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## Trophic Ecology of Northern Sea Otter (*Enhydra lutris*) in Southcentral and Southwest Alaska Utilizing Stable Isotope Ratios

D. Alex Mandi

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# Capstone of D. Alex Mandi

Submitted in Partial Fulfillment of the Requirements for the Degree of

## Master of Science Marine Science

Nova Southeastern University  
Halmos College of Arts and Sciences

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Approved:  
Capstone Committee

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HALMOS COLLEGE OF ARTS AND SCIENCES

TROPHIC ECOLOGY OF NORTHERN SEA OTTER (*Enhydra lutris*) IN SOUTHCENTRAL  
AND SOUTHWEST ALASKA UTILIZING STABLE ISOTOPE RATIOS

By

D. Alex Mandi

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in partial fulfillment of the requirements for  
the degree of Master of Science with a specialty in:

Marine Biology

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## Abstract

Sea otter populations in Alaskan waters have presented both growth and declines over the past years, which some researchers have attributed to changes in predator-prey dynamics. This project utilized stable isotope ratios to determine potential differences in the trophic ecology dynamics of the northern sea otter (*Enhydra lutris kenyoni*) in southern Alaskan waters. Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios from Prince William Sound otters, a relatively stable population, were compared to endangered sea otter populations from the Alaska Peninsula and Aleutian Island Archipelago. Location was a significant factor differentiating trophic ecology between southcentral and southwestern sea otter populations ( $p < 0.01$ ). Sea otter populations significantly varied in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between Prince William Sound, and the Aleutian Archipelago and Alaskan Peninsula ( $p < 0.01$ ). The southwest population had a greater enrichment in  $\delta^{15}\text{N}$  suggesting a trophic ecology in contrast to the southcentral population. There was no significant variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  within the Prince William Sound and within the Alaskan Peninsula and Aleutian Island Archipelago sea otter populations suggesting common trophic position within these populations. Neither  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  were significantly impacted by age or sex in either population. This indicates common trophic ecology within sea otter populations that are distinct from regional populations. Therefore, food availability or diet would not seem to be a driving factor distinguishing the endangered western population from the southcentral group from at least 1996 to 2003. This study emphasized the importance of considering trophic ecology within a species based on regional variations and further supports research regarding sea otter trophic ecology.

**Keywords:** Sea otters, Alaska, stable isotope ratios,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$

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## Statement of Significance

Southern Alaskan sea otter populations have faced dramatic declines over the past five decades that has led to differences in trophic structuring between regional populations. Northern sea otters in Alaska waters are divided into three distinct populations based on geography and size: southeast, southcentral, and southwestern Alaska. While the southeastern and southcentral populations are relatively stable, the southwestern population has experienced severe declines which has led to the listing of this population as endangered. For decades, the U.S. Fish and Wildlife service has worked collaboratively with the Alaska Sea Otter and Steller Sea Lion Commission, a non-profit tribal consortium, to collect sea otter data in an effort to understand both the similarities and distinctions among these populations and individuals.

This study set out to assess if differences in diet, or trophics, were a contributing factor in the different population declines. The potential for trophic differences among the southcentral and southwestern populations were measured in the stable carbon ( $\delta^{13}\text{C}$ ) and stable nitrogen ( $\delta^{15}\text{N}$ ) isotopes ratios of vibrissae (whiskers) from thirty-six northern sea otters from two regions in southern Alaska. Raw data allowed for comparison of trophic differences based location, age class (adult versus subadult), and sex.

Location of sea otter populations affects diet and thus foraging and diving habits. While sea otters are predominantly benthic foragers, they also forage on forage fishes, each group of prey having distinct isotopic values. Prince William Sound in southcentral Alaska includes Knight and Montague islands, Knight Island has predominately rocky-bottom sediments (Esslinger *et al.*, 2014). Montague Island has soft-bottom sediments along the southwestern coastline while the northwestern coastline consists of rocky bottom sediments which are common amongst southcentral Alaska (Clakins, 1978, Kvitek *et al.*, 1992). This is in contrast to portions of southwest Alaska's coastlines that are predominantly soft-bottom sediments with associated low-density sea otter populations (Estes and Bodkin, 2002). Regional differences and thus variations in bottom sediment affect sea otter diet and foraging behaviors. Sea otter populations in southcentral Alaska tend to have greater enrichment in stable carbon isotope ratios which suggests foraging on predominately benthic organisms associated with a more rocky-bottom environment (Kvitek *et al.*, 1992). Whereas southwestern sea otter populations are generally more enriched in nitrogen isotope ratios, eluding to a more pelagic-based organismal foraging strategy, coinciding with the soft-bottom environment (Clakins, 1978). Little to no

variation in carbon and nitrogen stable isotope ratios between adult -subadult and male-female otters suggest sea otter diets are generally consistent among location, age and sex. Likewise, as sea otter pups are weaned from their mothers, diet and foraging behaviors reflect regional variations rather than present significant inter-regional differentiations (Burek *et al.*, 2005). These interactions provide insight into the regional differences associated with diet and foraging behaviors of northern sea otter populations.

## **Background**

### *Range and Population Status*

Historically, populations of sea otter (*Enhydra lutris*) have extended from Baja California to the islands of Japan, following along the northern Pacific Rim (Bodkin and Monson, 2003). Sea otters are separated into various subspecies based on geographic location and extent. The southern sea otter (*E. lutris nereis*) ranges from the island of San Nicolas in southern California to Port Año Nuevo between San Francisco and Santa Cruz (USFWS, 2008d). The northern sea otter is found in the northeast Pacific Ocean from the northwest coast of North America to the Russian Far East. Northern sea otters are further divided into two subspecies. Subspecies *E. l. kenyoni* extends from Washington state to Amchitka Island in Alaska's Aleutian Archipelago. *E. lutris lutris* extends from the Commander Islands, the Russian side of the Aleutian Archipelago, southward through the Russian Kuril Islands (Bodkin and Monson, 2003; Bodkin, 2004; USFWS, 2008d; Jefferson *et al.*, 2015). The subspecies *E. l. kenyoni* is subdivided into three stocks based on genetics, morphology, and geographic distribution (Ferrero *et al.*, 2000) within Alaskan waters: Kodiak, Prince William Sound, and Southeastern Alaska (Figure 1). The U.S. Geological Survey (USGS) estimated in 2003 that approximately 150,000 sea otters were located along the North Pacific coast of the United States (USFWS, 2005a). In 2005, the U.S. Fish and Wildlife Service (USFWS) estimated that 70,000 sea otters were in Alaskan waters (USFWS, 2005b).

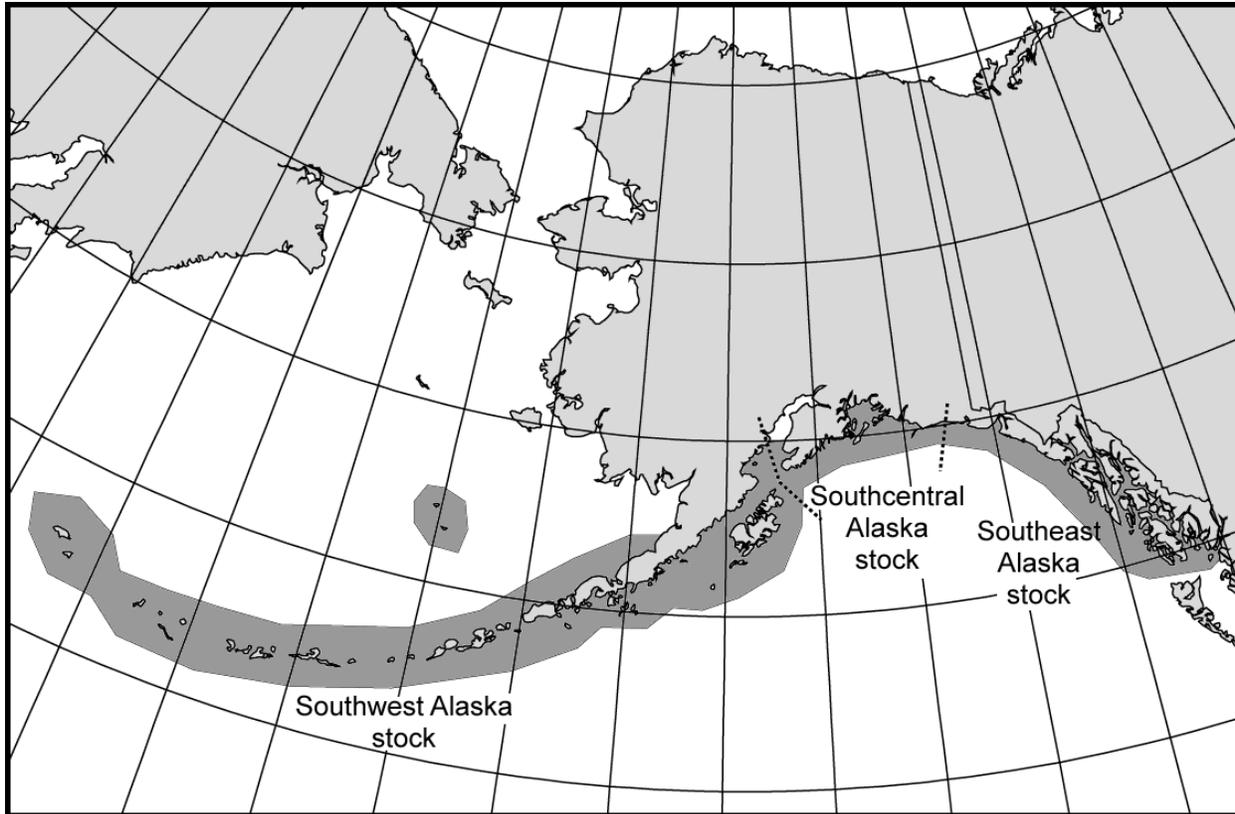
Sea otter populations vary both between the northern and southern subspecies and also vary among geographic regions. On January 14, 1997, the southern sea otter (*E. l. nereis*) was listed as a threatened species by the Marine Mammal Commission under the Endangered Species Act. On August 9, 2005 the southwestern stock of the northern sea otter (*E. l. kenyoni*) was listed as a threatened distinct population segment by the USFWS under the Endangered Species Act

(Federal Register, 2005). An organism listed as threatened under the Endangered Species Act will most likely become extinct throughout the majority of its range in the foreseeable future. The southwest Alaska threatened distinct population segment was believed to be suffering since it had undergone a population decline of approximately 55-67%, with as much as 90% in certain regions, hypothesized to be a result of predation by killer whales (*Orcinus orca*) or a combination of oceanographic changes and fisheries effects (Federal Register, 2005).

The Prince William Sound population has been relatively stable from 2011 to 2014 (Bodkin, 2004; Esslinger *et al.*, 2014) and is estimated to contain approximately 11,989 otters (USFWS, 2008c; Ballachey *et al.*, 2014). Along the northern part of Knight Island in the southern Sound, however, the population has yet to recover from the *Exxon Valdez* oil spill in 1989 (Bodkin, 2004). Contrary to the previous statement, sea otter populations in the western portion of Prince William Sound, part of the south central population stock, have increased between 1993 and 2000, the western population of Prince William Sound is not likely to be listed as “depleted” or “threatened” under the Endangered Species Act in the foreseeable future (USFWS, 2008c; USFWS, 2013). The USFWS survey found 47,676 sea otters in southwest Alaska (USFWS, 2008c). Comparisons of trophic ecology between the southwest Alaska threatened distinct population segments and the relatively stable Prince William Sound populations may provide insight into the stability of the southcentral stock over the southwest stock.

### *Biology and Anatomy*

Sea otters are members of the family Mustelidae and are related to river otters, minks, ferrets, and weasels (Levinton, 2001). Sea otters are the largest member of the Mustelids by body size and weight. Kenyon (1969) demonstrated a slight sexual dimorphism in sea otters; male sea otters can reach lengths of up to 148 cm (58 inches) and generally weigh approximately 45 kg (100 lbs) while female sea otters are typically smaller. Their overall length is up to 140 cm (55 inches) and they can weigh up to 32.5 kg (72 lbs). (Kenyon, 1969; Fisher, 1940; and Garrison, 2005). Sea otter lifespan also varies with sex; males typically live from 10-15 years in the wild, whereas females can live up to 20 years in the wild (Estes *et al.*, 1999). Sea otters, given the common name, are greatly adapted to life both in the sea as well as on land.



**Figure 1.** Approximate locations and distributions (shaded region) of the three stocks of northern sea otters in southern Alaska (USFWS, 2014).

The hind feet of sea otters are webbed for ease of swimming at depth and on the surface while their forefeet have un-webbed toes that are highly sensitive and dexterous for finding and manipulating food (Fischer, 1939; Jefferson *et al.*, 2015). Sea otters have three primary modes of aquatic movement: craniocaudally thrusting for short bursts of speed, paddling motion with the hind feet for long-distance traveling, and a lateral sweeping motion with the tail for slow, low energy movement (Estes and Bodkin, 2001).

Life in saltwater requires highly specialized adaptations especially with the intake of seawater while feeding and its high salt content. Sea otters and other marine mammals have evolved complex kidney systems that allow for the intake of saltwater as a result of consuming prey items. This kidney design is known as a reniculate kidney which is multi-lobed allowing the animal to survive in a greater range of salinities that terrestrial mammals lack (Costa, 1981; Atkinson, Aubin, and Ortiz, 2009). Sea otters have high metabolic rates, and as a result they must consume approximately 23-35% of their body weight each day (Estes *et al.*, 1974; Estes and Bodkin, 2001). To satiate this high metabolic cost, sea otters consume a variety of invertebrates, which have higher levels of electrolytes compared to teleost fish; subsequently, sea otters maintain a positive water balance by also consuming saltwater (Costa, 1981; Jefferson, Webber, Pitman, 2015). Primarily consuming invertebrates, sea otters have teeth designed for crushing and scooping, rather than containing sharp cutting cusps for tearing meat. To crush the shells of their prey, they have large, flat, and rounded molar teeth (Fisher 1941) and sharp canines for scooping the organisms out of the shells (Hilderbrand 1954; Timm-Davis *et al.*, 2015).

Sea otters are the only marine mammals that do not contain a layer of blubber; rather, they rely solely on the thickness of their fur to keep them warm. Their fur has the greatest density of hairs per square centimeter of any mammal on Earth (100,000 hairs/cm<sup>2</sup> or 850,000 to one million hairs/in<sup>2</sup>) (Kenyon, 1969; Estes and Bodkin, 2002; Jefferson *et al.*, 2015). Sea otter fur is composed of two layers, an undercoat and an overcoat. The undercoat consists of long, fine fibers and the overcoat consists of long and sparse, guard hairs. This design allows for a layer of air to become trapped in the undercoat, keeping the skin dry when under water (Eberhardt and Schneider, 1994; Jefferson *et al.*, 2015). Mammal fur is superior to blubber for heat regulation when in the air but is significantly less efficient in water. Fur is incapable of efficiently regulating heat flow, requires high levels of maintenance, and is highly compressible with

increased water depth and pressure. Sea otters require constant grooming of their fur to maintain the layer of air between their skin and the undercoat, taking up about 10% of their daily activities (Estes and Bodkin, 2002). They will float on their backs and gently blow air into the undercoat to maintain the layer of air between the skin and the undercoat (Jefferson *et al.*, 2015). This layer of air in the undercoat provides a heat barrier as sea otters dive to forage, while consuming and digesting prey provides additional heat gain at the surface (Estes and Bodkin, 2002).

### *Trophic Ecology*

Contrary to what might be expected, sea otters have poor vision underwater (Estes, 1980). Instead, otters rely on their vibrissae (whiskers) and their highly sensitive forepaws to hunt-down and manipulate their prey (Figure 2). When underwater, sea otters will detect prey vibrations with their vibrissae, then the otter will move any obstacles with their forepaws to grab the prey item (Kvitek *et al.*, 1992). Sea otters have flaps of skin under their forearm pits that act as pockets allowing otters to store prey and rocks for the ascent to the surface (Jefferson *et al.*, 2015). At the surface, sea otters will float on their backs and may use tools (e.g. rocks) collected to smash open shells of their prey to obtain the protein-packed meat and tissues (Kenyon, 1978; Estes, 1980).

Sea otters will often raft with other otters during feeding which enhances behavioral activities and the social structure. Garshelis (1984) found that sea otters in Prince William Sound would often share their food with both pups and other members of the raft, strengthening the social organization. Bodkin *et al.* (2004) noted that during sea otter dives, 64% of the time is devoted to foraging while only 36% is attributed to traveling. Average feeding dive durations for sea otters was 66 seconds, with an average of 59 seconds at a depth of 11.9 meters for males, and an average 67 seconds at a depth of 9.6 meters for females (Calkins, 1978). Caution should be noted when considering research done solely with direct visual observation on sea otters and their foraging activities as they tend to be biased as otters outside of the visual range cannot be properly observed (Estes and Bodkin, 2001).

More than 150 prey species are known to be included in sea otter diets while only a handful of species are consistent with the diets of individual otters (Calkins, 1978; Estes *et al.*, 2003; Jefferson *et al.*, 2015). Calkins (1978) observed that sea otters in Prince William Sound fed mostly on three major groups of bottom-dwelling invertebrates: mollusks (oysters, clams,

mussels, chiton, snails, and octopi), crustaceans (crabs), and echinoderms (sea urchins and sea stars). Calkins (1978) and Jefferson, Webber, and Pitman (2015) both noted that when invertebrate densities were low, sea otters relied on fish. Sea otters employ various hunting strategies depending on prey. Estes (1999) and Estes *et al.* (2003) observed that some sea otters replicated their mother's diet and hunting strategy; these individuals are known as specialist predators. These specialist sea otters can consume 25% more prey items per unit time than sea otters that do not replicate their mother's behaviors; these individuals are known as non-specialists. Therefore, it is more advantageous for the pup to mimic the mother's dietary and hunting behaviors (Tinker *et al.*, 2008).

Sea otters have a strong relationship and play a pivotal role within the coastal environment, so much so that sea otters are a keystone species; the removal of sea otters would trigger cascading ecological effects. Sea otters are also considered apex predators, meaning they have little predation threat and are at the highest trophic level of the local food chain, controlling population densities of prey species (Estes and Bodkin, 2002). Sea otters are known to help maintain biodiversity of their local communities in areas where sea otters are absent or recently reestablished (Jefferson *et al.*, 2015). Extensive evidence shows sea otters significantly alter prey abundance and modify community structure in rocky-bottom environments (Kvitek *et al.*, 1992). Contrary to rocky-bottom environments, little research has been conducted on structural altering by sea otters on soft-bottom environments. However, because of the depth at which infauna organisms' refuge in soft-bottom environments, sea otters may have less of an impact on these communities. Furthermore, sea otters living in soft-bottom communities act as a measure of disturbance as they tend to dig for prey. Also, the discarding of shells from prey increases potential settlement area of larval organisms (Kvitek *et al.*, 1992).

A major study on the role of sea otters as apex predators observed the trophic cascade of absent sea otters on kelp forests and sea urchin abundance. In kelp forest communities where sea otters prey on urchins, the kelp is abundant and healthy. Following the removal of sea otters, urchins proliferate and begin to feed on the kelp, thus reducing the kelp forest density. Overall, the removal of kelp resulted in a decrease in abundance of organisms that rely on the kelp forest, such as invertebrates, fish, and mammals (Estes and Bodkin, 2002; Bodkin *et al.*, 2004).



**Figure 2.** Northern sea otter vibrissae (<https://aquarium.org/how-sea-otters-keep-cozy/>).

### *Environment, Diet, and Feeding Behavior*

Montague and Knight Islands are located along the southern extent of Prince William Sound in southcentral Alaska. The southern and southwestern ends of Montague Island are predominantly composed of soft-bottom sediments (Kvitek *et al.*, 1992) while the northwestern end is composed of rocky shorelines (Calkins, 1978). The coastline of Knight Island, by contrast, tends to be rocky-bottomed overall; this is in contrast to the soft-bottom sediments that dominate the vast region of southcentral Alaska (Esslinger *et al.*, 2014). Estes and Bodkin (2002) demonstrated that the diets of sea otters will often vary according to location and local prey availability, season, and residence time. For example, Kodiak Island and Prince William Sound have predominantly rocky-bottom sediments and thus sea otters' primary diets consist of clams (Calkins, 1978). By contrast, in the Aleutian, Commander, and Kuril Islands - where bottom type is soft sediment and there are low-density populations of sea otters - prey consist primarily of sea urchins and fish (Estes and Bodkin, 2002). Sea otters display proficient and advanced survival skills to overcome difficulties (high metabolism, low-capacity energy stores, low food resources) faced in their harsh habitats (Estes *et al.*, 2003).

### *Anthropogenic Effects and Sea Otter Regulation*

Sea otters have a variety of natural predators, including both killer whales (*Orcinus orca*) and bald eagles (*Haliaeetus leucocephalus*) (Anthony *et al.*, 2008). Humans, however, have negatively impacted sea otter populations both directly and indirectly. Direct impacts include hunting of the sea otters and pinniped species for the fur trade in the mid-1700s; during this time sea otter populations declined and reached record low-densities in Alaska (Doroff *et al.*, 2003). Indirect impacts like the oil spill of the *Exxon Valdez* also have lasting effects that are still observed today (Monson *et al.*, 1999). On March 24, 1989 the *Exxon Valdez* tanker ran aground in Prince William Sound, spilling 42 million liters (10.8 million gallons) of crude oil into the waters over a three-day period. The *Exxon Valdez* spill is ranked as the second largest oil spill in U.S. waters (although the Deepwater Horizon oil spill is the largest to date, per Ramseur (2010)). Garrott *et al.* (1993) documented the effects of the *Exxon Valdez* oil spill on sea otter populations in Prince William Sound. Prior to the spill, sea otter populations were estimated to be approximately 6,546 individuals; following the spill that number dropped to 3,898 individuals.

By comparison, therefore approximately 2,648 sea otters were directly affected by the *Exxon Valdez* event (Garrott *et al.*, 2003).

Article V of the *Convention between Great Britain, Japan, Russia, and the United States for the Protection and Preservation of Fur Seals* resulted in the cessation of fur seal hunting in 1911, but also protected sea otters from being commercially hunted and exploited (Fanshawe *et al.*, 2003). Following this international treaty, approximately 1,000 to 2,000 sea otter individuals remained within the thirteen remnant populations that existed following the extensive fur-trade hunting, the southern sea otter is descended from one of these remnant colonies (Kenyon, 1969). In 1965, repopulation efforts were undertaken in unoccupied areas between California and Prince William Sound. Some sea otters found in Prince William Sound were relocated to southeast Alaska, British Columbia, Washington State, and Oregon. Forty-three otters were translocated to Washington State, 89 to British Columbia, and 412 to southeast Alaska. Of these translocated individuals, only 4 survived in Washington, 28 in British Columbia, and 150 in southeast Alaska (Bodkin and Monson, 2003). Interestingly, the growth rates of individual translocated sea otters were considerably greater than remnant individuals, with a 21% average growth rate as opposed to 9% growth rates of the remnants (Bodkin *et al.*, 1999; Bodkin and Monson, 2003).

By the mid-1980s, southwestern Alaska comprised roughly 80% of the world's sea otter populations (Burn, 2004). However, in recent times, sea otter populations have been declining with no specific cause. Estes *et al.* (1998) have hypothesized that changes in killer whale feeding behaviors could dramatically affect and alter the balance of marine ecosystems thus altering prey abundances, though this hypothesis has been proven to be controversial among scientists (Schrope, 2007; Garcia *et al.*, 2016). Changes in killer whale diet behavior have been attributed to increased ocean temperatures (Estes *et al.*, 1998). Furthermore, such a change may explain why southwestern sea otter populations in Alaska are declining overall. Researchers have continually proposed hypotheses to explain these decreases in Alaskan sea otter populations, though one particular hypothesis has yet to be adopted as the ultimate reason for the declines. Rather, a combination of certain factors is most likely the cause for population declines (Garcia *et al.*, 2016).

### *Stable Isotope Ratios*

Stable isotopes are used by researchers to better understand and quantify ecosystem structuring via trophic dynamic studies. A stable isotope is a naturally occurring, non-reactive form of an atom that is non-radioactive and thus not subject to decay. Stable isotopes have the same elemental atomic number but have additional neutrons, thus changing the atomic mass of the element. An example of a stable isotope would be carbon-13, which possesses one more neutron than carbon-12. Though additional neutrons affect the atomic mass, they do not affect electron shells, nor the chemical reactions within these shells (DeNiro and Epstein, 1978; Arnold, 1982; Minagawa and Wade, 1984; Peterson and Fry, 1987; Kling *et al.*, 1992; Kelly, 1999; Vander Zanden *et al.*, 1999; Post *et al.*, 2000; Fry, 2006). Atoms whose stable isotopes are commonly used for ecological analyses include carbon, nitrogen, oxygen, hydrogen, and sulfur.

Stable isotope analysis studies have included demonstrating increased carbon in the atmosphere from ice core samples in Antarctica to analyzing ancient human diets via isotope ratios from bone samples (Schoeninger and Moore, 1992; Stelling and Yu, 2019). Abundances of these stable isotopes vary naturally depending on the ecosystem in which they are extracted (Peterson and Fry, 1987; Fry, 2006; Laitha, 2007). Stable isotope analysis is a tool for overserving trophic structuring of the past as isotopes are considered natural tracers. Stable isotopes can be used to better comprehend the dynamics of marine ecosystems, focusing on the biological and physical contributions of life and ecosystems. Through the analysis of stable isotopes, marine and estuarine ecosystems' food web structure can be determined; furthermore, scientists have noted that the use of multiple stable isotopes when conducting research provide more accurate results (Laitha, 2007; Newsome *et al.*, 2010). Stable isotope ratios are utilized by ecologists to better understand the interaction of organisms with different ecological zones (Clementa and Koch, 2001). In the Aleutian Archipelago, for example, surface water productivity has been shown to decrease from east to westward by observing stable isotope ratios (Hunt and Stabeno, 2005).

Substantial interest in the use of stable isotopes has increased since the late 1970s, specifically carbon and nitrogen for analysis of the dynamics and structures of food web ecology and ecological communities (Peterson and Fry, 1987; Kling *et al.*, 1992; Kelly, 1999; Vander Zanden *et al.*, 1999; Post *et al.*, 2000; Newsome *et al.*, 2010). Food webs illustrate trophic interactions within ecological communities, but are difficult and time consuming to reconstruct and at times inadequately represent the mass flow within these ecological communities (Paine,

1998; Hairston and Hairston, 1993; Polis and Strong, 1996; Vander Zanden and Rasmussen, 1999; Post, 2002; and Newsome *et al.*, 2010). One of the most accurate measures of food web dynamics is to follow the pathway of organic matter; stable carbon and nitrogen isotopes are generally used (McCutchan and Lewis, 2001). The ratio between the carbon of a sample and a carbonate standard can be used to determine ultimate sources of carbon and represented by the ratio of carbon,  $\delta^{13}\text{C}$  (Post, 2002; and Newsome *et al.*, 2010). On the other hand, the ratio between nitrogen in a sample and atmospheric nitrogen gas ( $\text{N}_2$ ) can determine the trophic position of an organism,  $\delta^{15}\text{N}$  (Wada *et al.*, 1991; Post, 2002; and Newsome *et al.*, 2010). The  $^{13}\text{C}/^{12}\text{C}$  ratio responds conservatively due to the low trophic fractionation of carbon (i.e. the processes that affect relative abundances of stable isotopes), approximately 1-3‰ (DeNiro and Epstein, 1978; Fry and Arnold, 1982; Peterson and Howarth, 1987; and Schäuble, 2004), while nitrogen fractionation is larger approximately 3-5‰ (DeNiro and Epstein, 1981; Minagawa and Wade, 1984). Analysis of stable isotope ratios may reveal differences in trophic structure with geographic variations. Furthermore, stable isotope ratios may shed light on trophic variations within particular populations based on sex and age of individuals.

## **Objectives**

The purpose of this study was to examine differences in stable isotope ratios and content of thirty-six northern sea otter individuals from two southern Alaska regions. Regional differences among populations may affect foraging behaviors and thus diets of sea otters, which in turn may correlate with the variation in stable carbon and nitrogen isotopes. Differences in bottom sediment may lead to trophic ecology differences between populations (Calkins, 1978; Estes and Bodkin, 2002; Esslinger *et al.*, 2014). The goal of this study was to 1) determine what factors or combinations of factors (i.e. location, age class and sex) affect stable isotope ratios among sea otter individuals, and 2) determine if there are differences between the southcentral and southwestern sea otter populations.

## **Materials and Methods**

### *Sample Locations*

Sea otter vibrissae samples were collected from a total of 12 sea otters from southwestern Alaska and a total of 24 sea otters from Prince William Sound from 1996-2003 (Table 1).

**Table 1.** Northern sea otter vibrissae samples (mean  $\pm$  standard deviation) from Alaska, 1996-2003. Southcentral Alaska = 24 individuals, southwest Alaska = 12 individuals.

**Southcentral Alaska**

ID	N	Location	Sex	Age Class	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
NVP9642/SO-96-42	1	Knight Is.	F	Subadult	-15.90 $\pm$ 0.22	10.71 $\pm$ 0.46
NVP9644/SO-96-44	1	Knight Is.	M	Adult	-14.83 $\pm$ 0.22	12.32 $\pm$ 0.85
NVP9652/SO-96-52	1	Knight Is.	M	Subadult	-14.52 $\pm$ 0.42	11.43 $\pm$ 0.75
NVP9659/SO-96-59	1	Knight Is.	F	Adult	-12.14 $\pm$ 1.45	11.62 $\pm$ 0.48
SO-97-24	1	Knight Is.	F	Adult	-14.66 $\pm$ 0.22	11.40 $\pm$ 0.53
SO-97-47	1	Knight Is.	M	Adult	-14.75 $\pm$ 0.69	10.52 $\pm$ 0.73
SO-01-19	1	Knight Is.	F	Adult	-14.62 $\pm$ 0.52	11.66 $\pm$ 0.65
SO-01-26	1	Knight Is.	M	Adult	-15.13 $\pm$ 0.45	12.77 $\pm$ 0.95
SO-98-38	1	Knight Is.	M	Adult	-14.92 $\pm$ 0.53	10.16 $\pm$ 0.23
SO-02-33	1	Knight Is.	F	Subadult	-14.99 $\pm$ 0.49	10.69 $\pm$ 0.54
SO-02-09	1	Knight Is.	F	Adult	-13.92 $\pm$ 0.52	13.02 $\pm$ 0.72
NVP9623/SO-96-23	1	Montague Is.	F	Subadult	-14.83 $\pm$ 0.45	12.86 $\pm$ 0.46
NVP9627/SO-96-27	1	Montague Is.	M	Adult	-13.53 $\pm$ 0.22	12.36 $\pm$ 0.54
NVP9633/SO-96-33	1	Montague Is.	F	Adult	-12.98 $\pm$ 0.81	13.46 $\pm$ 0.95
NVP9638/SO-96-38	1	Montague Is.	M	Subadult	-14.75 $\pm$ 0.49	12.13 $\pm$ 0.52
SO-97-03	1	Montague Is.	M	Adult	-14.05 $\pm$ 0.39	11.88 $\pm$ 0.97
SO-97-14	1	Montague Is.	F	Adult	-13.85 $\pm$ 0.43	13.18 $\pm$ 0.63
SO-97-32	1	Montague Is.	M	Subadult	-13.38 $\pm$ 0.64	12.38 $\pm$ 0.82
SO-01-04	1	Montague Is.	F	Adult	-14.10 $\pm$ 0.46	11.64 $\pm$ 0.88
SO-01-10	1	Montague Is.	F	Subadult	-14.09 $\pm$ 0.75	11.81 $\pm$ 0.86
SO-01-11	1	Montague Is.	M	Adult	-14.60 $\pm$ 0.44	11.52 $\pm$ 0.62
SO-02-12	1	Montague Is.	M	Adult	-13.77 $\pm$ 0.73	10.88 $\pm$ 0.56
SO-02-13	1	Montague Is.	F	Subadult	-14.50 $\pm$ 1.31	9.57 $\pm$ 1.15
SO-02-11	1	Montague Is.	F	Adult	-13.34 $\pm$ 1.09	12.08 $\pm$ 0.35

**Southwest Alaska**

ID	N	Location	Sex	Age Class	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
600-015	1	AK Peninsula	M	Adult	-12.70 $\pm$ 0.31	13.44 $\pm$ 0.40
BS98014	1	AK Peninsula	M	Adult	-11.99 $\pm$ 0.76	17.42 $\pm$ 0.31
BS00014	1	AK Peninsula	M	Adult	-14.12 $\pm$ 0.62	14.21 $\pm$ 0.72
BS00019	1	AK Peninsula	F	Adult	-13.92 $\pm$ 0.58	14.99 $\pm$ 0.72
BS00020	1	AK Peninsula	M	Subadult	-15.09 $\pm$ 1.71	13.82 $\pm$ 5.33
BS95043	1	AK Peninsula	F	Adult	-12.83 $\pm$ 1.09	13.25 $\pm$ 1.67
ALE_04_001	1	Aleutians	F	Adult	-13.27 $\pm$ 0.45	11.87 $\pm$ 0.65
ALE_04_002	1	Aleutians	F	Subadult	-13.17 $\pm$ 1.11	14.36 $\pm$ 0.91
ALE_04_003	1	Aleutians	M	Subadult	-13.64 $\pm$ 0.72	13.15 $\pm$ 0.77
ALE_04_004	1	Aleutians	F	Subadult	-13.07 $\pm$ 1.39	13.67 $\pm$ 1.27
195-003	1	Aleutians	F	Adult	-12.00 $\pm$ 0.58	15.20 $\pm$ 0.87
BS00035	1	Aleutians	F	Adult	-13.75 $\pm$ 1.60	12.53 $\pm$ 1.41

Collection was accomplished in part by native hunters and federal agency personnel from the USFWS and United States Geological Survey (USGS). The southwest Alaska locations are found between 52° and 55° N and 160° and 177° W and included locations Kalekta Bay, Clam Lagoon, St. Catherine Cove, Cold Bay, Sand Point, King Cove, Zachary Bay, and Port Heiden in the Alaska Peninsula and Aleutian Archipelago. Sea otter tissue samples were also collected from Knight and Montague islands in southern Prince William Sound which are located at approximately 60° N and 147.5° W.

### *Sea Otter Samples*

Collection of sea otter vibrissae was accomplished via clipping of the vibrissae from deceased sea otters from all 36 northern sea otters. Vibrissae samples were collected from subsistence harvested and stranded sea otters from 1997-2014 in southern Alaska. All fissioned samples previously collected were under USFWS permit number MA041309-5 (V.A. Gill, co-PI). Previous chemical analyses were conducted under MMPA 806. No Institutional Animal Care and Use Committee (IACUC) permit was needed as no living organisms will be sampled for this study. Samples from southcentral Alaska were collected during July and August while southwestern samples were collected during the months of January, February, June, August, September, October, and November. Collection years included 1996-1998 and 2000-2003. Age classes for all organisms are sub-adults (1-3 years of age) and adults (4-9 years of age). Sea otter vibrissae samples will be evenly distributed among sample collections based on location, sex, and age class.

### *Statistical Analysis*

To determine if trophic contribution by sea otters in southern Alaska is predominantly benthic or pelagic, a comparison of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  by location, age class, and sex was conducted. Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each sea otter vibrissae were used in statistical analyses as there were no significant differences in either  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  within each segment. A combination of parametric analyses was employed and all statistical analyses were performed in R Studio. Analysis of Variance (*ANOVA*) tests and one sample t-tests (*t-test*) were used to test for individual stable isotopes while Multivariate Analysis of Variance (*MANOVA*) tests and Principal Component

Analysis (*PCA*) tested for the influence of location, age class, and sex on the combined stable carbon and nitrogen isotope ratios.

### *Stable Isotope Analysis*

Stable carbon and nitrogen isotope ratios were measured for each sea otter vibrissa. To remove unwanted debris and potential contaminating substances, vibrissae were cleaned with steel wool, dried, and cut into 2.5 mm segments from the proximal end to distal end of the vibrissae using surgical forceps and snippers. Every other segment of each whisker segment was analyzed for stable isotope ratios and each archived segment was treated as a pseudo-replicate if additional analyses were needed (e.g. the physical loss of a sample). Samples weighed approximately 0.6-0.8mg and placed in 3.5 x 5mm sterile aluminum tin capsules for stable isotope analysis at the Smithsonian Institution Museum Support Center in Suitland, Maryland. Samples were combusted and analyzed using a Thermo Delta V Advantage mass spectrometer in continuous flow mode coupled to an Elementar vario ISOTOPE Cube Elemental Analyzer (EA) via a Thermo ConFlo IV. For every 10-12 samples, a set of standards were run to ensure proper functioning of the mass spectrometer. Standards include Costech acetanilide D and a urea (Urea-UIN3) standard, both of which are calibrated to USGS40 (L-glutamic acid) and USGS41 (L-glutamic acid). All samples and standards were run with the same parameters and procedures, including an expected reproducibility of the standards to be  $\leq 0.2\%$  ( $1\sigma$ ) for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

The ratio of the heavy to light isotopes for each vibrissae sample was expressed in terms of  $\delta$  and were reported in comparison to the standard reference material Pee Dee Belemnite (PDB) for carbon and atmospheric air ( $\text{N}_2$ ) for nitrogen. The stable isotope values were obtained from the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is the isotope being analyzed (i.e.  $^{13}\text{C}$  or  $^{15}\text{N}$ ) and R is the ratio of the heavy to light isotope (i.e.  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ). The units of the  $\delta$  values were expressed in parts per thousand or per mil (‰). Raw isotope values were corrected using a 2-point linear correction on the calibrated Costech acetanilide and urea standards.

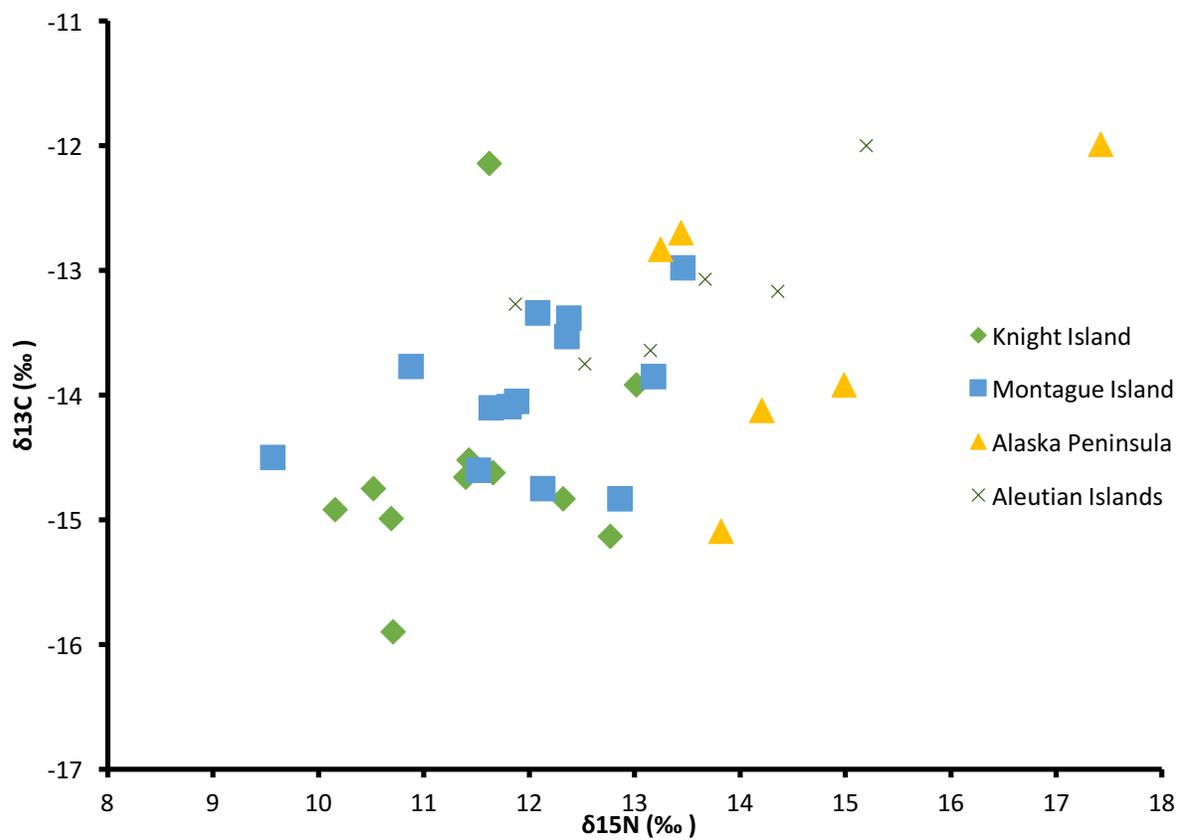
## Results and Discussion

### *Spatial*

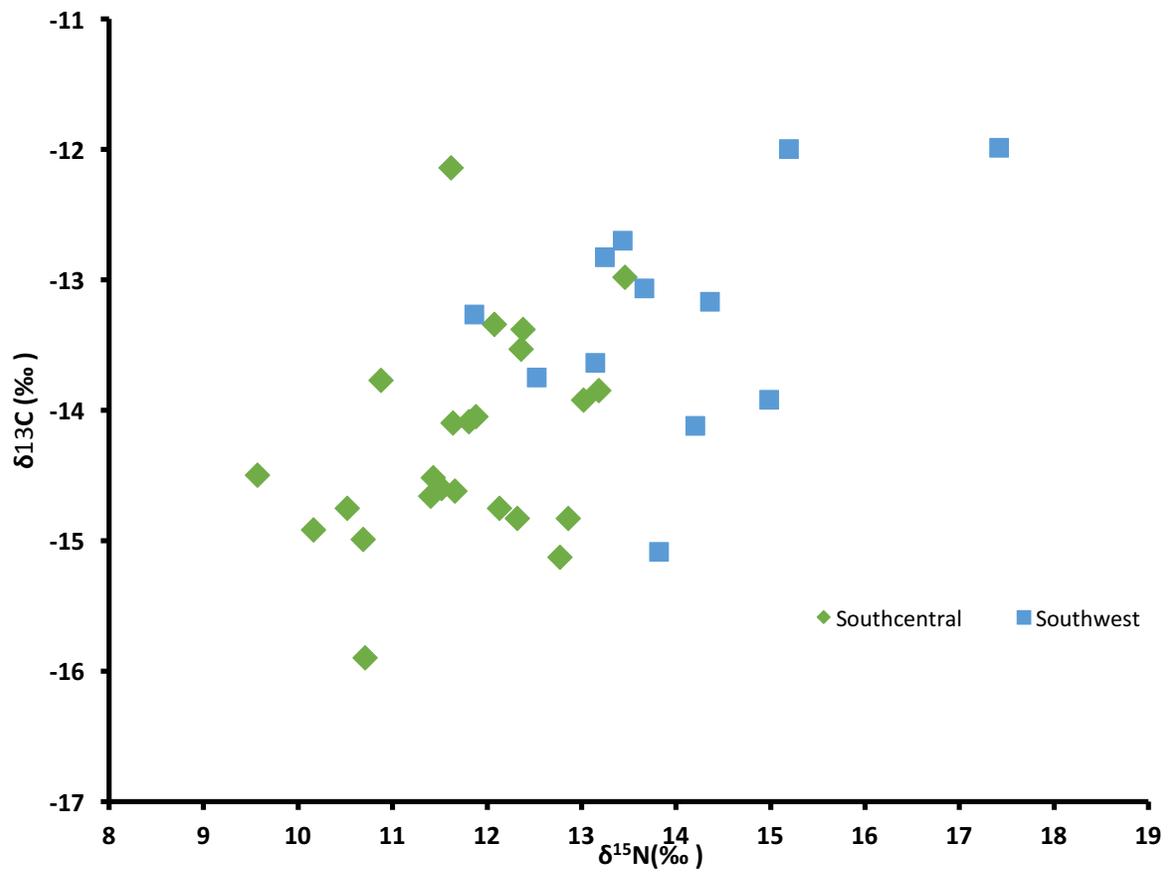
No significant differences were detected in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  along individual vibrissae; therefore, mean stable isotope values were used for the remaining statistical analyses (*t-test*:  $df = 35$ ,  $t = -88.848$ ,  $p = 1.000$ ;  $df = 35$ ,  $t = 48.073$ ,  $p = 1.000$ , respectively). The mean range in the  $\delta^{13}\text{C}$  in vibrissae in Prince William Sound was  $-15.90 \pm 0.22$  to  $-12.14 \pm 1.45$ . The mean range in the  $\delta^{15}\text{N}$  in vibrissae in Prince William Sound was  $9.57 \pm 1.15$  to  $13.46 \pm 0.95$  (Table 1). The mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each sea otter vibrissa combined were significantly affected by location (*ANOVA*:  $df = 3$ ,  $F = 4.9037$ ,  $p = 0.0065$ ;  $df = 3$ ,  $F = 11.947$ ,  $p < 0.0001$ , respectively; Figure 3). The combined mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were also significantly different between southcentral and southwest Alaska (*MANOVA*:  $df = 3$ ,  $F = 5.2455$ ,  $p = 0.0004$ ; Figure 4).

Within Prince William Sound, no significant differences, individually or combined, for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were found between Knight Island and Montague Island (*ANOVA*:  $df = 1$ ,  $F = 2.3298$ ,  $p = 0.1362$ ; *MANOVA*:  $df = 1$ ,  $F = 1.9734$ ,  $p = 0.1639$ ; Figure 5). Additionally, no significant differences, individually or combined, for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were found between the Alaskan Peninsula and the Aleutian Islands (*ANOVA*:  $df = 1$ ,  $F = 2.0468$ ,  $p = 0.1617$ ; *MANOVA*:  $df = 1$ ,  $F = 1.7366$ ,  $p = 0.2303$ ; Figure 6).

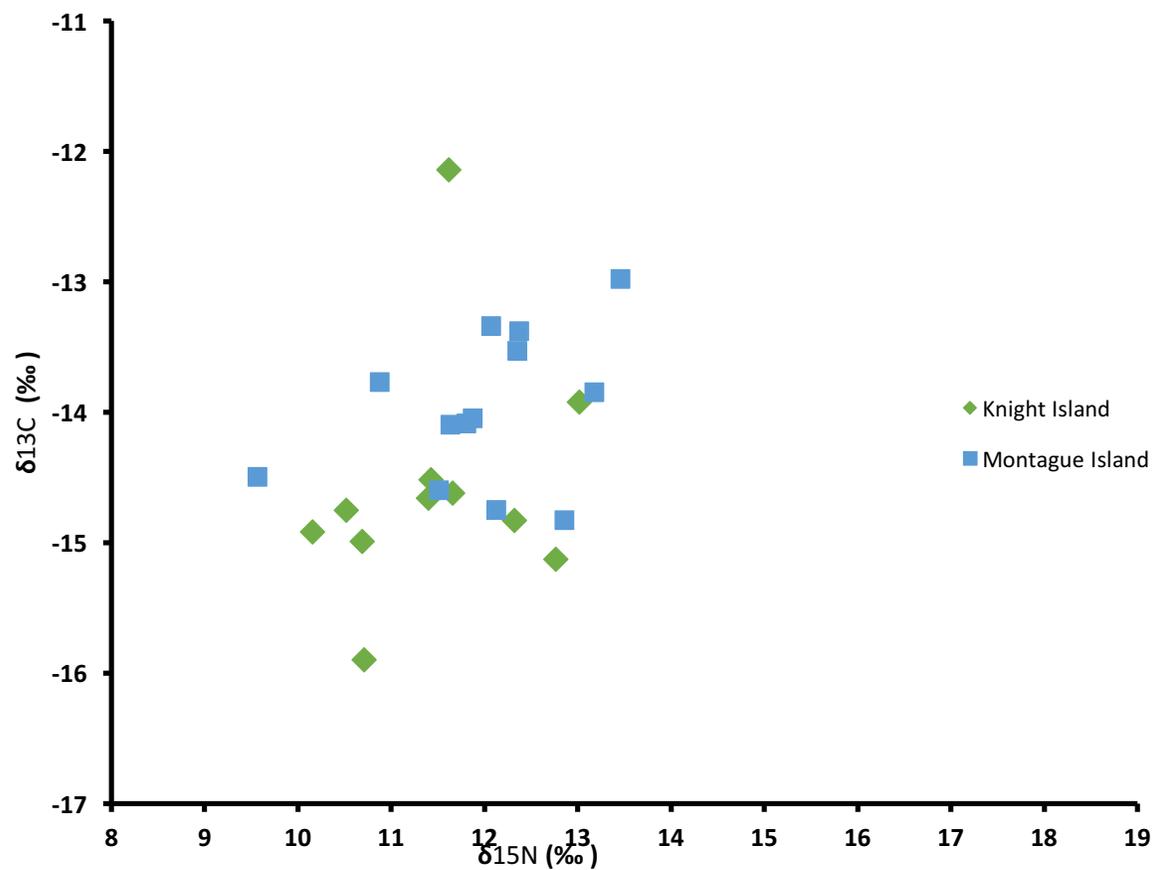
The two study locations, southcentral Alaska including Prince William Sound, and southwestern Alaska including the Aleutian Archipelago and Alaska Peninsula, are marked by different sediment substrata. Coastal southcentral Alaska (PWS) has a predominately rocky-bottom environment (Esslinger *et al.*, 2014). By contrast, the southwest Alaska (Alaska Peninsula and Aleutian Archipelago) margin has a generally soft-bottom environment (Calkins, 1978). As sea otters are largely benthic foragers, differing bottom types may affect the types of prey located in these locations. Likely benthic prey items consumed by sea otters in southcentral and southwest Alaska include, but are not limited to; sea urchins, clams, mussels, octopuses, sea cucumbers, some sea stars, etc., these organisms typically have a trophic level around 2 or 2.5. Likely pelagic prey items in the southwest Alaska populations include fish species, such as Pacific herring (*Clupea pallasii*), which have trophic levels of 3 (Trites, 2019). These varying foraging environments may correlate with the statistical findings of more enrichment in either carbon or nitrogen isotopes precluding benthic or pelagic feeding, respectively (Gorbics and Bodkin, 2006).



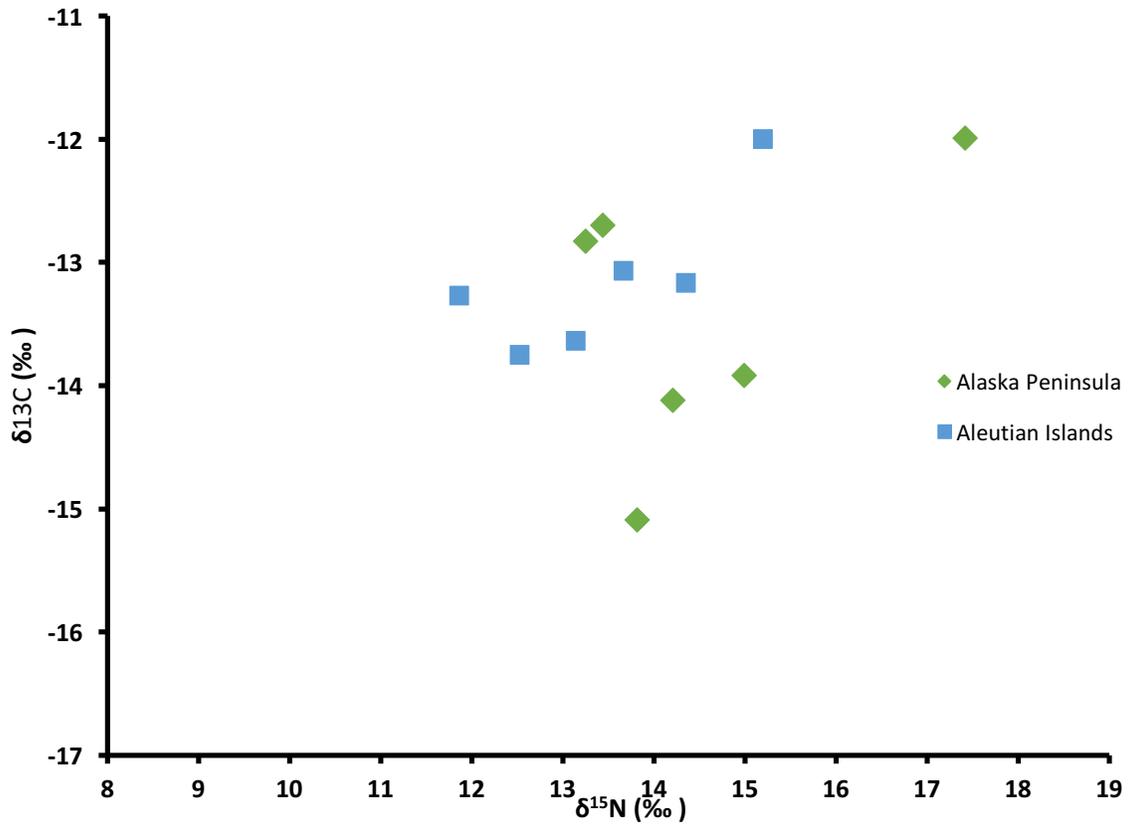
**Figure 3.** Isotope variation in sea otter samples based on location in southern Alaska.



**Figure 4.** Isotope variation in sea otter samples between southcentral and southwest Alaska.



**Figure 5.** Isotope variation in sea otter samples within Prince William Sound, comparing Knight Island and Montague Island.



**Figure 6.** Isotope variation in sea otter samples within southwest Alaska, comparing the Alaska Peninsula and the Aleutian Islands.

The otter vibrissae  $\delta^{13}\text{C}$  from PWS ranged just over 3‰ while  $\delta^{15}\text{N}$  ranged 4‰. Thus otters in PWS have heavier benthic diets. The southwest population was on average slightly more enriched in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than the otters in PWS. The otter vibrissae  $\delta^{13}\text{C}$  from the Peninsula and Aleutian Islands also ranged just over 3‰ while  $\delta^{15}\text{N}$  ranged 5‰. While the nitrogen isotopes reflect roughly a fluctuation within one trophic level, the carbon isotopes are more reflective of a change in prey habitat (DeNiro and Epstein, 1978, 1981). Carbon isotope enrichment is a hallmark of nutrient recycling as gross and particulate matter on the way to the benthos are digested and excreted, sometime multiple times, each time incrementally increasing the carbon isotope (France and Peters, 1997). Therefore, the range in the otters'  $\delta^{13}\text{C}$  likely reflects a mix of benthic (largely invertebrates) and neritic (fishes) foraging. The increased range in  $\delta^{15}\text{N}$  from southwest Alaska potentially reflects the inclusion of more fishes in the sea otter's diet (DeNiro and Epstein, 1981).

Sea otter populations in PWS have benthic invertebrate-dominated diets while sea otter populations in southwest Alaska have pelagic fish-dominated diets, though decadal shifts have been noted in more recent research (Calkins, 1978; J. Watt *et al.*, 2000; Reisewitz *et al.*, 2005). Research notes regional dietary variations among sea otter populations that have manifested as a result of the dramatic decline and increase in sea otter populations over the past five decades (Estes *et al.*, 2005). These findings support the hypotheses that sea otter populations in southern Alaska exhibit regional dietary variations via differentiation in stable carbon and nitrogen isotope values. Therefore, it is logical to suggest that the southcentral sea otter populations present a different trophic ecology when compared to the sea otter populations in southwestern Alaska. These results shed may light on how regional ecosystems are affected by population decreases and increases within decadal time spans. This study further adds to the complexities of trophic ecology studies, specifically of a coastal keystone species such as the northern sea otter.

However, a majority of the Knight Island population in PWS can be found within a range of 2‰  $\delta^{13}\text{C}$  and 3‰  $\delta^{15}\text{N}$ . The Montague Island population has a majority within 1 ‰ carbon and 3 ‰ nitrogen. The two remaining individuals, one from Knight Island and one from Montague Island, remain close to 3‰  $\delta^{15}\text{N}$  but the Knight Island individual is more enriched in  $\delta^{13}\text{C}$ . These findings are consistent with data acquired in previous studies. Sea otters in Prince William Sound generally feed on benthic invertebrates, preying less commonly on pelagic fishes (Calkins, 1978). Further research conducted by Watt *et al.* (2000) has noted decadal shifts in

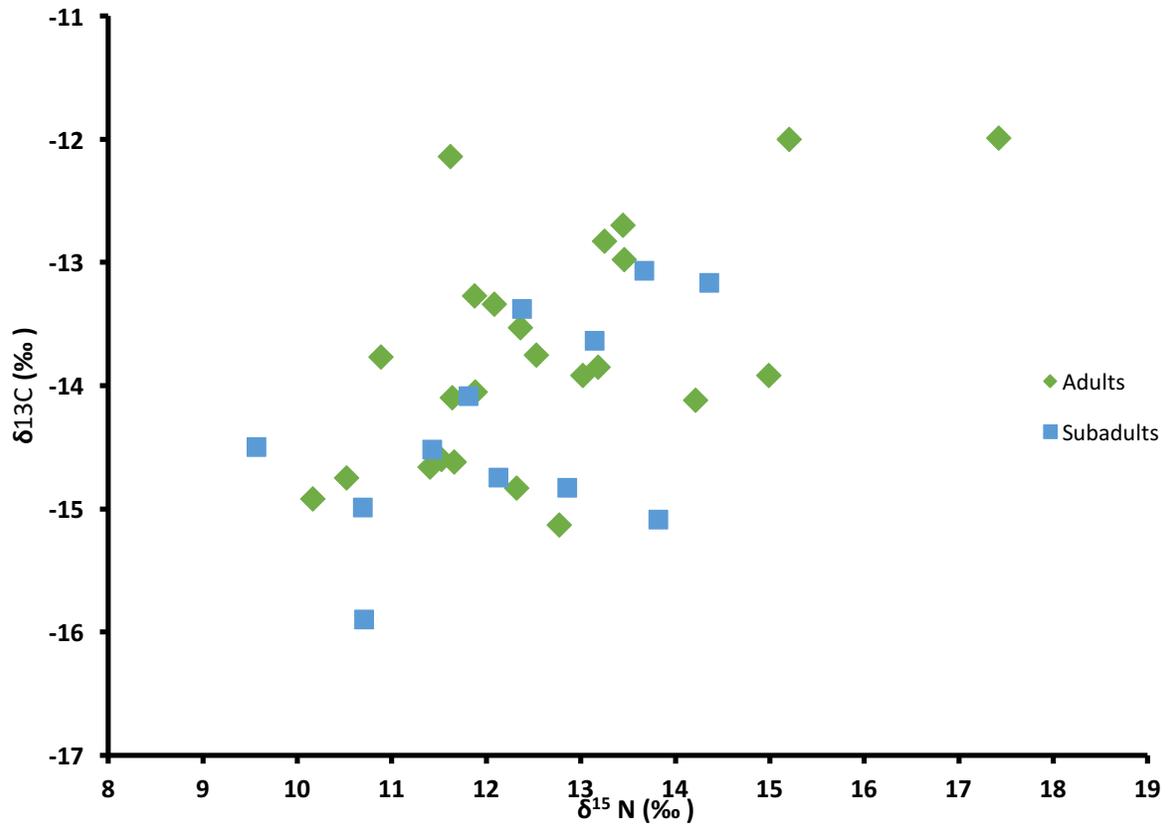
dietary preferences of PWS sea otters to be dominated by benthic invertebrates including, but not limited to, sea urchins, clams, crabs, and octopuses. Calkins (1978) further supported general foraging habits of sea otters in PWS presented by Kenyon (1969) in California, that showed mean dive times of 66 seconds. Furthermore, it was noted that males spent on average 59 seconds foraging while females spent 61 seconds foraging, a non-significant differences in forage times. Continued general foraging habits of sea otters in PWS include consuming of entire prey species such as octopuses and clams. Some larger clams are first broken open with a large stone and then consumed (Calkins, 1978). Interestingly, Larson *et al.* (2013) found that sea otters in PWS tend to rarely consume sea cucumbers, while they are seen as a minor importance to sea otters in southwestern Alaska. Recent studies show that sea otters in PWS are proficient in digging-up buried benthic invertebrates and thus do not rely on a heavy pelagic fish diet (Watt *et al.*, 2000). Overall, sea otters are opportunistic feeders though regional variations are noted.

There is no clear pattern between the Alaska Peninsula and Aleutian otter populations, however; 66% of the Peninsula otters are found within 1‰  $\delta^{13}\text{C}$ . and 3‰  $\delta^{15}\text{N}$ . Although both locations are predominately soft bottom the Peninsula otters also have a wider range in nitrogen isotopes suggesting a more pelagic foraging strategy. In general, southwestern Alaska sea otter populations have declined 56-68% since the mid-1980s (Burn *et al.*, 2005). This overall decline in sea otter populations has implication for sea otter foraging and dietary behaviors and preferences that are in contrast to sea otter populations in southcentral Alaska (PWS). For example, Evans *et al.* (1997) noted the keystone effect of the norther sea otter in the Aleutian Archipelago. That is, when sea otter populations were high, sea urchin populations were low and kelp forests were numerous along the coastline. As such, pelagic fishes were also abundant and due to the opportunistic nature of sea otters, a fish-dominated diet was common (Evans *et al.*, 1997). In more recent years, and corresponding with a decline in sea otter numbers, Watt *et al.* (2005) demonstrated a shift in foraging dynamics. Sea otters would feed on benthic organisms to satisfy dietary requirements. As southwestern sea otter populations have recently begun to equilibrate, fish abundance has slightly increased leading to an historic fish-dominated diet and foraging behavior. An interesting point noted by Watt *et al.* (2005) was that although kelp forests generally exist in soft-bottom environments, southwestern sea otter populations fed substantially less on benthic organisms and even were less successful in foraging buried prey items than their southcentral counterparts.

## Age

Adult sea otters comprised 66% of the study animals while 33% were subadult. The  $\delta^{13}\text{C}$  for all study adults ranged from  $-15.13 \pm 0.45$  to  $-11.99 \pm 0.76$  and  $\delta^{15}\text{N}$  ranged from  $10.16 \pm 0.23$  to  $17.42 \pm 0.31$ . The  $\delta^{13}\text{C}$  values for subadults ranged from  $-15.90 \pm 0.22$  to  $-13.07 \pm 1.39$  and  $\delta^{15}\text{N}$  ranged from  $9.57 \pm 1.15$  to  $14.36 \pm 0.91$  (Table 1). No significant difference in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was found based on age class between southcentral and southwestern Alaska (*ANOVA*:  $df = 1$ ,  $F = 3.3195$ ,  $p = 0.0773$ ;  $df = 1$ ,  $F = 0.5891$ ,  $p = 0.4481$ ; *MANOVA*:  $df = 1$ ,  $F = 1.6642$ ,  $p = 0.2048$ ; Figure 7). Within Prince William Sound no significant difference for age class was found between Knight Island and Montague Island (*MANOVA*:  $df = 1$ ,  $F = 1.4072$ ,  $p = 0.267$ ). Additionally, no significant difference based on age class was found between the Alaskan Peninsula and the Aleutian Islands (*MANOVA*:  $df = 1$ ,  $F = 0.7299$ ,  $p = 0.5058$ ).

Roughly 58% of the adults lie within the two trophic levels. Almost half of the subadults (42%) lie within the two trophic levels. Furthermore, about 47% of the sea otters that fell outside the range of the two trophic levels were from the southwest region. General trends in sea otter population declines and increases have led to common prey items consumed across all ages post-weaning (Watt *et al.*, 2000; Burek *et al.*, 2005). As these results have shown, there are no significant differences in foraging habits between age classes of sea otters regardless of location. Therefore, it is suggested that adult and subadult sea otters within their respective regional populations feed on common prey items. Research by Watt *et al.* (2000) and supported by Garlich-Miller *et al.* (2018) noted dietary shifts associated with kelp forest abundance linked to sea otter population numbers, affecting all ages post-weaning. Additionally, evidence shows seasonal variations can induce dietary shifts. For example, from early-summer to mid-winter benthic invertebrates are common prey, while late-winter and spring foraging shifts to pelagic fish (Watt *et al.*, 2000). Findings in this study have supported evidence that in southwestern Alaska sea otter populations, pelagic fish were preferentially consumed in the 1990s, though recent research has suggested that another shift from pelagic fish to benthic invertebrates may be occurring in southwestern Alaska (Reisewitz *et al.*, 2005).

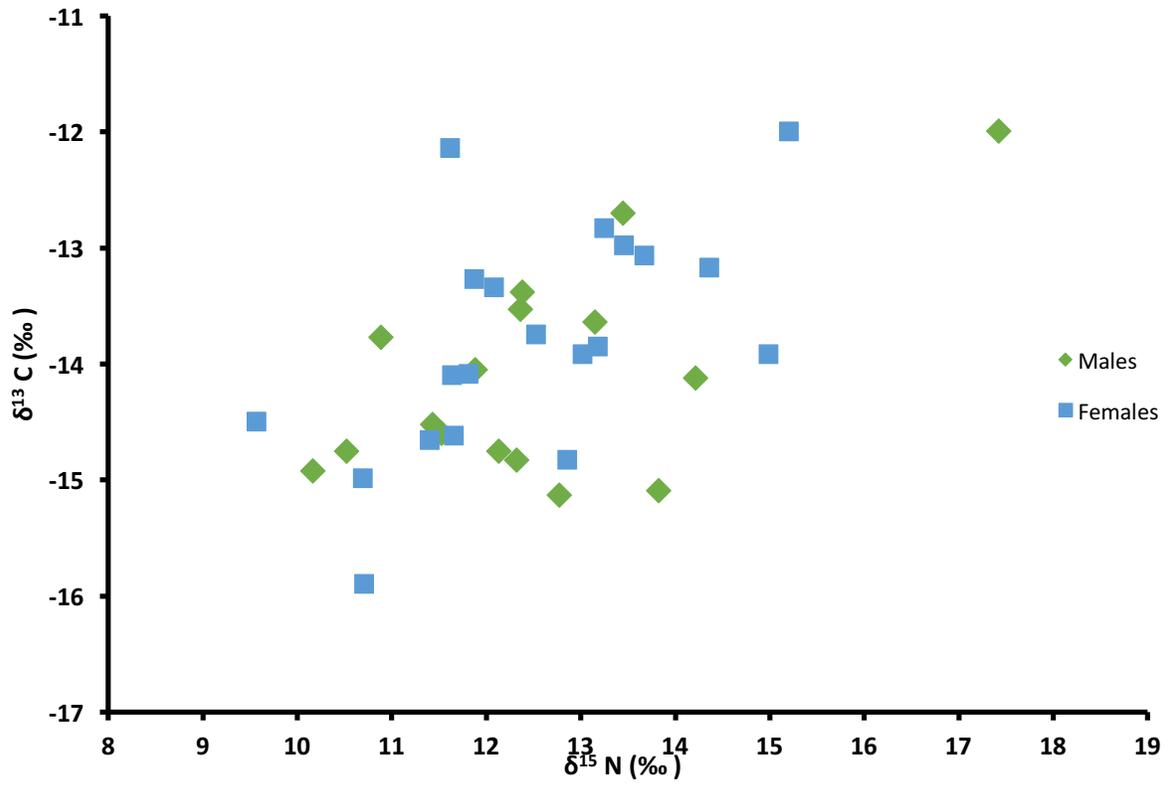


**Figure 7.** Isotope variation in sea otter samples based on age class in southern Alaska.

## Sex

Male sea otters comprised 44% of the study animals while 55% were female. The  $\delta^{13}\text{C}$  values for males ranged from  $-15.13 \pm 0.45$  to  $-11.99 \pm 0.76$  and  $\delta^{15}\text{N}$  values ranged from  $10.16 \pm 0.23$  to  $17.42 \pm 0.31$ . Female otter values ranged from  $-15.90 \pm 0.22$  to  $-12.00 \pm 0.58$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranged from  $9.57 \pm 1.15$  to  $15.20 \pm 0.87$  (Table 1). No significant differences in either  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , or combined, were found between sex between southcentral and southwestern Alaska (*ANOVA*:  $df = 1$ ,  $F = 0.99$ ,  $p = 0.3268$ ;  $df = 1$ ,  $F = 0.0075$ ,  $p = 0.9316$ ; *MANOVA*:  $df = 1$ ,  $F = 0.8178$ ,  $p = 0.4501$ ; Figure 8). Within Prince William Sound No significant sex differences were identified between Knight Island and Montague Island (*MANOVA*:  $df = 1$ ,  $F = 0.2473$ ,  $p = 0.7831$ ) or between the Alaskan Peninsula and the Aleutian Islands (*MANOVA*:  $df = 1$ ,  $F = 1.0226$ ,  $p = 0.3979$ ; Figure 8).

Principal component analysis revealed 25% of all female and 20% of all male sea otters isotopically fell within 1‰  $\delta^{13}\text{C}$  and 3‰  $\delta^{15}\text{N}$ , and 50% of females and 75% of males fell within 2‰  $\delta^{13}\text{C}$  and 3‰  $\delta^{15}\text{N}$ . Female otters have a predominantly wider range in  $\delta^{13}\text{C}$  while a wider range in  $\delta^{15}\text{N}$  is exhibited by male otters. One possible explanation for this may be that females tend to feed more predominantly on benthic organisms while males are feeding on more pelagic organisms. Female sea otters generally have a single pup at a time and will continuously nurture that single pup until it is weaned. A mother sea otter will only leave her pup unattended when she dives to forage, up to at most two minutes. Therefore, it is logical to suggest that mother sea otters would preferentially feed on benthic organisms as to remain as near to her pup as possible. In contrast, male sea otters have no obligation to care for pups and thus could embark on farther forage trips, including pelagic fishing. Results from this study loosely support this notion that mother otters may generally feed on benthic invertebrates, though more data is needed to further support this hypothesis. Weaning of sea otter pups takes three to six months (Burek *et al.*, 2005) and during this time the pup is close to its mother learning social behaviors as well as foraging techniques (Jefferson *et al.*, 2015). Post-weaning, sea otter pups are endowed with these lifestyle and survival skills including how to interact within a community raft, and what prey items present the greatest metabolic reward. The learned skills and prey identification of sea otter pups varies based on regional differences as seen with previous research and the results of this study (Reisewitz *et al.*, 2005).



**Figure 8.** Isotope variation in sea otter samples based on sex in southern Alaska.

## Conclusion

The results of this study showed distinct regional differences in stable carbon and nitrogen isotope ratios, and thus trophic ecologies, within sea otter populations between southcentral Alaska and southwest Alaska. Sea otters in Prince William Sound had a significantly different stable carbon and nitrogen content than sea otters from the Aleutian Archipelago and the Alaskan Peninsula.

- Overall, a significant effect of location on stable carbon and nitrogen isotope ratios was observed between southcentral Alaskan sea otter populations and southwest Alaskan sea otter populations. This distinction between trophic ecologies supports previous observations that sea otters in southcentral Alaska generally consume more benthic-invertebrate heavy diet due to a rocky-bottom environment (Esslinger *et al.*, 2014). By contrast, southwestern sea otters consume more pelagic organisms given the soft-bottom sediments and relatively abundant kelp forests (Estes and Bodkin, 2002).
- No significant isotopic differences were found within sea otter populations in both southcentral and southwestern Alaska. This is likely because these populations of sea otters consume similar prey items and thus do not differ significantly in stable carbon and nitrogen isotope content.
- Age class was not a significant factor in determining trophic differences between regions and within sea otter populations. This is most likely due to the fact that following a weaning period of 3-6 months, sea otter pups, and thus subadult sea otters, are endowed with the hunting skills required to feed on similar prey items as adult sea otters (Burek *et al.*, 2005).
- Lastly, sex had no significant effect on stable carbon and nitrogen isotope content in determining differences in trophic ecologies between regions and also within sea otter populations. A possible explanation for this result is similar to that of the age class comparison; female and male sea otters tend to have similar diets within regional trophic ecologies. Though a wider range in stable carbon within females may also suggest that at some point, females feed on a more benthic invertebrate-rich diet than males; however, this is a non-significant phenomenon.

This study compared stable carbon and nitrogen isotope ratios from vibrissae within 36 sea otter individuals from two regions in southern Alaska, and is the first to make trophic comparisons between two sea otter populations. Distinct differences were noted based on location, primarily between the two regions in southern Alaska, Prince William Sound (southcentral) and the Aleutian Archipelago and the Alaskan Peninsula (southwest). The results presented here illustrate the importance of considering regional variations in determining trophic ecology differences within a species, which is crucial for future research in understanding how stable isotope analysis can assess trophic dynamics within a species.

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