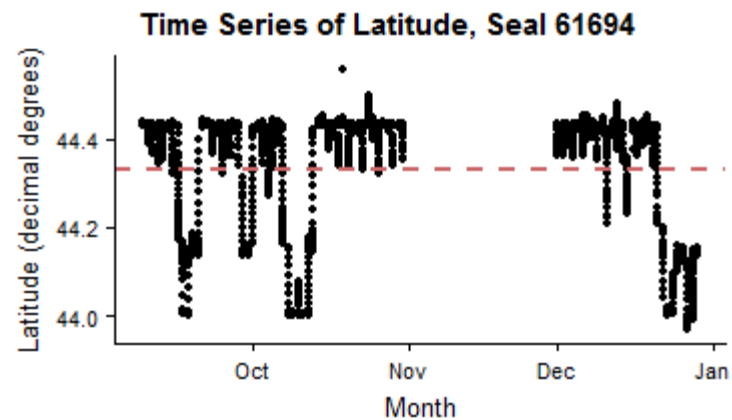
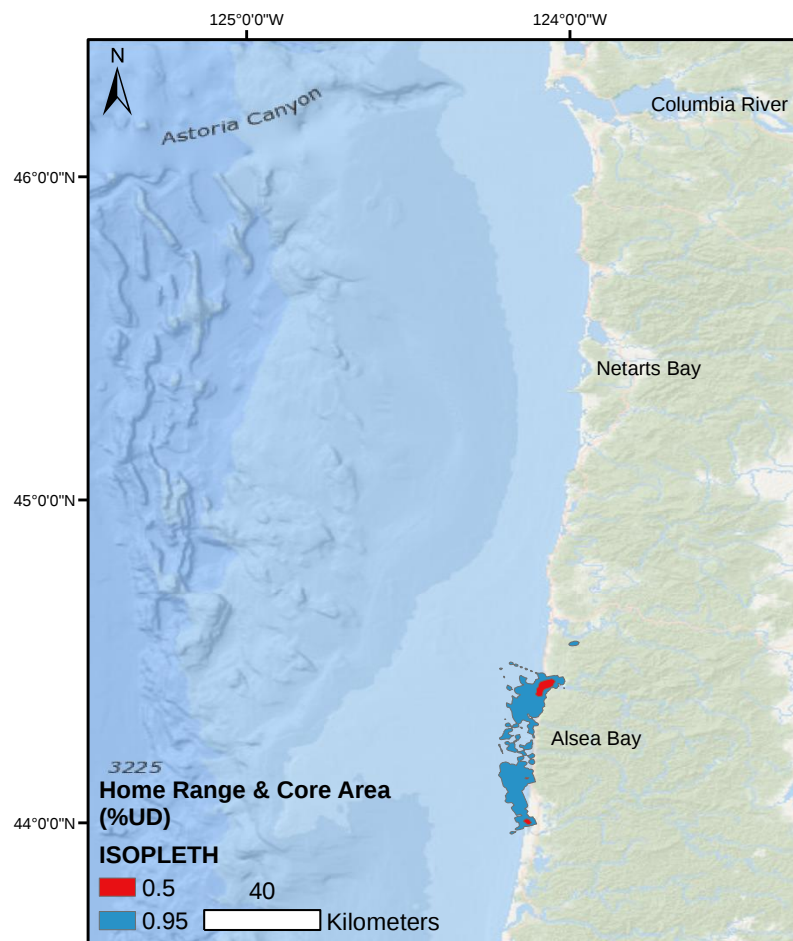
Seal 44614 Home Range and Core Area from 'crawled' Locations  
(n = 2786) 8 Apr. 2015 - 2 Aug. 2015



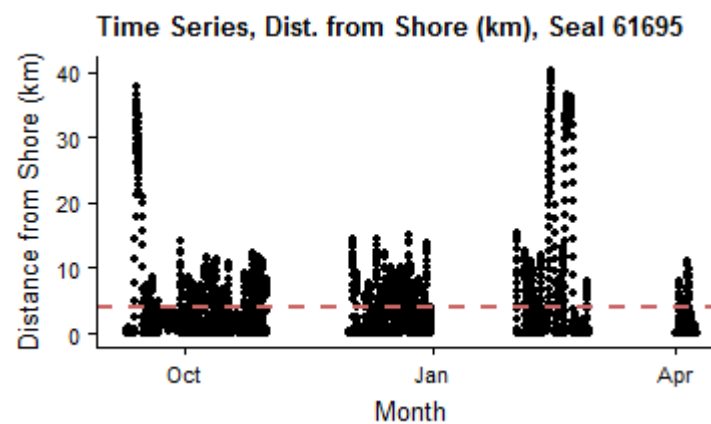
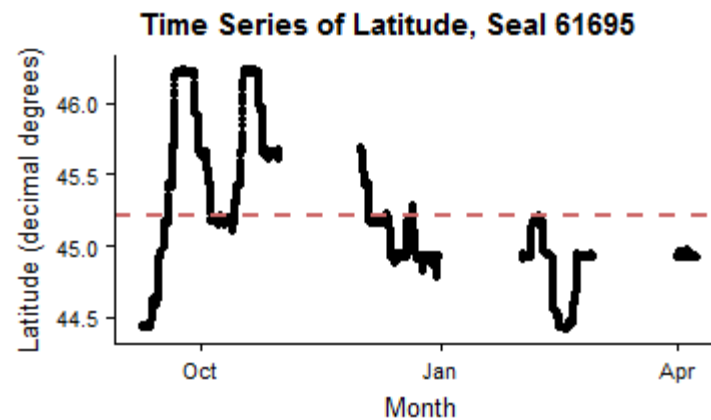
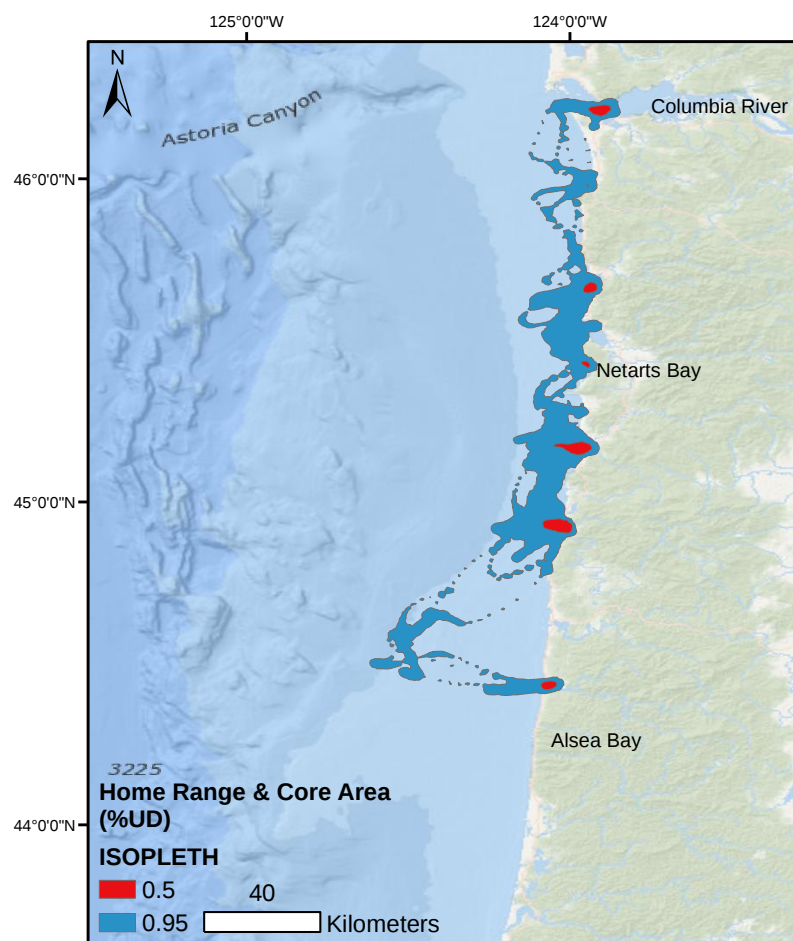
Seal 44615 Home Range and Core Area from 'crawled' Locations  
(n = 1039) 7 Apr. 2015 - 21 May 2015



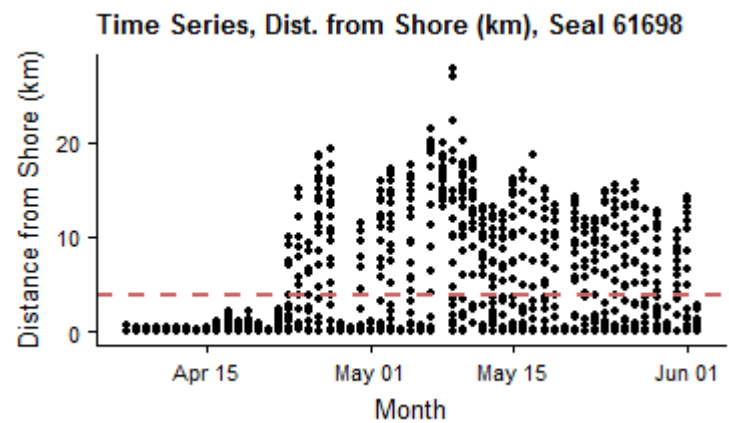
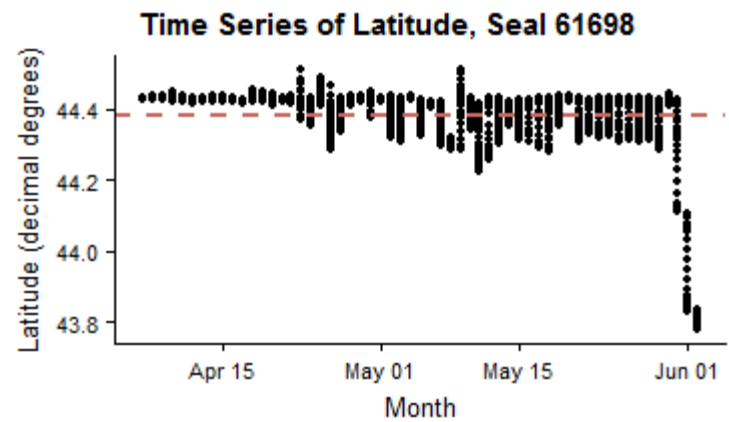
Seal 61694 Home Range and Core Area from 'crawled' Locations  
(n = 1927) 9 Sept. 2014 - 29 Dec. 2014



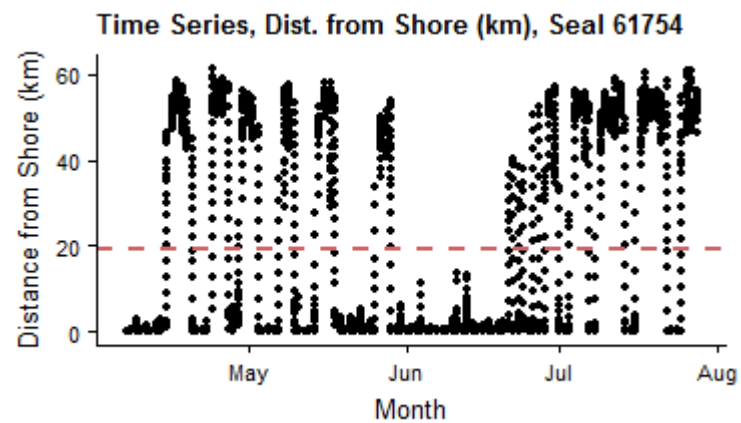
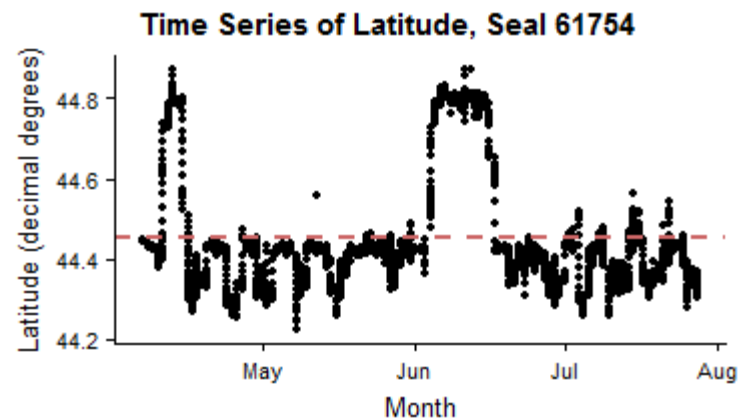
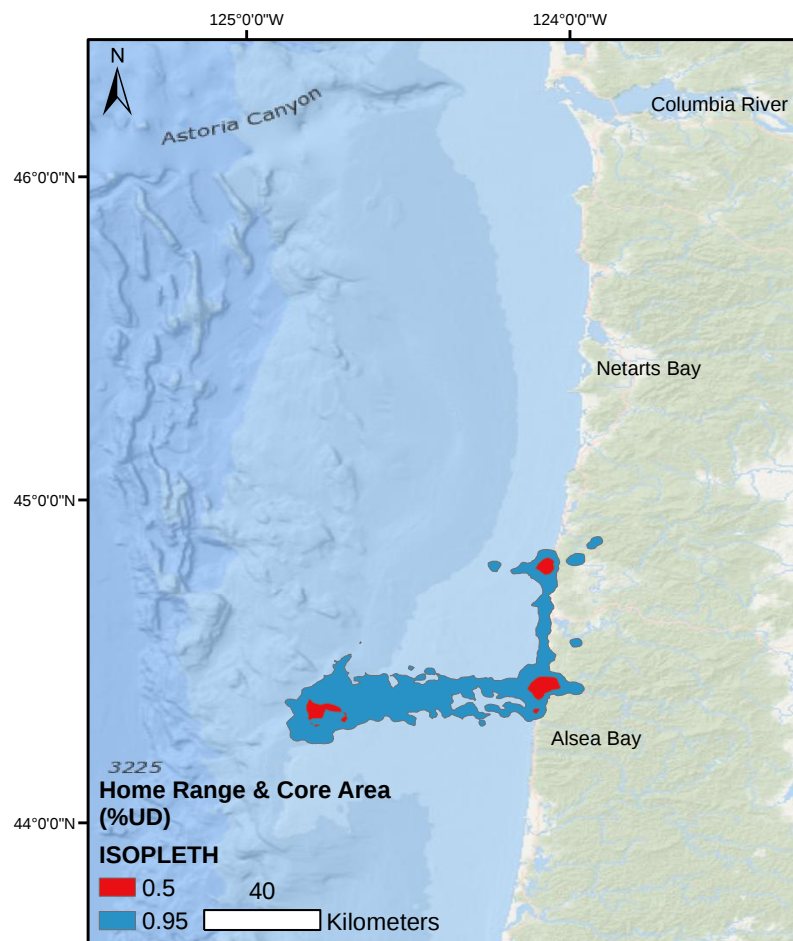
Seal 61695 Home Range and Core Area from 'crawled' Locations  
(n = 2848) 9 Sept. 2014 - 9 Apr. 2015



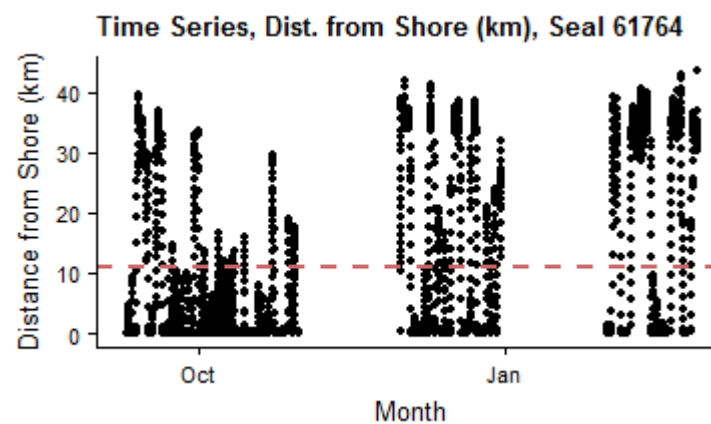
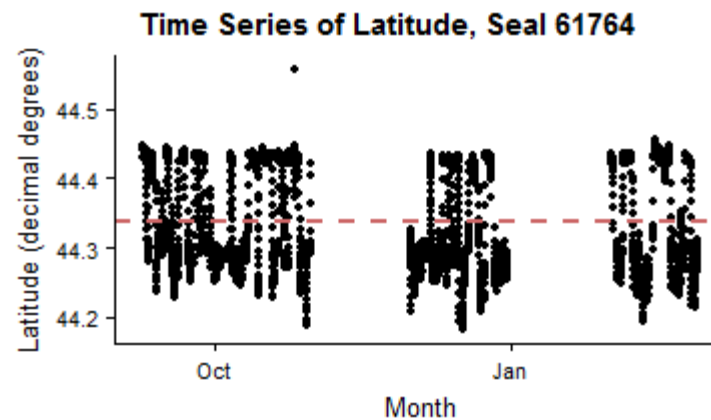
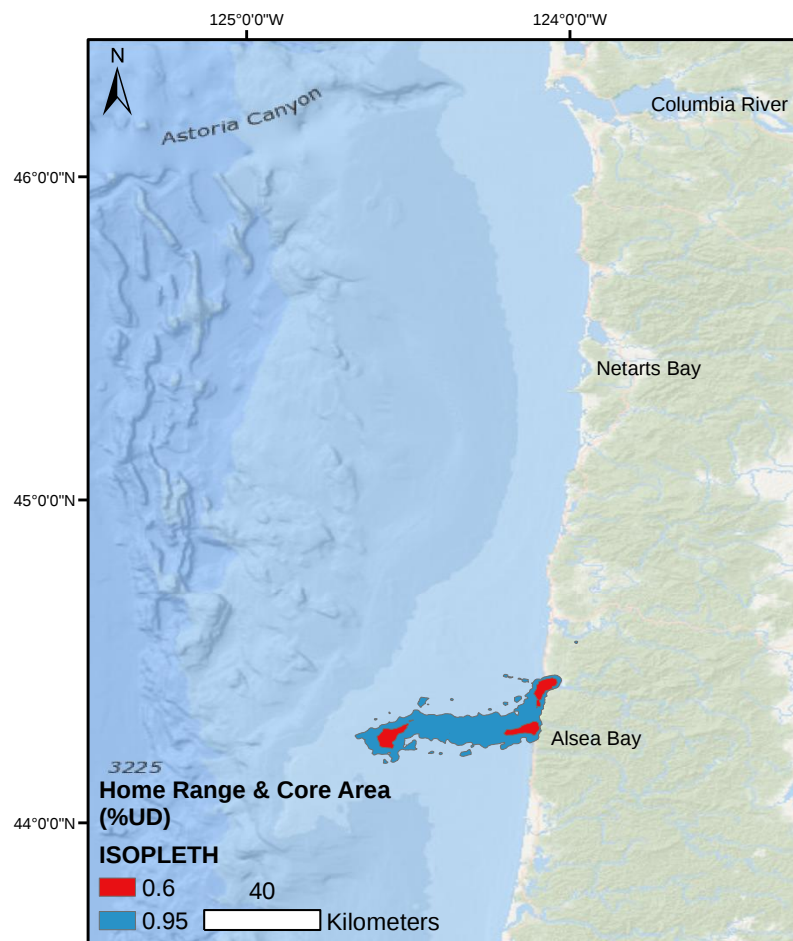
Seal 61698 Home Range and Core Area from 'crawled' Locations  
(n = 1339) 7 Apr. 2015 - 2 June 2015



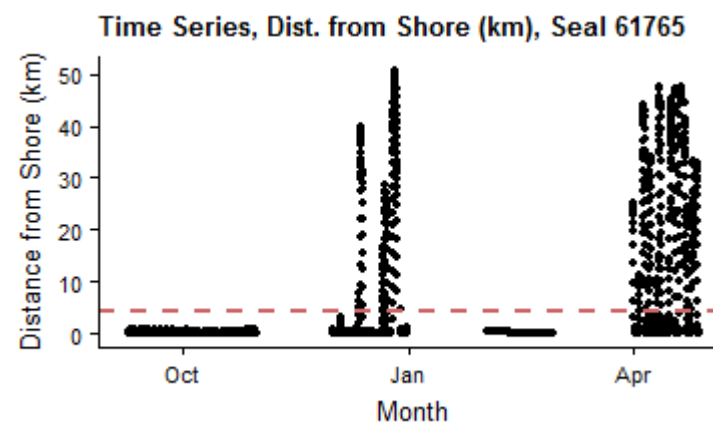
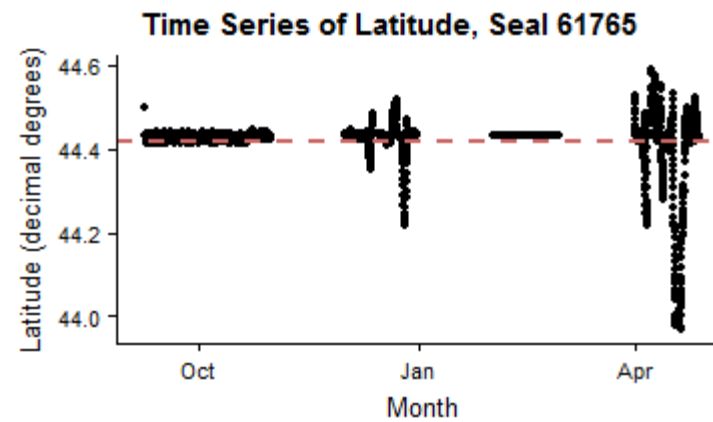
Seal 61754 Home Range and Core Area from 'crawled' Locations  
(n = 2679) 7 Apr. 2015 - 28 July 2015



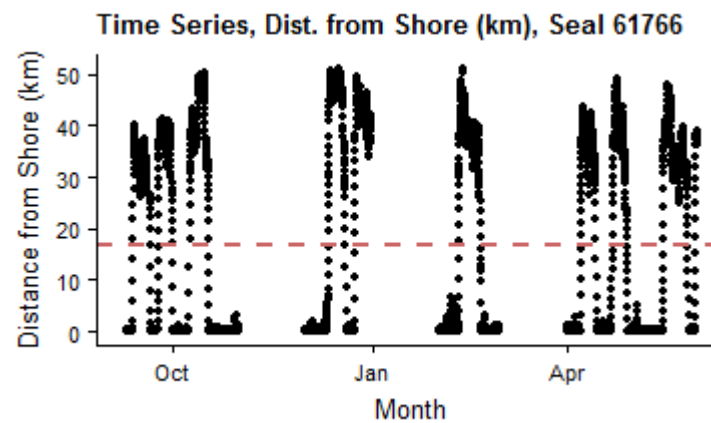
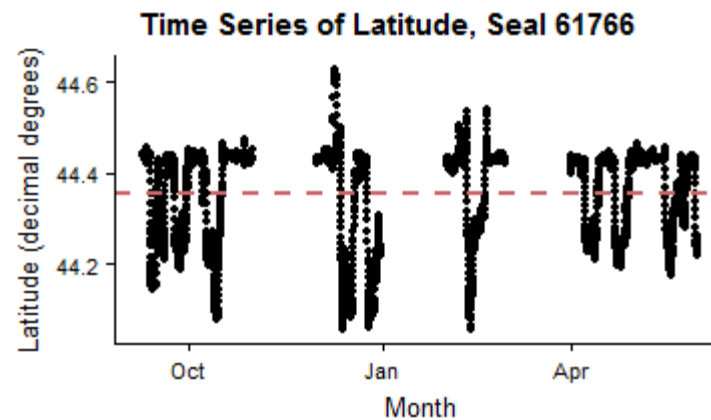
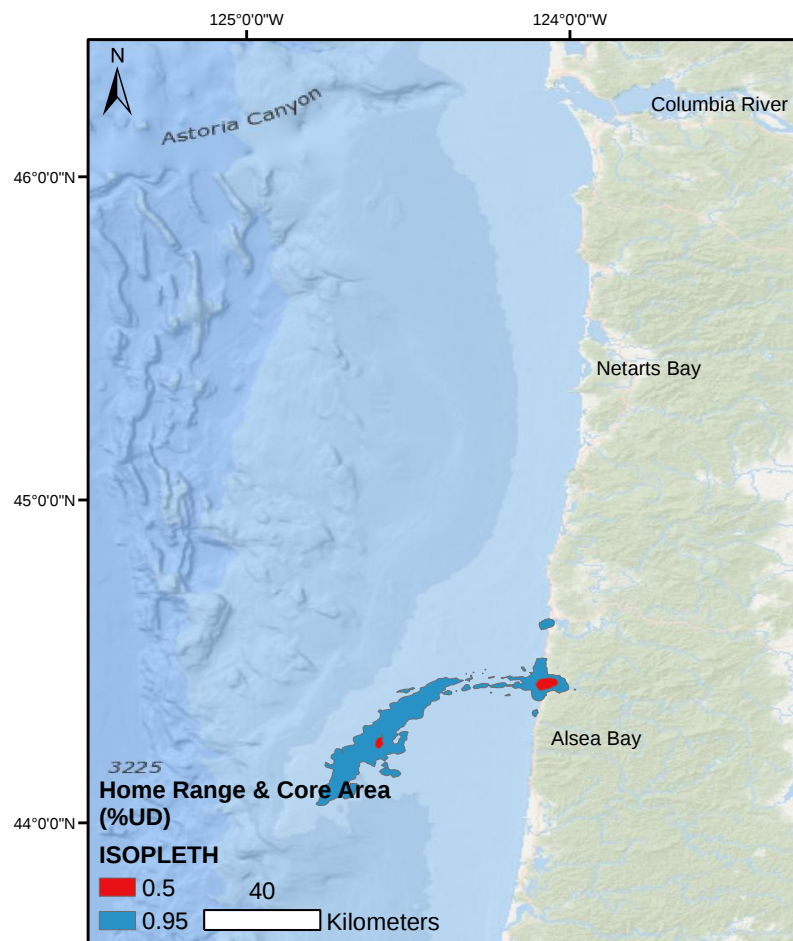
Seal 61764 Home Range and Core Area from 'crawled' Locations  
(n = 2661) 9 Sept. 2014 - 28 Feb. 2015



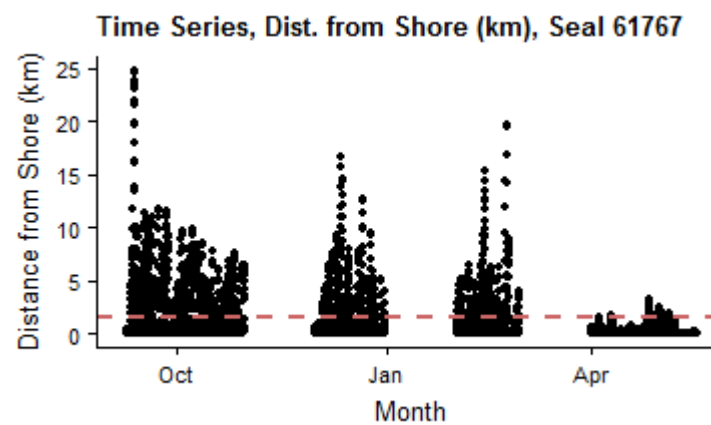
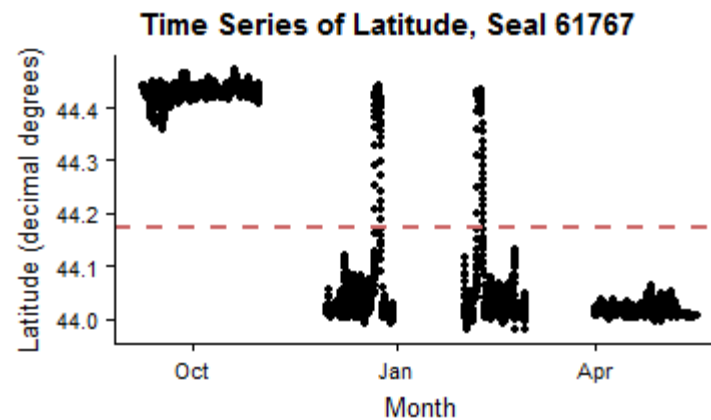
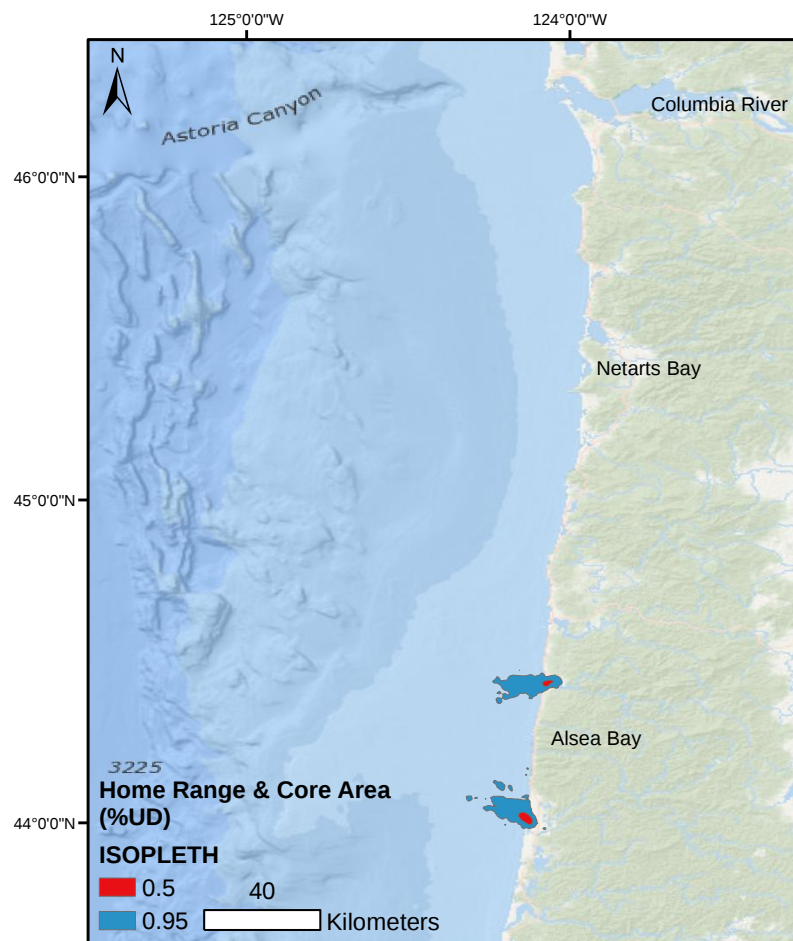
Seal 61765 Home Range and Core Area from 'crawled' Locations  
(n = 3288) 9 Sept. 2014 - 28 Apr. 2015



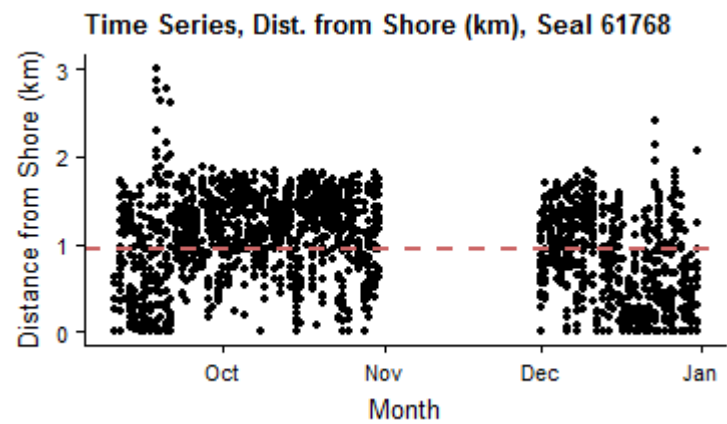
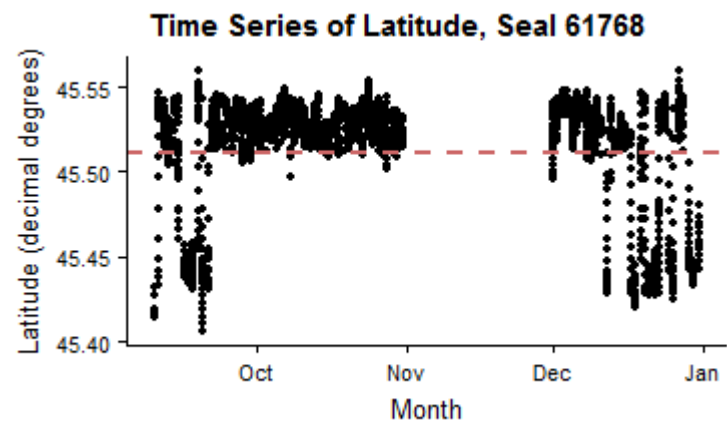
Seal 61766 Home Range and Core Area from 'crawled' Locations  
(n = 4114) 9 Sept. 2014 - 31 May 2015



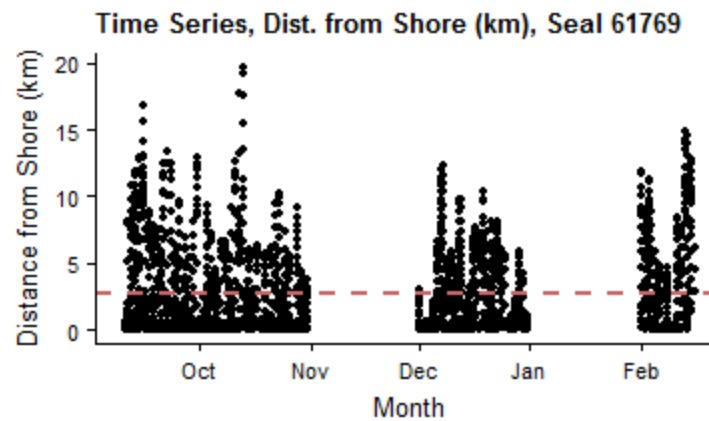
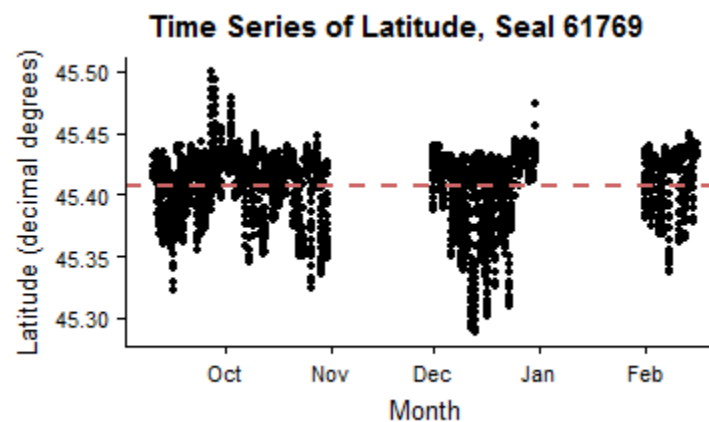
Seal 61767 Home Range and Core Area from 'crawled' Locations  
(n = 3759) 9 Sept. 2014 - 17 May 2015



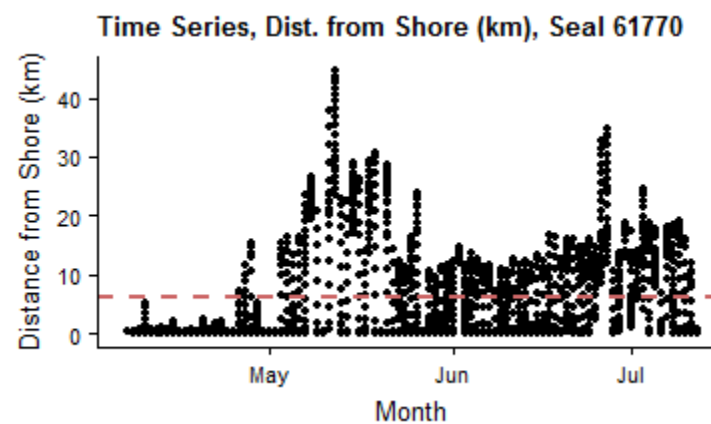
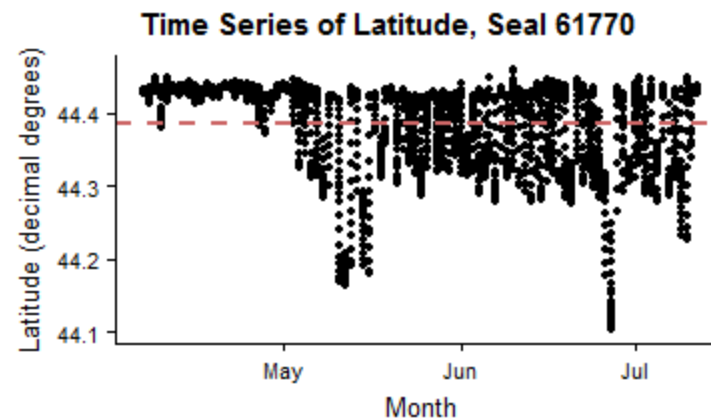
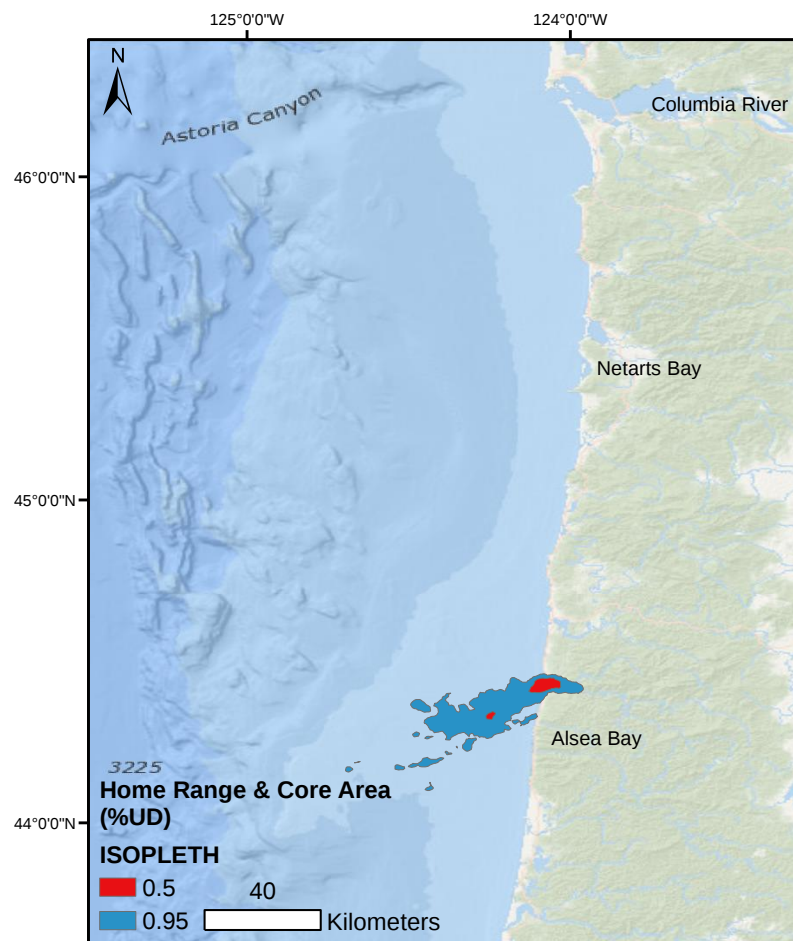
Seal 61768 Home Range and Core Area from 'crawled' Locations  
(n = 1956) 10 Sept. 2014 - 31 Dec. 2014



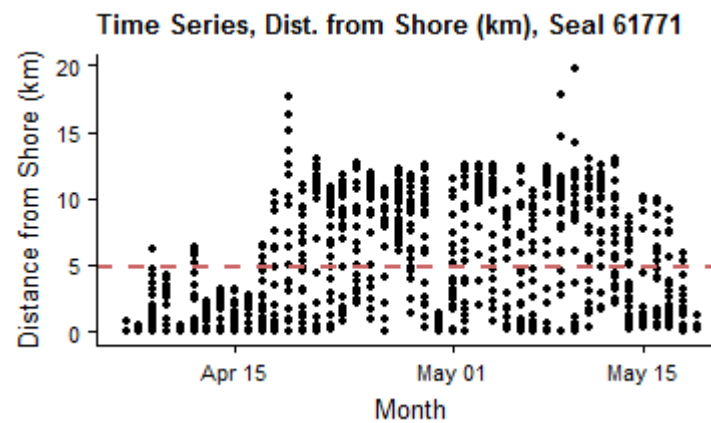
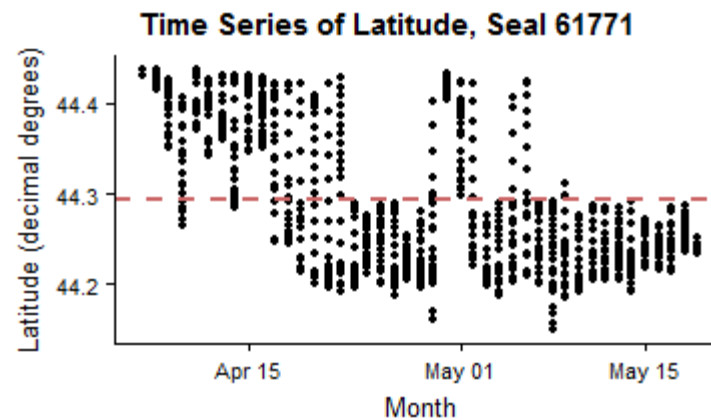
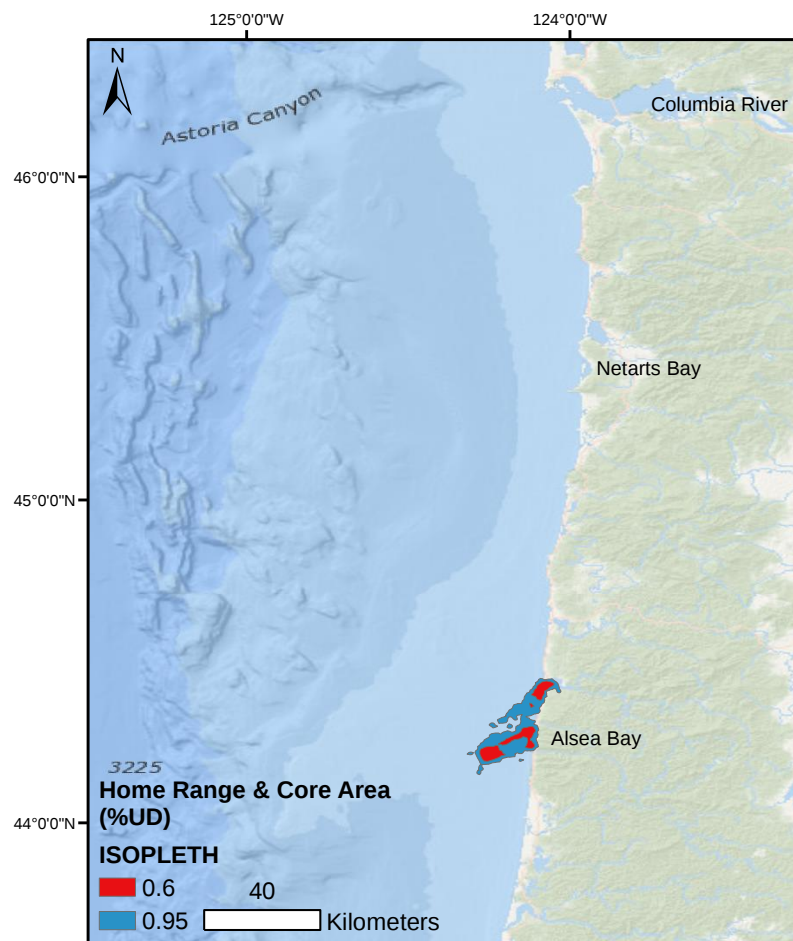
Seal 61769 Home Range and Core Area from 'crawled' Locations  
(n = 2332) 10 Sept. 2014 - 16 Feb. 2015



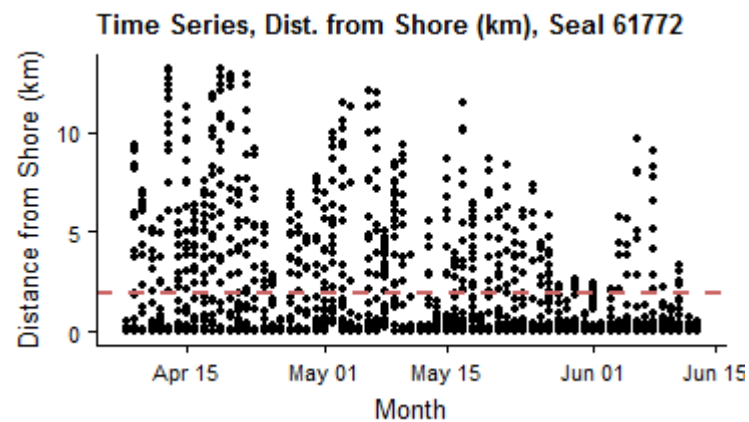
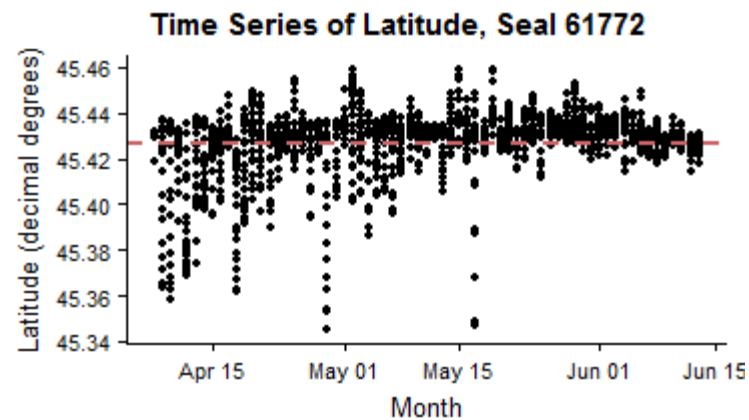
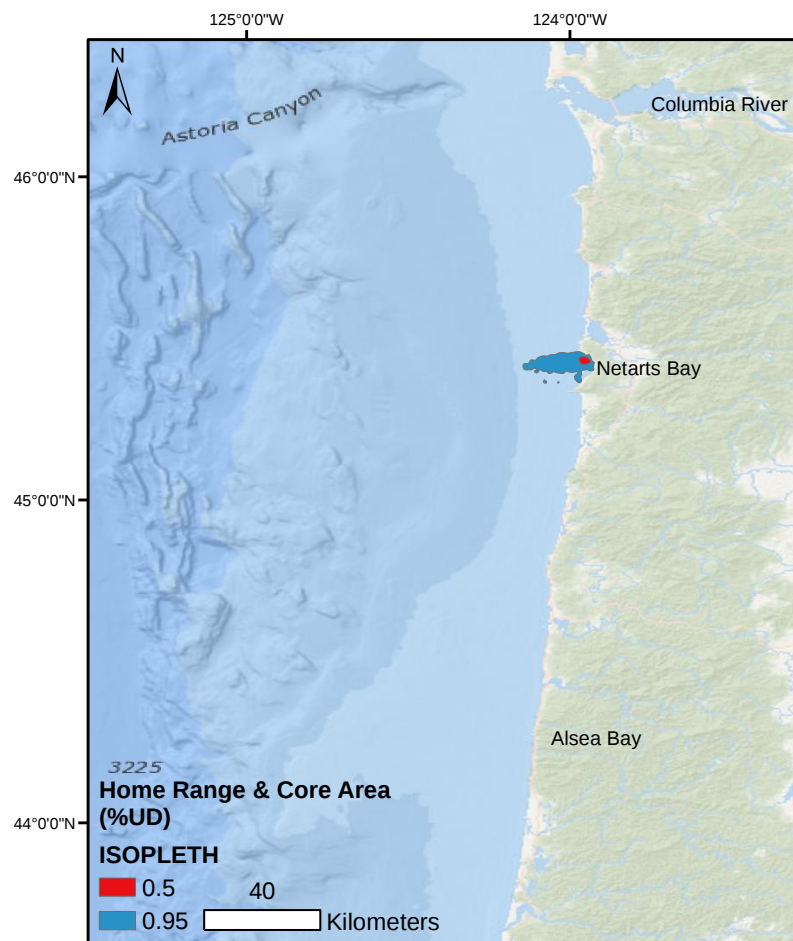
Seal 61770 Home Range and Core Area from 'crawled' Locations  
(n = 2292) 7 Apr. 2015 - 12 July 2015



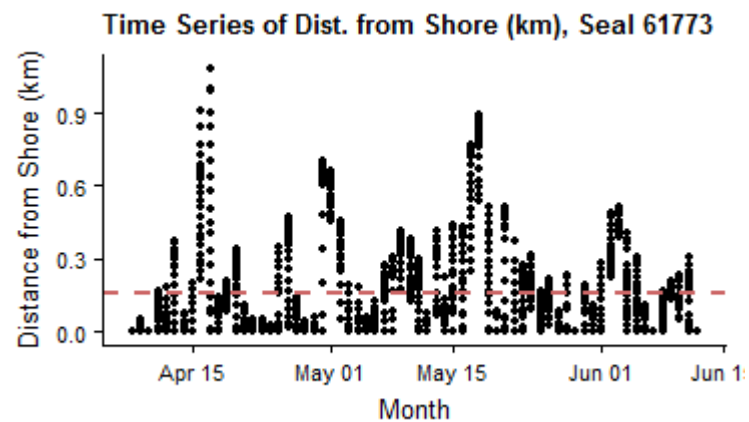
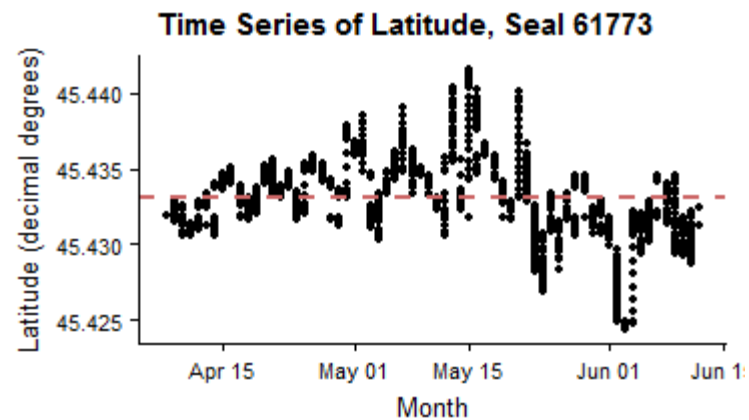
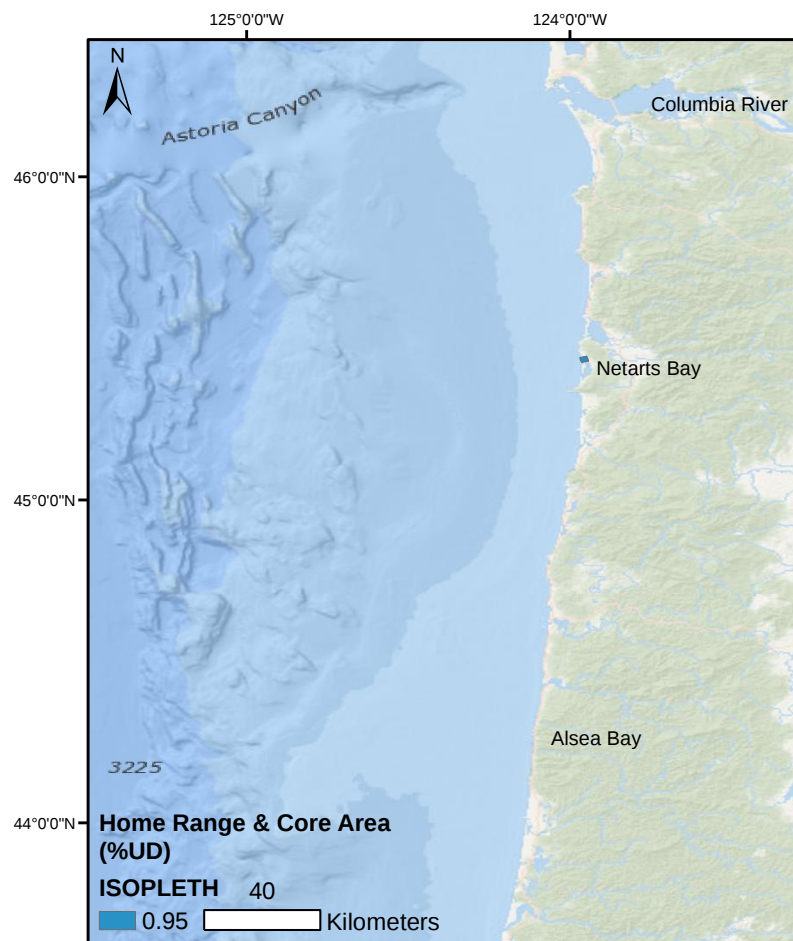
Seal 61771 Home Range and Core Area from 'crawled' Locations  
(n = 991) 7 Apr. 2015 - 19 May 2015



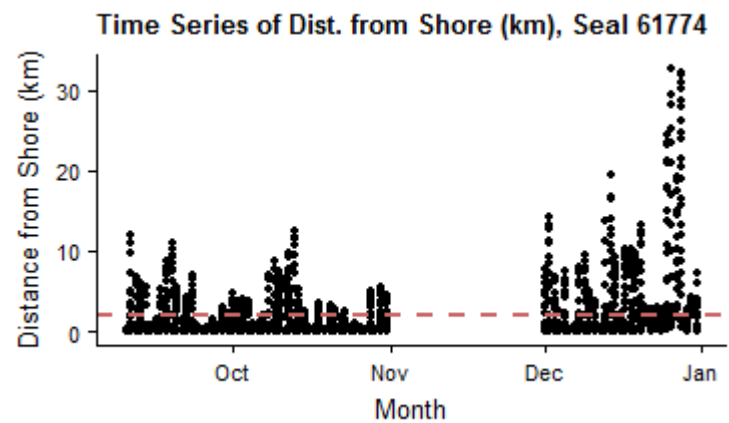
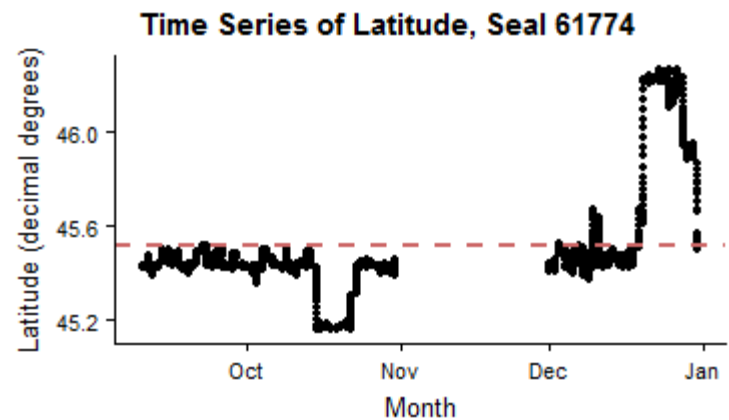
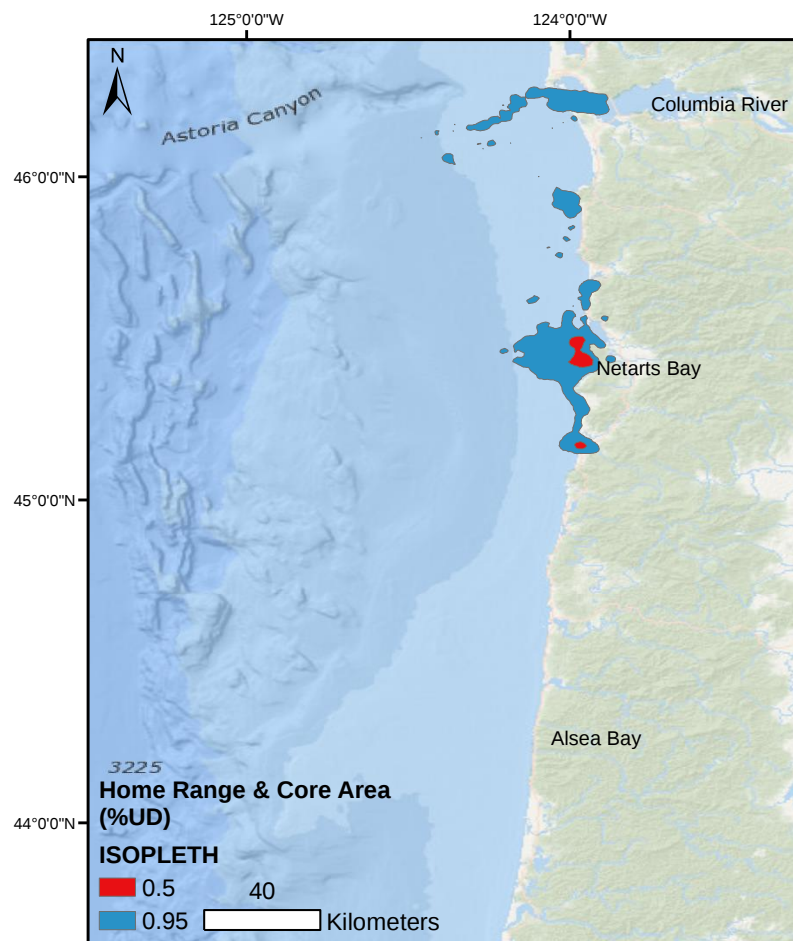
Seal 61772 Home Range and Core Area from 'crawled' Locations  
(n = 1587) 8 Apr. 2015 - 13 June 2015



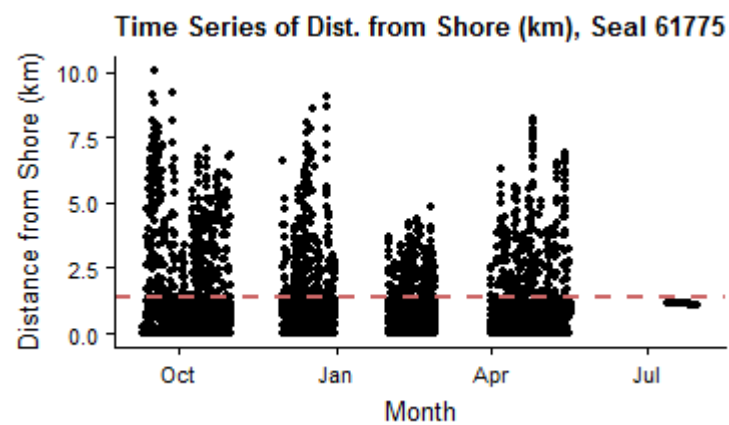
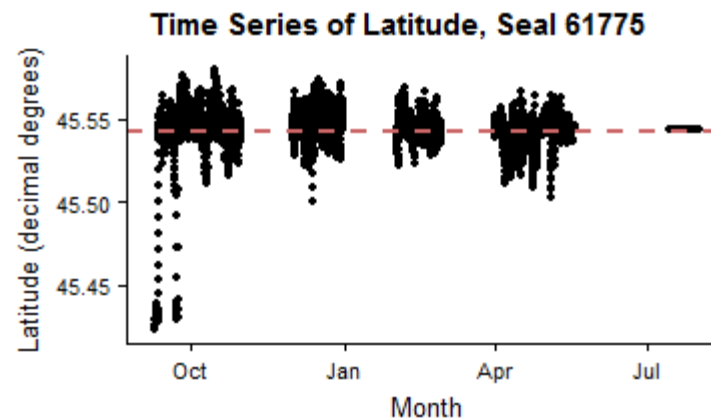
Seal 61773 Home Range from 'crawled' Locations  
(n = 1543) 8 Apr. 2015 - 12 June 2015



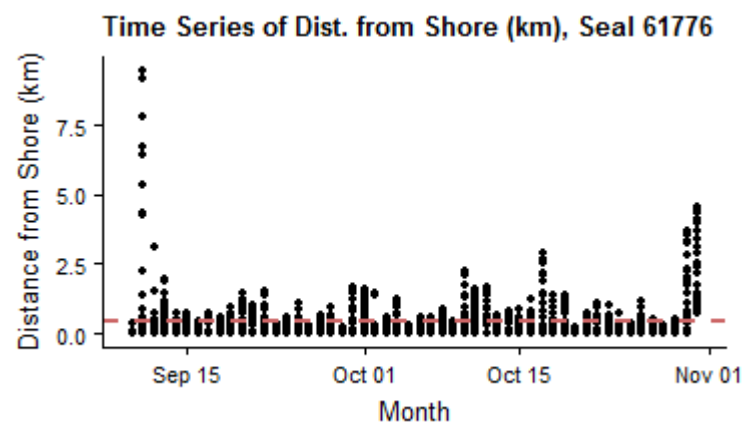
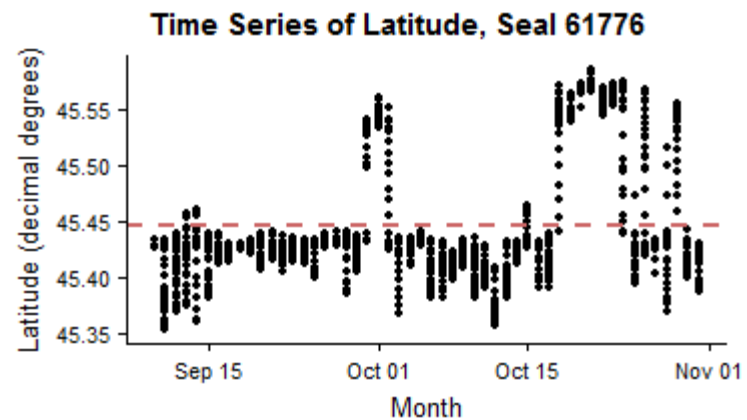
Seal 61774 Home Range and Core Area from 'crawled' Locations  
(n = 1967) 10 Sept. 2014 - 31 Dec. 2014



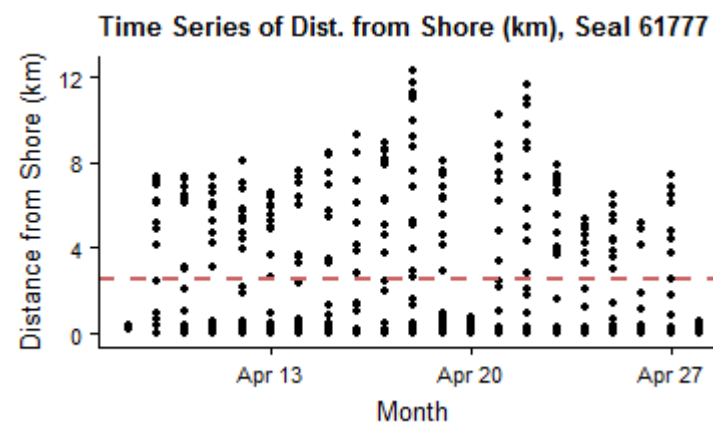
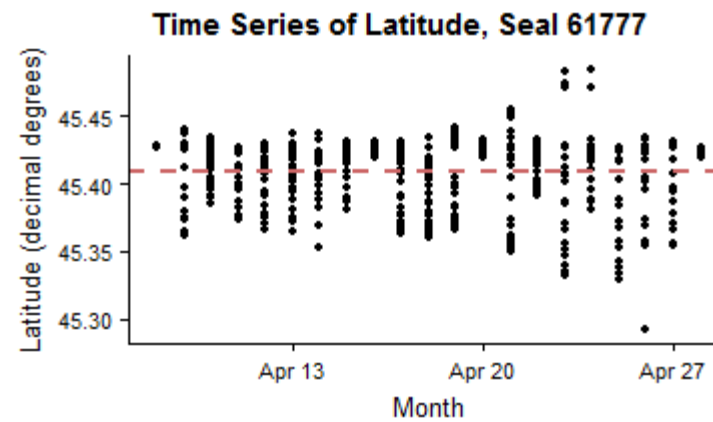
Seal 61775 Home Range and Core Area from 'crawled' Locations  
(n = 4208) 10 Sept. 2014 - 31 July 2015



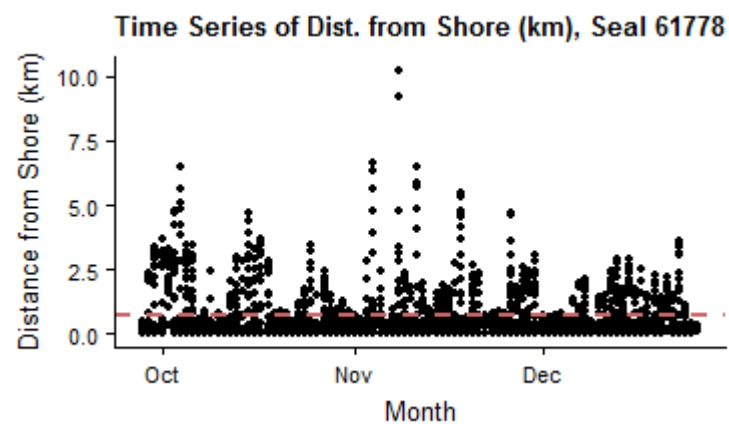
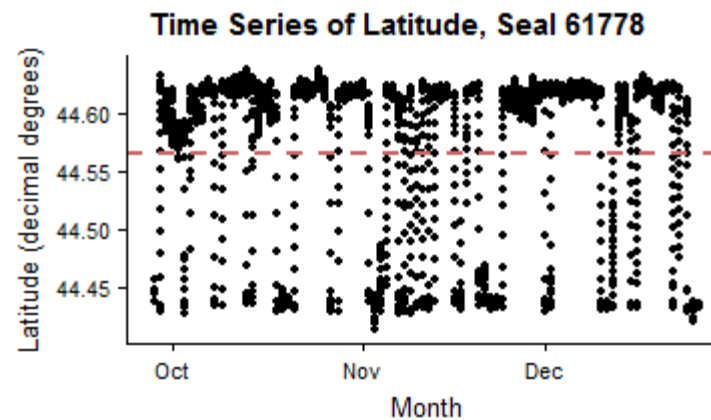
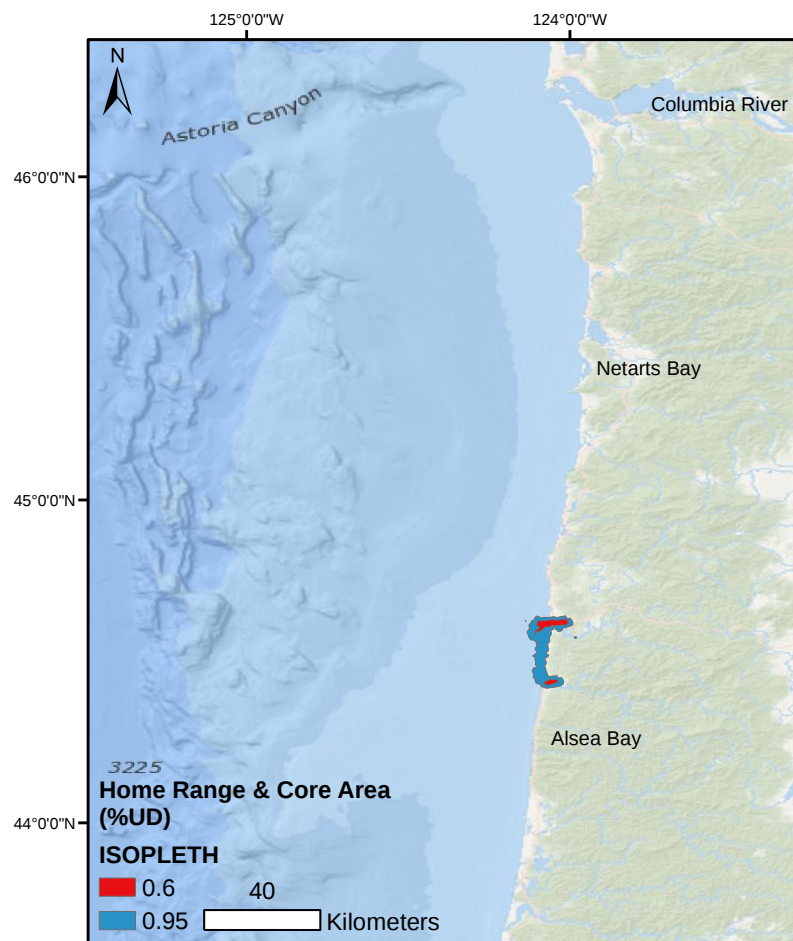
Seal 61776 Home Range and Core Area from 'crawled' Locations  
(n = 1227) 10 Sept. 2014 - 31 Oct. 2014



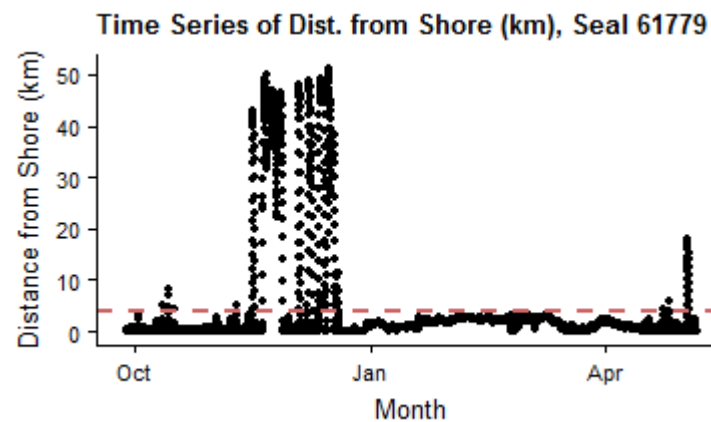
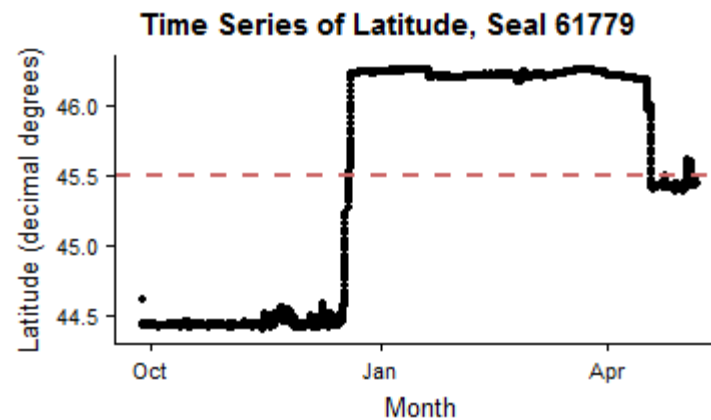
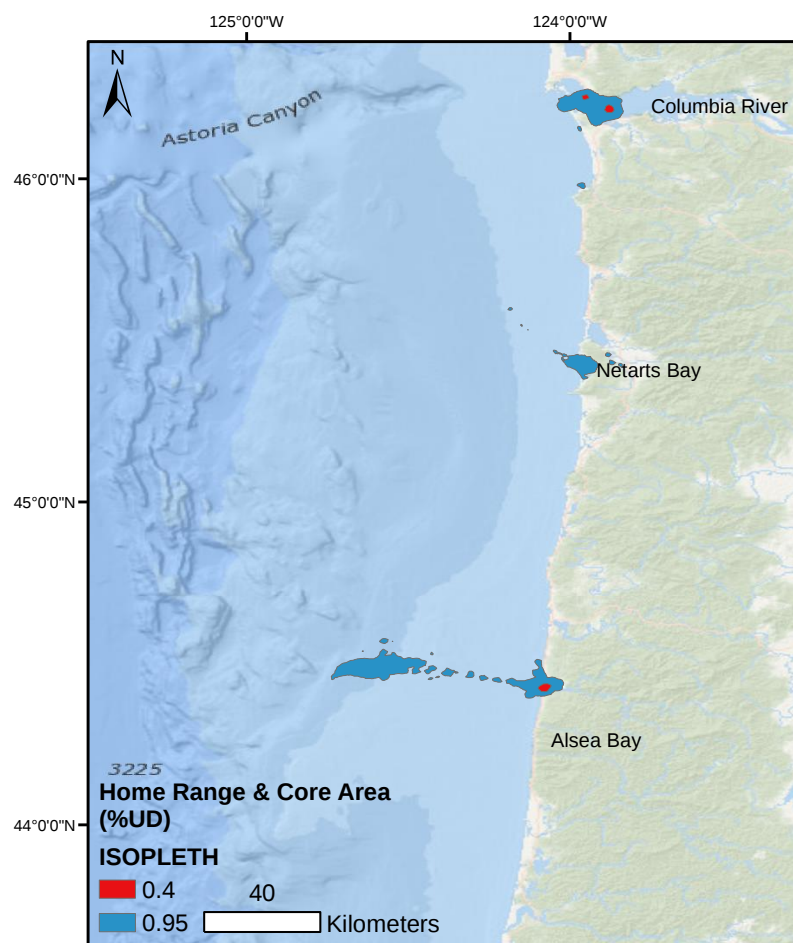
Seal 61777 Home Range and Core Area from 'crawled' Locations  
(n = 474) 8 Apr. 2015 - 28 Apr. 2015



Seal 61778 Home Range and Core Area from 'crawled' Locations  
(n = 2133) 28 Sept. 2015 - 26 Dec. 2015



Seal 61779 Home Range and Core Area from 'crawled' Locations  
(n =5315) 28 Sept. 2015 - 7 May 2016

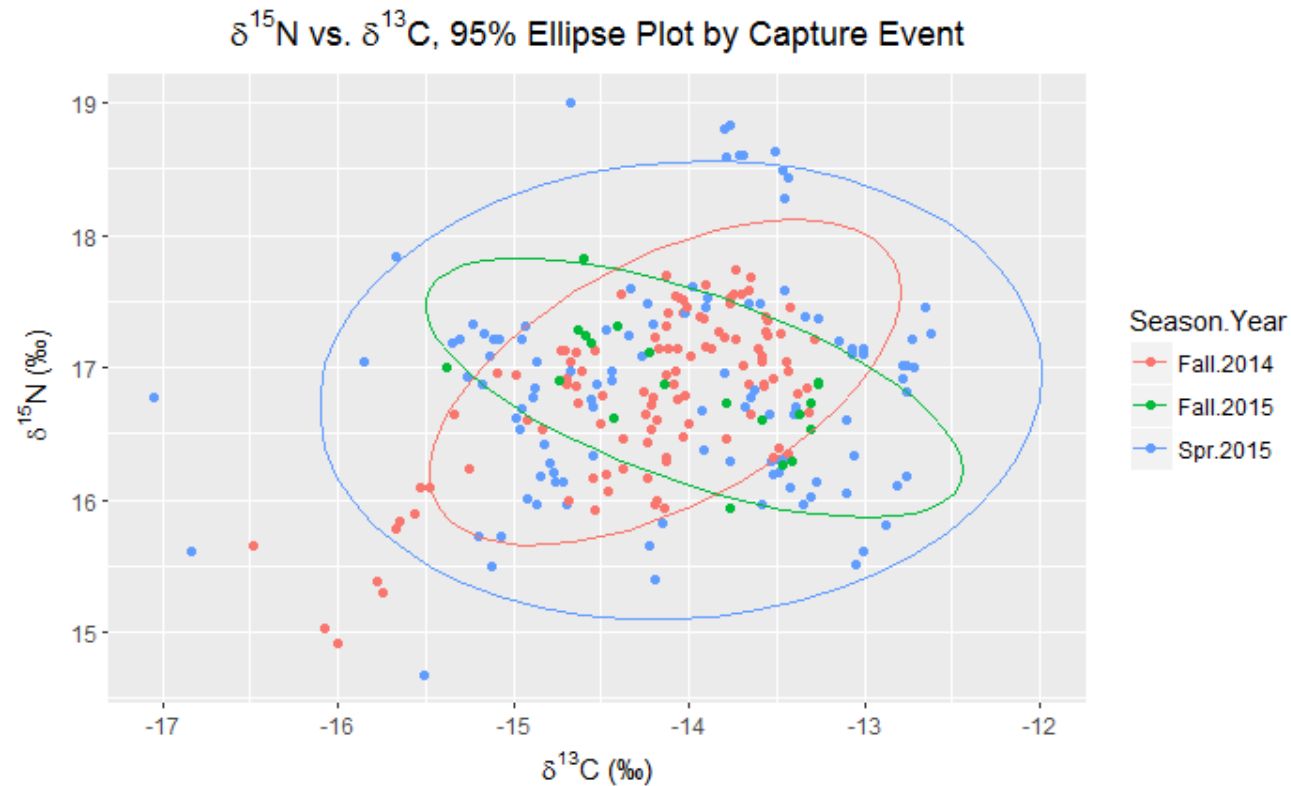


# APPENDIX II: CHAPTER 2 SUPPLEMENTARY TABLES AND FIGURES

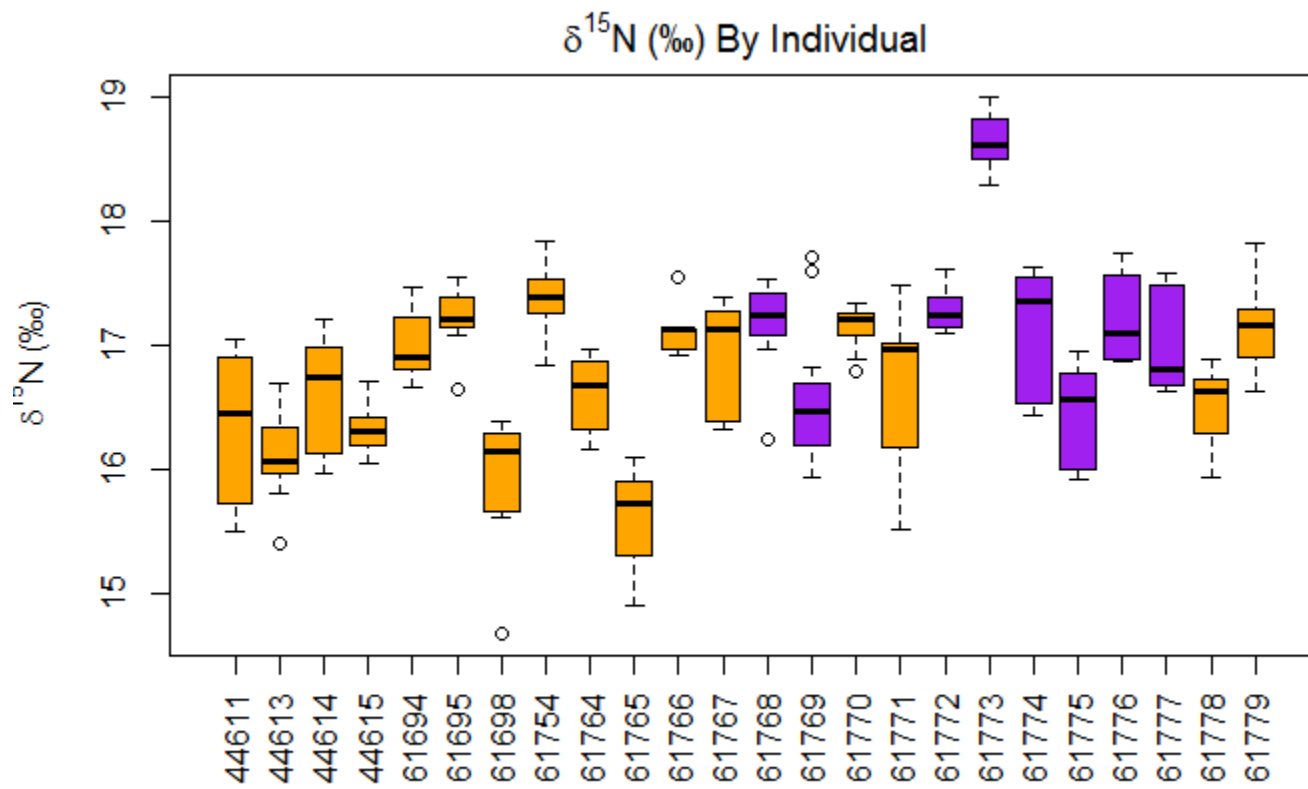
Supplementary Table 2.1. Stable  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , summarized by individual animal. Bold rows represent Alsea Bay Animals.

| Ptt          | Capture Location | Mean $\delta^{13}\text{C}$          | Mean $\delta^{15}\text{N}$         | Root $\delta^{13}\text{C}$ | Root $\delta^{15}\text{N}$ | Range $\delta^{13}\text{C}$  | Range $\delta^{15}\text{N}$ |
|--------------|------------------|-------------------------------------|------------------------------------|----------------------------|----------------------------|------------------------------|-----------------------------|
| 44611        | <b>Alsea</b>     | <b>-14.88 <math>\pm</math> 1.12</b> | <b>16.36 <math>\pm</math> 0.82</b> | <b>-15.85</b>              | <b>17.05</b>               | <b>1.41 (-15.85, -14.44)</b> | <b>1.55 (15.50, 17.05)</b>  |
| 44613        | <b>Alsea</b>     | <b>-13.50 <math>\pm</math> 0.75</b> | <b>16.12 <math>\pm</math> 1.02</b> | <b>-14.95</b>              | <b>16.69</b>               | <b>2.14 (-14.95, -12.81)</b> | <b>1.29 (15.40, 16.69)</b>  |
| 44614        | <b>Alsea</b>     | <b>-14.89 <math>\pm</math> 0.69</b> | <b>16.63 <math>\pm</math> 0.87</b> | <b>-15.31</b>              | <b>17.21</b>               | <b>0.76 (-15.31, -14.55)</b> | <b>1.24 (15.97, 17.21)</b>  |
| 44615        | <b>Alsea</b>     | <b>-13.55 <math>\pm</math> 0.61</b> | <b>16.32 <math>\pm</math> 0.98</b> | <b>-14.82</b>              | <b>16.42</b>               | <b>1.72 (-14.82, -13.10)</b> | <b>0.66 (16.05, 16.71)</b>  |
| 61694        | <b>Alsea</b>     | <b>-13.50 <math>\pm</math> 0.67</b> | <b>16.98 <math>\pm</math> 0.90</b> | <b>-14.21</b>              | <b>16.72</b>               | <b>0.93 (-14.21, -13.28)</b> | <b>0.80 (16.66, 17.46)</b>  |
| 61695        | <b>Alsea</b>     | <b>-13.99 <math>\pm</math> 0.88</b> | <b>17.20 <math>\pm</math> 0.83</b> | <b>-15.34</b>              | <b>16.64</b>               | <b>1.86 (-15.34, -13.48)</b> | <b>0.90 (16.64, 17.54)</b>  |
| 61698        | <b>Alsea</b>     | <b>-14.70 <math>\pm</math> 0.75</b> | <b>15.92 <math>\pm</math> 0.96</b> | <b>-16.84</b>              | <b>15.61</b>               | <b>3.42 (16.84, -13.42)</b>  | <b>1.70 (14.68, 16.38)</b>  |
| 61754        | <b>Alsea</b>     | <b>-14.36 <math>\pm</math> 0.82</b> | <b>17.36 <math>\pm</math> 0.79</b> | <b>-15.67</b>              | <b>17.84</b>               | <b>1.78 (-15.67, -13.89)</b> | <b>1.00 (16.84, 17.84)</b>  |
| 61764        | <b>Alsea</b>     | <b>-14.61 <math>\pm</math> 0.79</b> | <b>16.61 <math>\pm</math> 0.84</b> | <b>-15.09</b>              | <b>16.96</b>               | <b>0.96 (-15.09, -14.13)</b> | <b>0.80 (16.16, 16.96)</b>  |
| 61765        | <b>Alsea</b>     | <b>-15.80 <math>\pm</math> 0.80</b> | <b>15.60 <math>\pm</math> 0.82</b> | <b>-16.48</b>              | <b>15.66</b>               | <b>0.14 (-15.48, -15.34)</b> | <b>0.55 (16.09, 16.64)</b>  |
| 61766        | <b>Alsea</b>     | <b>-14.67 <math>\pm</math> 0.68</b> | <b>17.11 <math>\pm</math> 0.52</b> | <b>-14.71</b>              | <b>17.13</b>               | <b>1.69 (-16.08, -14.39)</b> | <b>2.52 (15.03, 17.55)</b>  |
| 61767        | <b>Alsea</b>     | <b>-13.66 <math>\pm</math> 1.00</b> | <b>16.91 <math>\pm</math> 0.47</b> | <b>-14.58</b>              | <b>16.65</b>               | <b>0.82 (-14.25, -13.43)</b> | <b>1.07 (16.32, 17.39)</b>  |
| <b>61768</b> | Netarts          | -14.18 $\pm$ 0.92                   | 17.17 $\pm$ 0.87                   | -15.25                     | 16.24                      | 1.33 (-15.25, -13.92)        | 1.28 (16.24, 17.52)         |
| <b>61769</b> | Netarts          | -14.36 $\pm$ 0.95                   | 16.58 $\pm$ 0.86                   | -14.55                     | 16.16                      | 1.84 (-15.65, -13.79)        | 1.76 (15.94, 17.70)         |
| 61770        | <b>Alsea</b>     | <b>-15.32 <math>\pm</math> 1.17</b> | <b>17.15 <math>\pm</math> 0.62</b> | <b>-17.05</b>              | <b>16.78</b>               | <b>2.12 (-17.05, -14.93)</b> | <b>0.55 (16.78, 17.33)</b>  |
| 61771        | <b>Alsea</b>     | <b>-12.96 <math>\pm</math> 1.01</b> | <b>16.68 <math>\pm</math> 0.57</b> | <b>-14.24</b>              | <b>17.48</b>               | <b>1.52 (-14.24, -12.72)</b> | <b>1.97 (15.51, 17.48)</b>  |
| <b>61772</b> | Netarts          | -13.15 $\pm$ 0.76                   | 17.27 $\pm$ 0.57                   | -14.33                     | 17.60                      | 1.72 (-14.33, -12.62)        | 0.50 (17.10, 17.60)         |
| <b>61773</b> | Netarts          | -13.73 $\pm$ 0.69                   | 18.63 $\pm$ 0.46                   | -14.67                     | 19.00                      | 1.24 (-14.67, -13.43)        | 0.72 (18.28, 19.00)         |
| <b>61774</b> | Netarts          | -14.03 $\pm$ 0.67                   | 17.10 $\pm$ 0.47                   | -14.19                     | 17.23                      | 0.71 (-14.37, -13.66)        | 1.19 (16.43, 17.62)         |
| <b>61775</b> | Netarts          | -14.17 $\pm$ 0.67                   | 16.43 $\pm$ 0.38                   | -14.13                     | 16.94                      | 1.03 (-14.68, -13.65)        | 1.02 (15.92, 16.94)         |
| <b>61776</b> | Netarts          | -13.70 $\pm$ 0.86                   | 17.23 $\pm$ 0.40                   | -14.09                     | 16.88                      | 0.52 (-14.09, -13.57)        | 0.88 (16.86, 17.74)         |
| <b>61777</b> | Netarts          | -13.79 $\pm$ 0.77                   | 16.97 $\pm$ 0.57                   | -14.98                     | 16.62                      | 1.53 (-14.98, -13.45)        | 0.96 (16.62, 17.58)         |
| 61778        | <b>Alsea</b>     | <b>-13.45 <math>\pm</math> 0.64</b> | <b>16.55 <math>\pm</math> 0.40</b> | <b>-13.79</b>              | <b>16.73</b>               | <b>0.53 (-13.79, -13.26)</b> | <b>0.95 (15.94, 16.89)</b>  |
| 61779        | <b>Alsea</b>     | <b>-14.57 <math>\pm</math> 0.64</b> | <b>17.14 <math>\pm</math> 0.37</b> | <b>-15.38</b>              | <b>17.00</b>               | <b>1.24 (-15.38, -14.14)</b> | <b>1.20 (16.62, 17.82)</b>  |

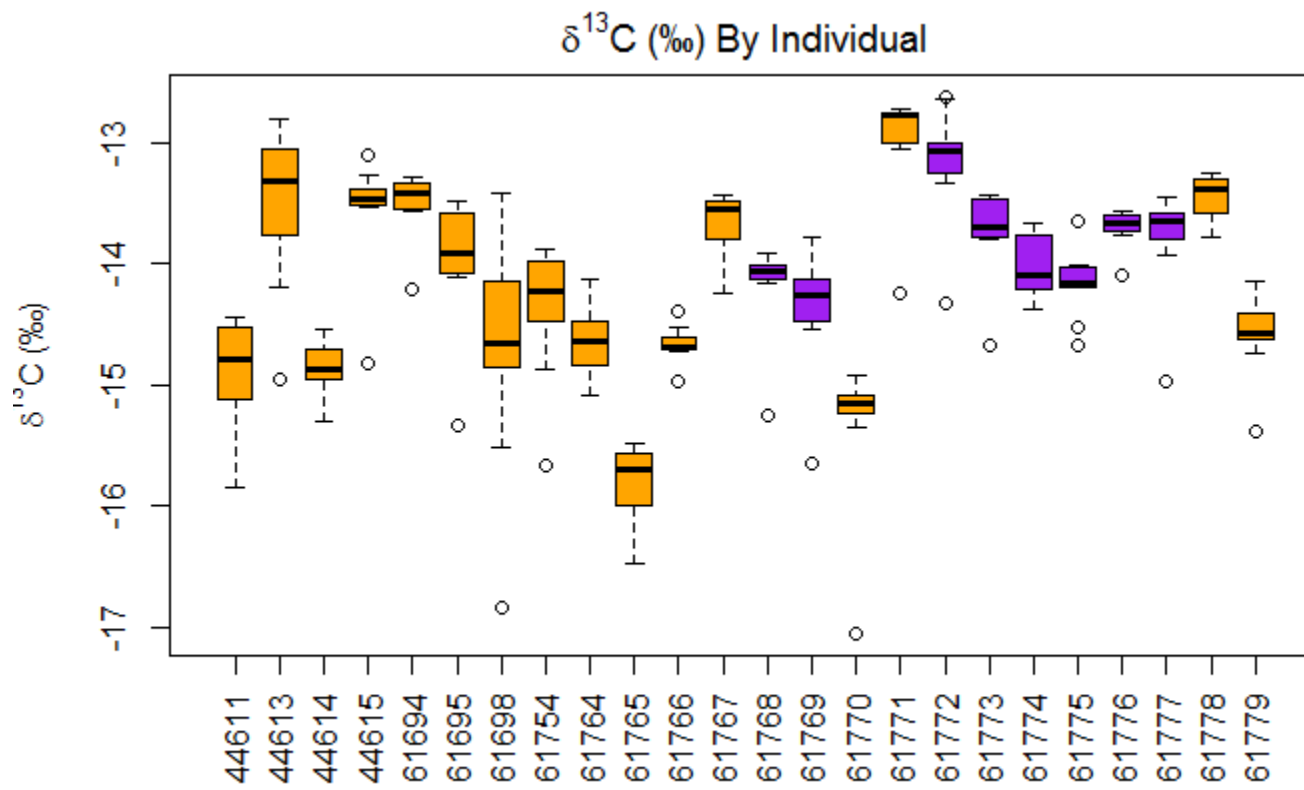
APPENDIX III: CHAPTER 3 SUPPLEMENTARY TABLES AND FIGURES



Supplemental Figure 3.1. 95% ellipse plot of isotope values between capture events (Fall 2014, Fall 2015, and Spring 2015). Individual trophic niche (range  $\delta^{15}\text{N}$ ) varied from 0.137 to 0.342. Individual range in  $\delta^{13}\text{C}$  varied from 0.54 to 2.53. Seals tagged in spring 2015 had a wider overall measured trophic niche than animals captured in fall 2014 or 2015.



Supplemental Figure 3.2. Box-and-whisker plot of  $\delta^{15}\text{N}$  by individual, separated by capture site. Alsea Bay animals are represented in orange and Netarts Bay animals represented in purple. A wider box represents a wider dietary niche, and higher  $\delta^{15}\text{N}$  represents a higher relative trophic level.



Supplemental Figure 3.3. Box-and-whisker plot of  $\delta^{13}\text{C}$  by individual, separated by capture site. Alsea Bay animals are represented in orange and Netarts Bay animals represented in purple.