

SEA OTTER DIET COMPOSITION WITH RESPECT TO RECOLONIZATION, LIFE
HISTORY, AND SEASON IN SOUTHERN SOUTHEAST ALASKA

By

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Abstract

Until translocation efforts in the 1960s, sea otters (*Enhydra lutris*) were absent from Southeast Alaska due to extirpation by the fur trade in the 18th and 19th centuries. About 400 sea otters were reintroduced to six Southeast Alaska locations, including two sites near Prince of Wales Island in southern Southeast Alaska. The most recent US Fish and Wildlife Service population count, completed in 2012, estimated that about 25,000 sea otters inhabited Southeast Alaska. Sea otters will reduce invertebrate prey biomass when recolonizing an area. By quantifying sea otter diets and caloric intake according to recolonization patterns, we can better understand the ecosystem impacts of sea otter population increase and range expansion. The goal of this study was to quantify changes in seasonal diet composition and assess the energetic quality of sea otter prey in southern Southeast Alaska. I made visual foraging observations of 3,385 sea otter dives around Prince of Wales Island (POW) to determine diet composition during the spring and summer months. I then collected vibrissae from 45 sea otters obtained from subsistence hunters to assess year-round sea otter diets using stable isotopes. I collected sea otter prey items throughout POW in three seasons (May 2018, August 2018, and February 2019) to measure energy, lipid and protein content, and $\delta^{13}\text{C}$ (carbon) and $\delta^{15}\text{N}$ (nitrogen) values. Sea otter diets mainly consisted of clams, as quantified both from visual observations and stable isotope analysis. However, there was more variation in the diet estimates from stable isotope analysis. Stable isotope analysis revealed variation among individual diets of sea otters and individuality in diet within the POW region of sea otters. Sea otters seasonally increased consumption of some prey when the prey was highest in lipid and overall caloric content. Sea otters switched prey types when the prey was more energetically valuable. The results of this study will aid in future management of shellfisheries, subsistence hunting, and implementing co-management of a protected species by

providing quantitative diet composition data for stakeholders. This work is a part of a large-scale project examining how the recovery of sea otters structures nearshore marine ecosystems, provides ecosystem services, and affects community sustainability.

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General Introduction

Overview

Sea otters (*Enhydra lutris*) are a keystone predator, a species that can quickly change the dynamics and food web diversity of the nearshore marine ecosystem (Estes & Palmisano 1974). Because of this, sea otters can serve as a magnifying glass into ocean health and benthic habitat composition (Tinker et al. 2019). Sea otters sample benthic invertebrates at a high rate and with better skill than people can attain with SCUBA surveys (Riedman & Estes 1990, Oftedal et al. 2007). Previous research throughout the sea otter range has revealed consistent evidence of inverse relationships between sea otter density and prey resources (Estes & Palmisano 1974, Estes & Duggins 1995, Larson et al. 2013, Weitzman 2013, Hoyt 2015).

Historical records of sea otters show that they once inhabited nearshore ecosystems of the Pacific Ocean from Japan to Baja California. However, by the late 19th Century, there were only 11 remnant populations within their once continuous distribution due to the lucrative fur markets in Russia and China. In 1911, sea otters were protected from hunting by the International Fur Seal Treaty. By this time, sea otters were extirpated from Southeast Alaska (Jameson et al. 1982). To restore sea otters to their historical range, the Alaska Department of Fish and Game (ADFG) and the Atomic Energy Commission initiated a translocation program and, in the 1960s, relocated about 400 sea otters from the Aleutian Islands to six locations in Southeast Alaska (Burriss & McKnight 1973, Jameson et al. 1982). Since the translocation, sea otters have expanded their range and increased in numbers. The most recent sea otter aerial counts in 2012 estimated that approximately 25,000 sea otters were present in Southeast Alaska (USFWS 2014).

The expansion of sea otters from the six translocation sites in Southeast Alaska into unoccupied habitat over time allows for a ‘space-for-time’ substitution (Pickett 1989), in which the longer-term effects (positive, neutral, and negative) of sea otters on the nearshore ecosystem can be seen in areas of prolonged occupation.

Sea otters, unlike most marine mammals, do not have blubber to keep them warm in the marine environment. Instead, sea otters maintain very high metabolisms, consuming 20–39% of their body weight in food per day (dependent on life history state) to sustain these elevated metabolic costs (Costa & Kooyman 1982, Davis 2020). In kelp forests, sea otters suppress the grazer population (sea urchins, *Strongylocentrotus* spp.), which relieves pressure on the giant kelp (*Macrocystis pyrifera*). This relief of grazing pressure helps to increase kelp forest abundance, which has been shown to increase juvenile fish habitat (Estes & Duggins 1995, Hughes et al. 2013).

In Southeast Alaska, top-down effects of sea otter predation are evident in rocky habitats that support kelp forests (Estes & Duggins 1995). Still, most nearshore habitats consist of a combination of soft and mixed sediment (Kvitek & Oliver 1992, Kvitek et al. 1993, Weitzman 2013). Soft sediment habitats have little three-dimensional structure, while mixed sediment habitats are more complex with a greater range of structure consisting of both rock and sediment substrate (Harper & Morris 2014). Sea otters in soft and mixed sediment habitats have clam dominated diets; however, they are known to consume > 100 different species within these habitats (Newsome et al. 2015).

For over 100 years while sea otters were absent from Southeast Alaska, the nearshore ecosystem lacked a keystone predator, allowing populations of commercially valuable organisms such as geoduck clams (*Panopea generosa*), red sea urchin (*S. franciscanus*), Dungeness crab

(*Metacarcinus magister*), and sea cucumber (*Apostichopus californicus*) to flourish (Pritchett & Hoyt 2008, Larson et al. 2013, Hoyt 2015). Once sea otters recolonized, the biomass of their preferred prey was reduced (Hoyt 2015, Larson et al. 2013). Prince of Wales Island (POW) and its neighboring islands in southern Southeast Alaska have two original sea otter release locations and commercial fishing for shellfish. Hoyt (2015) studied sea otter diets throughout southern Southeast Alaska for three seasons (2010–2012), focusing on sea otter impacts on commercially important species. Hoyt (2015) found that the number of species consumed by sea otters increases as time since recolonization increases, and abundance of commercially important species was reduced where sea otters were present vs. absent. An example of a commercial shellfishery impacted by sea otters is the sea cucumber fishery. Once sea otters recolonized the western side of POW, sea cucumber dive fisheries were closed due to declining sea cucumber numbers and test size in ADFG dive surveys (Larson et al. 2013).

As sea otters recolonize Southeast Alaska, regional entities are beginning to work towards creating ecosystem-based management plans. In Alaska, tribal governments are working to be more involved in the management of land and marine resources alongside state and federal governments. Working on ecosystem-based co-management plans would be advantageous for all Alaskan residents, making sure that all voices are heard. This study is an essential step in an ecosystem-based management approach because management plans need quantitative data to work with federal and state organizations. Wide-ranging studies of sea otter diets can aid in the management of commercially important and subsistence species in Southeast Alaska while co-managing for a protected apex predator. Producing quantitative reports of sea otter diet composition and detailed macronutrient analyses can bridge a gap in crucial future management plans for state, federal, tribal groups, and coastal communities to produce co-management plans

for sea otter hunting and preserving subsistence foods, such as butter clams (*Saxidomus gigantea*), Dungeness crab, sea urchin, and sea cucumbers.

Thesis Goals

The overall goal of this study was to analyze sea otter diet composition according to age, reproductive class, season, and time since recolonization. To achieve this goal, I had two objectives. In Chapter 1, I addressed changes in seasonal diet composition using stable isotopes from sea otter vibrissae and potential sea otter prey. Both were analyzed to identify intra-annual diet shifts within individual sea otters. In Chapter 2, I addressed the energetic quality of sea otter prey in southern Southeast Alaska. Diets of sea otters throughout the POW region were compared using different sea otter and environmental metrics; 1) adult versus juvenile sea otters, 2) reproductive class and sex of sea otters, 3) time since recolonization, and 4) season. Prey were evaluated by lipid and protein content and compared according to overall diet composition across the different sea otter metrics. These objectives were addressed to gain a better understanding of sea otter diets in a growing population in Southeast Alaska.

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Chapter 1: Behavioral observations and stable isotopes reveal high individual variation and little seasonal variation in sea otter diets in Southeast Alaska¹

Abstract

Our goal was to assess year-round variation in sea otter (*Enhydra lutris*) diet around Prince of Wales Island (POW) in southern Southeast Alaska, a region characterized by mixed bottom habitat, using two complementary approaches. We observed sea otter foraging to determine diet composition during the spring and summer and obtained sea otter vibrissae, which embed temporal foraging patterns as they grow, from subsistence hunters to identify year-round changes in sea otter diets via stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). We compared the stable isotopes from sea otter vibrissae and sea otter prey items that were collected during spring, summer, and winter. Overall, year-round sea otter diet estimates from stable isotope signatures and visual observations from spring and summer were dominated by clams in terms of biomass, with butter clams (*Saxidomus gigantea*) as the most common clam species seen during visual observations. Our results indicate that these sea otters, when considered together at a regional level around POW, do not exhibit shifts in the main prey source by season or location, however individual sea otter diets identified by stable isotopes had strong individual-level variation, which suggests some individuals may vary their diet seasonally. Behavioral variation among individual sea otters may be a primary driving factor in sea otter diet composition. This study aids in the future management of shellfisheries, subsistence hunting, and founding co-

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management strategies for a protected species by providing quantitative diet composition data for modeling predictions of invertebrate population estimates.

1. Introduction

The importance of sea otters (*Enhydra lutris*) in shaping nearshore marine ecosystems is well documented along the northeast Pacific coast (Estes & Palmisano 1974, Hughes et al. 2013, Rechsteiner et al. 2019, Hale et al. 2019). Sea otters are keystone predators with voracious appetites, capable of causing major ecological shifts in nearshore marine ecosystems (Estes & Palmisano 1974). Unlike most marine mammals, sea otters do not have blubber for warmth. Instead, sea otters maintain very high metabolic rates, resulting in the need to consume 19–39% of their body weight in food per day, dependent on reproductive status (Costa 1982, Davis 2020). Sea otter consumption can control populations of sea urchins (*Strongylocentrotus* spp.) in rocky habitats, relieving grazing pressure on canopy-forming kelps. Decreased grazing increases kelp forest cover, in turn, providing habitat for juvenile fishes and invertebrates (Estes & Palmisano 1974, Estes & Duggins 1995). Trophic cascades also have been documented in seagrass communities, where sea otter presence is positively correlated with eelgrass (*Zostera marina*) biomass (Raymond et al. in review, Hughes et al. 2013).

Sea otter recolonization patterns have shaped nearshore ecosystems (Estes & Duggins, 1995). Sea otters once inhabited nearshore Pacific Ocean ecosystems from Japan to Baja California. However, due to hunting for lucrative fur markets in Russia and China, by the late 19th Century, only 11 remnant populations remained of the once-continuous distribution. In 1911, sea otter hunting was prohibited by the International Fur Seal Treaty (Burriss & McKnight

1973). While sea otters were absent, the nearshore ecosystem lacked a keystone predator, allowing commercially-valuable organisms such as geoduck clams (*Panopea generosa*), red sea urchin (*S. franciscanus*), Dungeness crab (*Metacarcinus magister*), and sea cucumber (*Apostichopus californicus*) to flourish (Pritchett & Hoyt 2008, Larson et al. 2013, Hoyt 2015). In Southeast Alaska, the Alaska Department of Fish and Game and Atomic Energy Commission initiated a translocation program to restore sea otters to their historical range. In total, about 400 sea otters were relocated to six locations in Southeast Alaska in the 1960s (Burris & McKnight 1973, Jameson et al. 1982). Since then, sea otter range and abundance in Southeast Alaska have increased. In 2012, aerial counts estimated that approximately 25,000 sea otters were present in Southeast Alaska (USFWS 2014), and very few locations within Southeast Alaska were estimated to be at carrying capacity at the time of that survey (Tinker et al. 2019).

Time since sea otter recolonization in Southeast Alaska plays an important role in sea otter diet diversity (Hoyt 2015). At newly recolonized sites, sea otters consume fewer species as compared to sites where sea otters have been present for more extended periods. Sea otters in a newly colonized rocky habitat consume red sea urchins (*S. franciscanus*) at very high rates before moving on to smaller, less caloric-rich prey sources (e.g., sea cucumbers). As sea otter populations increase and reach carrying capacity, overall prey diversity increases (Hoyt 2015).

While time since recolonization affects sea otter diets on a population level (Hoyt 2015), sea otters often exhibit diet variations on an individual level (Tinker et al. 2008). In regions of California where sea otters are at or near carrying capacity, sea otters often specialize on a small subgroup of prey items (Estes et al. 2003, Tinker et al. 2008, Newsome et al. 2009). Sea otter individuality is also evident in rocky sediment habitats where populations are at carrying

capacity. To date, studies of sea otters in mixed and soft sediment habitats have not revealed prey specialization among individuals (Newsome et al. 2015).

Year-round studies from regions with populations at or near carrying capacity show that diet remains consistent over seasons but can vary at an individual level (Tinker et al. 2008, Newsome et al. 2009). However, environmental conditions can hinder year-round diet studies. For example, in Alaska, the rugged terrain, harsh weather conditions, and lack of daylight during the winter make year-round observations difficult. Therefore, observational studies of sea otter diet in Alaska are limited to April through October (Weitzman 2013, Larson et al. 2013, Coletti 2014, Hoyt 2015). Thus, alternative methods are needed to examine diet on a year-round basis in regions such as Alaska.

Stable isotopes are a common tool for assessing diet composition in ecological studies that can be obtained from a range of soft and hard tissues (e.g., blood, muscle, hair) (Fry 2006, Crawford et al. 2008, Newsome et al. 2010, Wild et al. 2020). As compared to visual observations, stable isotopes can: i) provide temporally-integrated estimates of prey contributions with lower cost and field effort, ii) be used in situations where field observations are impossible (e.g., no access roads or poor weather conditions), iii) detect cryptic foraging patterns due to factors such as small prey size and offshore ranging patterns, and iv) provide a measure of assimilated diet as opposed to ingested diet. In ecological studies, nitrogen and carbon stable isotopes are commonly used in the analysis of food web structure (Fry 2006). Nitrogen isotope ratios ($\delta^{15}\text{N}$) can determine a species' relative trophic level within a food web, as heavier nitrogen (^{15}N) accumulates in an organism relative to its prey (Robinson 2001). Carbon isotope values ($\delta^{13}\text{C}$) can aid in identifying the original carbon source at sequestration, i.e., the primary producer at the base of the food web. In marine systems, heavier carbon (^{13}C)

accumulates more in benthic primary producers, such as kelp. Carbon in pelagic ecosystems where phytoplankton forms the base of the food web have lighter carbon (^{12}C) and less ^{13}C accumulation (Bell et al. 2016). In the nearshore marine system of which sea otters are a part, filter feeders, such as clams and mussels, exhibit pelagic signals and kelp grazers, such as sea urchins, snails, and sea cucumbers, exhibit benthic signals (Bell et al. 2016).

To investigate seasonal variation in diet, keratinous tissues can be used as an isotopic record (Newsome et al. 2009, Cardona et al. 2017, Chilvers 2019). Vibrissae, the whiskers that grow on the base of the muzzle of sea otters, embed temporal foraging patterns as they grow via changes in carbon and nitrogen isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). The root of the vibrissa, closest to the muzzle, carries the most recent dietary signature. Growth rates for marine mammal vibrissa have been studied in captive settings, allowing for standard rates to be applied to wild populations (Tyrrell et al. 2013, Beltran et al. 2015). Vibrissae in adult sea otters show consistent growth of approximately 7.7 cm per year (Tyrrell et al. 2013). Serial samples along a single vibrissa can thus show dietary shifts for an individual over time as the vibrissa grows.

To test the diets of sea otters, we concentrated studies around the western side of Prince of Wales Island (POW) and the surrounding islands (Figure 1.1). This region is within the Southeast Alaska population of sea otters. POW is an ideal study region because there are previous sea otter foraging studies upon which to build (Kvitek et al. 1993, Larson et al. 2013, Hoyt 2015). POW also contains two original sea otter relocation sites (Burriss & McKnight 1973, Jameson et al. 1982), creating a natural gradient for assessing changes in the sea otter diet due to recolonization patterns. The sea otter population that resides in the POW region is currently estimated to be below carrying capacity with a few small sub-regions reaching carrying capacity (Tinker et al. 2019). According to traditional ecological knowledge, sea otters in some regions

around POW change their locations and diet during the winter months. Thus, using summer observations to estimate sea otter prey consumption year-round could lead to biased data. By using carbon and nitrogen stable isotopes from sea otter vibrissae, we can fill the gap in knowledge regarding sea otter foraging behavior during the winter in Southeast Alaska.

Our goal was to determine if there is seasonal variation in: sea otter diet, foraging locations around POW, and individual variation throughout the region. Our objectives were to 1) confirm that visual foraging observation and stable isotope analysis results provide similar sea otter diet estimates, 2) determine if sea otters diets vary by i) season and ii) sea otter location, and 3) determine sea otter individuality in diet from stable isotope analysis. A year-round diet profile for the sea otters of the POW region provides a more comprehensive understanding of sea otter nearshore habitat use. This understanding can aid in efforts for both sea otter management and their prey, which are important components of commercial and subsistence fisheries in Southeast Alaska.

2. Methods

2.1 Observational diet data

Sea otter foraging data were collected from May to August 2018 via visual observations. Data were collected from locations spanning the west coast of POW, encompassing soft and rocky habitats where sea otters occur in high densities (Figure 1.1). Foraging observations were made from shore to assess sea otter diet composition, using standardized methods (Dean et al. 2002). In brief, we followed individual sea otters using Questar telescopes (20–50X) for one

foraging bout, defined as sequential dives by one sea otter for a maximum of 20 dives or until the sea otter was lost by the observer. Twenty dives were used as this is the maximum number of dives required to determine significant relationships between prey type and diving success (D. Monson, personal communication). Two trained observers conducted observations. For each surface interval (i.e., the time between two consecutive foraging dives), the observer recorded the prey item, to species level when possible (Calkins 1978). Visual observations were separated into Spring (May 6 – June 20) or Summer (June 21 – August 13). Prey biomass for each season was estimated from a Bayesian model using a Monte Carlo based simulation to factor in unknown prey items that were recorded (Tinker et al. 2008).

2.2 Prey tissue collection

The most commonly reported sea otter prey species from visual observations in other regions of Alaska (Anthony 1995, Oftedal et al. 2007, Weitzman 2013, Coletti 2014, Hoyt 2015, Cartagena 2016, Brown et al. 2019) were collected for stable isotope analysis. Prey species were grouped into functional prey groups (to genus or family), consisting of clams, crabs, sea cucumbers, snails, sea urchins, and mussels (Figure 1.2). Potential prey items were collected at two sites around POW at three different time periods (May 2018, August 2018, February 2019) to reflect possible geographic and temporal isotopic variation in the region. Site 1 (N 55.532, W 133.147) was near the town of Craig, AK. Site 2 (N 55.268, W 133.003) was in Soda Bay, AK (Figure 1.1). All sampling was conducted in the intertidal zone at low tide by digging (for clams), via Fukui minnow and crab traps (for crabs), or by hand while snorkeling (for all other species). Five replicates per species were collected, or as many as possible if five replicates were

not present. Occasionally, sea otter prey species were not present at either site. In such cases, those prey species were collected opportunistically at nearby sites (Appendix A.1). When prey items were collected outside of the main sites, mussels (*Mytilus trossulus*) were also collected for baseline isotopic comparison as they are prevalent across POW and are filter feeders (i.e., primary consumer).

After collection, samples were cleaned with freshwater to remove sediment and debris, then frozen at -20°C until analysis. For analysis, samples were thawed and separated into soft tissues and hard parts. We removed all hard parts to remove their influence on carbon values during stable isotope analysis. The soft tissues were weighed and homogenized in a food processor (Cuisinart Mini-prep). Samples were then dried in a LECO Thermogravimetric Analyzer 701 (TGA) dryer at 135°C or in a gravity convection oven (VWR Symphony 414004-552) at 70°C.

2.3 Sea otter vibrissae collection

Sea otter vibrissae were collected through the US Fish and Wildlife Service (USFWS) tagging program associated with subsistence harvest. Per the Marine Mammal Protection Act (Marine Mammal Commission 2018), Alaskan Natives, who live in coastal Alaskan communities, can legally harvest sea otters. Hunters report all takes with the USFWS through the sea otter tagging program (FWS-30 Marine Mammals Management, Marking, Tagging and Reporting Program 2018). Each harvested sea otter received a tag that contains information on harvest date, location, sex, age (if known), and group size. We worked with hunters and taggers on POW who collected and submitted vibrissae to the USFWS as part of their standard harvest.

Forty-five sea otters harvested by subsistence hunters from July to October 2019 were included in this study. Between one and three whiskers were collected from the base of the muzzle of each harvested sea otter. Previous research has shown that a sample size > 10 sea otters per region is ideal for assessing regional-level diet composition using carbon and nitrogen stable isotopes (Elliott Smith et al. 2015).

In the lab, sea otter vibrissae were cleaned with 70% ethanol and cut into subsections approximately every 0.7 cm (Figure 1.3). Depending on individual vibrissa length, there were 5–14 subsections per vibrissa. Approximately 0.4 mg of each subsection was weighed using a Sartorius MC210S balance (Sartorius AG, Göttingen, Germany) and sealed into a tin capsule (3.3 x 5 mm). Each sea otter vibrissa was measured after subsections were made, and based on the length from the root and date collected, were grouped into seasons according to the known growth estimate of 7.7 cm per year (Tyrrell et al. 2013). Subsections were assigned seasons for spring (March 21 – June 20), summer (June 21 – September 20), fall (September 21 – December 20), and winter (December 21 – March 20).

2.4 Trophic discrimination factors

Trophic discrimination factors (TDF) are used to correct for isotopic differences between a consumer and its prey. A TDF, on average $\sim 1.0\text{--}2.5\text{‰}$ for $\delta^{13}\text{C}$ and $\sim 2.0\text{--}3.5\text{‰}$ for $\delta^{15}\text{N}$, is one trophic step up the food web from source to consumer (Post 2002, Sponheimer et al. 2003, Caut et al. 2009). As a consumer changes its diet and feeds up the food web, typically correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are highly positive because of the trophic discrimination (Cardona et al. 2017).

Estimating TDF depends on individual metabolic needs and the prey consumed. Because we did not do a direct test of TDFs in this study, we conducted a sensitivity analysis of previously used TDFs for similar consumers to determine the appropriate TDFs for our Bayesian mixing model (see below) (Lesage et al. 2002, Caut et al. 2009, Wolf et al. 2009, Newsome et al. 2010, Beltran et al. 2016). We tested 1.5, 1.8, and 2.0‰ for $\delta^{13}\text{C}$, and 2.8 and 3.1‰ for $\delta^{15}\text{N}$. TDFs of 2.0‰ for $\delta^{13}\text{C}$ and 2.8‰ for $\delta^{15}\text{N}$ were chosen based on similarity to other marine mammals and similarity in testing.

2.5 Isotopic methods

All tissue samples (i.e., prey and vibrissae) were analyzed for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios at the NOAA Fisheries Recruitment Energetics and Coastal Assessment Chemistry Laboratory (Juneau, AK). We used a FlashSmart elemental analyzer coupled to a Delta-V continuous-flow isotope ratio mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA). We report stable isotope ratios in per mil (‰) using the delta (δ) notation and the following equations:

$$\delta^{13}\text{C} = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] * 1000$$

$$\delta^{15}\text{N} = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] * 1000$$

where R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Isotope ratios are reported relative to Vienna-Pee Dee Belemnite for carbon and air for nitrogen. Replicated measurements of internal laboratory standards (purified methionine, homogenized Chinook salmon (*Oncorhynchus tshawytscha*) muscle, and homogenized pollock (*Gadus chalcogrammus*) muscle) were used as

quality controls (standard deviation of ± 0.10 for $\delta^{13}\text{C}$ and ± 0.15 for $\delta^{15}\text{N}$). We measured the C:N ratio for each subsample to control for the quality of vibrissae protein (Ambrose 1990). Sea otter prey tissue samples were corrected for lipid-rich samples that were higher than 3.5:1 carbon to nitrogen ratio, with the following equation (Post et al. 2007).

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 * \text{C: N}$$

2.6 Statistical analyses

To test seasonal variation in sea otter diet, a Bayesian mixing model was run in R v. 4.0.0 (R Core Team 2020) using the program MixSIAR (Stock & Semmens 2016). For each functional prey group, we estimated the mean proportional contribution by season at the sea otter regional level. We combined sites for the mixing model, as we had small sample sizes for certain species (i.e., sea cucumbers and snails). We tested mixing model sensitivity across prey collected in every season by running separate models for each season prey were collected (Appendix A.3). There were no significant changes in the mixing model outputs, so we combined all seasons. Mixing models were created for each harvest site, with season as a fixed factor and an informed prior from proportional diet estimates (Figure 1.2). Posterior probabilities were estimated using three chains of length 1,000,000 after a burn-in of 50,000 iterations, and chains were thinned by subsampling every 500th iteration. Each site was run separately, with an approximately 50 hour run time. Sea cucumbers and snails were combined in stable isotope analyses because their mean and standard deviation for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ overlapped and were isotopically indistinguishable.

To test seasonal variation of sea otter diet around POW, we created a linear mixed effect model (LME) with an analysis of variance (ANOVA) for each sea otter harvest site's $\delta^{13}\text{C}$ and

$\delta^{15}\text{N}$ values with season as a fixed effect and sea otter ID as a random effect to account for the multiple sub-samples for each vibrissa ($\alpha = 0.05$). Post hoc comparisons to determine pairwise differences between seasons were conducted with a Tukey's procedure. We ran all statistical analyses in R v. 4.0.0 (R Core Team 2020) with packages nlme (Pinheiro et al. 2020), emmeans (Lenth 2019), and MuMIn (Bartoń 2019).

To account for individuality across the POW region, we calculated a Pearson's correlation of serial $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each individual using R v. 4.0.0 (R Core Team 2020). All datasets are archived in a publicly accessible database with the Knowledge Network for Biocomplexity (LaRoche et al. 2020, LaRoche and Rogers 2020).

3. Results

3.1 Visual foraging observations

Between May 6 and August 13, 2018, we recorded 3,385 foraging dives from 362 sea otter foraging bouts. Foraging bouts were evenly distributed around the western side of POW. Sea otters were observed to consume a total of 44 invertebrate categories (to species, when possible) (LaRoche 2020). The most frequently consumed functional prey group across spring and summer was clams (82.9% in spring, 78.6% in summer), followed by sea cucumbers (6.0% in spring, 10.8% in summer), crabs (2.9% in spring, 4.6% in summer), snails (2.9% in spring and 1.6% in summer), sea urchins (1.2% in spring and 2.2% in summer), and mussels (1.2% in spring and 0.2% in summer) (Figure 1.2, Table 1.1). Within the clam group, butter clam (*Saxidomus gigantea*) was the most frequently consumed species.

3.2 Stable isotopes of sea otter prey

For each functional prey group, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were compared by site and season, and did not have uniform variations across sites (Table 1.1). Filter feeders, including clams and mussels, had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Craig than Soda Bay for all seasons, but this pattern was not seen in higher level consumers or sea urchins (Appendix A.3).

3.3 Stable isotopes of sea otter vibrissae

Across all harvest locations, mean sea otter vibrissae $\delta^{13}\text{C}$ values ranged from -15.54 to -12.46‰ and mean $\delta^{15}\text{N}$ values ranged from 12.15 to 14.20‰ (Figure 1.4, Appendix A.2). Sea otter $\delta^{13}\text{C}$ values significantly varied by season within each harvest site (ANOVA: Tonowek Narrows $df = 3$, $F\text{-value} = 3.05$, $p = 0.03$, Shinaku Inlet $df = 3$, $F\text{-value} = 3.60$, $p = 0.02$, Sukkwan Strait $df = 3$, $F\text{-value} = 3.36$, $p = 0.02$). Sea otter $\delta^{15}\text{N}$ values significantly varied by season only within the Tonowek Narrows harvest site (ANOVA: $df = 3$, $F\text{-value} = 18.98$, $p < 0.0001$) but not the other two sites. For sea otters harvested from Tonowek narrows, pairwise comparisons of $\delta^{13}\text{C}$ values between spring and fall along with $\delta^{15}\text{N}$ values between spring and fall, spring and winter, summer and fall, and summer and winter revealed significant differences. For sea otters harvested from Shinaku Inlet, pairwise comparisons of $\delta^{13}\text{C}$ values between summer and winter, and fall and winter revealed significant differences. For sea otters harvested from Sukkwan Strait pairwise comparisons of $\delta^{13}\text{C}$ values between spring and summer revealed significant differences (Table 1.2). Linear mixed effects models for each isotope and harvest site suggested that seasonal variability (R^2_m) accounted for 1 to 14% of the variability in isotope

values and that the remaining variability showed similar levels of variability between sea otters (σ_b) and within a sea otter (σ_e) ($\delta^{13}\text{C}$ Tonowek Narrows: $R^2_m = 0.02$, $\sigma_b = 0.62$, $\sigma_e = 0.49$; Shinaku Inlet: $R^2_m = 0.12$, $\sigma_b = 0.45$, $\sigma_e = 0.66$; Sukkwan Strait: $R^2_m = 0.04$, $\sigma_b = 0.39$, $\sigma_e = 0.41$. $\delta^{15}\text{N}$ Tonowek Narrows: $R^2_m = 0.14$, $\sigma_b = 0.30$, $\sigma_e = 0.42$; Shinaku Inlet: $R^2_m = 0.04$, $\sigma_b = 0.66$, $\sigma_e = 0.51$, Sukkwan Strait: $R^2_m = 0.01$, $\sigma_b = 0.25$, $\sigma_e = 0.35$).

Isotope ratios of sea otter vibrissae and functional prey groups are shown in an isospace plot (Figure 1.5). Isotopic information obtained from sea otter vibrissae were within the range of the sea otter prey isospace, which indicates that mixing models can be used to assess sea otter diets in this region and that the prey isotopic signatures and TDFs are appropriate for the individuals in this study.

Across all vibrissae, mean variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across individual vibrissa were 1.43‰ and 1.29‰, respectively, indicating little variation at the regional level. However, at the individual level, distinct patterns emerged (Figure 1.6). The highest variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ occurred in sea otter “521”, which had a change in $\delta^{13}\text{C}$ of 3.95‰ and change in $\delta^{15}\text{N}$ of 2.51‰ (Figure 1.6, B). The relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in sea otter vibrissa, as determined by Pearson’s correlation, varied among individuals, from highly negative ($r = -0.77$, $p = 0.025$, sea otter “752”, Figure 1.6C) to highly positive ($r = 0.97$, $p = <0.001$, sea otter “287”, Figure 1.6D). Thirty-four sea otters (75%) had a positive correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the vibrissa, and 11 sea otters (25%) had a negative correlation (Appendix A.2).

3.4 Mixing model results

Each site exhibited seasonal variation in diet (Figure 1.7). Clams comprised the largest proportion of the diet during every season, but the overall estimates of diet composition were variable with coefficients of variation ranging from 0.06 to 0.25. The range in coefficients of variation reflects a high degree of variability in the diet and a high degree of uncertainty. Seasonal variation was most apparent at the Shinaku Inlet site, where the mean proportion of clams in sea otter diets ranged from 40 to 78% across seasons, but sample size at this site is lower than the other two sites. Diet proportions during fall exhibited little inter-site variation.

4. Discussion

Stable isotopes from sea otter vibrissae in Southeast Alaska gave insight into year-round diets of sea otters around POW, which are challenging to obtain from visual observations. The year-round diet estimates from stable isotopes suggest diets have slight site and seasonal variations and were similar to the diet compositions determined by visual observations in summer months. However, there was greater variation in sea otter diet estimates from stable isotope analysis when compared to visual foraging observations. Clams were the dominant prey using visual and isotopic methods across all sites and seasons. Supplemental prey items, on the other hand, varied in the diet composition across site and seasons. Unlike studies in rocky habitats where 23% of sea otters had > 2‰ variation in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Newsome et al. 2009), our study had only one individual with pelagic to benthic ($\delta^{13}\text{C}$) or trophic ($\delta^{15}\text{N}$) level transitions over the length of the vibrissa. Although most sea otters did not exhibit large shifts, there was

strong individual-level variation in whisker stable isotope values, which suggests some individuals may vary their diet seasonally and that sea otter behavior is an important factor driving sea otter diet composition.

4.1 Seasonal Variation

4.1.1 Seasonal patterns throughout Prince of Wales Island

Shifts in $\delta^{13}\text{C}$ values resemble a shift in the base consumer in the food web (Bell et al. 2016). Mean $\delta^{13}\text{C}$ values across seasons exhibited little overall variation across the POW region. The change in mean $\delta^{13}\text{C}$ values across seasons and sites was $< 1\text{‰}$, which is not ecologically significant and is below the confidence intervals of the testing methods used. This shows that at the regional level, sea otters were not making large shifts in diets that vary in their base carbon source (i.e., shifting from majority clams to majority sea urchins). However, there are likely inter-individual differences in dietary composition or foraging location due to 9% of the data residing outside the 99.5% confidence interval (Figure 1.4).

Generally, large shifts ($\sim 3\text{‰}$) in $\delta^{15}\text{N}$ values signal trophic level in the food web (Robinson 2001). Mean $\delta^{15}\text{N}$ values across seasons and sites had a variation of approximately 1‰ . This change, similar to $\delta^{13}\text{C}$, is likely not ecologically significant because it is approximating the confidence intervals of the testing methods. Therefore, sea otters at a regional level do not exhibit seasonal differences in the overall diet. However, nitrogen exhibited more inter-site variability than carbon. The inter-site and inter-seasonal individual variation that was present could indicate shifts in supplementary diet items (i.e., crabs, sea cucumbers, sea urchins

and snails,); this was apparent in the mixing model results that vary by site and season for non-clam diet items.

4.1.2 Seasonal patterns across harvest sites

Seasonal effects on sea otter diet varied by sea otter harvest site. Shinaku Inlet had the highest diet uncertainty in the mixing model, which is likely attributed to the low sample size ($n = 5$) at this site. According to local observations (A. Frisby, personal communication), Shinaku Inlet is an area with seasonal variation in sea otter presence. This variability could be due in part to the strong hunting pressure in the winter and spring months (B. Benter, personal communication).

In contrast to Shinaku Inlet, Tonowek Narrows had less uncertainty in diet composition as inferred from stable isotope values. $\delta^{15}\text{N}$ values were lower in the warmer spring to summer months in comparison to the cooler fall to winter months. Tonowek Narrows is in a region with a high sea otter density that is nearing carrying capacity (Tinker et al. 2019). The diet composition from this location could be due in part to high resource competition (Tinker et al. 2012).

Sukkwan Strait is the most recently recolonized site. There was very little regional variation of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across all seasons. In previous studies, sea otters in newly recolonized areas have low prey diversity due to more plentiful, energetically-rich prey resources (Tinker et al. 2008, Hoyt 2015).

We collected prey throughout the year to account for seasonal variation in prey isotopes. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across seasons were not consistent for all prey species. Filter feeding bivalves (mussels and clams) expressed minimal isotopic variation across seasons;

however, mobile animals such as crabs, sea cucumbers, snails, and sea urchins showed elevated seasonal variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Although there was isotopic variation in sea otter prey across seasons, seasonal variation in sea otter diet was not attributed to isotopic variation in prey types. These differences across seasons, although not significant at the sea otter regional level, could potentially impact isotopic variation at the individual sea otter level.

4.2 Sea otter individuality

Across all three sites, there was individuality among sea otters, as evidenced by the wide range of prey (33 identified species) recorded during visual observations. Individuality in sea otter diets has been previously shown where sea otters become specialists for certain prey types in rocky habitats (Tinker et al. 2008). However, sea otter individuality is typically not as apparent in mixed sediment habitats (Newsome et al. 2015). Previous findings are similar to this study, where we did not find many large shifts in individual vibrissa, however the small-scale variations show individuality, as well as patterns across harvest sites.

Individual sea otter variation was apparent when looking at the correlation of carbon and nitrogen throughout each vibrissa. Most marine mammal species only have positive correlations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along a vibrissa (Cardona et al. 2017, Chilvers 2019). Our study had mostly positive correlations, but 25% (11/45) of vibrissae had negative correlations, with two sea otters exhibiting a significant negative correlation. Tonowek Narrows had the most positive correlations, with only one negative correlation. Most of the negative correlations were from Sukkwan Strait, the site most recently recolonized. A negative correlation of values depicts a decoupling of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which could signal sea otter movements (e.g., feeding inshore vs

offshore); however the exact locations are unknown. Sukkwan Strait, the location with significantly negative correlations is the site with the newest sea otter colonization, and a high rate of hunting pressure (T. Peele, personal communication), both promoting more sea otter movements (Lafferty & Tinker 2014, Hoyt 2015).

Despite the regional-level specialization on clams throughout POW, there was inter-individual dietary variation that was driven by individual sea otter behavior. Individual diet variability has been documented in other marine mammal species. For example, some female bottlenose dolphins (*Tursiops truncatus*) in Shark Bay, Australia, have developed a unique foraging pattern called sponging where they dig for prey by carrying a sponge on their rostra (Mann & Sargeant 2003, Mann et al. 2008, 2012). This unique foraging pattern was not present throughout the entire dolphin population. For sea otters, some individuals use tools to open hard shells, whereas other individuals within the same population do not use tools (Fujii et al. 2015). Overall, dietary specialization in sea otters may be an example of vertical culture (Whitehead et al. 2004) as the behavior is transmitted from mother to offspring (Staedler 2011).

4.3 Future work

All vibrissae for this study were collected during the summer and fall months, which may lead to a more accurate estimate of summer and fall isotope values vs. winter and spring values. As the vibrissa grows, the growth rates become more variable depending on factors such as thickness of the keratin and individual growth patterns (Tyrrell et al. 2013, Beltran et al. 2015). Thus, future work with sea otter vibrissae collected at different times of the year could be compared to get more root and tip estimations of each season, comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Since we found that using stable isotopes has similar outcomes to visual foraging results, future efforts could focus on stable isotopes to document sea otter diets over time and space. Stable isotopes may be a more cost-effective research tool to monitor sea otters in the future as they recolonize and reach carrying capacity around POW. Continued work with harvesters, and including local tribes and stakeholders, could be an alternative to visual foraging surveys in developing a long-term dietary dataset. Continuing diet studies focused at the individual level can provide insight into the fine-scale behavioral differences in the sea otter population, and better explain the population-level changes in this nearshore system. Southeast Alaska is a unique region for sea otters because there is strong hunting pressure, which often occurs in pulses. This hunting pressure likely affects the population status and promotes more movement.

Southeast Alaska is a unique population of sea otters due to the strong pulses of hunting that affect the population on a local scale (Raymond et al. 2019). Effects of sea otter hunting could change the social structure of sea otter sub-populations. More movements were apparent in female home ranges when hunting increased around Kuiu Island (Hoyt 2015). Understanding the dynamics of the sea otter social structures in Southeast Alaska could provide insight to where sea otters are likely to move and recolonize in the future.

Conclusions

Our study found there were no ecologically significant shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ over seasons, indicating that, at the regional level, sea otters did not shift diets across seasons. There is individual variation, so while clams, a subsistence harvest food for local communities (Moss 1998), are consumed in high numbers at the regional level, individual sea otters consume a wide

range of prey. Parallel studies conducted on POW show the positive effects of sea otter recolonization on canopy-forming kelps (Bell et al. in prep.) and negative effects of sea otter recolonization on subsistence shellfish harvest (Ibarra in prep). As sea otters return to their historical range, it is likely that the benthic community structure will diversify (Estes & Palmisano 1974) while commercial and subsistence shellfish fisheries will decline (Larson et al. 2013). This study provides quantifiable diet estimates for sea otters around POW, which can be incorporated into future models to more effectively account for and project sea otter effects concerning commercial and subsistence foods for the Southeast Alaska region.

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Figures

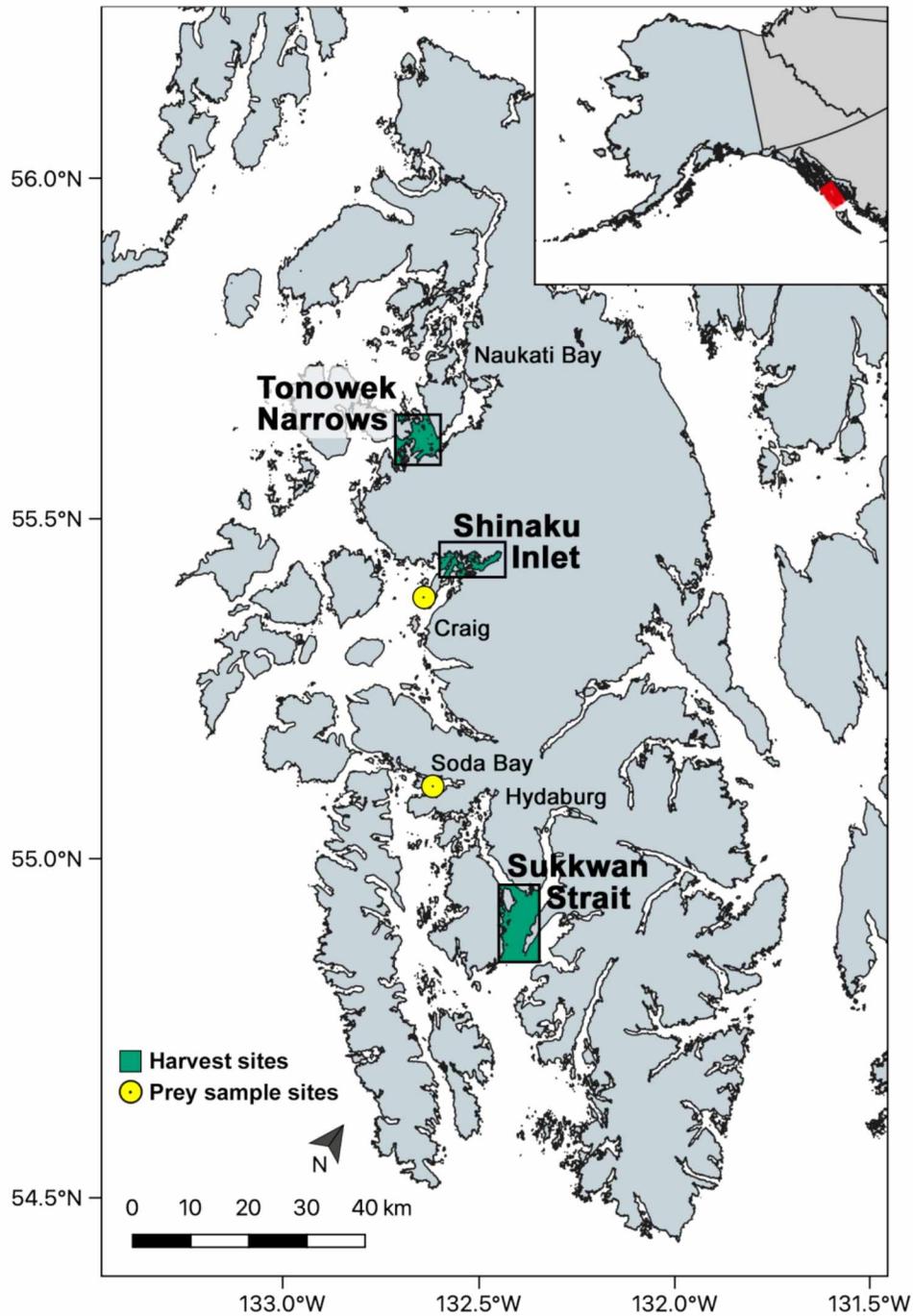


Figure 1.1: Prince of Wales Island, Southeast Alaska. Yellow circles indicate invertebrate sampling sites (Craig and Soda Bay), and green boxes indicate where vibrissae were collected from harvested sea otters.

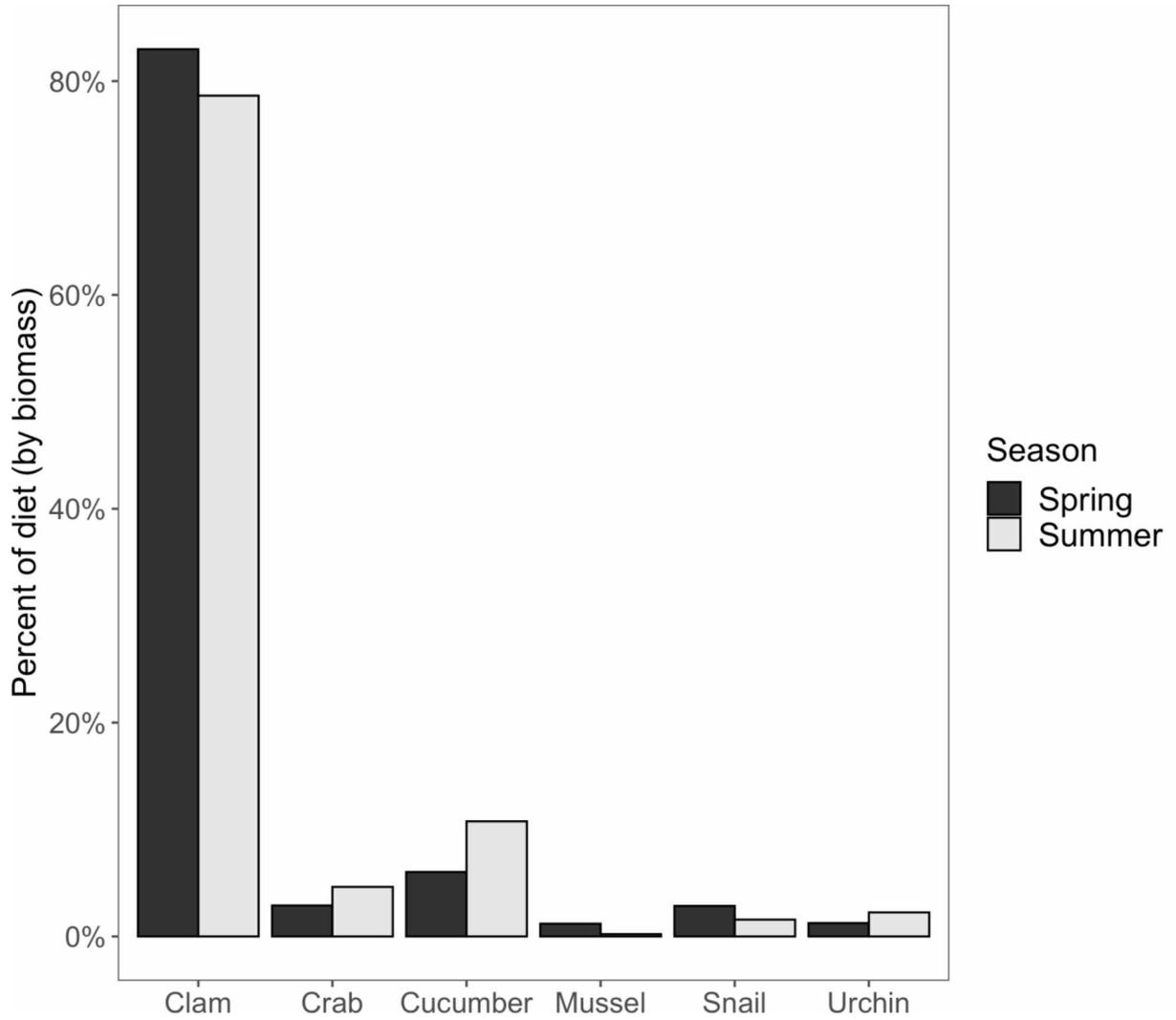


Figure 1.2: Proportion of diet by biomass from visual observations of sea otter foraging around the western side of Prince of Wales Island. Spring includes May 6– June 20, 2018 (n= 1557), and summer includes June 21– August 15, 2018 (n= 1610).

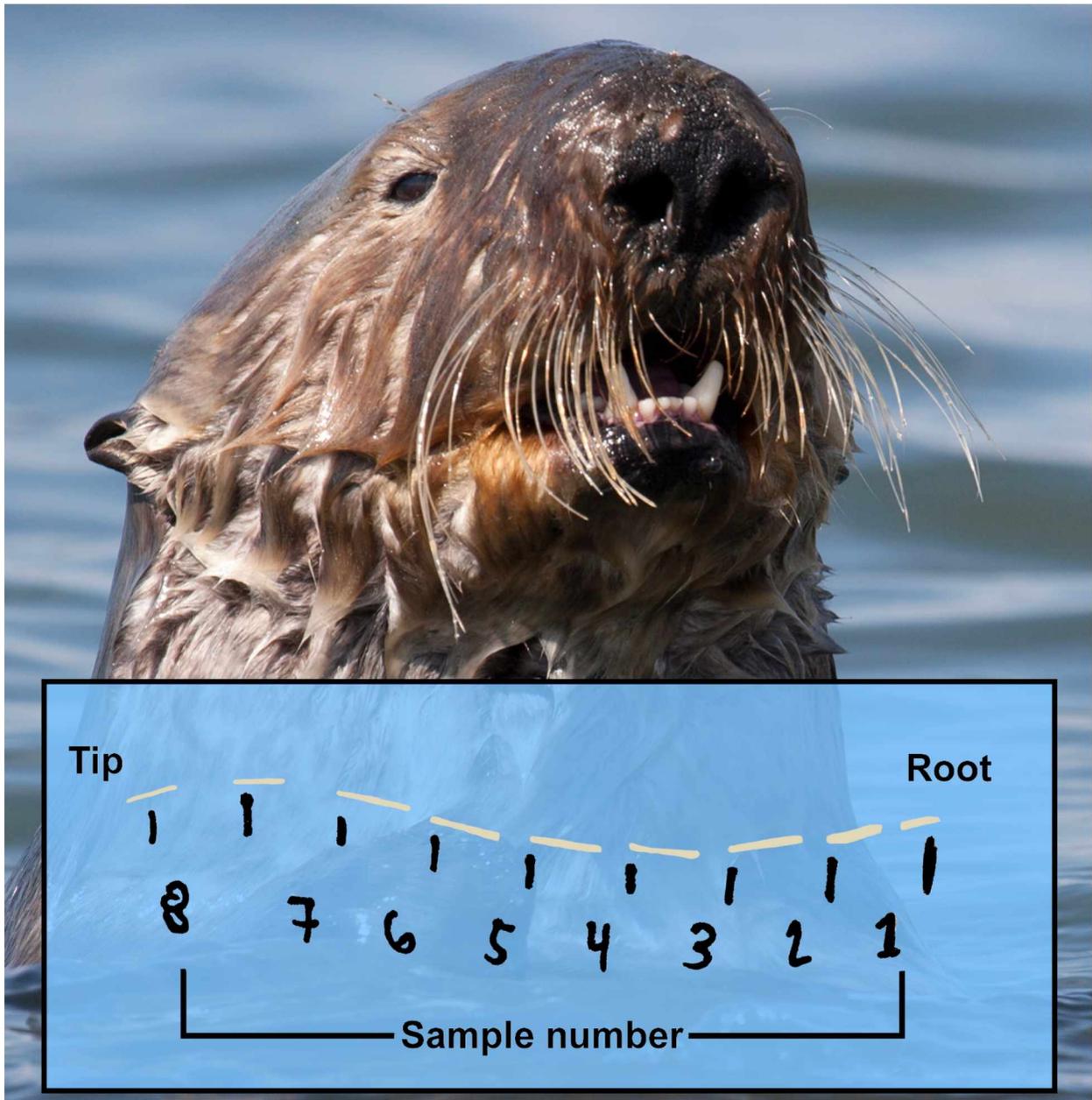


Figure 1.3: Sea otter vibrissa with subsections removed for sampling. Vibrissa was taped down in 0.7 cm increments (representing approximately one month of growth) marked with a line. The season was estimated by measuring from the cut location to the root.

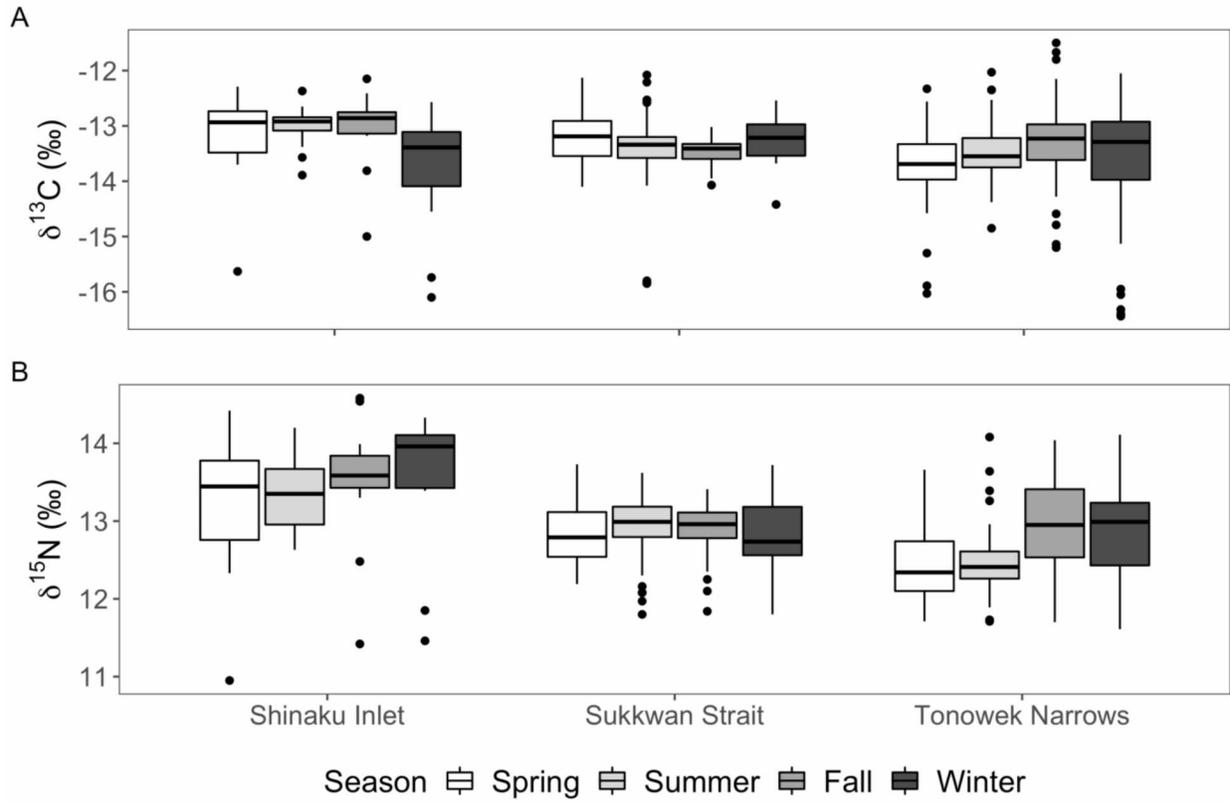


Figure 1.4: Sea otter vibrissae stable isotope ratios $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) by harvest site and season. Seasons were estimated from vibrissae growth rate (7.7 cm/year) and sample distance from the root. Shinaku Inlet n=54, Sukkwan Strait n=132, Tonowek Narrows n=235.

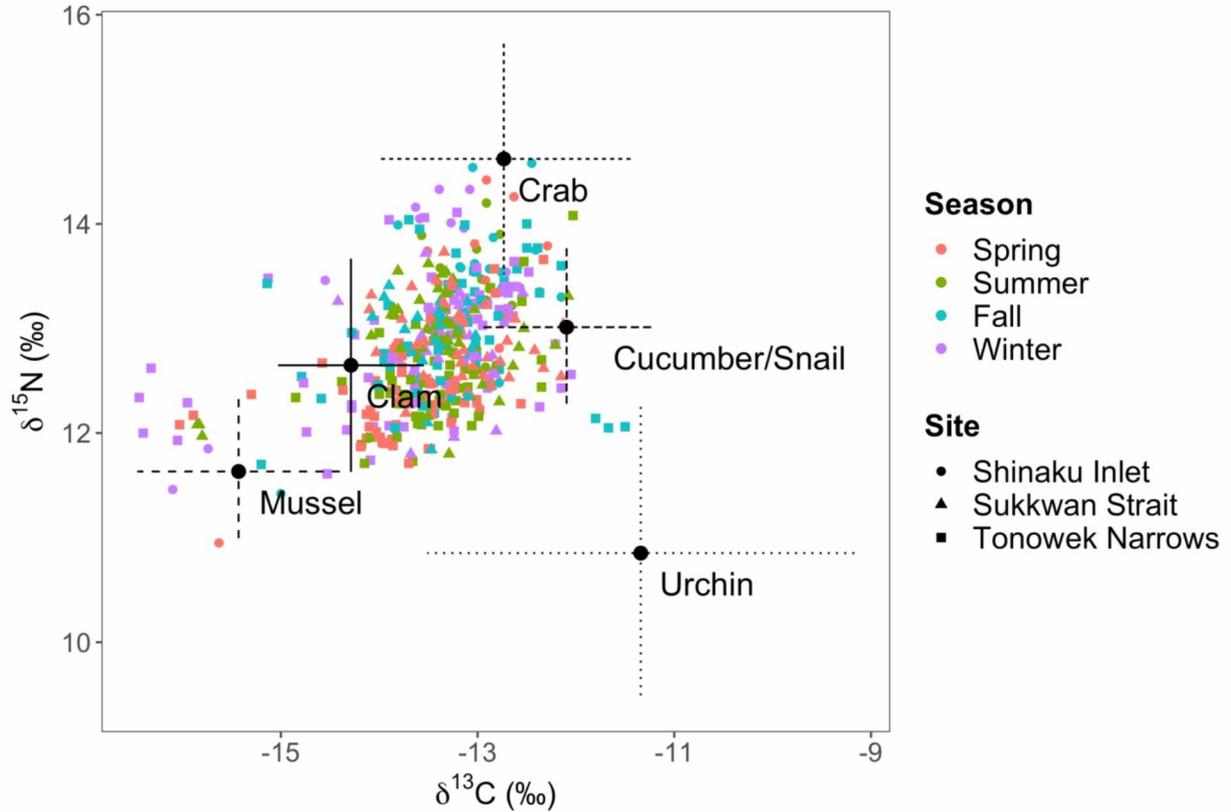


Figure 1.5: Stable isotope ratios $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sea otters (as determined by vibrissae) and their prey (mean with standard deviation error bars). Sea otter prey values were corrected for trophic discrimination by subtracting 2.0‰ and 2.8‰ from carbon and nitrogen isotope values, respectively. Carbon values were normalized for lipid content following Post et al. (2007). Each season was derived from estimated growth rates of sea otter vibrissae and sample distance from the root. Site indicates where the sea otter was harvested.

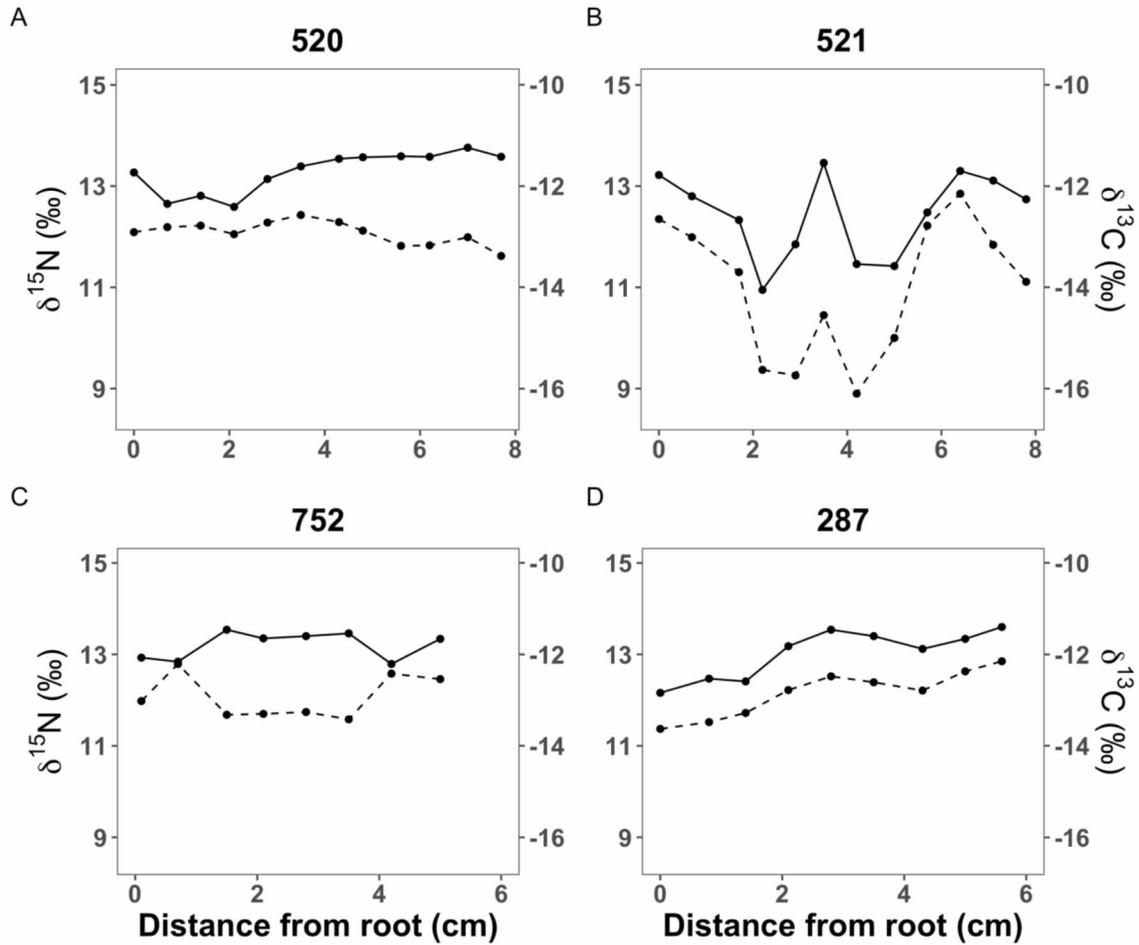


Figure 1.6: Stable isotope ratios, $\delta^{15}\text{N}$ (solid line, primary y-axis) and $\delta^{13}\text{C}$ (dotted line, secondary y-axis), for four sea otter vibrissae from root to tip, with a maximum length of 8 cm. (A) Individual 520 (from Shinaku Inlet) has little temporal variation in both carbon and nitrogen ratios, with a non-significant negative correlation ($r = -0.36$, $p = 0.244$). (B) Individual 521 (from Shinaku Inlet) shows a high temporal variation in both carbon and nitrogen, which are positively correlated ($r = 0.78$, $p = 0.003$). (C) Individual 752 (from Sukkwan Strait) has a significant negative correlation between carbon and nitrogen ($r = -0.77$, $p = 0.025$). (D) Individual 287 (from Tonowek Narrows) demonstrates increases in stable isotope ratios over the length of the vibrissa, with a high correlation between carbon and nitrogen ($r = 0.97$, $p = <0.001$).

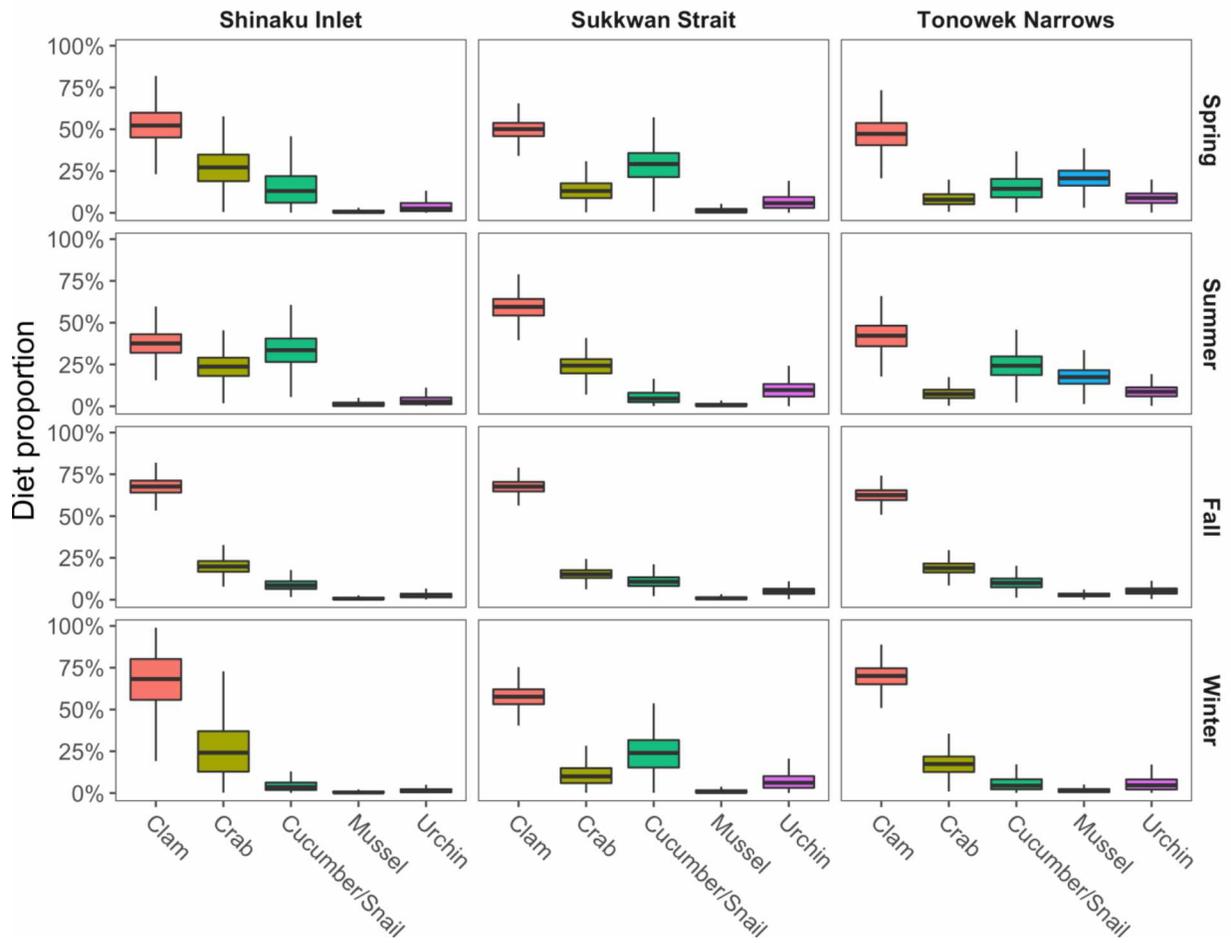


Figure 1.7: Sea otter diets estimated by an informed mixing model as a function of harvest location and season for the five functional prey groups. Boxes are upper and lower quantiles with a median horizontal line and 95% credible interval. Models were based on sea otter vibrissae samples from Tonowek Narrows ($n = 24$), Shinaku Inlet ($n = 5$), and Sukkwan Strait ($n = 16$).

Table 1.1: Summary of stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) ratios by sea otter functional prey group and season. Dietary percent is proportion of diet by biomass for the whole Prince of Wales Island region. *Sea cucumbers and snails were combined for analysis because of isotopic overlap.

Functional Prey Group	Species	Spring				Summer				Winter				All Seasons			
		$\delta^{13}\text{C}$ mean \pm sd	$\delta^{15}\text{N}$ mean \pm sd	n	Dietary %	$\delta^{13}\text{C}$ mean \pm sd	$\delta^{15}\text{N}$ mean \pm sd	n	Dietary %	$\delta^{13}\text{C}$ mean \pm sd	$\delta^{15}\text{N}$ mean \pm sd	n	Dietary %	$\delta^{13}\text{C}$ mean \pm sd	$\delta^{15}\text{N}$ mean \pm sd	n	Dietary %
Clam	<i>Clinocardium nuttallii</i>	-16.13 \pm 0.77	9.57 \pm 1.05	34	82.9%	-16.22 \pm 0.64	10.19 \pm 1.01	29	78.6%	-16.6 \pm 0.76	9.83 \pm 0.89	23	-	-16.29 \pm 0.74	9.85 \pm 1.02	86	81.0%
	<i>Leukoma staminea</i>																
	<i>Saxidomus gigantea</i>																
Crab	<i>Metacarcinus magister</i>																
	<i>Cancer oregonensis</i>																
	<i>Cancer productus</i>	-14.25 \pm 1.05	11.8 \pm 1.28	19	2.9%	-14.74 \pm 1.21	12.01 \pm 0.97	20	4.6%	-15.72 \pm 1.46	11.44 \pm 0.98	9	-	-14.73 \pm 1.29	11.82 \pm 1.1	48	3.8%
	<i>Pugettia productus</i>																
Sea cucumber*	<i>Apostichopus californicus</i>	-13.67 \pm 1.19	9.75 \pm 0.74	5	6.0%	-14.84 \pm 0.54	10.23 \pm 0.71	5	10.8%	-14.47 \pm 0.19	10.94 \pm 1.03	5	-	-14.33 \pm 0.87	10.3 \pm 0.93	15	8.5%
Mussel	<i>Mytilus trossulus</i>	-17.03 \pm 0.66	8.92 \pm 0.77	9	1.2%	-17.75 \pm 1.18	8.59 \pm 0.59	9	1.2%	-17.49 \pm 1.12	8.96 \pm 0.71	11	-	-17.43 \pm 1.03	8.83 \pm 0.69	29	0.4%
Snail*	<i>Tegula spp.</i>	-13.37 \pm 0.55	10.08 \pm 0.34	5	2.9%	-14.21 \pm 0.93	9.92 \pm 0.25	3	2.8%	-13.87	10.37	1	-	-13.71 \pm 0.73	10.06 \pm 0.31	9	2.7%
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	-12.49 \pm 2.15	7.64 \pm 1.6	7	1.2%	-14.15 \pm 2.05	8.52 \pm 1.49	15	1.3%	-12.46 \pm 2.05	7.46 \pm 0.46	7	-	-13.34 \pm 2.17	8.05 \pm 1.4	29	1.5%
	<i>Strongylocentrotus franciscanus</i>																

Table 1.2: Tukey's non-additivity pairwise comparisons for each season with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values separated for each site. Significant values are in bold. Shinaku Inlet spring n=14, Shinaku Inlet summer n=15, Shinaku Inlet fall n=14, Shinaku Inlet winter n=11, Sukkwon Strait spring, n=43, Sukkwon Strait summer, n=47, Sukkwon Strait fall, n=22, Sukkwon Strait winter n=20, Tonowek Narrows spring n=57, Tonowek Narrows summer n=53, Tonowek Narrows fall n=58, Tonowek Narrows winter n=67.

Site	Pairwise Season		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
			p-value	p-value
Tonowek Narrows	Spring	Summer	0.10	0.87
	Spring	Fall	0.02	<0.0001
	Spring	Winter	0.30	<0.0001
	Summer	Fall	0.95	<0.0001
	Summer	Winter	0.91	0.00
	Fall	Winter	0.60	0.78
Shinaku Inlet	Spring	Summer	0.65	0.35
	Spring	Fall	0.76	0.15
	Spring	Winter	0.26	0.15
	Summer	Fall	1.00	0.95
	Summer	Winter	0.02	0.93
	Fall	Winter	0.04	1.00
Sukkwon Strait	Spring	Summer	0.04	0.88
	Spring	Fall	0.26	1.00
	Spring	Winter	1.00	0.78
	Summer	Fall	0.99	0.94
	Summer	Winter	0.12	0.43
	Fall	Winter	0.34	0.83

Chapter 2: Sea otter diet nutrient composition with respect to recolonization, life history, and season in southern Southeast Alaska²

Abstract

The sea otter (*Enhydra lutris*) population of Southeast Alaska has been growing at a higher rate than other regions along the Pacific coast. While good for the recovery of this endangered species, rapid population growth can negatively impact commercial and subsistence fishing. Previous foraging studies throughout the sea otter range have shown that sea otters will reduce invertebrate prey biomass when recolonizing an area. The goal of this study was to examine and quantify the energetic content of sea otter diets through direct observation of foraging and collection of prey. Our study area, Prince of Wales Island in southern Southeast Alaska, exhibits a gradient of sea otter recolonization, thus providing a natural experiment to test diet change in regions with different recolonization history. Sea otter prey items were collected in three seasons (spring, summer, and winter) to measure caloric value and lipid and protein content. We observed 3,523 sea otter dives during the spring and summer months. A majority of the sea otter diet consisted of clams across all variables tested. Sea otters in newly recolonized areas had lower diet diversity, higher kcal/gram intake rates, and higher energetic intake rates. Sea otters with pups had the highest diet diversity and the lowest energetic intake rates (calories per gram consumed). Sea otter energetic intake rates were higher in the fall and winter months

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than the spring and summer months. Sea cucumber energy and lipid content appeared to correspond with times when sea otters consumed the highest proportion of sea cucumbers.

1. Introduction

The nutritional ecology of marine predators is poorly understood compared to terrestrial predators (Machovsky-Capuska et al., 2018). Classic foraging theory suggests that consumers should target prey that maximizes their net rate of energetic gain (Kleiber, 1961; Stephens & Krebs, 1986). As energetic intake was the focus, studies have focused on a consumer's overall net energetic consumption as a factor in prey selection. However, recent studies focus on predators' nutritional needs and how prey choice varies according to macronutrient composition (Machovsky-Capuska et al., 2018; Oftedal et al., 2007; Vollenweider et al., 2011). Consumers may target lower energy prey for various reasons, including reproductive status. For example, Machovsky-Capuska et al. (2018) revealed that male Australasian gannets (*Morus serrator*) consistently foraged for fish with higher protein-to-lipid ratios, whereas females foraged for fish with higher lipid-to-protein ratios. One potential explanation is the female and male parents responding to the chicks needs as they grow by changing their diets. Similarly, female sea otters (*Enhydra lutris*) will switch their foraging tactics when caring for a pup, which may represent a trade-off between maximizing potential energy return to meet pup needs (Staedler, 2011).

Sea otters are a dynamic species in which to study nutritional ecology because of their unique adaptations to the marine environment. Unlike most marine mammals, sea otters do not have blubber to keep them warm in the marine environment. Instead, sea otters maintain very high metabolisms. Various studies estimate sea otters consume anywhere from 19 to 39% of

their body weight in food per day to sustain these elevated metabolic costs (Costa, 1982; Davis, 2020). Because of their voracious appetites, sea otters can exert large effects on the nearshore marine ecosystem within relatively short periods (Estes & Palmisano, 1974). These effects are particularly evident in kelp forests, where sea otters suppress the grazers, sea urchins (*Strongylocentrotus* spp.), which in turn relieves pressure on giant kelp (*Macrocystis pyrifera*). This relief of grazing pressure helps to increase kelp forest density, which has been shown to increase juvenile fish habitat (Estes & Duggins, 1995) and increase overall species diversity in the system.

Historical records show that sea otters once inhabited nearshore ecosystems of the Pacific Ocean from Japan to Baja California. However, by the late 19th Century, there were only 11 remnant populations within their once continuous distribution due to hunting for the lucrative fur markets in Russia and China. In 1911, sea otters were protected from hunting by the International Fur Seal Treaty. By this time, sea otters were extirpated from Southeast Alaska (Jameson et al., 1982). To restore sea otters to their historical range, the Alaska Department of Fish and Game and the Atomic Energy Commission initiated a translocation program and, in the 1960s, relocated about 400 sea otters from the Aleutian Islands to six locations in Southeast Alaska (Burris & McKnight, 1973; Jameson et al., 1982). Since the translocation, sea otters have expanded their range and increased in numbers. The most recent sea otter aerial counts in 2010–2012 estimated that approximately 25,000 sea otters were present in Southeast Alaska (USFWS, 2014). The expansion of sea otters from the six translocation sites in Southeast Alaska into unoccupied habitat over time allows for a ‘space-for-time’ substitution (Pickett, 1989), in which the longer-term effects (positive, neutral, and negative) of sea otters on the nearshore ecosystem can be seen in areas of longer occupation.

Prince of Wales Island (POW), along with its neighboring islands, in southern Southeast Alaska has two original release locations. Hoyt (2015) studied sea otter diets around POW for three years (2010–2012), focusing on sea otter impacts on commercially important species. Hoyt (2015) found that the number of species consumed by sea otters increased as time since recolonization increased, and sea otters reduced the abundance of commercially important species. The sea cucumber (*Apostichopus californicus*) fishery is an example of a commercial shellfishery impacted by sea otters. Previous studies showed that sea otter presence caused a decline of sea cucumbers in all regions where sea otters were present for > 15 years (Larson et al., 2013). Many sea cucumber fishery regions have been closed due to declining survey numbers after sea otters have recolonized the regions (Hebert, 2017).

Measuring sea otter energetic intake rate is a widely used method to measure changes in diet and to assign quantitative values to sea otter nutritional needs (Tinker et al., 2008). In Alaska, the Alaska Science Center, a part of the United States Geological Survey (USGS), maintains a database on species- and size-specific energetic values for sea otter prey items. Many of these values come from California invertebrate collections and published literature (Ofstedal et al., 2007; Tinker, 2004). These values are used to create energetic models and biomass estimates for each sea otter prey species; however, using prey values from other regions could lead to inaccurate consumption estimates for sea otters in Alaska. Similarly, a comprehensive analysis of the biochemical composition of sea otter prey was conducted in varying seasons in California, but is absent for Alaskan prey (Ofstedal et al., 2007). A preliminary study in Sitka, Alaska, showed that the preferred prey of sea otters (clams) was not highest in overall caloric content or lipid content when compared to all available prey items (Cartagena, 2016). This preliminary work is a driver for further investigation of sea otter diet analysis in Southeast Alaska.

Our goal for this study was to analyze the relationship between sea otter diet and prey nutritional composition. Our objectives were to 1) examine diet composition according to prey macronutrient composition across different sea otter metrics: i) time since recolonization, ii) juvenile versus adult sea otters, iii) sea otter sex and reproductive class, and iv) season and 2) investigate the macronutrient quality of sea otter prey in southern Southeast Alaska across seasons. This work increases our understanding of sea otter prey composition according to the energy and macronutrient content in Southeast Alaska, which, in turn, gives us a better understanding of the invertebrates removed from the nearshore system due to sea otter predation, and why. This increases the potential to predict future reductions in commercial and subsistence species due to sea otter predation.

2. Methods

2.1 Visual foraging observations

We observed sea otter foraging behavior from May to August 2018 on the western side and neighboring islands of POW. Sampling was stratified by time since recolonization, based on US Fish and Wildlife Service (USFWS) aerial surveys. Three periods were denoted from the surveys; zone 1 (> 30 years present), zone 2 (< 30 years and > 15 years present), and zone 3 (< 15 years and > 7 years present) (Fig. 2.1). In each zone, a minimum of 300 foraging dives were recorded. Because zone 2 makes up a majority of POW, most foraging dives occurred in this zone.

Foraging observations were made from shore to assess sea otter diet composition. Questar telescopes (50X) were used to follow individual sea otters for one bout (up to 20 dives per sea otter). The observer recorded the following foraging metrics: prey item (to species level when possible), prey size (based on an estimated sea otter paw width of 5 cm and categorized into less than $\frac{1}{3}$ of the paw, less than $\frac{2}{3}$ of the paw, or less than the whole paw), the proportion of the prey item consumed, location, prey handling time, time spent diving, and total time spent at the surface. The following sea otter metrics were also recorded for each foraging bout: sex, reproductive status, and age class. Males were identified by the presence of a penile bulge, whereas females were identified if there was a clear lack of penile bulge, or if they had a pup. If sex was not confirmed, nor pup was observed, the sex was categorized as “unknown.” When possible, age class was determined as adult or juvenile by visual assessment of size and amount of grizzled fur (Lee et al., 2010).

We calculated the caloric intake for sea otters based on visual foraging observations using the Sea Otter Foraging Analysis (SOFA) program, which is based in Matlab (MathWorks) and maintained by the USGS Alaska Science Center in Anchorage, AK. SOFA uses a Monte Carlo-based simulation to account for unknown prey items and potential sample bias. SOFA is a Bayesian model, with estimated biomass for individual prey types across time since recolonization, age, and reproductive status and sex. All SOFA outputs are reported as means with standard deviation. The consumption rates for each prey species were assigned for each foraging bout (Tinker et al., 2008) using the estimated prey size relative to a sea otter paw width. Prey diversity for each region was calculated using the Shannon-Wiener Index (Shannon, 1948) in SOFA.

2.2 Prey sampling

Potential prey items to be collected for macronutrient and energetic analyses were selected based on existing literature on sea otter diets in Southeast Alaska (Hoyt, 2015; Weitzman, 2013). Five functional prey groups were identified that were composed of 13 target species (Appendix B.2) for analysis: crabs, clams, sea cucumbers, snails, and sea urchins. These groups made up 95% of sea otter diets (in terms of biomass) from visual foraging observations. Five individuals of each target species were collected at two sites (Fig. 2.1) in May 2018, August 2018, and February 2019. All samples were collected in the intertidal zone. Two collection sites were selected that encompassed the foraging observation sites and had reliable access. Craig (Site 1) and Soda Bay (Site 2) represented differences in sea otter occupation time (> 15 years for Craig, and > 7 years for Soda Bay). Where there were more sea otters present, there were less abundant invertebrate species for collection. Additional samples were opportunistically collected around POW if they were not present or in high enough abundance in the two designated sites (Appendix A.1). Samples were held in seawater-filled buckets, cleaned of sand and dirt, and then frozen at -18°C.

In the lab, samples were thawed, weighed, measured, and separated into edible and inedible tissues. For bivalves, decapods, gastropods, and sea urchins, all hard parts were removed and discarded, as they were considered inedible as the sea otter excretes these contents (Kenyon, 1969). For sea cucumbers, the entire organism was considered edible. Only crabs were processed separately by sex. Remaining edible tissues were weighed and homogenized in a Cuisinart Mini-prep food processor. A maximum of 4 g of tissue was dried in a LECO Thermogravimetric Analyzer 701 (TGA) dryer at 135°C, or in a gravity convection oven (VWR Symphony 414004-

552) at 70°C. Standards and duplicates were run with each dryer to confirm consistent moisture values.

2.3 Energy content nutritional analysis

We measured energetic value and proximate composition (the proportion of protein content, lipid content, moisture, and percent ash) for sea otter prey items. We used previously established methods (Fergusson et al., 2010) to measure energy density using a Parr 6725 semi-micro bomb calorimeter. Standards and replicates were used to confirm consistent calorimeter readings. Lipid content was determined using previously established methods (Fergusson et al., 2020) using a sulfo-phospho-vanillin colorimetric analysis. Protein content was estimated by multiplying total nitrogen content by 6.25, which accounts for the nitrogen content of protein (Craig et al., 1978). Nitrogen content was measured with a FlashSmart elemental analyzer coupled to a Delta-V continuous-flow isotope ratio mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA). Carbohydrate content was not assessed as it is assumed to be negligible in marine invertebrates (Ofstedal et al., 2007; Vollenweider et al., 2011). Ash content was processed at 600°C and measured with a LECO Thermogravimetric Analyzer 701 (TGA) dryer. Only samples with > 1 g of dried material were able to be combusted for percent ash content.

2.4 Statistical analysis of sea otter prey

To test our first objective (investigate the macronutrient quality of sea otter prey across seasons), we calculated the percent protein and lipid of each prey group using the energy equivalents of 9.5 kcal/g for lipid and 5.7 kcal/g for protein (Kleiber, 1961). We used PRIMER v7 (Clarke & Gorley, 2015) with a one-way analysis of similarity (ANOSIM) procedure with season as factors for each prey group, excluding crabs ($\alpha = 0.01$). Snails had too few samples to conduct pairwise seasonal comparisons. Mussels were excluded from results because they were a very small portion (< 1%) of the sea otter diet around POW. Crabs were analyzed separately with season and sex as factors, using a two-way ANOSIM ($\alpha = 0.01$).

To test our second objective (compare diet composition and prey macronutrient composition across different sea otter metrics), we calculated regional-level concentrations of macronutrient composition of sea otter diets using established methods (Ofstedal et al., 2007). In brief, first, we converted the dry mass average (kcal, lipid, and protein) for each functional prey group to a wet mass value. Second, using the proportion of diet (also in wet mass) from SOFA outputs for each functional prey group and the average prey value (kcal, lipid, and protein), we calculated an average for each prey and macronutrient and added all individual groups together. Finally, we divided this newly calculated wet mass by dry mass to get the nutrient composition of dry mass. Statistical comparison between sea otter metrics tested were not possible because we did not use known sea otters for this study and all data were used at a regional scale (Western POW and surrounding islands).

Due to weather and light limitations, it was only possible to conduct visual foraging observations during spring and summer. To estimate year-round diets, we used results from

stable isotope analysis (Chapter 1). Diets estimates were made using stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis of both sea otter vibrissae and the prey present around POW using a Bayesian model to estimate percent of total diet for functional prey groups. These diet estimates were used in the calculations for seasonal sea otter macronutrient contribution and comparison to changes in sea otter prey. All datasets are archived in a publicly accessible database with the Knowledge Network for Biocomplexity (LaRoche, Fergusson, & Pearson, 2020; LaRoche, King, & Pearson, 2020).

3. Results

3.1 Sea otter diets across Prince of Wales

Foraging records consisted of 362 foraging bouts (each bout is one sea otter). In total, 3,523 dives were recorded between May 6, 2018, and August 13, 2018. The overall success rate was 89.9%, and diet diversity (H') was 0.81. Mean dive time was 88.4 seconds (± 44.5), and mean surface time was 56.4 seconds (± 42.3). The mean energy intake rate was 7.3 ± 0.22 Kcal/min. Sea otters were observed to consume a total of 44 prey items (Appendix B.1). When prey selection was examined irrespective of habitat type or site, the dominant prey categories (making up 97.5% of the total diet by biomass) were clams ($80.9 \pm 2.21\%$), sea cucumbers ($8.5 \pm 1.13\%$), crabs ($3.8 \pm 0.44\%$), snails ($2.7 \pm 0.39\%$), and sea urchins ($1.6\% \pm 0.28\%$). Within the clam category, butter clams (*Saxidomus gigantea*) were the predominant species, comprising $36.9 \pm 1.61\%$ of the overall diet.

We observed differences in sea otter diets across recolonization zones, age group and reproductive status. Species diversity and intake rate (kcal/min) varied by recolonization zone (Table 2.1). The newest recolonization zone (> 7 years) had the lowest species diversity ($H' = 0.39$) and highest intake rate (11.06 ± 0.8 Kcal/min). The zone with sea otters for the longest period of time (> 30 years) had the highest species diversity ($H' = 1.19$) and lowest intake rate (5.7 ± 0.8 Kcal/min). Clams were the main prey consumed across all recolonization zones (Fig. 2.2A) and for both adults and juveniles (Fig. 2.2B). Intake rate varied by age group and reproductive status (Table 2.1). Juveniles had a slightly lower species diversity than adults ($H' = 0.79, 0.86$ respectively) and lower intake rate than adults ($5.8 \pm 0.6, 7.2 \pm 0.3$ Kcal/min, respectively). Although clams were the dominant prey, sea otter diets varied by reproductive status; females with pups had a more varied diet and higher Shannon-Weiner diversity index than females without pups and males (Table 2.1, Fig. 2.2C). Females with pups had the highest species diversity ($H' = 1.23$) whereas males had the lowest species diversity ($H' = 0.34$).

3.2 Macronutrient content in sea otter diets

Energetic intake (kcal/gram) and percent protein composition varied by recolonization zone, age class, and reproductive status (Figs 2.3, A–C). Energetic intake and percent lipid and protein composition varied by season (Fig. 2.3, D). For example, the fall and winter seasons varied from spring and summer seasons in overall energetic intake (fall: 4.3 Kcal/gram, winter: 4.2 Kcal/gram, spring: 3.8 Kcal/gram, and summer: 3.8 Kcal/gram). The variation in energetic intake is driven by both percent protein and percent lipid (fall: 8.0% lipid and 58.4% protein, winter: 8.1% lipid and 58.0% protein, spring: 7.4% lipid and 51.3% protein, summer: 7.5% lipid

and 51.1% protein). In contrast, Females with and without pups had variation in overall energetic content driven only by the percent protein in the diet (with pup: 3.9 Kcal/gram, 7.2% lipid, and 53.6% protein, without pup: 4.4 Kcal/gram, 7.4% lipid, and 61.2% protein).

3.3 Energetic content of sea otter prey

Overall, sea otter prey had a similar makeup of protein and lipid content; sea urchins were the only prey that was significantly different from other prey groups for lipid-to-protein ratio (Fig. 2.4). Functional prey groups varied their energy, lipid, and protein content across seasons (Table 2.2). Across all seasons, sea cucumbers exhibited lower energy than all other prey types (Fig. 2.5), and their energy and lipid varied significantly by season. Sea urchins had significant variability in lipid content across seasons. Clams exhibited a significant change in energy and lipid over seasons as well, but R values were low, which means the overall seasonal effect was low. Crabs did not vary significantly across seasons or sex. Snails did not vary significantly across seasons. Pairwise comparisons for all prey groups and seasons revealed significant differences in energy for clams and sea cucumbers (Table 2.3). Lipid varied for clams, sea cucumbers, and sea urchins, whereas protein only varied between seasons for clams. Snails were not compared across seasons due to the small sample size.

When we compared year-round energetic changes in sea otter prey with diet proportion estimates, we found consumption rates of most functional prey groups did not correlate with energy density. Clam consumption, the major diet item for sea otters in this study, did not correspond with changes in energy (Fig. 2.6, A) or lipid (Fig. 2.6, C). Based on Chapter 1 results, sea otters consumed more clams in the fall and winter months, when the energetic and lipid

contents of clams were lower than the spring season. Sea cucumber consumption, the second most abundant diet contribution, did appear to correspond with changes in energy (Fig. 2.6, B) and lipid (Fig. 2.6, D). Sea otters decreased their consumption of sea cucumber in the fall and winter months, which corresponded with declining energetic value.

4. Discussion

The main sea otter diet component regardless of location, sex, age, and season was clams. Sea otter intake rates at the POW regional level were comparable to studies of sea otters in California and British Columbia at or near carrying capacity (Oftedal et al., 2007; Rechsteiner et al., 2019; Tinker et al., 2008), showing that locations around POW may be reaching carrying capacity. There were differences in the proportion of diet and prey composition according to time since recolonization, reproductive status, and season, but no differences observed between age classes.

4.1 Time since recolonization

Time since recolonization affects the prey composition of sea otter diets. Although clams comprise the majority of the diet in all regions of POW, there were differences in prey items across recolonization zones. The areas of POW that have been colonized for the least amount of time (zone 3, colonized for > 7 years) had the lowest species diversity in prey and highest energy recovery rates. In this zone, clams were overwhelmingly present in the diets of sea otters. This was similar to previous studies in mixed sediment communities in Southeast Alaska, where sea

otters focus on fewer, high-quality prey species (e.g., sea urchins in rocky habitats, and large clams in soft-sediment habitats) in newly occupied areas, and eventually diversify prey species as sea otter populations persist (Hoyt, 2015; Weitzman, 2013). Lipid content in sea otter diets was consistent across recolonization zones, but overall energy rate gain was slightly higher in zone 3, which may be due to the ability to obtain larger prey in newly colonized areas. Foraging records for the areas where sea otters had been present the longest (zone 1, colonized for > 30 years) had an intake rate that was comparable to previous studies where sea otters were at carrying capacity (Rechsteiner et al., 2019; Tinker et al., 2008). This shows that the sea otters in this recolonization zone of POW are likely at or near carrying capacity, which is in line with modeling from aerial survey data from the region (Tinker, Gill, et al., 2019).

When considering sea otter diets and how sea otter invertebrate removal can affect the nearshore system, it is important to look at diet variation across recolonization zones as diets in the newly colonized areas were less diverse, which is similar to past studies in Alaska (Hoyt, 2015). In rocky habitats of Southeast Alaska and British Columbia, sea otters in newly colonized regions consumed a majority of red sea urchins (Hoyt, 2015; Rechsteiner et al., 2019). In the present study, the areas we observed where sea otters are newly colonizing were soft-sediment habitat ripe with large butter clams, which were the overwhelmingly predominant prey item.

4.2 Reproductive status

Female sea otters with pups had a more varied diet composition than females without pups and males. The difference in the diet was the largest shift among all tested metrics. Females with pups ate a higher proportion of crabs, sea cucumbers, and sea urchins than sea otters

without pups. Sea cucumbers are the functional prey group with the lowest energetic content, therefore females with pups are obtaining less calories per gram of food consumed. This is likely due to females with pups opting for a risk-averse strategy, instead of searching for the highest quality prey and risking no success at all. One possibility could be that a female with a pup would rather come up with prey every dive instead of risking no success for a higher effort prey (such as choosing a slow-moving sea cucumber laying the ocean floor, instead of digging for a clam). Success rates were high across the POW region, but females with pups had the highest success rate (90% success). Other studies have reported females to vary their diet according to reproductive state. In California, tagged female sea otters switched their foraging strategies and prey types consumed when they had no pup, small pups, and large pups (Staedler, 2011).

There were other sex-specific differences in prey type. Males were observed to eat more snails than females, and females with pups were never observed to eat snails. In previous studies, snail specialists have been linked to poor overall body condition and higher death rates due to disease (Tinker, Tomoleoni, et al., 2019). Because we did not follow individuals in this study, we were unable to determine if there was a similar pattern in Southeast Alaska sea otters. In addition, although the prevalence of geoduck clams (*Panopea generosa*) in diets was low in our study (only seven observations of geoduck clams consumed throughout the region), these were only consumed by males. Geoduck clams are higher risk prey because of the increased effort needed to excavate them, thus, sea otters generally make several dives to recover one geoduck clam (Kvitek et al., 1993). We did not observe sea otters foraging for geoduck clams in the most recently colonized zones, which matches previous studies in the same region (Hoyt, 2015). These areas may have larger clams that reside in shallower areas (e.g., butter clams) creating a more efficient risk-reward ratio. Dietary differences between males and females are worth noting, as

males are more likely to expand into new regions first (Garshelis & Garshelis, 1984; Lafferty & Tinker, 2014). As new regions are being recolonized, knowing the diet preferences of males can help to predict invertebrate predation with relation to species that are of interest to humans.

Lipid content and energetic gain per gram were lowest for females with pups. There were no significant differences in dive or surface times for females with pups vs. other age/sex classes, which could be an artifact of eating less calorically-rich prey. However, females with pups have the highest foraging success rate when compared to females without pups and males, which could indicate that females with pups select less energy-rich prey items over the risk of no success. Previous studies of sea otter energetics showed that female sea otters with large pups operate at an energetic deficit by the time a pup reaches weaning age (Chinn et al., 2016; Thometz et al., 2016). In the present study, this deficit may be evidenced by the lower energetic gain per gram for females with pups. However, there are a multitude of other risks females with pups must contend with while foraging. In areas where food is limited, females with large pups may reach a maximum physical amount of time allowable for foraging (Tinker, Tomoleoni, et al., 2019). They also encounter constraints with respect to allocating energy to nursing vs. providing prey to their pup (Thometz et al., 2014).

4.3 Seasonal diet shifts

Sea otters consume prey with higher percent lipid in the fall and winter months. This change in nutrient composition could be to compensate for colder temperatures in winter months and the need to obtain more calories to metabolize for warmth. Average sea surface temperatures (SST) for nearby Ketchikan range from a low of 6°C in the winter to a high of 14°C in the

summer (“NCEI Coastal Water Temperature Guide - Alaska Coast Table”). Currently, to our knowledge, there are no published studies that test the density and characteristics of sea otter fur across seasons, so it is unknown if the fur is thicker and can add additional warmth in the winter months. Sea otters may need to increase the consumption of lipids to assist in thermoregulation. The low end of the water temperature range in which a sea otter can remain in a thermoneutral zone (i.e., a physiological state whereby the animal maintains its normal core body temperature without metabolic heat production or active cooling) is about 15°C (Davis, 2020; Murray, 2015). This temperature is slightly above the typical summer SST on POW, meaning that at temperatures below this critical level, sea otters must consume more energy to generate additional heat. Previous studies have shown that sea otters adjust their foraging patterns to environmental conditions (Esslinger et al., 2014), which could affect diet composition.

Based on sea otter diet estimates from Chapter 1, clam consumption in spring and summer was lower than fall and winter. This change, which does not correlate with seasonal changes in energy or lipid content, could be due to paralytic shellfish poisoning (PSP). PSP is a toxin in algae that blooms in the spring and summer months along the Pacific coast (Kvitek et al., 1991). Studies have shown that sea otters will still eat bivalves that have PSP toxins present, but will avoid bivalves with very high amounts, as well as only consuming the foot and discarding the siphon, which usually has the highest concentration of PSP (Kvitek et al., 1991).

Sea otter consumption of sea cucumbers across seasons positively corresponded with sea cucumber total energy and lipid content. Sea cucumbers are broadcast spawners. They move into shallow waters in the late spring to begin spawning in the summer months (Cameron & Fankboner, 1989). During the fall and winter months, they retreat to deeper water. Their highest percent lipid and caloric content were in the summer when they are preparing to spawn.

Estimates from stable isotope analyses show the highest diet proportion in the summer, with spring slightly lower, and a drastic drop in the fall and winter months. This correlates with sea cucumber life history. The visual foraging observations show higher consumption in the summer than the spring. This correlation can be due to increased caloric content. Additionally, their shallow-water summer habitat makes them more easily obtainable for sea otters. At other times of the year, sea cucumbers inhabit depths up to 250 m, which is outside of a sea otter's diving ability (Cameron & Fankboner, 1989; Costa & Kooyman, 1982).

4.4 Future Work

It is important for managers to consider the whole ecosystem and not only focus on each single species individually. Because sea otters are removing biomass similar to a fishery, their impact on invertebrate prey should be considered in management strategies. It is also important to incorporate how sea otters prioritize and change their diets, for example, this study showed that sea otters increase their sea cucumber consumption in the summer months. Currently, there is a lack of invertebrate surveys to assess current population levels. Dungeness crabs, butter clams, or other substance bivalves like cockles are not surveyed. Creating a complete ecosystem level management for the Alaska nearshore system with subsistence foods surveyed would account for the needs people both local and commercial fishing, as well as the health of the ecosystem.

Within our study area only three aerial surveys were conducted over a 30-year period to estimate the sea otter abundance and geographic range (USFWS 2014). More fine scale outcomes of sea otter diet changes were not possible because of the long gaps in population data. More frequent range-wide surveys are needed to better understand the population size and

distribution. The current Southeast Alaska population movements and growth rates are currently estimated on surveys that were conducted a decade ago (Tinker, Gill, et al., 2019; USFWS, 2014).

Conclusions

Sea otters can be used as a looking glass into the overall ecosystem because of their foraging habits. Sea otters sample benthic invertebrates at a higher rate and with better skill than people can attain with SCUBA surveys (Oftedal et al., 2007; Riedman & Estes, 1990). This study provides quantitative data that can inform an ecosystem-based management approach that also considers local subsistence harvest needs and stakeholder input. However, for a more comprehensive understanding of the sea otter population in Southeast Alaska, abundance surveys of both sea otters and invertebrates need to be conducted more frequently. If used in conjunction with more comprehensive abundance surveys, the quantitative results presented here regarding sex and location-specific diet composition can be used to predict current and future sea otter ecosystem effects, thus informing co-management plans for this apex predator in addition to commercially-important and subsistence foods.

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Figures

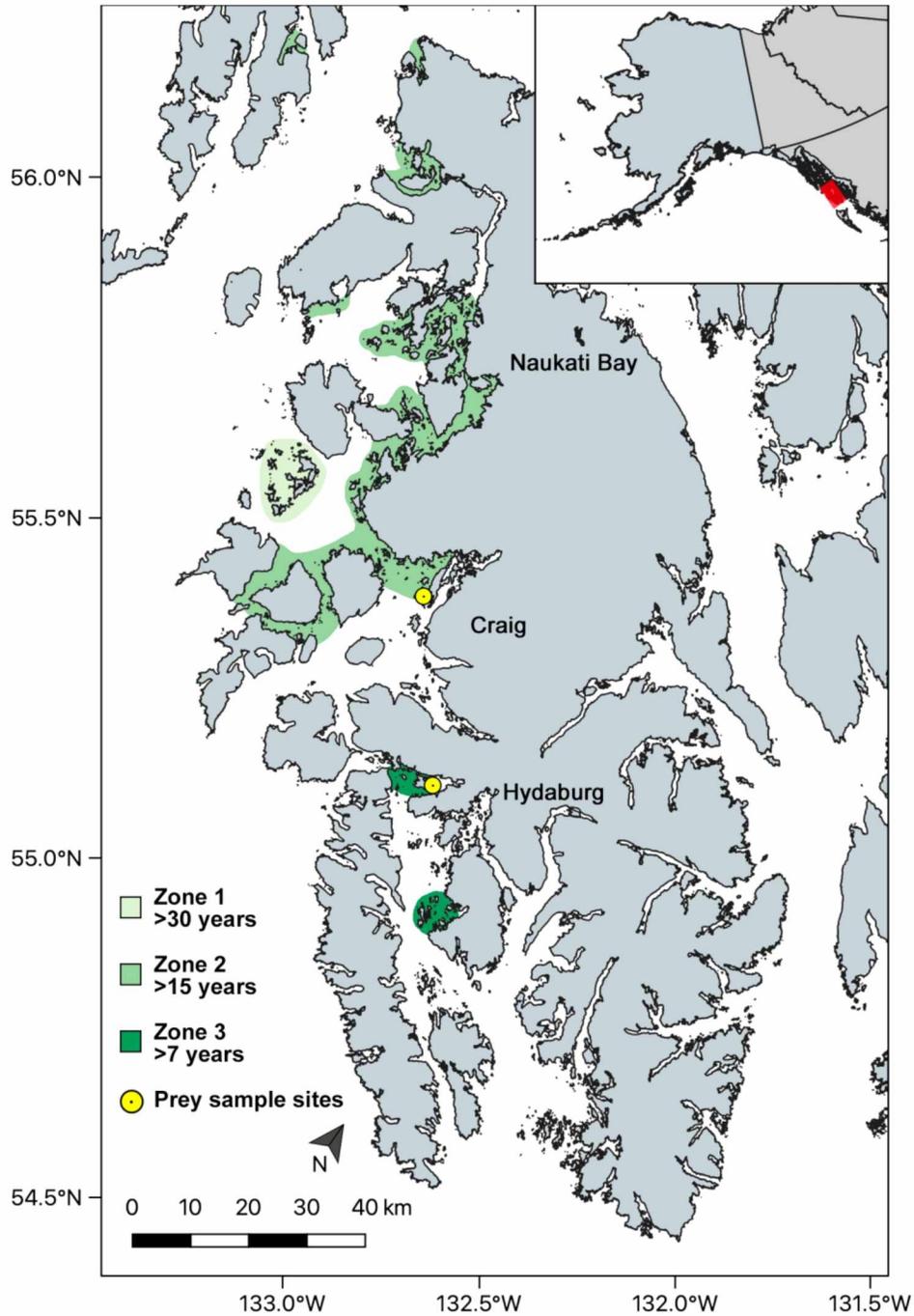


Figure 2.1: Sea otter visual foraging observations were made within three foraging zones (shaded areas with zone numbers listed) on Prince of Wales Island in southern Southeast Alaska. Each zone was designated by time-since-recolonization based on US Fish and Wildlife Service aerial surveys.

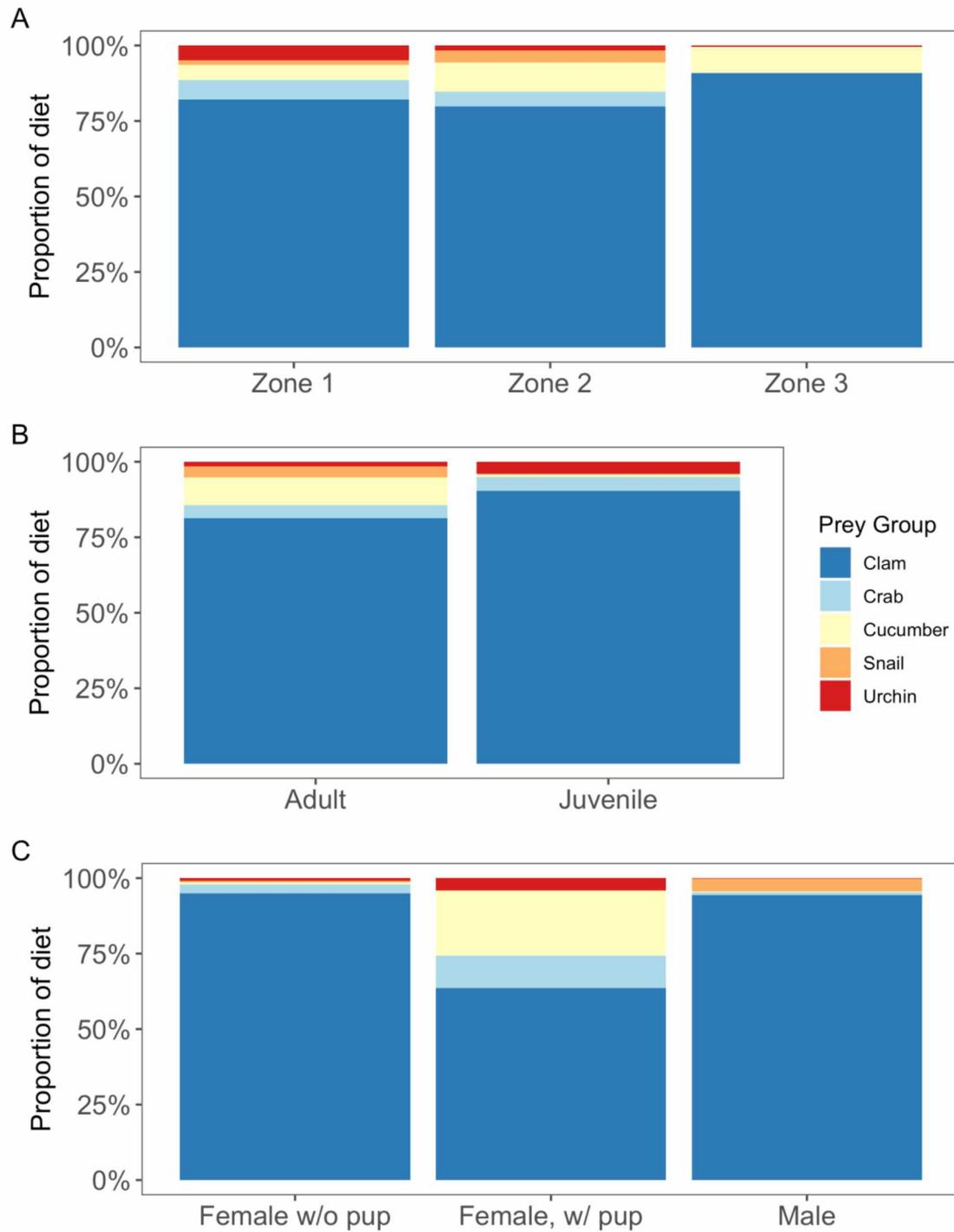


Figure 2.2: Proportion of diet from biomass estimates for time-since-recolonization zones (A), sea otter age class (B), and sea otter reproductive status/sex (C). Zones are based on US Fish and Wildlife Service aerial surveys. Zone 1 is the area occupied for > 30 years, Zone 2 is the area occupied >15 years, and Zone 3 is the area occupied >7 years.

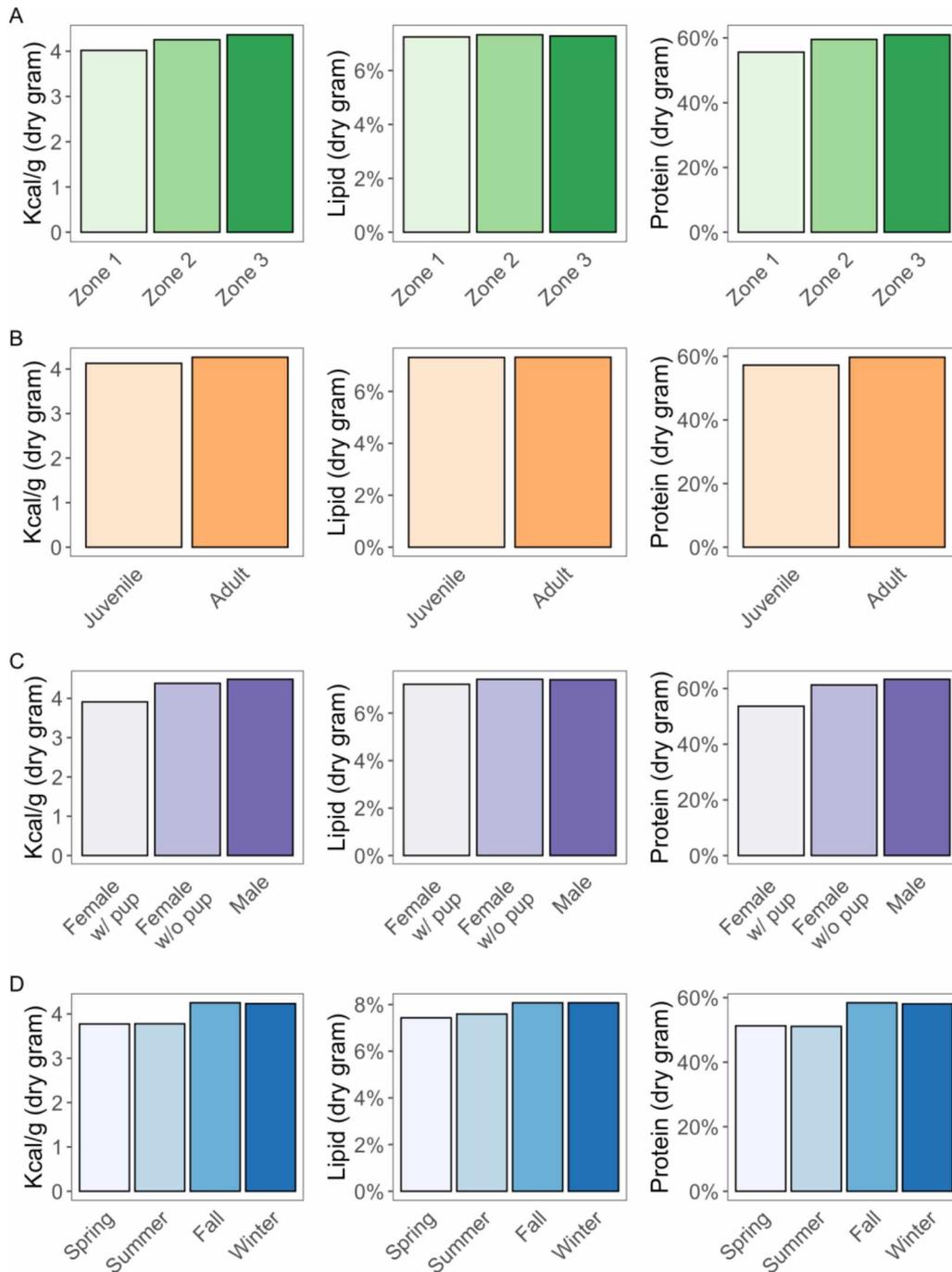


Figure 2.3: Comparison of the energy, lipid, and protein concentrations in population-level diets for time-since-recolonization zone (A), sea otter age class (B), sea otter reproductive status/sex (C), and season (D). All calculations are made from the wet mass (as a sea otter would eat the item) and converted to dry mass for comparison. Zones are based on US Fish and Wildlife Service aerial surveys. Zone 1 is the area occupied for > 30 years, Zone 2 is the area occupied >15 years, and Zone 3 is the area occupied >7 years.

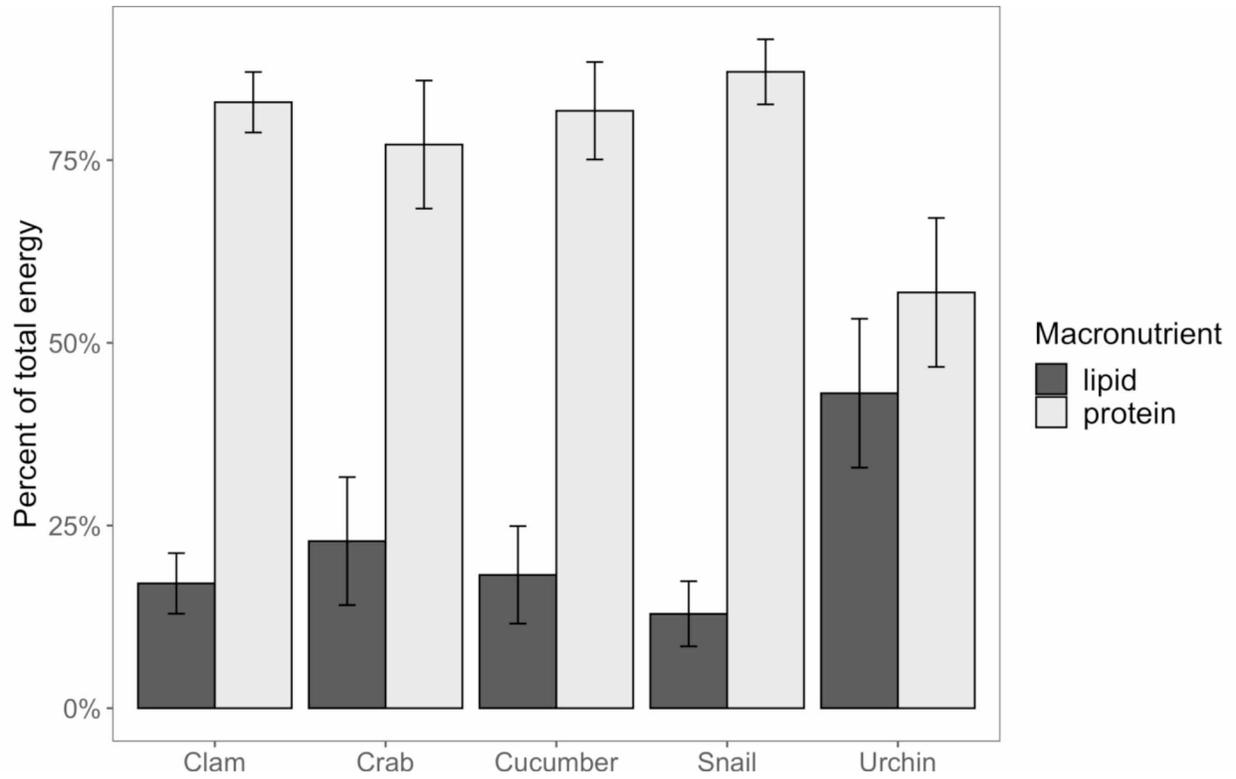


Figure 2.4: Proportion of energy in each functional prey group of sea otters derived from lipid and protein.

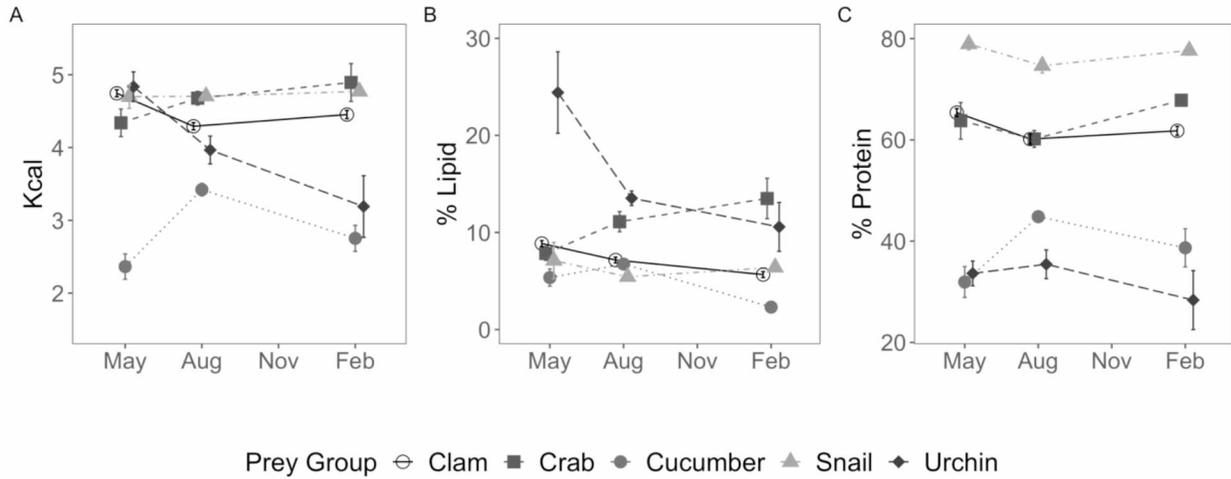


Figure 2.5: Seasonal whole-body nutrition of functional prey groups of sea otters in dry mass. Panel A depicts the energy content in kilocalories per dry gram (\pm one standard error), panel B depicts the lipid content in dry gram (\pm one standard error), and panel C depicts the protein content in dry grams (\pm one standard error).

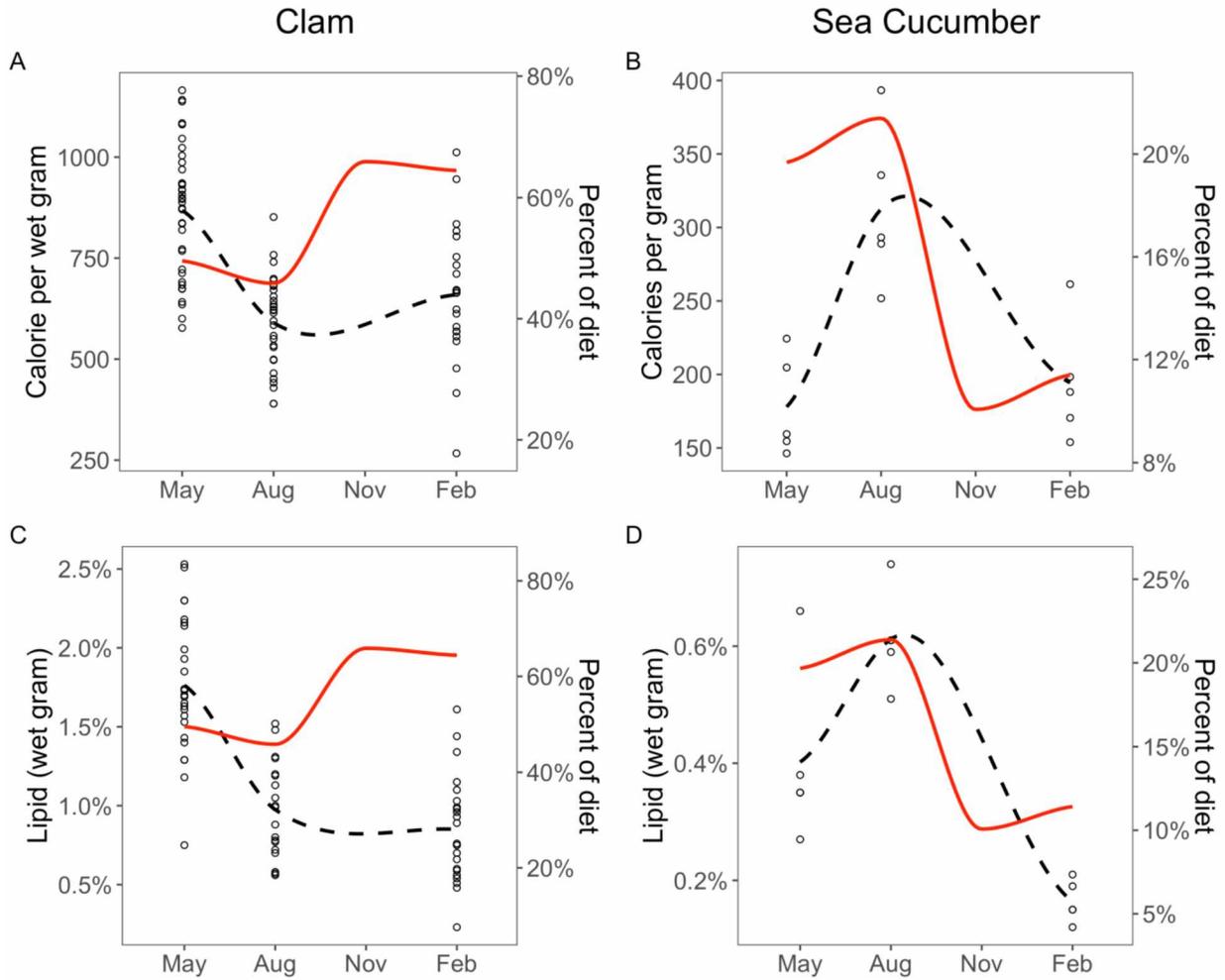


Figure 2.6: Seasonal variation in the nutrition of sea otter prey (A and C are clams, and B and D are sea cucumbers. Circles are individual samples and dotted lines are the mean, with percent on the left axes) and frequency of occurrence of that prey species in the diet (red solid lines, with percent on the right axes) from Chapter 1. A and B are energy density (calorie per gram of edible wet mass), and C and D are lipid content (percent per gram of edible wet mass).

Tables

Table 2.1: Sea otter intake rates (in kilocalorie per minute of foraging), species diversity (H' , Shannon Weiner Index), and dive statistics by recolonization zone, age class, and reproductive status/sex.

	n (bouts)	n (dives)	Kcal/min intake rate (sd)	H'	Mean Dive Time (sd)	Mean Surface Time (sd)	Success Rate
Recolonization zones (years occupied)							
Zone 1 (> 30 years)	34	305	5.7 (0.8)	1.19	104.6 (46.2)	58.4 (39.7)	90.2%
Zone 2 (> 15 years)	270	2864	7.0 (0.4)	0.90	83.7 (43.6)	52.2 (40.0)	89.6%
Zone 3 (> 7 years)	58	354	11.6 (0.8)	0.39	101.9 (41.6)	85.2 (50.6)	90.9%
Age class							
Adult	230	2481	7.2 (0.3)	0.86	86.4 (43.7)	56.0 (41.8)	90.0%
Juvenile	30	310	5.8 (0.6)	0.78	83.5 (43.5)	56.9 (43.6)	87.8%
Reproductive status/ sex							
Female no pup	37	484	7.0 (0.7)	0.44	84.1 (43.3)	50.7 (35.6)	90.1%
Female with pup	75	849	6.0 (0.4)	1.23	80.9 (45.3)	53.3 (38.9)	93.0%
Male	69	821	7.1 (0.5)	0.34	87.4 (40.7)	58.9 (45.4)	85.7%

Table 2.2: Statistical comparison of sea otter prey groups with (A) season and (B) sex (for crabs only) as factors using analysis of similarity (ANOSIM). The R statistic ranges from near 0 (no difference between groups) and 1 (differences between groups) with bold numbers denoting significance ($p < 0.01$).

A. Season

Functional Prey Group	Energy R statistic	Lipid R statistic	Protein R statistic
Clam	0.300	0.213	0.058
Crab	0.077	0.024	0.133
Sea Cucumber	0.472	0.778	0.267
Sea Urchin	0.172	0.404	0.067
Snail	-0.157	-0.158	0.096

B. Sex

Functional Prey Group	Energy R statistic	Lipid R statistic	Protein R statistic
Crab	0.057	0.065	0.181

Table 2.3: Statistical pairwise comparisons of sea otter prey groups with season and sex (for crabs only) using analysis of similarity (ANOSIM). The R statistic ranges from near 0 (no difference between groups) and 1 (differences between groups) with bold numbers denoting significance ($p < 0.01$).

Functional Prey Group	Season		Energy R statistic	Lipid R statistic	Protein R statistic
Clam	Spring	Summer	0.470	0.082	0.125
	Spring	Winter	0.228	0.397	0.034
	Summer	Winter	0.117	0.117	-0.018
Crab	Spring	Summer	0.021	0.069	0.155
	Spring	Winter	0.073	-0.102	-0.039
	Summer	Winter	0.150	-0.151	0.070
Sea Cucumber	Spring	Summer	0.824	0.536	0.624
	Spring	Winter	0.068	0.672	0.016
	Summer	Winter	0.472	1.000	0.156
Sea Urchin	Spring	Summer	0.133	0.426	-0.089
	Spring	Winter	0.380	0.270	0.052
	Summer	Winter	0.140	0.410	0.205

General Conclusion

The sea otter population in Southeast Alaska has recovered at rates high above sea otter populations in other regions. While this is a success for a recovering endangered species, commercial and subsistence fishers see this as a threat. Understanding what sea otters are eating, and documenting potential diet changes, it is vital to understand this keystone species better. The goal of this study was to quantify the diets of sea otters around Prince of Wales Island (POW) building upon prior studies (Kvitek et al. 1993, Larson et al. 2013, Hoyt 2015) to produce diet estimates for all seasons, which has not yet been done, and to compare the macronutrients of their diets to understand better what sea otters need.

In chapter 1, I used stable isotope chemistry to estimate sea otter diets throughout the year. Using vibrissae from legally harvested sea otters, I was able to estimate year-round diets of sea otters by using serial samples along the vibrissa. Samples closer to the muzzle are more recent, whereas samples near the tip of the vibrissa are older. Previous studies on sea otters estimated growth rates of vibrissae at 7.7 cm per year (Tyrrell et al. 2013). We were able to obtain vibrissae from three different harvest locations, allowing for analysis of seasonal and locational variations. We found that a majority of the sea otter diet, regardless of season or location, is clams, but the supplementary diet items varied. Sea otters eat the highest proportion of clams in the fall and winter months. Shinaku inlet had the highest variation in diet estimates, which is likely due to a low sample size and one sea otter with a considerable variation of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across the length of the vibrissa. Using stable isotopes, we were able to assess sea otter individuality. Correlation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values over the length of the vibrissa varied from significantly highly correlated (both positive and negative) to no correlation. These

findings are similar to other studies with serial samples (Cardona et al. 2017, Chilvers 2019), but unlike most studies, I also saw both positive and negative correlation. A significant negative correlation is not often observed and could be an important focus of future studies with sea otter vibrissae to determine if the negative correlation can be a pattern that shows movement of sea otters seasonally. A range of significant correlations, both positive and negative, in one population of sea otters is a sign that individuals that have behavioral distinctions from one another.

In chapter 2, I analyzed sea otter diets according to the macronutrient content of their prey. Sea otter prey, except sea urchins, was low in lipid and high in protein. Previous studies show sea otters are not protein-limited in their diets (Ofstedal et al. 2007, Monson & Bowen 2015). Sea otter diets across sites, seasons, and life history traits consisted mostly of clams, so the variation of macronutrient makeup was not apparent in all metrics. The most noticeable change in caloric gain per gram consumed was across seasons. Sea otters consumed more calories per gram in the fall and winter months. This increase in calories likely is due to increased metabolic needs during the cold winter months. Winter sea surface temperatures drop below a sea otter's thermoneutral zone, requiring sea otters to obtain additional energy to generate heat (Davis 2020; Murray 2015). Female reproductive status is another metric that had varying caloric rates. Females with pups had more diversity in their diets, lower calories per gram, and lower lipid content in their prey. These variations could be due to altered needs while nursing or pregnant, or reduced abilities to forage for high-quality prey. Another finding arose from the seasonal prey variations of sea cucumbers. Sea cucumbers double their energy content and increase their lipid content in the summer months. Sea otter consumption of sea cucumbers increases in the summer months. This increase in sea cucumber predation is likely due to the rise

in caloric content. Sea cucumbers also come to shallower waters during summer months, making them more available to sea otters. These results could assist sea cucumber fishery managers in models of sea cucumber decline due to sea otter predation.

As sea otters recolonize Southeast Alaska, their voracious predation on commercially important and local subsistence invertebrates will continue to increase resource competition with commercially important and local subsistence invertebrates. Sea otter populations at regional scales fluctuate with hunting pressure (Raymond et al. 2019). As populations fluctuate, resource competition has the potential to be lessened in hunted regions. This regional variation is important for management as all regions in the Southeast Alaska population may not have uniform effects. The management of such a species is not a simple endeavor, as resource competition between a federally protected marine mammal and commercially important species brings many issues (USFWS 2012). Local indigenous tribes have managed sea otter and subsistence foods for thousands of years (Lee et al. 2019). This study offers a suite of quantitative data for local management as well as state and federal management agencies. Continued diet studies on sea otters in Southeast Alaska can increase the understanding of individual behavioral patterns in diet choice, as well as continue to follow sea otter diet variations as populations near carrying capacity and expand into varied habitat types.

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Appendix

Appendix A: Supplemental Tables for Chapter 1

Appendix A.1: Number of potential sea otter prey collected throughout three seasons (Spring 2018, Summer 2018, Winter 2019) at each site (Craig and Soda Bay). Supplemental items collected opportunistically at listed locations with a rocky and soft sediment habitat for each location. *Sites nearby Soda Bay used for supplemental collections

Common name	Scientific name	Season	Craig		Soda Bay				Additional Sites		
			Wadleigh Is <i>N 55.5315,</i> <i>W 133.1470</i>	Alberto Is <i>N 55.5372,</i> <i>W 133.1822</i>	Soft sediment <i>N 55.2680,</i> <i>W 133.0026</i>	Rocky <i>N 55.2490,</i> <i>W 133.0199</i>	North Pass* <i>N 55.2294,</i> <i>W 132.9322</i>	South Pass* <i>N 55.1902,</i> <i>W 132.8530</i>	Nossuk Bay <i>N 55.7284,</i> <i>W 133.3755</i>	Maurelle Is <i>N 55.6646,</i> <i>W 133.7236</i>	Kaguk Cove <i>N 55.7391,</i> <i>W 133.2993</i>
Sea cucumber	<i>Apostichopus oalyformicus</i>	Spring			2	3					
		Summer				5					
		Winter			1	4					
Dungeness crab	<i>Metacarcinus magister</i>	Spring					5				
		Summer	3				3				2
		Winter	4		3						
Graceful rock crab	<i>Cancer oregonensis</i>	Spring		2							
		Summer		2							
Red rock crab	<i>Cancer productus</i>	Spring					5				
		Summer	1	1			2				
Leafy Hornmouth	<i>Ceratosoma foliatum</i>	Spring		5		2					
		Summer		1		2					
Nuttall's cockle	<i>Clinocardium nuttalli</i>	Spring	5							4	
		Summer	5								
Mottled sea star	<i>Evasterias troschelii</i>	Spring		1							
		Summer					2				
Dire whelk	<i>Lirabuccinum dirum</i>	Spring									
		Summer		2							
Puppet margarite snail	<i>Margarites pupillus</i>	Spring									
		Summer		3		3					
Bay mussel	<i>Mytilus trossulus</i>	Spring	3	3	2	1					
		Summer	3			3	3				
		Winter	3	3	3	3					
Dog wrinkle	<i>Nucella lima</i>	Spring	5		1						
		Summer	6						2		
		Winter		3							
Ochre sea star	<i>Pisaster ochraceus</i>	Spring		3							
		Summer					9				
		Winter		3							
Green falsejingle	<i>Pododesmus macrochisma</i>	Spring									
		Summer				1					
Littleneck clam	<i>Leukoma staminea</i>	Spring	5		5					4	
		Summer	5				5				
		Winter	5		4						
Kelp crab	<i>Pugettia productus</i>	Spring		2							
		Summer		3							
Butter clam	<i>Saxidomus gigantea</i>	Spring	5		5					1	
		Summer	5				5				
		Winter	5		5						
Green sea urchin	<i>Strongylocentrotus droebachiensis</i>	Spring		2			4				
		Summer		4			5				
		Winter					3				
Red sea urchin	<i>Strongylocentrotus franciscanus</i>	Spring								2	
		Summer		1			5				
Helmet crab	<i>Telmessus cheiragonus</i>	Spring									
		Summer		2		1				5	
Turban snail	<i>Tegula spp.</i>	Spring		5							
		Summer		3							
		Winter		1							

Appendix A.2: Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for 45 sea otter vibrissae, the mean and standard deviation for each individual sea otter, number of subsections (n), and Pearson's correlation (r) between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ per otter.

Otter ID	Harvest Location	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		n	Pearson's correlation	
		mean	sd	mean	sd		r	p
280	Tonowek	-13.65	0.29	12.40	0.46	14	0.82	<0.001
281	Tonowek	-13.63	0.21	13.52	0.68	9	0.44	0.239
284	Tonowek	-13.40	0.37	12.59	0.43	12	0.48	0.114
285	Tonowek	-13.18	0.29	12.77	0.63	11	0.77	0.006
286	Tonowek	-13.45	0.29	12.68	0.39	10	0.77	0.009
287	Tonowek	-12.84	0.51	13.02	0.54	9	0.97	<0.001
297	Tonowek	-13.06	0.63	13.08	0.77	10	0.87	0.001
298	Tonowek	-13.93	0.37	12.18	0.46	12	0.58	0.048
299	Tonowek	-13.11	0.33	13.09	0.63	10	0.40	0.253
300	Tonowek	-13.80	0.53	12.57	0.49	9	0.90	0.001
478	Tonowek	-13.13	0.66	12.23	0.34	8	0.80	0.016
479	Tonowek	-13.00	0.38	12.98	0.53	9	0.93	<0.001
480	Tonowek	-13.95	0.60	12.61	0.28	9	0.53	0.144
520	Shinaku	-12.92	0.23	13.29	0.40	12	-0.36	0.244
521	Shinaku	-14.03	1.35	12.43	0.83	12	0.78	0.003
522	Shinaku	-13.16	0.33	13.61	0.36	11	0.15	0.659
523	Shinaku	-13.06	0.46	13.67	0.44	10	-0.47	0.167
524	Shinaku	-12.79	0.37	14.20	0.39	9	-0.56	0.118
525	Tonowek	-12.46	0.68	12.29	0.16	11	-0.54	0.085
526	Tonowek	-13.08	0.43	12.65	0.32	10	0.02	0.963
527	Tonowek	-12.92	0.34	13.02	0.37	9	0.88	0.002
528	Tonowek	-13.17	0.16	12.92	0.44	10	0.59	0.071
529	Tonowek	-15.54	0.83	12.21	0.20	8	0.85	0.007
530	Tonowek	-13.43	0.53	12.80	0.60	9	0.92	<0.001
531	Tonowek	-13.92	0.22	12.78	0.26	8	0.24	0.564
533	Tonowek	-13.80	0.34	12.15	0.25	8	0.86	0.007
534	Tonowek	-14.66	1.19	12.84	0.38	9	0.09	0.813
535	Tonowek	-13.19	0.28	13.00	0.50	10	0.45	0.190
536	Tonowek	-14.12	0.51	12.37	0.42	11	0.28	0.409
751	Sukkwan	-13.60	0.36	13.00	0.13	10	-0.43	0.211
752	Sukkwan	-12.94	0.47	13.21	0.30	8	-0.77	0.025
754	Sukkwan	-13.44	0.20	12.88	0.33	8	0.22	0.593
755	Sukkwan	-13.20	0.21	12.80	0.32	8	-0.66	0.074
757	Sukkwan	-13.47	0.14	12.77	0.23	6	-0.10	0.854
758	Sukkwan	-13.59	0.20	12.52	0.52	8	0.74	0.034
760	Sukkwan	-13.66	0.29	13.48	0.20	8	0.66	0.077
762	Sukkwan	-13.35	0.18	13.17	0.22	10	0.60	0.068
763	Sukkwan	-13.10	0.40	12.68	0.10	9	0.03	0.937
765	Sukkwan	-13.17	0.34	12.78	0.26	11	-0.74	0.009
766	Sukkwan	-14.44	0.99	12.78	0.56	10	0.87	0.001
767	Sukkwan	-12.91	0.28	12.74	0.23	8	-0.09	0.831
768	Sukkwan	-13.18	0.35	12.51	0.42	10	-0.45	0.189
769	Sukkwan	-13.45	0.43	13.21	0.05	5	0.14	0.827
771	Sukkwan	-13.15	0.32	12.92	0.57	6	0.50	0.316
772	Sukkwan	-12.66	0.62	12.56	0.50	7	0.82	0.025

Appendix A.3: Site and seasonal variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ prey sources

Invertebrate variability across sites was a limiting factor in acquiring all potential sea otter prey types. Because we were unable to collect all species at both sites, we combined the two sites for analysis. Filter feeders, including clams and mussels, had consistent changes in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between sites, but this consistency was not seen across all functional prey groups (Figure D1) therefore a correction between sites based on the shift observed in mussels was not appropriate. To confirm that the results of the mixing model would not vary significantly by combining prey across seasons, we ran an analysis to test the response of the model results to seasonal variation in the existing sea otter vibrissa data (Figure D2).

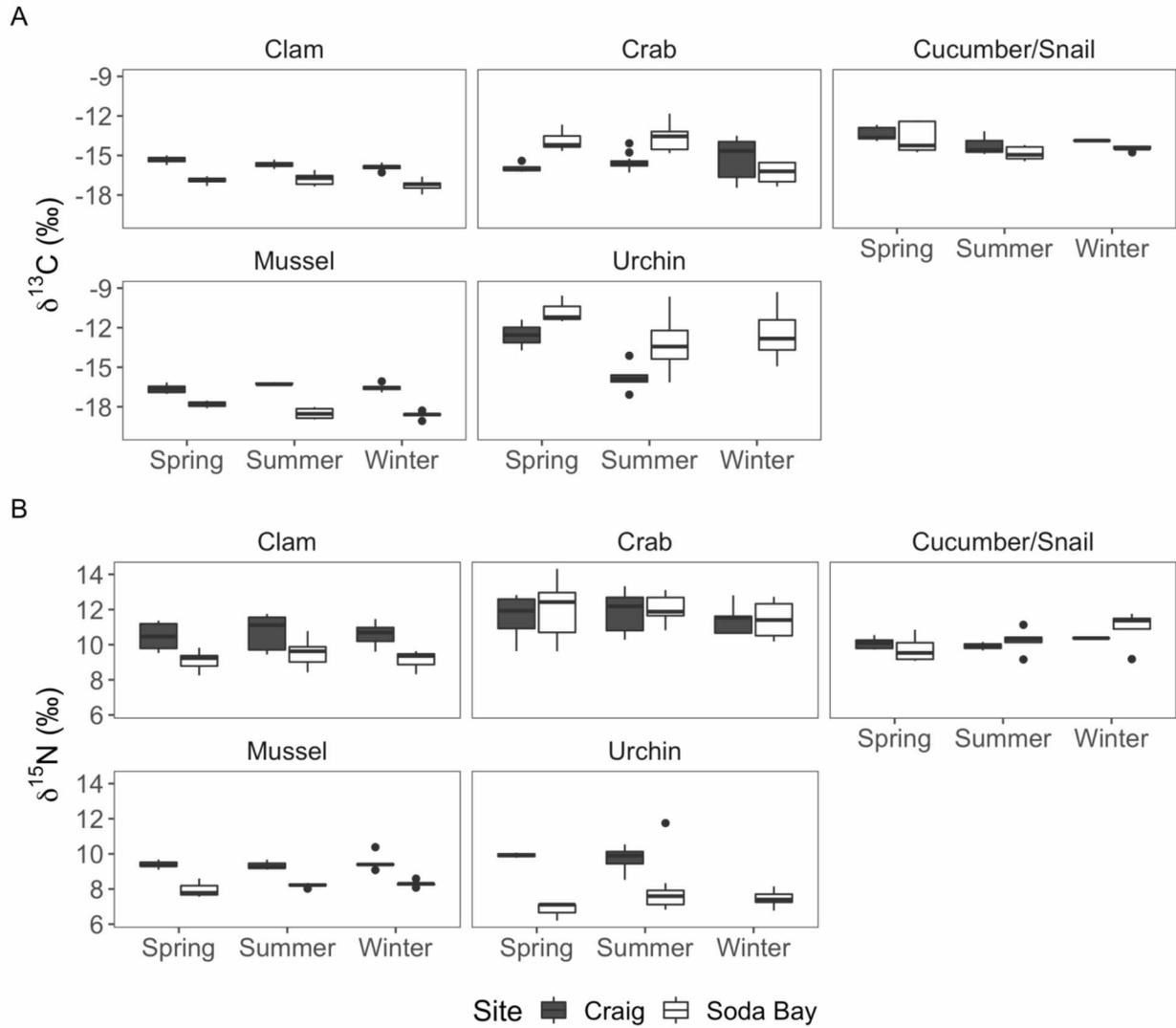


Figure A1: Sea otter prey stable isotope ratios $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) by site and season for each functional group. Boxes denote upper and lower quantiles with a mean horizontal line and 95% credible interval. No sea urchins were collected in Craig during winter.

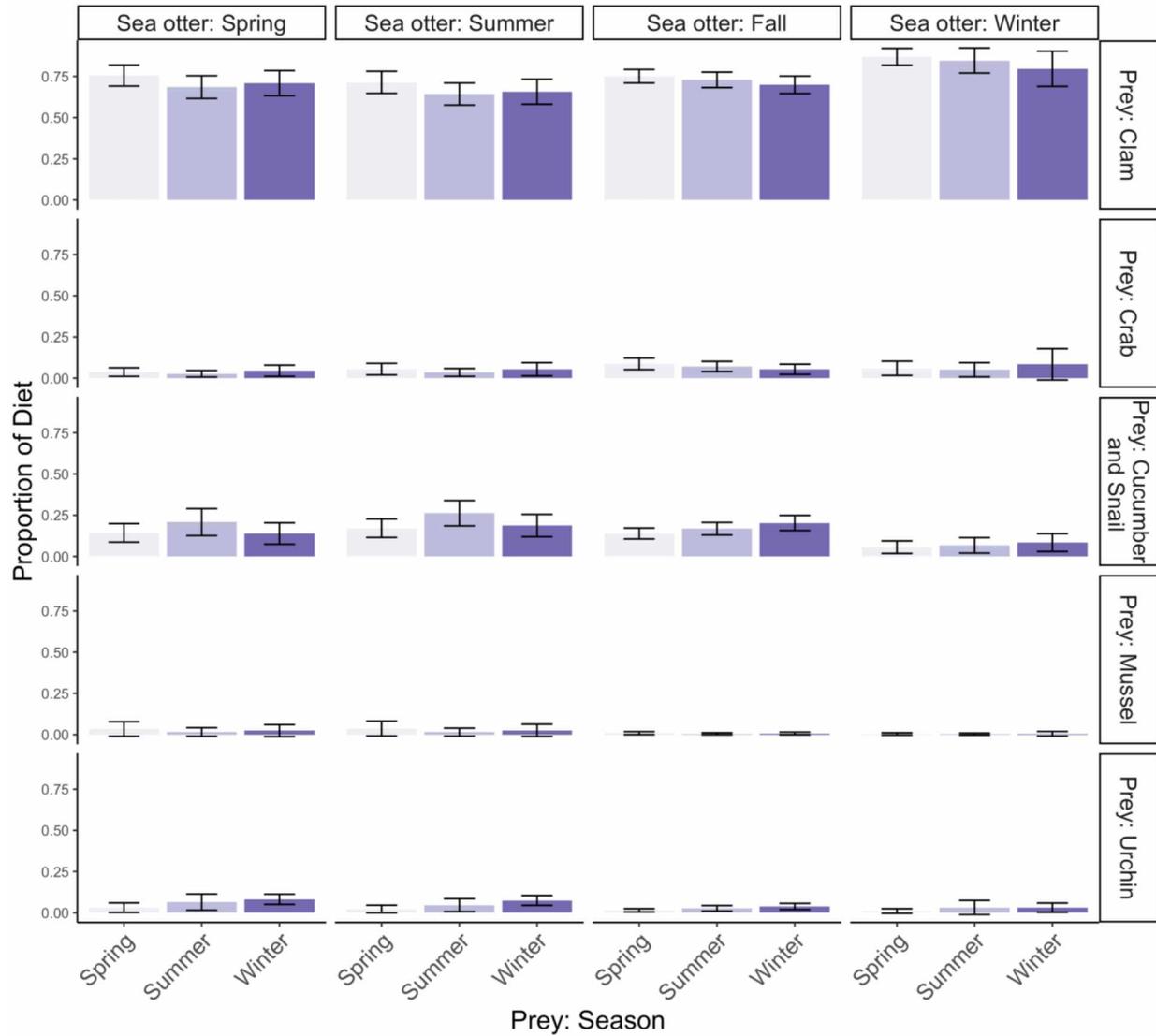


Figure A2: Mean and standard deviation proportion of sea otter diet by season for the five functional prey groups from an informed mixing model. Colors represent the season prey isotopic samples were collected. Each model was run with only isotope values from one season. There is no significant variation for each prey group according to season, which indicates that variation in seasonal effects of prey isotope signatures does not change the mixing model output.

Appendix B: Supplemental Tables for Chapter 2

Appendix B.1: Sea otter prey recorded in visual observations with estimated proportion of diet and standard deviation based on biomass.

Phylum	Class/Order	Species	Proportion (biomass)	sd
Mollusca	Bivalve	Unidentified clam	0.398	0.014
Mollusca	Bivalve	Butter clam (<i>Saxidomus giganteus</i>)	0.369	0.016
Echinodermata	Sea cucumber	California sea cucumber (<i>Apostichopus californicus</i>)	0.084	0.011
Mollusca	Gastropod	Unidentified snail species	0.026	0.004
Mollusca	Bivalve	Truncate soft-shelled clam (<i>Mya truncata</i>)	0.017	0.003
Crustacea	Decapod	Northern kelp crab (<i>Pugettia producta</i>)	0.014	0.004
Crustacea	Decapod	Unidentified rock crab	0.013	0.002
Mollusca	Bivalve	Nuttall's cockle (<i>Clinocardium nuttallii</i>)	0.013	0.004
Mollusca	Bivalve	Littleneck clam (<i>Leukoma staminea</i>)	0.010	0.003
Echinodermata	Sea urchin	Red sea urchin (<i>Strongylocentrotus franciscanus</i>)	0.010	0.002
Crustacea	Decapod	Unidentified crab species	0.009	0.001
Echinodermata	Sea star	Ochre star (<i>Pisaster ochraceus</i>)	0.007	0.002
Echinodermata	Sea urchin	Green sea urchin (<i>Strongylocentrotus droebachiensis</i>)	0.006	0.001
Mollusca	Bivalve	Bay mussel (<i>Mytilus trossulus</i>)	0.003	0.001
Mollusca	Chiton	Gumboot chiton (<i>Cryptochiton stelleri</i>)	0.003	0.001
Tunicata	Sea squirts	Pacific sea peach (<i>halocynthia aurantium</i>)	0.002	0.001
Crustacea	Decapod	Pandalus shrimp	0.002	0.001
Mollusca	Bivalve	Unidentified bivalve species	0.002	0.001
Mollusca	Bivalve	California sunset clam (<i>Gari californica</i>)	0.001	0.001
Mollusca	Gastropod	Pinto abalone (<i>Haliotis kamtschatkana</i>)	0.001	0.001
Mollusca	Bivalve	Horse mussel (<i>Modiolus modiolus</i>)	0.001	0.001
Mollusca	Chiton	Unidentified chiton species	0.001	0.000
Echinodermata	Sea cucumber	Unidentified sea cucumber species	0.001	0.000
Crustacea	Decapod	Dungeness crab (<i>Metacarcinus magister</i>)	0.001	0.001
Mollusca	Bivalve	Unidentified <i>Macoma</i> spp.	0.001	0.000
Echinodermata	Sea star	Unidentified sea star species	0.001	0.000
Echinodermata	Sea cucumber	orange sea cucumber (<i>Cucumaria miniata</i>)	0.001	0.001
Mollusca	Bivalve	Pink Scallop (<i>Chlamys rubdia</i>)	0.000	0.000
Mollusca	Bivalve	Green falsejingle (<i>Pododesmus macrochisma</i>)	0.000	0.000
Crustacea	Decapod	Helmet crab (<i>Telmessus cheiragonus</i>)	0.000	0.000
Crustacea	Decapod	Red rock crab (<i>Cancer productus</i>)	0.000	0.000
Mollusca	Gastropod	Moon snail (<i>Euspira lewisii</i>)	0.000	0.000
Echinodermata	Sea star	Mottled sea star (<i>Evasteria troscheli</i>)	0.000	0.000
Mollusca	Bivalve	Arctic Surfclam (<i>mactromeris polynyma</i>)	0.000	0.000
Echinodermata	Sea urchin	Unidentified sea urchin	0.000	0.000
Mollusca	Bivalve	Gaper clam (<i>Tresus capax</i>)	0.000	0.000
Mollusca	Bivalve	Unidentified <i>Mya</i> spp.	0.000	0.000
Mollusca	Bivalve	Soft-shelled clam (<i>Mya arenaria</i>)	0.000	0.000
Annelida		Unidentified worm	0.000	0.000
Crustacea	Decapod	Graceful decorator crab (<i>Oregonia gracilis</i>)	0.000	0.000
Crustacea	Decapod	Pygmy rock crab (<i>Cancer oregonensis</i>)	0.000	0.000
Mollusca	Bivalve	Unidentified scallop	0.000	0.000
Mollusca	Bivalve	Geoduck (<i>Panopea abrupta</i>)	0.000	0.000
Crustacea	Barnacle	Unidentified barnacle species	0.000	0.000

Appendix B.2: (A) Total length, dissected mass, and percent edible, (B) energy (kilocalories per dry gram), (C) lipid content (percent lipid per dry gram), (D) protein content (percent protein per dry gram), (E) percent ash, (F) percent moisture, for sea otter prey species separated by season with mean \pm standard deviation and number of samples processed.

A. Length / Mass / % Edible

Category	Species	Spring				Summer				Winter			
		length mean \pm sd	mass mean \pm sd	% edible mean \pm sd	n	mean length	mean mass	mean % edible	n	mean length	mean mass	mean % edible	n
Clam	<i>Climocardium nuttallii</i>	38.5 \pm 11.5	10.4 \pm 8.9	46.8 \pm 4.9	9	51.8 \pm 8.1	20.1 \pm 10.4	45.8 \pm 5.3	9	53.4 \pm 8.0	23.1 \pm 12.2	48.8 \pm 2.8	4
	<i>Leukoma staminea</i>	45.5 \pm 12.1	12.1 \pm 11.1	38.0 \pm 5.8	14	51.4 \pm 6.1	17.5 \pm 6.9	37.8 \pm 4.6	10	48.7 \pm 6.4	16.9 \pm 7.8	44.1 \pm 4.7	9
	<i>Saxidomus gigantea</i>	58.7 \pm 22.9	27.3 \pm 22.7	41.9 \pm 8.0	11	60.5 \pm 8.7	32.6 \pm 13.9	47.0 \pm 4.6	10	66.2 \pm 15.0	42.6 \pm 24.2	45.0 \pm 3.0	10
Crab	<i>Metacarcinus magister</i>	71.9 \pm 63.3	65.1 \pm 139.3	23.4 \pm 12.8	5	82.4 \pm 34.1	57.2 \pm 86.8	43.6 \pm 6.4	8	66.1 \pm 6.6	21.5 \pm 5.9	39.8 \pm 4.1	4
	<i>Cancer oregonensis</i>	29.25 \pm 0.4	1.7 \pm 0.6	23.5 \pm 9.8	2	32.0 \pm 0.7	2.745 \pm 0.6	26.0 \pm 8.0	2	-	-	-	-
	<i>Cancer productus</i>	139.5 \pm 14.0	136.1 \pm 32.9	40.3 \pm 4.9	5	127.5 \pm 36.8	123.6 \pm 87.6	40.7 \pm 6.8	4	78.0	34.9	49.5	1
	<i>Pugettia productus</i>	51.3 \pm 27.9	27.3 \pm 36.6	23.3 \pm 6.0	2	50.7 \pm 12.7	19.4 \pm 16.6	29.9 \pm 9.9	3	-	-	-	-
	<i>Telmesus cheiragonus</i>	57.8 \pm 5.3	19.4 \pm 10.5	35.9 \pm 7.7	5	61.5 \pm 19.1	29.3 \pm 25.2	40.3 \pm 7.4	2	45.0	17.7	38.9	1
Sea cucumber	<i>Apostichopus californicus</i>	266 \pm 193.1	305.1 \pm 349.8	100	5	230.0 \pm 25.5	289.5 \pm 57.2	100	5	234.8 \pm 99.8	354.7 \pm 272.6	100	5
Mussel	<i>Mytilus trossulus</i>	31.1 \pm 6.9	1.0 \pm 0.6	33.6 \pm 5.8	9	42.3 \pm 4.5	3.5 \pm 0.7	43.3 \pm 7.0	9	33.5 \pm 5.1	1.5 \pm 0.6	41.2 \pm 9.9	12
Snail	<i>Tegula spp.</i>	23.6 \pm 1.8	1.2 \pm 1.0	19.7 \pm 12.8	5	25.2 \pm 1.0	1.0 \pm 0.2	13.5 \pm 2.3	3	21.0	0.4	9.6	1
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	32.7 \pm 7.8	0.6 \pm 0.5	4.0 \pm 2.0	6	36.2 \pm 7.1	5.0 \pm 2.8	24.7 \pm 3.7	9	38.5 \pm 2.3	7.5 \pm 2.2	37.9 \pm 9.7	3
	<i>Strongylocentrotus franciscanus</i>	54.5 \pm 3.5	4.0 \pm 1.2	7.5 \pm 0.5	2	42.3 \pm 6.5	7.7 \pm 5.0	25.7 \pm 9.6	7	37.8 \pm 14.4	5.9 \pm 3.4	22.2 \pm 4.4	4

Appendix B.2 continued

B. Energy, Kcal per dry gram

Category	Species	Spring		Summer		Winter	
		mean	n	mean	n	mean	n
Clam	<i>Clinocardium nuttallii</i>	4.7 ± 0.3	9	4.3 ± 0.4	9	4.6 ± 0.2	4
	<i>Leukoma staminea</i>	4.8 ± 0.4	14	4.3 ± 0.2	10	4.4 ± 0.3	9
	<i>Saxidomus gigantea</i>	4.8 ± 0.1	11	4.3 ± 0.2	10	4.5 ± 0.3	10
Crab	<i>Metacarcinus magister</i>	3.5 ± 1.5	4	4.6 ± 0.4	8	5.1 ± 0.6	4
	<i>Cancer oregonensis</i>	4.4 ± 0.7	2	4.8 ± 0.3	2	-	-
	<i>Cancer productus</i>	4.6 ± 0.3	5	4.5 ± 0.5	3	4.9	1
	<i>Pugettia productus</i>	4.4 ± 0.1	2	4.1 ± 0.6	3	-	-
	<i>Telmeus cheiragonus</i>	4.7 ± 0.3	5	4.8 ± 0.1	2	4.0	1
Sea cucumber	<i>Apostichopus californicus</i>	2.4 ± 0.4	5	3.4 ± 0.2	5	2.8 ± 0.4	5
Mussel	<i>Mytilus trossulus</i>	-	-	4.6 ± 0.2	8	4.6 ± 0.1	2
Snail	<i>Tegula spp.</i>	4.7 ± 0.4	5	4.7 ± 0.1	3	4.8	1
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	31.2 ± 6.7	5	35.4 ± 4.7	9	42.6 ± 5.8	3
	<i>Strongylocentrotus franciscanus</i>	39.6 ± 2.4	2	35.5 ± 18.1	6	17.6 ± 9.8	4

C. % Protein (dry mass)

Category	Species	Spring		Summer		Winter	
		mean	n	mean	n	mean	n
Clam	<i>Clinocardium nuttallii</i>	67.6 ± 4.9	9	60.8 ± 5.7	9	63.4 ± 2.4	4
	<i>Leukoma staminea</i>	37.9 ± 3.2	14	58.9 ± 5.4	10	58.9 ± 3.9	9
	<i>Saxidomus gigantea</i>	65.8 ± 5.5	11	60.8 ± 5.6	10	63.7 ± 3.7	10
Crab	<i>Metacarcinus magister</i>	49.6 ± 22.8	5	64.8 ± 6.2	8	69.0 ± 1.2	4
	<i>Cancer oregonensis</i>	58.2 ± 1.7	2	54.9 ± 2.3	2	-	-
	<i>Cancer productus</i>	72.9 ± 5.2	5	63.5 ± 6.6	3	66.9	1
	<i>Pugettia productus</i>	56.5 ± 8.3	2	47.4 ± 2.9	3	-	-
	<i>Telmeus cheiragonus</i>	74.0 ± 5.0	5	61.0 ± 6.9	2	64.1	1
Sea cucumber	<i>Apostichopus californicus</i>	31.9 ± 6.8	5	44.8 ± 2.1	5	38.7 ± 8.4	5
Mussel	<i>Mytilus trossulus</i>	64.2 ± 3.3	9	54.1 ± 3.9	9	64.7 ± 3.6	11
Snail	<i>Tegula spp.</i>	78.9 ± 2.5	5	74.6 ± 2.5	3	74.5	1
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	31.7 ± 7.6	4	34.7 ± 4.5	8	39.3 ± 0.9	2
	<i>Strongylocentrotus franciscanus</i>	37.9	1	40.2 ± 21.2	4	13.1 ± 4.5	3

D. % Lipid (dry mass)

Category	Species	Spring		Summer		Winter	
		mean	n	mean	n	mean	n
Clam	<i>Clinocardium nuttallii</i>	9.23	5	7.1 ± 1.3	6	5.3 ± 1.1	4
	<i>Leukoma staminea</i>	8.71	10	7.9 ± 1.5	8	4.6 ± 1.2	9
	<i>Saxidomus gigantea</i>	8.83	10	6.1 ± 1.7	5	6.8 ± 1.1	10
Crab	<i>Metacarcinus magister</i>	7.7 ± 2.9	4	11.1 ± 2.7	6	14.4 ± 5.4	4
	<i>Cancer productus</i>	7.4 ± 3.3	5	10.7 ± 6.9	3	9.8	1
	<i>Pugettia productus</i>	9.3 ± 4.7	2	8.5 ± 6.0	3	-	-
Sea cucumber	<i>Apostichopus californicus</i>	5.4 ± 2.0	5	6.7 ± 0.6	5	2.3 ± 0.3	5
Snail	<i>Tegula spp.</i>	7.1 ± 4.2	4	5.4 ± 0.6	3	6.4	1
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	28.8 ± 18.3	2	14.0 ± 2.2	9	15.5 ± 7.2	3
	<i>Strongylocentrotus franciscanus</i>	20.0 ± 3.2	2	12.9 ± 4.1	6	6.9 ± 3.6	4

E. % Ash

Category	Species	Spring		Summer		Winter	
		mean	n	mean	n	mean	n
Clam	<i>Clinocardium nuttallii</i>	2.5 ± 0.3	6	2.7 ± 0.3	9	2.4 ± 0.2	4
	<i>Leukoma staminea</i>	2.6 ± 0.4	10	2.5 ± 0.2	10	2.5 ± 0.9	9
	<i>Saxidomus gigantea</i>	2.6 ± 0.3	8	2.6 ± 0.4	10	2.1 ± 0.2	5
Crab	<i>Metacarcinus magister</i>	-	-	3.0 ± 0.3	8	2.4 ± 0.4	4
	<i>Cancer productus</i>	2.5	1	2.5 ± 0.2	3	3.2	1
	<i>Telmeus cheiragonus</i>	-	-	2.7 ± 0.2	2	-	-
Sea cucumber	<i>Apostichopus californicus</i>	3.9 ± 0.5	5	3.3 ± 0.2	5	3.3 ± 0.7	5.00
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	-	-	2.0	1	-	-
	<i>Strongylocentrotus franciscanus</i>	-	-	2.6 ± 0.2	2	7.8	1

F. % Moisture

Category	Species	Spring		Summer		Winter	
		mean	n	mean	n	mean	n
Clam	<i>Clinocardium nuttallii</i>	82.5 ± 3.5	9	87.7 ± 1.8	9	85.1 ± 2.0	4
	<i>Leukoma staminea</i>	83.0 ± 3.1	14	86.5 ± 2.1	10	86.9 ± 2.6	9
	<i>Saxidomus gigantea</i>	79.5 ± 3.5	11	84.8 ± 2.0	10	84.1 ± 3.3	10
Crab	<i>Metacarcinus magister</i>	76.8 ± 6.6	5	83.1 ± 4.4	8	76.2 ± 7.2	4
	<i>Cancer oregonensis</i>	78.5 ± 8.9	2	83.7 ± 6.4	2	-	-
	<i>Cancer productus</i>	83.8 ± 3.6	5	88.9 ± 3.5	3	75.8	1
	<i>Pugettia productus</i>	74.6 ± 5.6	2	82.4 ± 3.5	3	-	-
	<i>Telmeus cheiragonus</i>	81.1 ± 3.6	5	83.0 ± 0.3	2	89.3	1
Sea cucumber	<i>Apostichopus californicus</i>	92.5 ± 0.5	5	90.9 ± 1.1	5	92.9 ± 0.9	5
Mussel	<i>Mytilus trossulus</i>	79.8 ± 1.4	9	82.8 ± 1.8	9	83.3 ± 0.9	12
Snail	<i>Tegula spp.</i>	76.0 ± 2.7	5	75.0 ± 1.0	3	75.7	1
Sea urchin	<i>Strongylocentrotus droebachiensis</i>	75.1 ± 1.6	6	88.7 ± 2.7	9	83.4 ± 3.3	3
	<i>Strongylocentrotus franciscanus</i>	84.8 ± 1.2	2	92.4 ± 1.3	7	74.99	4

Appendix C: Permits

Appendix C.1: 2018 ADFG collection permit



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-18-065**

Expires: **12/31/2018**

AQUATIC RESOURCE PERMIT
(For Scientific/Collection Purposes)

This permit authorizes:

Nicole LaRoche
(whose signature is required on page 2 for permit validation)
of
University of Alaska Fairbanks
17101 Point Lena Loop Rd., Juneau, AK 99801
(650)219-5061 nlaroche@alaska.edu

to conduct the following activities from **April 24, 2018** to **December 31, 2018** in accordance with AS 16.05.930 and AS 16.05.340(b), and 5 AAC 41.600.

Purpose: To collect sea otter prey species for stable isotope and caloric analysis.

Location: Prince of Wales and surrounding islands, Juneau road system

Species: See **Species List** on page 3-4.

Method of Collection: Hand collection, shovel, crap pots. See **Stipulations** section.

Disposition: Species will be sacrificed for analysis and disposed of as directed. See **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2019 and a COMPLETION REPORT IS DUE June 30, 2019. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfa.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 4/12/18

Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

Appendix C.2: 2019 ADFG Collection permit



STATE OF ALASKA
DEPARTMENT OF FISH AND GAME

P.O. Box 115526
JUNEAU, ALASKA 99811-5526

AQUATIC RESOURCE PERMIT
(For Scientific/Collection Purposes)

Permit No. **CF-19-027**

Expires: **12/31/2019**

This permit authorizes:

Nicole LaRoche

(whose signature is required on page 2 for permit validation)

of

University of Alaska Fairbanks

17101 Point Lena Loop Rd., Juneau, AK 99801

(650)219-5061

nlaroche@alaska.edu

to conduct the following activities from **January 2, 2019** to **December 31, 2019** in accordance with AS 16.05.930 and AS 16.05.340(b), and 5 AAC 41.600.

Purpose: To collect sea otter prey species for stable isotope and caloric analysis.

Location: Prince of Wales and surrounding islands

Species: See **Species List** on page 3.

Method of Collection: Hand collection, shovel, crap pots. See **Stipulations** section.

Disposition: Species will be sacrificed for analysis and disposed of as directed. See **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2020 and a COMPLETION REPORT IS DUE June 30, 2020. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. **UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE** the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 1/2/19

**Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game**

Appendix C.3: UAF IACUC Approval



(907) 474-7800
(907) 474-5993 fax
uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 10, 2017

To: Ginny Eckert
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [926969-3] Trophic linkages in seagrass ecosystems

The IACUC reviewed and approved the Amendment/Modification to the Personnel List referenced above by Administrative Review.

Received:	July 5, 2017
Approval Date:	July 10, 2017
Initial Approval Date:	June 29, 2016
Expiration Date:	June 29, 2018

This action is included on the July 13, 2017 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix C.4: USFWS MMPA Permit



United States Department of the Interior



U.S. FISH AND WILDLIFE SERVICE
1011 East Tudor Road
Anchorage, Alaska 99503-6199

IN REPLY REFER TO:

AFES/MMM

DEC 07 2017

Memorandum

To: Chief, Branch of Permits, Division of Management Authority
From: Chief, Marine Mammals Management 
Subject: Designation of Co-Investigator Ginny L. Eckert, Ph.D., to Marine Mammal Research Permit MA041309-6.

As per Permit MA041309-6 condition L, I have designated Dr. Ginny L. Eckert as a Co-investigator to conduct activities under this permit. Dr. Eckert is collaborating with Wildlife Biologist Ms. Michelle Kissling, a Principal Investigator on the permit, to study sea otters and their role as apex predators in seagrass ecosystems in southeastern Alaska. The field component of the project is expected to last through summer 2020 and analysis and reporting will be completed by fall 2022.

I confirm that Dr. Eckert has received appropriate training and possesses adequate proficiency to conduct research activities on sea otters in accordance with permit conditions. Additionally, as per permit Condition L, attached is Dr. Eckert's curriculum vita for your records. Dr. Eckert will carry a copy of this memorandum and the permit while conducting research activities. A summary of her activities will be included in our annual report.

Additionally, as our permit is scheduled to expire on July 25, 2018, we will be submitting a request for renewal prior to that date and plan to retain Dr. Eckert as a Co-investigator.

If you have concerns or questions, please contact me via email at patrick_lemmons@fws.gov or by phone at (907) 786-3668. Alternatively, contact Wildlife Biologist, Ms. Michelle Kissling, by email at michelle_kissling@fws.gov or phone at (907) 780-1168.

Attachment