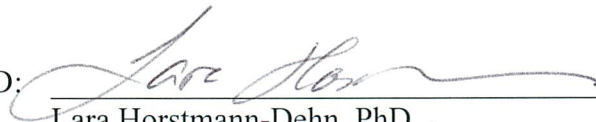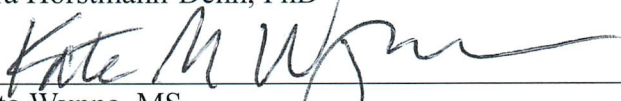VARIABILITY IN FORAGING BY HUMPBACK WHALES (*MEGAPTERA NOVAENANGLIAE*) ON THE KODIAK, AK, FEEDING GROUND

By

Dana Louise Wright
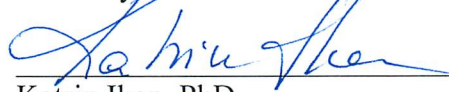
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Lara Horstmann-Dehn, PhD

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Kate Wynne, MS
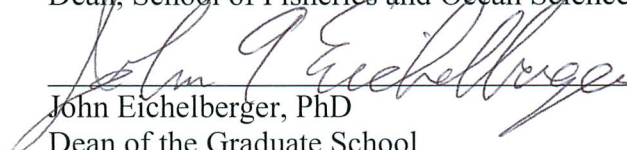
_____
Terrance Quinn II, PhD

_____
Briana Witteveen, PhD
Advisory Committee Chair

_____
Katrin Iken, PhD
Head, Graduate Program in Marine Sciences and Limnology

APPROVED: _____
Michael Castellini, PhD
Dean, School of Fisheries and Ocean Sciences

_____
John Eichelberger, PhD
Dean of the Graduate School

_____
12/8/14
Date

VARIABILITY IN FORAGING BY HUMPBACK WHALES (*MEGAPTERA NOVAENANGLIAE*) ON THE KODIAK, AK, FEEDING GROUND

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Dana Louise Wright, B.S.

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Abstract

The North Pacific humpback whale (*Megaptera novaeangliae*) population has been growing rapidly following a moratorium on commercial whaling in 1986. Knowledge of humpback whale foraging on feeding grounds is becoming increasingly important as the growing population consumes more prey, including economically important commercial fishes. The goal of this thesis is to better understand how marine resources are shared among the growing humpback whale population and sympatric apex predators, including western Steller sea lions (SSLs; *Eumetopias jubatus*), on the Kodiak, AK, feeding ground. To address this, we explored spatial and temporal (inter-annual and within-feeding season) variability in summer foraging by humpback whales along the eastern side of the Kodiak Archipelago as described by stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios of humpback whale skin ($n = 118$; 2004 – 2013). We found evidence for the existence of two sub-aggregations of humpback whales ('North', 'South') on the feeding ground that fed at different trophic levels (TLs) throughout the study period. Bayesian stable isotopic mixing models were applied to describe the proportional contribution of prey species to the diet of humpback whales for the two regions. The 'North' region humpback whale sub-aggregation consumed a mixed diet of euphausiids and forage fishes, whereas the 'South' region sub-aggregation foraged predominantly on euphausiids. Results from these analyses were compared to diet composition of Kodiak SSLs of the recovering western SSL population estimated from fecal samples ($n = 656$; 2000 – 2005), to explore spatial differences in the degree of overlap in trophic niche between these predators. Western SSLs underwent a marked population decline starting in the late 1970's and have shown slow and variable signs of recovery. Regional

variability in SSL and humpback whale diets resulted in a higher degree of overlap in trophic niche, although not biologically significant ($O_{jk} < 0.60$), for individuals in the 'North' region compared with the 'South'. However, humpback whale consumption appears to overlap considerably with multiple piscivorous fishes that are prominent prey for SSLs, and thus, consumption by humpback whales may indirectly impact the prey resources of SSLs. Therefore, this study highlights the complexity of the Kodiak ecosystem and suggests consumption by an increasing population of humpback whales has the potential to indirectly impact the recovery of SSLs on a regional scale depending on the biomass of prey species and diet composition of humpback whales in the region.

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Chapter 1: Introduction

The humpback whale (*Megaptera novaeangliae*) is a baleen whale that occurs in all major ocean basins (Clapham 2000). In general, individuals migrate between high latitude feeding grounds in summer, where they exhibit site fidelity to specific feeding aggregations, to low latitude breeding grounds in winter (Dawbin and Norris 1966, Rice 1978, Straley *et al.* 1994, Calambokidis *et al.* 1996, Zerbini *et al.* 2006, Witteveen *et al.* 2007). While migrating and on the breeding grounds, individuals fast or feed minimally, relying on fat stores accrued while on the feeding grounds for sustenance (Lockyer 1981). Therefore, foraging by humpback whales at higher latitudes is critical to an individual whale's reproduction and survival.

Humpback whales are mechanistic filter feeders that use large baleen plates to sieve aggregate fish and zooplankton species before swallowing (Nemato 1970, Hain *et al.* 1981). This mode of feeding has a high energetic cost (Goldbogen *et al.* 2011), and thus individuals are generalists in their consumption, feeding on regionally aggregate prey above a threshold density to ensure positive net energy gain from the feeding event (Dolphin 1988, Piatt and Methven 1990). As a result, the abundance, distribution, and species of prey present on a feeding ground will highly influence which prey species are targeted and consequently the trophic competitive interactions among predators in a system. Therefore, the foraging ecology of humpback whales likely differs across feeding aggregations and should be studied regionally.

The Kodiak Archipelago, located in the Gulf of Alaska (GOA; Fig. 1.1), is a hydrographically complex and productive region (Kendall *et al.* 1980, Stabeno *et al.* 2004). Kodiak waters seasonally support a wide variety of predator species including marine mammals, birds, and piscivorous fishes (Harris and Hartt 1977, Anderson *et al.* 1997, Waite *et al.* 1999, Spalinger 2006, McKenzie and Wynne 2008, Witteveen *et al.* 2012). In addition, commercial

and subsistence fisheries annually remove large volumes of fishes, including walleye pollock (*Gadus chalcogrammus;* hereafter 'pollock') and various salmon species (*Oncorhynchus* spp.; Hartill *et al.* 2013). Prey consumption by sympatric predators in the region may directly or indirectly impact culturally and commercially important fish stocks depending in part on the volume of prey consumed in relation to the biomass of available prey species. In regions where predators consume the same species, local competition may occur if predator populations increase in abundance and limit the biomass of prey species (Connell 1961).

North Pacific humpback whales have undergone substantial population fluctuations over the past several decades due to targeted commercial harvest and recovery. Baleen whales, including humpback whales, were harvested throughout the North Pacific in the early-20th century resulting in near extinction of their populations (Rice 1978). Illegal Soviet whaling also occurred from 1948 – 1987. During that time period almost twice the recorded catch of humpback whales were illegally harvested in the North Pacific (Ivashchenko *et al.* 2013). Pre-whaling numbers for humpback whales in the North Pacific were estimated between 15,000 – 20,000 animals (Rice 1978). Prior to the moratorium on whaling that occurred in 1986, humpback whales in the North Pacific may have been reduced to as few as 1,000 animals (Perry *et al.* 1990). Following the moratorium in 1986, the North Pacific population has increased and is now estimated between 18,000 - 21,000 animals (Barlow *et al.* 2011, Baker *et al.* 2013).

Multiple other fish and marine mammal species within the GOA have also experienced extensive population fluctuations throughout the 20th century (Anderson and Piatt 1999). Gadid and flatfish populations in the GOA, such as pollock and arrowtooth flounder (*Atheresthes stomias*), began to increase in the late 1970's (Anderson *et al.* 1997). Soon after, small pelagic fish species, including Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*) declined

(Anderson *et al.* 1997, Mueter and Norcross 2000). In addition to these fish species, one of the most substantial changes in abundance has been seen in the western Steller sea lion (SSL; *Eumetopias jubatus*) population segment (west of Cape Suckling, AK), which declined by ~ 85 % between the early 1970's and 2000 and has shown slow and variable signs of recovery (Fritz *et al.* 2013).

Many hypotheses have been proposed to explain the recorded population fluctuations in the GOA, but most studies suggest that variations in oceanographic conditions play a role (Mueter and Norcross 2000, Trites *et al.* 2007). Some of these population changes may have been influenced, at least in part, by changes in balaenopterid abundance (Merrick 1997). Stomach-content analysis of humpback whales harvested in the late 1930's indicate that whales in the Kodiak region foraged heavily on euphausiid species and surf smelts (*Hypomesus pretiosus*; Thompson 1940). Euphausiids are prominent prey for multiple species of piscivorous fishes at early life stages (*e.g.*, arrowtooth flounder; Knoth and Foy 2008) and forage fishes during all life stages (Livingston *et al.* 1993, Yang and Nelson 2000). Kodiak humpback whales are estimated to consume 370 kg/day (Witteveen *et al.* 2006), and thus, predation by humpback whales on large quantities of euphausiids in pre-whaling conditions may have impacted recruitment levels of piscivorous and forage fish species at multiple life stages in this region. Growth in forage fish populations may have continued to support increasing piscivorous fish populations at later life stages resulting in reduced forage fish numbers (Merrick 1997). This top-down fish predation hypothesis is supported by the finding that Kodiak demersal fish communities in most regions appear to have increased in abundance from 1980-1982 prior to a decrease in shrimp and forage fish communities starting in 1981, suggesting predation by piscivorous fishes resulted in decreased forage fish numbers (Mueter and Norcross 2000).

The continued recovery of the North Pacific humpback whale population has undoubtedly resulted in their increased demand for aggregate prey species in the Kodiak region. In turn, the recovery has likely influenced trophic interactions around the archipelago. The Gulf Apex Predator-prey (GAP) study was initiated in 1999 by University of Alaska, Fairbanks, researchers stationed in Kodiak with the goal to better understand trophic interactions among sympatric apex predators within the Kodiak Archipelago while simultaneously collecting data on prey distribution and abundance. Past GAP efforts include identifying regional differences in SSL diet compositions, investigating the physiology of piscivorous fish species, and exploring potential linkages between foraging and reproduction in a variety of seabird species (*e.g.*, Hanna *et al.* 2008, McKenzie and Wynne 2008, Williams *et al.* 2008). GAP studies have also investigated broad aspects of Kodiak humpback whale diets and recorded annual variability in consumption of forage fishes and euphausiids (Witteveen *et al.* 2006, 2012). However, studies have not explored variability in diet composition or trophic level of humpback whales in the Kodiak region on fine temporal or spatial scales nor compared their diet to those of other predators. Understanding fine-scale variability in foraging by Kodiak humpback whales is becoming increasingly important as the population continues to recover from commercial whaling and consume ecologically important prey species (Calambokidis *et al.* 2008, Witteveen *et al.* 2012).

It is inherently difficult to study the diet of humpback whales due to their mobility and time spent under the water's surface. Traditional methods to estimate marine mammal diets have relied on gut content analysis, fecal samples, or direct observations of foraging events (Nemato 1957, Mann 1999, Parsons *et al.* 1999). Obtaining cetacean gut content data *in situ* from feces, subsistence harvests, or strandings is possible (Clarke 1996, Santos *et al.* 2001, Parsons *et al.*

2003, Horstmann-Dehn *et al.* 2012), but the diet data are limited to recently consumed prey items and may be influenced by differential digestion rates of prey items (Carss and Parkinson 1996). Similarly, direct observations of foraging events are also opportunistic and may be biased by foraging behavior for specific prey species (Mann 1999). Analysis of stable isotope ratios of animal tissues is becoming a popular method for investigating the trophic position or diet of marine mammals (Newsome *et al.* 2010). Stable isotopes are stable variants of an element with differing numbers of neutrons (*e.g*, ^{14}N, ^{15}N; Hobson and Wassenaar 1999). The preferential incorporation of the lighter isotope in thermodynamic and physiochemical reactions (*e.g*., urea production, photosynthesis) results in isotopic differences, or fractionation, between the source (prey) and product (consumer; DeNiro and Epstein 1978, 1981, Minagawa and Wada 1984). The stability and presumably predictable incorporation of stable isotope ratios in tissues makes stable isotope analysis (SIA) an appropriate tool for food web studies (Peterson and Fry 1987, Hobson and Wassenaar 1999).

Different stable isotope elements provide unique information about the life history of a consumer. Stable nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) and carbon ($^{13}C/^{12}C$; $\delta^{13}C$) isotope ratios yield insight into relative trophic position and location of foraging (DeNiro and Epstein 1978, Hobson and Wassenaar 1999, Post 2002). Following consumption, a consumer's tissues become enriched in ^{15}N relative to ^{14}N (~3 ‰ per TL) due to preferential incorporation of ^{14}N in biochemical reactions (Minagawa and Wada 1984). Thus, $\delta^{15}N$ values of tissue samples can be used as a proxy of the relative trophic position of a consumer (Hobson *et al.* 1994, Post 2002). These data can then be used with basal food web $\delta^{15}N$ data to estimate the trophic level (TL) of foraging of a consumer, and the TL results can be compared across food webs (Post 2002). Stable carbon isotope patterns result primarily from processes associated with photosynthesis and ratios

increase minimally with each TL (~1 ‰; DeNiro and Epstein 1977, 1978, Farquhar *et al.* 1989). As a result, $\delta^{13}C$ values are often used to describe location of foraging (*e.g.*, marine inshore *vs.* offshore habitats; Fry 1981, Rau *et al.* 1982, Hobson *et al.* 1994, Horstmann-Dehn *et al.* 2012).

The composition of stable isotopes present in an animal's tissue reflects the isotopic composition of its assimilated diet (DeNiro and Epstein 1977, Rau *et al.* 1982, Fry and Sherr 1984). Therefore, stable carbon and nitrogen isotope ratios can be used to estimate a consumer's diet composition using stable isotope mixing models (SIMMs; Phillips and Gregg 2003, Hall-Aspland *et al.* 2005, Phillips *et al.* 2005). Initial SIMMs were used in systems involving a single consumer (or a single mean of multiple consumers) that yielded a linear system with one solution by limiting the number of sources to one more than the number of stable isotopes used (Phillips and Gregg 2001). While informative, this simple model framework does not account for variability in source, consumer, or stable isotope discrimination values (Phillips and Gregg 2001, 2003). In addition, this framework is not applicable in complex food webs, where multiple sources may comprise the consumer's stable isotope composition (Phillips and Gregg 2003, Phillips *et al.* 2005). Model advancements relaxed the limitation with regard to the number of sources (Phillips and Gregg 2001, 2003), and recently, Bayesian modeling has been implemented to allow for probability distributions of dietary proportions, while accounting for variability in source, product, and stable isotope discrimination values (Moore and Semmens 2008, Parnell *et al.* 2010). Therefore, SIMMs can now better model generalist predator diets, such as those of the humpback whale. The ability to re-create diet compositions of cetaceans makes it possible to quantify and assess the degree of overlap in trophic niche among sympatric species (Parnell *et al.* 2010).

In ecology, the term 'niche' is often considered an '*n*-dimensional hypervolume' (Hutchinson 1957) defined by all the resources exploited by a population that is in practice impossible to quantify. However, niche provides a useful conceptual framework when investigating trophic interactions among species in a system. Following niche theory, the successful coexistence of sympatric species depends on the species' ability to differ along other niche axes, for instance temporal avoidance or diet differences (MacArthur and Pianka 1966, Siemers and Schnitzler 2004). Thus, it is of interest to investigate the degree of overlap in trophic niche among sympatric apex predators on the Kodiak feeding ground.

Humpback whales and SSLs are both generalist predators that are recovering from population declines in Kodiak waters (Pendleton *et al.* 2006, Calambokidis *et al.* 2008, Fritz *et al.* 2013). Distinct morphological adaptations of these species translate into distinct feeding strategies, often targeted at different prey species (Nemato 1957, Pitcher 1981, Goldbogen *et al.* 2011). Separate studies on the diet composition of humpback whales and SSLs in the Kodiak region show differences in the dominant prey species consumed (McKenzie and Wynne 2008, Witteveen *et al.* 2012). However, these studies also indicate the potential for shared prey resources between these predators, including schooling forage fishes and early life stage piscivorous fish species. It is unknown what impacts the differential population recovery of humpback whales and SSLs will have to sympatric species in the region as well as to each other. An average Kodiak humpback whale can consume 370 kg prey/day (Witteveen *et al.* 2006), whereas a GOA SSL only needs 18 kg/day (Winship and Trites 2003). Therefore, consumption by humpback whales may impact the recovery of SSLs depending on their population growth and the degree of overlap in diet between both predators. A quantified measure of regional diet

overlap between humpback whales and SSLs is needed to investigate potential impacts of recovering predator populations to the Kodiak region on a fine scale.

Thesis objectives

The goal of this thesis is to understand how resources are shared between two sympatric marine mammal species around the Kodiak Archipelago (Fig. 1.1), and how this may be impacted by a growing humpback whale population. Chapter 2 explores temporal and spatial variability in the trophic level (TL) of humpback whales sampled along the eastern side of the Kodiak Archipelago between 2004 – 2013 using stable isotope analysis (SIA). Chapter 2 shows the utility of SIA in exploring the existence of sub-aggregations of humpback whales on a feeding ground. This information can be combined with fine-scale TL data collected on other humpback whale feeding aggregations in the North Pacific to better understand the foraging ecology of North Pacific humpback whales on their respective feeding grounds. Methodology used in this chapter can be applied to future foraging studies to discern spatial and temporal variability in the TL of a generalist consumer.

Chapter 3 utilizes the regions defined in Chapter 2 to explore spatial variability in the diet composition of Kodiak humpback whales and Steller sea lions (SSLs) along the eastern side of the Kodiak Archipelago. Chapter 3 also uses the Pianka niche overlap index (Pianka 1974) to quantify the degree of overlap in trophic niche (O_{jk}) between humpback whales and SSLs. Results from these analyses can be used with prey data of other sympatric marine mammal and their prey collected in the Kodiak region to increase the resolution of trophic interactions and prey removal estimation in the Kodiak region.

Finally, Chapter 4 discusses how this study contributes to the understanding of shared prey resources among sympatric marine mammals in the Kodiak region, addresses the limitations

of the study, and suggests areas of future research. This thesis represents the first attempt to explore the ecological implications of fine-scale variability in foraging by humpback whales on a feeding ground in the North Pacific. Results from each chapter combine to provide new insight into spatial variability in diet of humpback whales and SSLs on the Kodiak feeding ground. These data will help unravel the complex trophic interactions involving endangered species, their recovery, and economically important fish stocks in the Kodiak region.

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Figure
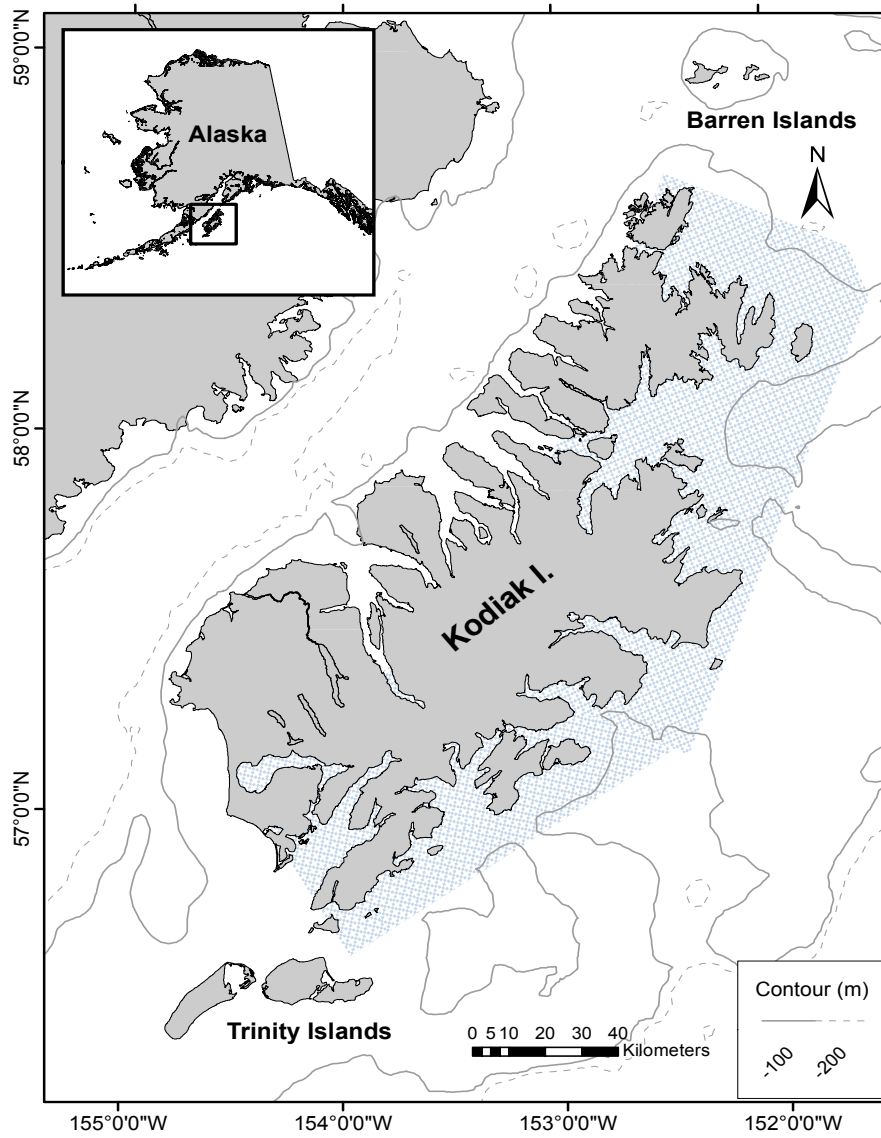
Figure 1.1 Map of the Kodiak Archipelago including the study area (blue crosshatch).

Chapter 2: Variability in foraging by humpback whales on the Kodiak, AK, feeding ground revealed from stable isotope analysis[1]

Abstract

Knowledge of humpback whale (*Megaptera novaeangliae*) foraging on feeding grounds is becoming increasingly important as the growing North Pacific population continues to recover from commercial whaling and consume more prey, including economically important fishes. We explored spatial and temporal (inter-annual; within-season) variability in summer foraging by humpback whales along the eastern side of the Kodiak Archipelago as described by stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios of humpback whale skin ($n = 118$; 2004 – 2013). The trophic level (TL) of individual whales was calculated using basal food web δ^{15}N values collected within the study area. We found evidence for the existence of two sub-aggregations of humpback whales ('North', 'South') on the feeding ground that fed at different TLs throughout the study period. Linear mixed models suggest that within an average year, Kodiak humpback whales forage at a consistent TL during the feeding season. TL estimates support mixed consumption of fish and zooplankton species in the 'North' (mean ± SE; 3.3±0.1) and predominant foraging on zooplankton in the 'South' (3.0±0.1). This trend appears to reflect spatial differences in prey abundance, and thus, our results suggest North Pacific humpback whales may segregate on feeding aggregations and target discrete prey species.

Introduction

Humpback whales (*Megaptera novaeangliae*) are balaenopterid cetaceans found in all major ocean basins (Dawbin and Norris 1966, Clapham 2000). In the North Pacific, humpback whales feed primarily during summer months (June – October) in discrete aggregations from California to the Chukchi Sea, before migrating to lower latitudes, including Hawaii and Mexico, to breed and give birth over the winter (Dawbin and Norris 1966, Urban *et al.* 2000, Calambokidis *et al.* 2001, Mizroch *et al.* 2004). During migration and on the breeding grounds, humpback whales fast or feed only minimally, relying on fat stores accrued while on the foraging grounds for sustenance (Dawbin and Norris 1966, Lockyer 1976). Therefore, foraging by humpback whales at higher latitudes is critical to the success of humpback whale populations.

Through long-term (> 10-yr) photo-identification studies, researchers have revealed inter-annual site fidelity by humpback whales to specific feeding regions in the Gulf of Alaska (GOA), including the Kodiak Archipelago (Calambokidis *et al.* 1996, Baker *et al.* 1998, Waite *et al.* 1999, Witteveen *et al.* 2007, 2011). The Kodiak Archipelago is one of the most productive regions in the GOA, supporting multiple marine predator and prey species (Kendall *et al.* 1980, Stabeno *et al.* 2004). Many species in the Kodiak region, including humpback whales, have undergone extensive population fluctuations across the past few decades (Piatt and Anderson 1996, Anderson *et al.* 1997, Anderson and Piatt 1999). Humpback whales were harvested throughout the North Pacific in the early 20th century, but have experienced considerable recovery following the moratorium on commercial whaling beginning in 1986 (Zerbini *et al.* 2006, Calambokidis *et al.* 2008, Barlow *et al.* 2011). It is unknown what effect the population recovery will have on the trophic dynamics of the Kodiak ecosystem.

Studies have investigated broad aspects of humpback whale diet in Kodiak waters

(Witteveen *et al.* 2006, 2012). These studies support previous work that concluded humpback

whales are generalist consumers that feed on a variety of forage fish and zooplankton species

(Nemato 1957, 1959, Hain *et al.* 1981, Krieger and Wing 1984). Witteveen *et al.* (2012)

described appreciable annual variability in Kodiak humpback whale foraging on euphausiids,

walleye pollock (*Gadus chalcogrammus*; hereafter 'pollock'), capelin (*Mallotus villosus*), and

Pacific sand lance (*Ammodytes hexapterus;* hereafter 'sand lance') in 2004 – 2006. However,

studies have not explored variability in trophic level (TL) of Kodiak humpback whales on fine

temporal or spatial scales. Understanding variability in foraging by humpback whales on finer

scales within the Kodiak feeding ground could yield insight into regional differences in prey

availability or foraging behavior, which will become useful as the increasing population

consumes proportionally more prey biomass.

Spatial variability in the prey species consumed by humpback whales around the

archipelago has been observed during boat surveys, but these observations are temporally limited

(Gulf Apex Predator-prey (GAP) study, NOAA, Kodiak, AK, unpubl. data). Studying cetacean

foraging using stomach content analysis or fecal samples is difficult to undertake and may be

biased when undertaken (Norris 1961, Parsons *et al.* 1999). Measuring the ratio of stable

nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, $\delta^{13}C$) isotopes from tissue samples has proven an

effective and widely-used tool to explore aspects of predator foraging ecology (Todd *et al.* 1997,

Hobson and Schell 1998, Hobson 1999, Hobson and Wassenaar 2008, Todd *et al.* 2009,

Newsome *et al.* 2010, Horstmann-Dehn *et al.* 2012, Witteveen *et al.* 2012). Following

consumption, a consumer's tissues become enriched in ^{15}N relative to ^{14}N (~3 ‰ per TL) due to

preferential incorporation of ^{14}N in biochemical reactions (Minigawa and Wada 1984). Thus,

$\delta^{15}N$ values of tissue samples can be used as a marker to determine the relative trophic position

of a consumer in a food web (Minagawa and Wada 1984, Hobson 1993, Hobson *et al.* 1994). The consumer $\delta^{15}N$ data can be combined with basal food web $\delta^{15}N$ data to estimate the TL of the consumer and consequently compare consumer TLs across food webs (Post 2002). Stable carbon isotope ratios yield insight into sources of primary production (Farquhar *et al.* 1989) and increase minimally with increasing TL (~1 ‰; DeNiro and Epstein 1978). Therefore, $\delta^{13}C$ values can be used as a tool to explore foraging location (*e.g.*, inshore *vs.* offshore; Fry 1981, Rau *et al.* 1982, Hobson *et al.* 1994, Horstmann-Dehn *et al.* 2012).

It has been proposed that fasting or nutritional stress of an individual can cause elevated $\delta^{15}N$ values in tissues, known as the fasting-^{15}N enrichment hypothesis (Hobson 1993). Under this hypothesis humpback whale skin $\delta^{15}N$ values should decrease linearly across the summer feeding season, reflecting a shift in diet from fasting, when individuals are essentially feeding on themselves, to foraging on prey species. However, in opposition to the fasting-^{15}N enrichment hypothesis, an increase in $\delta^{15}N$ values during feeding periods and a decrease with fasting periods has been recorded for multiple mysticete species for both baleen and muscle tissues (Best and Schell 1996, Summers *et al.* 2006, Aguilar *et al.* 2014). This trend is hypothesized to be the combined result of changes in isoscape during migration, catabolism of lipid reserves, and reduction in excretion (Aguilar *et al.* 2014). It has been shown the time frame reflected in a consumer's tissue depends on the turnover (*i.e.*, replacement) rate of the tissue sampled, and can vary with tissue sampled, growth rate, age, and metabolism (Tieszen *et al.* 1983, MacAvoy *et al.* 2005, Browning *et al.* 2014). The turnover rate of humpback whale skin is currently unknown, but previous studies suggest a turnover of approximately 70 days for cetacean skin (Hicks *et al.* 1985, St. Aubin *et al.* 1990, Browning *et al.* 2014). Therefore, it was of interest to investigate if

humpback whale skin $\delta^{15}N$ values follow a similar trend to mysticete baleen and muscle over the feeding season.

The objective of this study was to explore the utility of stable isotope analysis (SIA) to detect regional, inter-annual, and within-season variability in foraging by humpback whales on a feeding ground. In this study, skin samples from humpback whales were grouped into sub-aggregations on the Kodiak feeding ground based on observations of foraging behavior and location of sampling. We then tested for differences in humpback whale TL between the sub-aggregations using analysis of stable nitrogen and carbon isotope ratios from the skin samples and a primary consumer, *Patinopecten caurinus*. Temporal variability in foraging was explored within the foraging season and across years. We hypothesized that significant differences in annual $\delta^{15}N$ values within the study period would reflect annual fluctuations in prey availability. We also hypothesized a positive linear trend in $\delta^{15}N$ values across the summer foraging season as has been shown for other mysticete species baleen and muscle tissues.

Methods

Field sampling

The study area encompasses the eastern side of the Kodiak Archipelago (57°48'N, 152°24'W; Fig. 2.1). Skin samples from the flank of free-ranging humpback whales were collected intermittently for stable isotope analysis (SIA) using a pneumatic-dart system with a modified 0.22 rifle from June 21st – Sept. 10th, 2004 – 2013 (Table 2.1; Fig. 2.1). The samples were kept on ice while in the field and were then transferred to 1.2 mL polypropylene cryogenic vials and stored at -80 °C until processing for SIA. This study used new (2007 – 2013) and previously published (2004 – 2006) adult and juvenile humpback whale samples (Witteveen *et al.* 2009, 2012). The date, location (latitude, longitude), role of individual (*e.g.*, mother), and

individual identification (if known) were recorded at each sampling event. Individual whales were identified by natural markings (*e.g.*, scars, pigmentation) and shape of the ventral side of the fluke (Hammond *et al.* 1990). The role of each whale was determined from body size, behavior, and associations and categorized as calf, juvenile, mother, or adult.

Stable isotope ratios propagate from phytoplankton to higher TLs through consumption (Post 2002). Thus, fluctuations in basal food web $\delta^{15}N$ values could skew the interpretation of consumer trophic position when only the consumer $\delta^{15}N$ values are considered. Including basal food web isotope data into analyses can account for basal differences and allow for comparison across food webs (Post 2002). Thus, the TL of individual Kodiak humpback whales was calculated using $\delta^{15}N$ values from their skin and a primary consumer, the weathervane scallop *P. caurinus*. Adductor muscles of the scallops were collected during Alaska Department of Fish and Game (ADG&G) annual bottom-trawl surveys. Scallops were collected from an eastern otter trawl (400-mesh) between June and August in 2009 and 2012 (Fig. 2.1), and frozen whole at -80 °C in plastic bags until processing.

Sample preparation and stable isotope analysis (SIA)

Humpback whale skin samples were prepared for SIA using the protocol defined in Witteveen *et al.* (2009). In short, the skin from each sample was separated from the blubber and diced with a razor blade before ~ 50 mg aliquots were oven-dried at 60 °C for 24 hours, defatted using a Soxhlet extractor with petroleum ether (Dobush *et al.* 1985), re-dried at 60 °C for 12-24 hours, and individually homogenized using a Wig-L-Bug amalgamator for ~ 10 s (Dentsply, model 3110B, York, PA, USA). Adductor muscles from scallops were ground using a blender before ~ 0.15 g aliquots were measured into vials and dried and defatted using the protocol above. All samples were defatted before SIA to reduce lipid bias of $\delta^{13}C$ values, because lipids

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are depleted in ^{13}C relative to bulk diet, and thus can skew stable carbon isotope measures (DeNiro and Epstein 1978). On the other hand, defatting samples can bias stable nitrogen isotope ratios toward higher $\delta^{15}N$ values (Dobush *et al.* 1985, Post *et al.* 2007), but all samples were defatted using the same solvent and extraction protocol to allow comparison of the new and previously published (Witteveen *et al.* 2009, 2012) humpback whale data.

Approximately 1 mg of homogenized, defatted sample was weighed into a 5 mm x 9 mm tin capsule. Humpback whale skin and scallop samples were analyzed for stable nitrogen and carbon isotopes using a Costech Elemental Analyzer (ESC 4010) coupled to a Finnigan MAT Delta Plus XL stable isotope ratio mass spectrometer (IRMS) at the University of Georgia Institute of Ecology Stable Isotope Laboratory. All stable nitrogen and carbon isotope ratios were reported in δ notation as per mil (‰) as determined from:

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1000 \tag{2.1}$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$ of sample and standard, respectively. A laboratory standard (bovine liver) was used to calibrate samples to international standards, atmospheric air for nitrogen and Vienna PeeDee Belemnite for carbon. Replicate measurements of $\delta^{15}N$ and $\delta^{13}C$ values were tracked using the internal laboratory standard and indicated an instrument error of < 0.2 ‰ for both $\delta^{15}N$ and $\delta^{13}C$ values of humpback whales and scallops ($n = 64$).

Statistical analysis

The locale where humpback whales were sampled was assumed to represent the location of foraging as constituted by the stable isotope ratios. Only juveniles and adults without calves were used in analyses, because $\delta^{15}N$ values of mothers may be lower due to lactation (Koch 1997, Kurle 2002, Fuller *et al.* 2004), and calf tissues may be enriched in ^{15}N from milk

consumption (Hobson and Sease 1998, Polischuk *et al.* 2001). In 2009, only one humpback whale skin sample was collected and was therefore excluded from analysis. Stable isotope ratios of individual humpback whales sampled twice within a year ($n = 4$) were averaged by individual to prevent twice-weighting animals in analyses.

The normality of the humpback whale skin $\delta^{15}N$ and $\delta^{13}C$ values and scallop adductor $\delta^{15}N$ values was tested using the Shapiro-Wilks test to determine the appropriate statistical analyses. All statistics were conducted using statistical packages within R 2.13.1 (R Development Core Team 2008) and hypothesis tests were made with a significance level of $\alpha = 0.05$. Values are presented as mean ± 1 standard error (SE).

To explore regional differences in foraging, stable isotope ratios from humpback whale samples were initially separated into three regional sub-aggregations on the Kodiak feeding ground ('North', 'East', 'South'; Fig. 2.1) based on sampling effort and previous observations of foraging behaviors. Discriminant function analysis (DFA) with jack-knifed predictions (R package 'MASS'; Venables and Ripley 2002) then predicted sub-aggregation assignment of whales using their $\delta^{15}N$ and $\delta^{13}C$ values. A χ^2 goodness of fit test was used to assess the accuracy of the sub-aggregation assignments by determining if DFA assignments were significantly different from geographic field assignments.

To explore regional and annual differences in stable isotope ratios, the following type II two-way analysis of variance (ANOVA) model was computed:

$$\delta X_{itk} = \mu + SA_i + Year_t + \gamma_{it} + \varepsilon_{itk}, \text{ where } \varepsilon_{itk} \sim N(0,\sigma^2) \tag{2.2}$$

where X is ^{15}N or ^{13}C of observation k, μ is the grand mean, SA_i is the sub-aggregation (defined from the DFA), $year_t$ is the sampling year (2004 – 2013), and γ_{it} is the interaction of SA_i and $Year_t$. Non-significant interaction terms for $\delta^{15}N$ ($F_{3,106} = 0.69$, $P = 0.56$) and $\delta^{13}C$ models ($F_{3,106}$

= 1.47, $P = 0.23$) were removed, and the models were re-run. Tukey Honest Significant

Differences *post-hoc* tests were applied to compare means (R package 'agricolae'; Mendiburu

2013).

We hypothesized that humpback whale skin $\delta^{15}N$ values would increase linearly across

the feeding season as has been shown for other mysticete species using baleen and muscle tissues

(Best and Schell 1996, Summers *et al.* 2006, Aguilar *et al.* 2014). To determine the within-

season (June – September) trend in humpback whale foraging for an average year, the following

linear mixed model (LMM) was computed:

$$\delta X_{ijk} = \mu + SA_i + a_t + \beta_1 DOY_j + \beta_2 DOY_j^2 + \gamma_{ij} + \gamma_{ij}^2 + \varepsilon_{ijk} \qquad (2.3)$$

$$\text{where } a_t \sim N(0,\sigma_t^2) \text{ and } \varepsilon_{itk} \sim N(0,\sigma^2)$$

where X is ^{15}N or ^{13}C for observation k, μ is the grand mean, SA_i is the sub-aggregation (defined

from the DFA), DOY_j is the day of sample collection, γ_{it} is the interaction of SA_i and DOY_j, β's

are regression parameters, and a_t is random effect 'year' (t = years 2004 – 2013; R package

'lme4'; Bates *et al.* 2013). 'Year' accounts for additional random factors that affect mean stable

nitrogen and carbon isotopes in a given sampling year that were not accounted for in the model

as fixed effects (*e.g.,* water temperature). Both stable isotope ratios were modeled with a

quadratic trend with DOY following exploratory generalized additive modeling (R package

'gam'; Hastie 2013). Potential spatial correlation was accounted for by using an exponential

correlation structure with nugget effect (Dormann *et al.* 2007, R packages 'maps' Brownrigg and

Minka 2013 and 'mapproj'; McIlroy *et al.* 2013). When spatial correlation structure did not

improve model fit, it was removed in preliminary analyses. Temporal autocorrelation was

addressed by reviewing all model diagnostics and looking for trends in the residuals.

It is recommended (Zuur *et al.* 2007) that for LMM models, a two-phase procedure be used: (1) fitting models using maximum likelihood (ML) estimation for model selection using AICc, and (2) fitting the lowest AICc model for each stable isotope using restricted maximum likelihood (REML) estimation. The full model, and all combinations of reduced models with the parameters, were fitted using ML estimation and compared utilizing AICc (Burnham and Anderson 2004; R package 'AICcmodavg'; Mazerolle 2012). The selected ML model for each stable isotope was defined as the model with the lowest AICc value. However, if a less parameterized model was within 2 AICc units of the selected model, then the less-parameterized model became the selected model (Burnham and Anderson 2004). Selected models were re-computed for parameter estimates using restricted maximum likelihood estimation (REML) to produce the optimal model for each isotope. When significant interaction terms occurred, a LMM was constructed for humpback whale each sub-aggregation. To determine the proportion of variability explained in LMMs, marginal and conditional R^2 values were computed using equations defined in Nakagawa and Schielzeth (2013). In short, marginal R^2 is defined as the variance explained in LMMs by the fixed effects, and conditional R^2 is the variance explained by the fixed and random effects (Nakagawa and Schielzeth 2013).

Basal $\delta^{15}N$ and humpback whale trophic level (TL)

The TL of individual Kodiak humpback whales was calculated using $\delta^{15}N$ values of humpback whale skin and *P. caurinus* adductor muscle $\delta^{15}N$ values. *P. caurinus* was utilized to derive long-term basal $\delta^{15}N$ signatures of the Kodiak region because of their long-lived, sedentary lifestyle (MacDonald and Bourne 1987, Post 2002). However, *P. caurinus* occupies the benthos and stable nitrogen isotope ratios have been shown to increase with water depth due to remineralization (Saino and Hattori 1987). Potential $\delta^{15}N$ relationships with depth or DOY

were examined with local polynomial regression fitting (LOESS) trend-lines with span = 0.75 (R package 'stats'). A Student's t-test was used to test for annual differences in scallop δ^{15}N values.

Mean regional scallop δ^{15}N values were utilized to estimate the TL of individual humpback whales in each sub-aggregation using the following equation:

$$TL = 2 + (\delta^{15}N_{\text{humpback whale}} - \delta^{15}N_{\text{scallop}})/2.8 \qquad (2.4)$$

where 2 is the assumed TL of *P. caurinus* (primary consumer) and 2.8 is the isotopic discrimination between euphausiids and fin whale (*Balaenoptera physalus*) skin (Post 2002, Borrell *et al.* 2012). This discrimination value was chosen, because it represents the only published value for skin in a baleen whale species. Only overall mean sub-aggregation TLs were formally compared using a Student's t-test, because trends in humpback whale TL estimates are representative of trends in whale δ^{15}N values (see results sub-section *Basal δ^{15}N and humpback whale trophic level (TL)*). Annual mean TLs of both sub-aggregations were still computed to visualize trends in TL of foraging across years. The mean TL for the Kodiak Archipelago feeding aggregation was determined by averaging the TL from all individual whales.

Results

A total of 118 Kodiak humpback whale skin samples were used in the analyses (Table 2.1). Of these, 98 were individually identified whales, ten of which were sampled twice during the study period (four within-year and six among years). All but two of these repeat-sampled individuals were sampled in the same aggregation. Out of the samples used in statistical analyses, the most samples were collected in 2005 (*n* = 45) and the fewest in 2008 (*n* = 3; Table 2.1). Sampling dates and sample sizes varied annually by year and sub-aggregation (Table 2.1) due to vessel time, location, and weather constraints.

Stable isotope data from humpback whale skin were normally distributed (W = 0.99, *P* =

0.92 for δ^{15}N: W = 0.98, P = 0.06 for δ^{13}C). Individual humpback whale δ^{15}N values ranged from a minimum of +11.2 ‰ (August 2005, 'North') to a maximum of +15.5 ‰ (June 2005, 'North'). Stable carbon isotope ratios ranged from a minimum of -19.2 ‰ (August 2012, 'North') to a maximum of -15.9 ‰ (July 2004, 'North').

Overall, the three-region linear DFA ('North', 'East', South') correctly assigned 54 % of whales to the sub-aggregation they were sampled in when both stable isotope ratios were used (δ^{15}N, δ^{13}C) and when δ^{15}N was the only independent variable. Zero whales were correctly identified to the 'North' region in the three-region DFA. As a result, the 'North' and 'East' regions were combined and re-named 'North' and a two-region DFA was computed for comparison ('North', 'South'; Fig. 2.1). Sixty-seven percent of individuals were correctly assigned (80/118) when two sub-aggregations were assumed ('North' 71 %, 'South' 62 %). Cross-validation class membership misclassified more animals in the 'South' sub-aggregation (DFA membership/field assignment: 45/63 for 'North'; 34/53 for 'South'). Chi-squared test resulted revealed the two-region DFA-based assignments were significantly different from field assignments (χ^2 = 13.10, n = 118, P < 0.001). Nevertheless, the two sub-aggregation assignment ('North', 'South') was used in subsequent analyses.

Results of the humpback whale δ^{15}N two-way ANOVA model indicate that the 'North' sub-aggregation mean δ^{15}N value (13.7±0.1) was significantly higher than the 'South' (13.0±0.1; $F_{1, 106}$ = 15.22, P = 0.002; Table 2.1, 2.2). Main effect 'year' was not significant ($F_{7,106}$ = 2.07, P = 0.05; Table 2.2). Results were opposite for the δ^{13}C ANOVA model: the 'North' sub-aggregation mean δ^{13}C value (-18.0±0.1) was not significantly different from the 'South' (-17.9±0.1; $F_{1,106}$ = 1.43, P = 0.23), and year varied significantly across years ($F_{7,106}$ = 11.50, P < 0.001; Table 2.2). However, no single annual mean δ^{13}C value differed significantly from all

other years as shown by *post-hoc* tests (Table 2.1). Visual inspection of sub-aggregation annual means revealed higher $\delta^{15}N$ values in the 'North' sub-aggregation for all years compared with the 'South', and higher $\delta^{13}C$ values in the 'North' sub-aggregation for all years except 2004 (Fig. 2.2). The non-significant intra-annual sub-aggregation differences may be due to low sample sizes (Table 2.1).

Five linear mixed models (LMM) were computed for the humpback whale skin $\delta^{15}N$ and $\delta^{13}C$ data to explore trends in humpback whale foraging within a feeding season (Table 2.3). The best-fit $\delta^{15}N$ LMM had only the single fixed effect 'sub-aggregation' (SA) and random effect 'year' (Table 2.3, 2.4). Fixed effect SA appeared in all $\delta^{15}N$ models (Table 2.3). In contrast, fixed effects DOY, and the interaction between SA and DOY, were not significant for any $\delta^{15}N$ models (Table 2.3). Fixed effect SA explained the majority of the variance for the optimal model (Table 2.3). Overall, the $\delta^{15}N$ LMMs suggest that $\delta^{15}N$ values in skin of Kodiak humpback whales do not follow a trend within the summer feeding season (Table 2.3, 2.4; Fig. 2.3).

The optimal $\delta^{13}C$ LMM had all three fixed effect variables (DOY, SA, γ_{it}) and the random effect 'year' (Table 2.3). The significant interaction term (t_{107}= -9.74, $P < 0.001$; Table 2.4) resulted in computation of $\delta^{13}C$ LMMs for each sub-aggregation separately (Table 2.3). Fixed effect DOY was significant for the 'South' sub-aggregation model (t_{50}= 4.20, $P < 0.001$), but not the 'North' (t_{54}= -1.35, $P = 0.18$; Table 2.4). In addition, fixed effect DOY explained most of the variance of the 'South' region model, while the random effect 'year' explained most of the variance in the 'North' (Table 2.3). Moreover, the difference between fixed effect 'year' within-year variance and among-year variance was greatest for the 'South' region (Table 2.4). These results support a positive linear trend in $\delta^{13}C$ values over the summer foraging season for the 'South' sub-aggregation (Fig. 2.3, 2.4).

Basal δ¹⁵N and humpback whale trophic level (TL)

Scallop samples were collected in more areas close to humpback whale sample collection in the 'South' region compared with the 'North' in both years (Fig. 2.1). Specifically, scallop samples were not collected nearshore South of Marmot Bay in the 'North' region. More scallop samples were collected in 2009 ($n = 101$) than 2012 ($n = 80$), and more samples were collected in the 'South' region ($n = 140$) than the 'North' ($n = 40$). Thus, trophic level estimates of humpback whales should be treated as a first approximation until more homogenous scallop sample collection occurs in both regions.

Scallop δ^{15}N values were normally distributed (W = 0.99, $P = 0.20$) and did not differ significantly between years ($t_{179} = -1.63$, $P = 0.11$; Fig. 2.2). LOESS trend-lines revealed no prominent trends between scallop δ^{15}N data and depth or DOY (Fig. 2.5). As a result, scallop δ^{15}N data were pooled across years to compare regional means. Mean scallop δ^{15}N values were identical for both regions ($+10.2\pm0.1$), indicating trends in humpback whale TL estimates are representative of trends in humpback whale δ^{15}N values in both sub-aggregations. As a result, TL SE estimates are equivalent to mean δ^{15}N SE estimates divided by 2.8 (see Eq. 2.4). SE < 0.05 are still listed as 0.1 as this is the precision of the machinery used in stable isotope analysis.

A Student's t-test revealed that the 'North' sub-aggregation mean humpback whale TL estimate (3.3 ± 0.1) was significantly higher than the 'South' TL (3.0 ± 0.1; $t_{116} = 4.99$, $P < 0.001$). Visual inspection of the data suggests higher TL of foraging in the 'North' across all years (Fig. 2.6). The overall mean TL for all samples was 3.1 ± 0.1.

Discussion

We found evidence for the existence of two sub-aggregations of humpback whales on the Kodiak feeding ground ('North', 'South') using SIA. The 'North' sub-aggregation TL estimate

(3.3±0.1) supports previous studies that conclude humpback whales in Kodiak waters consume a mixed diet of zooplankton and forage fish species (Fig. 2.6; Witteveen *et al.* 2006, 2012). In contrast, the 'South' sub-aggregation TL estimate (3.0±0.1) is similar to TL estimates of cetacean species that are thought to forage predominantly on zooplankton, such as the bowhead whale (*Balaena mysticetus*; 2.8-3.0; Hoekstra *et al.* 2002). The regional difference in humpback whale TL support field observations that documented humpback whale feeding on forage fish species in the 'North' region (Witteveen *et al.* 2008) and swarms of euphausiids in the 'South' region (GAP, unpubl. data). These findings are supported by stable isotope data of euphausiids and forage fish species from the Kodiak region. Kodiak euphausiids had lower $\delta^{15}N$ values compared with forage fish species around the Kodiak Archipelago that are prey of humpback whales (Witteveen *et al.* 2012). Therefore, the recorded difference in humpback whale foraging between sub-aggregations may reflect variability in prey assemblages.

Regional prey assemblages can be shaped by complex topography and flow patterns along the eastern side of the archipelago that result in marked thermal features within and around troughs on the shelf, including Chiniak Trough in the 'North' region and Barnabas Trough in the 'South' (Fig. 2.1; Kendall *et al.* 1980, Hollowed *et al.* 2007). For example, capelin, an assumed common prey of Kodiak humpback whales (Witteveen *et al.* 2006, 2012), have been connected to frontal systems during summer months (Marchand *et al.* 1999, Hollowed *et al.* 2007). Thermal fronts have been observed at the mouth of Chiniak Trough near the shelf-break ('North' region) and midway through Barnabas Trough ('South' region; Hollowed *et al.* 2007). A high biomass of capelin is frequently recorded in nearshore regions on the western edge of Chiniak Trough, while capelin appears to peak in the 'South' region on the outer edge of Barnabas Trough (Wilson *et al.* 2003, Guttormsen and Yasenak 2007, Hollowed *et al.* 2007). Cross-shelf current patterns are

hypothesized to advect zooplankton inshore of Barnabas Trough in the 'South' region (Hollowed *et al.* 2007). High euphausiid biomass over Barnabas Trough is supported by preliminary analysis of hydroacoustic backscatter from mid-summer (2005, 2011, and 2013)[2]. Most humpback whales in our study were sampled inshore (Fig. 2.1) suggesting the stable isotope signatures of our whales reflect nearshore foraging choices. Therefore, the regional difference in foraging by humpback whales appears to be driven by prey availability.

Foraging by humpback whales based on available aggregate prey is reasonable given the feeding behavior of these animals. Baleen whales are mechanistic filter feeders, engulfing large volumes of water with their prey before sieving out the prey species through baleen plates (Hain *et al.* 1981, Baraff *et al.* 1991). However, this method of feeding has a high energetic cost (Goldbogen *et al.* 2011). Thus, individual baleen whales feed only on discrete prey patches above a threshold limit of prey density to ensure positive net energy gain from a feeding event (Dolphin 1988, Piatt and Methven 1990, Hazen *et al.* 2009). Additional studies focused on the spatial variability in forage fish species around the Kodiak Archipelago will help to further elucidate the foraging choices of humpback whales in this region.

The misclassification of 38 individual whales in the two-region DFA may be due to the generalist foraging strategy of these whales as a whole combined with the turnover rate of humpback whale skin. As stated, humpback whales feed opportunistically on available aggregate prey (Dolphin 1988, Piatt and Methven 1990, Hazen *et al.* 2009). In Kodiak waters, humpback whales consume some forage fish and krill species that have similar or overlapping stable nitrogen and carbon isotope ratios (Witteveen *et al.* 2012). In addition, humpback whales are large (30 ton; 13-15 m long), mobile marine mammals, and the turnover rate of skin has not been

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estimated for a marine mammal of comparable size. Thus, a corroborated measure of humpback whale skin turnover rate remains unknown. The half-life of bottlenose dolphin (*Tursiops truncutus*) skin tissue has been estimated at ~ 20 days for $\delta^{13}C$ and $\delta^{15}N$ values (Browning *et al.* 2014). Bottlenose dolphins have a marked smaller body mass compared with humpback whales, and thus, the overall isotopic turnover of humpback whale skin is likely significantly slower compared with bottlenose dolphins (Read *et al.* 1993, Newsome *et al.* 2010). Humpback whale skin may reflect a signature that masks fine-scale temporal variability in foraging (*i.e.*, hours or days) if consumed prey have similar stable isotope signatures, distinct prey are consumed intermittently, or the turnover rate of skin tissue is longer than the scale of foraging variability. Therefore, we accepted the two sub-aggregation DFA assignment and found a significant difference in $\delta^{15}N$ value between the sub-aggregations using LMM (t_{109}=88.38; $P < 0.001$) and ANOVA ($F_{1, 106} = 15.22$; $P = 0.002$) analyses. Because observations of foraging events led to the initial separation of samples into the regional sub-aggregations, this study highlights the important role that field observations can have when conducting stable isotope studies on generalist species.

Annual $\delta^{15}N$ values indicate that the prey types consumed by Kodiak humpback whales did not fluctuate significantly among years. However, within the 'North' sub-aggregation, the 2012 TL estimate was lower than all other years and was instead similar to the 'South' sub-aggregation values (Fig. 2.5). The lower $\delta^{15}N$ and $\delta^{13}C$ value in 2012 in the 'North' (Fig. 2.2) could be explained by fluctuations in consumption of zooplankton resulting from variability in zooplankton biomass from oceanographic conditions. Preliminary hydroacoustic backscatter results suggest annual variability in euphausiid biomass within trough regions on the shelf of the

archipelago[2]. GAP surveys conducted during 2012 and 2013 recorded acoustic backscatter

signatures consistent with high zooplankton biomass in 2012 and very low zooplankton biomass

in 2013 in Marmot and Perenosa bays in the 'North' region (Fig. 2.1; GAP, unpubl. data).

Moreover, during these surveys, humpback and fin whales were observed foraging on euphausiid

swarms in Marmot Bay during 2012 and fish in Perenosa Bay in 2013 (GAP, unpubl. data),

supporting the findings of this study. Therefore, we suggest that humpback whales in the 'North'

sub-aggregation likely forage on fish and zooplankton species, but the extent of foraging on each

is dependent on locally available prey densities. Lower estimated TLs were also observed for

both sub-aggregations in 2006 and 2010 (Fig. 2.6) and may indicate proportionally higher

zooplankton biomass around the archipelago in those years.

Annual differences in humpback whale mean $\delta^{13}C$ values were recorded. Stable carbon

isotope ratios reflect variability in carbon sources, which can be influenced by a myriad of

factors, both biotic (*e.g.*, phytoplankton species, size and growth rate) and abiotic (*e.g.*, water

masses, water temperature; Farquhar *et al.* 1989, Kelly 2000). Major marine and marginal

marine habitat types (*e.g.*, open ocean, nearshore, sea grass, kelp forest) have distinct $\delta^{13}C$ values

(Clementz and Koch 2001). In addition, the ratio of the heavier isotope has been shown to

increase with decreasing distance to shore in marine systems in the absence of freshwater

influences (Hobson *et al.* 1994, France 1995). The Kodiak Archipelago is a hydrographically and

bathymetically complex region with distinct water masses (*e.g.*, Alaska Coastal Current, Alaska

Stream, Kodiak coastal water) that interact at varying spatial scales in the study area (Kendall *et al.* 1980, Stabeno *et al.* 2004, Hollowed *et al.* 2007). The strength and direction of water mass

movement around the archipelago varies in response to physical variables (*e.g.*, temperature,

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winds, tides, upwelling, freshwater influence), thus influencing carbon signatures of the water that propagate through the food web. Additionally, the variable oceanographic conditions could influence regional prey composition and abundance, which could in turn influence the location of humpback whale foraging. Thus, variability in annual mean $\delta^{13}C$ vales of humpback whale skin tissue may indicate fluctuations in location of foraging or variability in oceanographic conditions in the study region.

We hypothesized that the humpback whale $\delta^{15}N$ values would increase linearly with DOY as has been shown for other mysticete species (Best and Schell 1996, Summers *et al.* 2006, Aguilar *et al.* 2014). Non-significant DOY trends for all humpback whale $\delta^{15}N$ models did not support our hypothesis. However, the random effect 'year' within-year variance was greater than among-year variance for the optimal $\delta^{15}N$ model (Table 2.4). Because within-year variance is an estimate of the variance that will occur in an average year based on the input data, the 'year' variance output implies humpback whales are foraging on more diverse prey species within an average year than across years. We conclude the larger random effect within-year variance is likely an artifact of sampling different individuals with feeding preferences each summer. Stable isotope ratios of a tissue could also be affected by differences in temporal integration of amino acids from differing pools that are used in tissue synthesis, as was shown for keratin synthesis of fasting King penguins (*Aptenodytes patagonicus*; Cherel *et al.* 2005). The lack of change in humpback whale $\delta^{15}N$ values with DOY from our dataset is likely influenced by the relatively long assumed half life of humpback whale skin (> 20 day) that may mask short-term changes in feeding behavior. Acoustic time-depth recorders affixed to whales that collect short-term (*i.e.,* hours to days) dive data can provide high-resolution foraging information for shorter temporal scales than the presumed skin tissue turnover time-frame (Croll *et al.* 1998, Johnson and Tyack

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2003, Witteveen *et al.* 2008). Future tagging studies of humpback whales in the Kodiak region will help provide a more holistic picture of humpback whale foraging across the summer feeding season.

The increase in 'South' sub-aggregation humpback whale skin δ^{13}C value with DOY could be due to movement of whales inshore to enhance optimal foraging. In the Kodiak region, forage fish species spawn during different months (Robards *et al.* 1999, Doyle *et al.* 2002). In addition, biomass of different euphausiid species varies across the Northern GOA shelf with depth (Coyle and Pinchuk 2005, Pinchuk *et al.* 2008), and euphausiid biomass around the archipelago is estimated to peak on Barnabas Trough in the 'South' region[2]. Thus, the positive linear 'South' sub-aggregation δ^{13}C trend may be the result of whales moving inshore to feed on increased abundances of euphausiids or spawning/larval forage fishes, such as capelin or sand lance. Additional sampling of individual humpback whales for SIA throughout the foraging season, with emphasis on early summer (*e.g*, May and June; Fig. 2.3), is needed in both sub-aggregations to help clarify if the established 'South' sub-aggregation δ^{13}C-DOY trend is supported by the biology, oceanography, and overall ecology of the system.

Similarity of sub-aggregation trophic levels to other aggregations in the North Pacific

Mean TL estimates were previously calculated for humpback whale feeding aggregations in the North Pacific using a stable isotope discrimination value that is 0.4 ‰ lower than the one used in this study (Witteveen *et al.* 2011). To compare our findings with Witteveen *et al.* (2011), we re-calculated the TL estimates of the humpback whale feeding aggregations defined in Witteveen *et al.* (2011) by using our stable isotope discrimination value (2.8 ‰), while keeping all other input variables the same. After re-scaling, our 'South' sub-aggregation TL estimate

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(3.0±0.1) is similar to the re-scaled TL estimates of the western Aleutian Islands (WEST; 3.1±0.1). On the other hand, our 'North' sub-aggregation TL estimate (3.3±0.1) is similar to the re-scaled central Aleutian Islands (CENT; 3.3±0.0) and northern British Columbia (NBC; 3.3±0.0) feeding aggregation estimates. Interestingly, even after re-scaling, neither the 'North' sub-aggregation estimate nor the mean Kodiak TL estimate (3.1±0.1) was similar to the Northern GOA TL value (NGOA; 3.7±0.0), which included whales biopsied in Kodiak waters. However, NGOA included animals sampled in Cook Inlet, the Barren Islands, and Prince William Sound in addition to Kodiak, and whales in these regions may have markedly different diet compositions. Fine-scale diet studies of humpback whales in the sub-aggregations defined in our study and other feeding aggregations in the North Pacific are needed to explore similarities in humpback whale diets across regions.

Conclusion

Humpback whales on the Kodiak feeding ground appear to segregate into at least two distinct feeding sub-aggregations, 'North' and 'South', and feed at different TLs across the summer feeding season. Kodiak humpback whales may rely on zooplankton to a greater extent than previously thought, especially in the 'South' sub-aggregation. Regional differences in TL appear to be influenced by prey availability, and thus humpback whales may segregate within feeding grounds in the North Pacific and target discrete species. A better understanding of the variability in foraging by humpback whales on their respective feeding grounds will help elucidate differences in diet choice and foraging behavior across feeding aggregations in the North Pacific. This type of foraging data will become useful as humpback whale populations continue to recover from overexploitation.

Acknowledgements

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Tables

Table 2.1. Humpback whale skin stable isotope data. Table includes number of Kodiak Archipelago humpback whale skin samples (*n*) collected by year (2004 – 2013) for each sub-aggregation ('North', 'South') and pooled across sub-aggregations (Arch.). Also shown are mean (±1 SE) $\delta^{15}N$ and $\delta^{13}C$ (‰) values. SE < 0.05 are listed as 0.1 as this is the precision of the machinery used in stable isotope analysis. Letters (*a,b*) indicate groupings for years in which humpback whale skin mean $\delta^{15}N$ values were not significantly different, and Roman numerals (*i,ii*) indicate years in which humpback whale mean $\delta^{13}C$ values were not significantly different as shown by *post hoc* tests. A significant difference between sub-aggregations is designated with the following superscript symbols: 0.05 – 0.01 ([*]); 0.01 – 0.001 ([**]); ≤ 0.001 ([***]).

Year	*n* 'North'	*n* 'South'	*n* Arch.	$\delta^{15}N$ 'North'	$\delta^{15}N$ 'South'	$\delta^{15}N$ Arch.	$\delta^{13}C$ 'North'	$\delta^{13}C$ 'South'	$\delta^{13}C$ Arch.	TL North	TL South	TL Arch.
2004	11	12	23	+13.6 ± 0.2	+13.3 ± 0.2	+13.4 ± 0.1[*a,b*]	-17.3 ± 0.2	-17.0 ± 0.2	-17.1 ± 0.1[*i*]	3.2 ± 0.1	3.1 ± 0.1	3.2 ± 0.1
2005	20	25	45	+13.8 ± 0.2	+13.0 ± 0.2	+13.4 ± 0.2[*a,b*]	-17.9 ± 0.1	-18.1 ± 0.1	-18.0 ± 0.1[*ii*]	3.3 ± 0.1	3.0 ± 0.1	3.1 ± 0.1
2006	4	13	17	+13.6 ± 0.3	+12.7 ± 0.1	+12.9 ± 0.2[*b*]	-18.1 ± 0.1	-18.4 ± 0.1	-18.3 ± 0.1[*ii*]	3.2 ± 0.1	2.9 ± 0.1	3.0 ± 0.1
2007	4	--	4	+14.0 ± 0.6	--	+14.0 ± 0.6[*a,b*]	-17.7 ± 0.4	--	-17.7 ± 0.4[*i,ii*]	3.4 ± 0.2	--	3.4 ± 0.2
2008	3	--	3	+14.6 ± 0.1	--	+14.6 ± 0.1[*a*]	-17.6 ± 0.1	--	-17.6 ± 0.1[*i,ii*]	3.6 ± 0.1	--	3.6 ± 0.1
2010	5	5	10	+13.5 ± 0.2	+12.9 ± 0.3	+13.2 ± 0.2[*a,b*]	-17.8 ± 0.1	-17.9 ± 0.2	-17.9 ± 0.1[*ii*]	3.2 ± 0.1	3.0 ± 0.1	3.1 ± 0.1
2012	8	--	8	+13.1 ± 0.3	--	+13.1 ± 0.3[*a,b*]	-18.4 ± 0.1	--	-18.4 ± 0.1[*ii*]	3.0 ± 0.1	--	3.0 ± 0.1
2013	8	--	8	+14.2 ± 0.2	--	+14.2 ± 0.2[*a*]	-17.7 ± 0.2	--	-17.7 ± 0.2[*i,ii*]	3.4 ± 0.1	--	3.4 ± 0.1
Total	63	55	118	+13.7 ± 0.1[**]	+13.0 ± 0.1[**]	+13.4 ± 0.1	-18.0 ± 0.1	-17.9 ± 0.1	-17.9 ± 0.6	3.3 ± 0.1[***]	3.0 ± 0.1[***]	3.1 ± 0.1

Table 2.2. Two-way ANOVA of humpback whale stable isotope values. Model parameters include dependent variables $\delta^{15}N$ and $\delta^{13}C$, and the independent variables 'sub-aggregation' (SA) and 'year'. Table includes sources (SA; year), sum of squares, degrees of freedom (*df*), mean squared error, F-value (F), and P-values (*P*). Also shown are the sum of squares, *df*, and mean squared error for the model residuals.

Stable Isotope Ratio	Source	Sum of Squares	df	Mean Square	F	P
$\delta^{15}N$	SA	9.17	1	0.17	15.22	0.002
$\delta^{15}N$	Year	8.72	7	1.25	2.07	0.05
$\delta^{15}N$	Residuals	65.71	109	0.6		
$\delta^{13}C$	SA	0.35	1	0.35	1.43	0.23
$\delta^{13}C$	Year	19.49	7	2.78	11.5	< 0.001
$\delta^{13}C$	Residuals	26.5	109	0.24		

Table 2.3. AICc comparison of candidate linear mixed models (LMM). LMMs were used to explain variability in δ^{15}N or δ^{13}C values from Kodiak Archipelago humpback whale skin samples. Parameters in candidate models include 'sub-aggregation' (SA: 'North', 'South'), 'day of year' (DOY), interaction between SA and DOY (γ), and random effect 'year' (a_t). Fixed effects are shown in bold. Comparison table includes model equation, number of parameters (k), AICc value, difference in AICc value (ΔAICc), AICc weight (AICC Wt.), cumulative AICc weight (Cum. Wt), and negative log likelihood estimates (LL). Also shown are R^2 estimates for fixed effects (Mar. R^2) and fixed plus random effects (Cond. R^2) as defined in Nakagawa and Schielzeth (2013). In addition, δ^{13}C LMM with linear 'DOY' trends are shown for 'North' and 'South' humpback whale sub-aggregations following the significant interaction term in the archipelago δ^{13}C model.

Isotope	Candidate Models	k	AICc	ΔAICc	AICc Wt.	Cum. Wt	LL	Mar. R^2	Cond. R^2
δ^{15}N	a_t+**SA**	4	288.84	--	0.47	0.47	-140.25	0.16	0.22
δ^{15}N	a_t+**SA+DOY+γ**	6	290.69	1.84	0.19	0.66	-138.97	0.18	0.24
δ^{15}N	a_t+**SA+DOY**	5	290.92	2.08	0.17	0.82	-140.19	0.16	0.23
δ^{15}N	a_t+**SA+DOY+DOY^2**	6	291.11	2.26	0.15	0.98	-139.18	0.17	0.28
δ^{15}N	a_t+**SA+DOY+DOY^2+γ+γ^2**	8	294.72	5.88	0.02	1.00	-138.70	0.18	0.30
δ^{13}C	a_t+**SA+DOY+γ**	6	186.11	--	0.70	0.07	-86.67	0.09	0.37
δ^{13}C	a_t+**SA+DOY+DOY^2+γ+γ^2**	8	189.72	3.62	0.11	0.81	-86.20	0.09	0.38
δ^{13}C	a_t+**SA+DOY+DOY^2**	6	189.75	3.64	0.11	0.93	-88.50	0.04	0.44
δ^{13}C	a_t+**SA+DOY**	5	191.53	5.42	0.05	0.97	-90.50	0.02	0.42
δ^{13}C	a_t+**SA**	5	192.57	6.47	0.03	1.00	-91.02	0.00	0.41
δ^{13}C	a_t+**DOY** ('North' sub-aggregation)	4	118.91	--	--	--	--	0.03	0.30
δ^{13}C	a_t+**DOY** ('South' sub-aggregation)	4	97.05	--	--	--	--	0.43	0.50

Table 2.4. Parameter estimates from optimal linear mixed models (LMM). LMMs were used to explain variability in δ^{15}N or δ^{13}C values from Kodiak Archipelago humpback whale skin samples by sub-aggregation ('North', 'South') and pooled across sub-aggregations (Arch.). Parameters in candidate models include 'sub-aggregation' (SA: 'North', 'South'), 'day of year' (DOY), interaction between 'sub-aggregation' and 'DOY' (γ), and random effect 'year' (a_t). Fixed effects are shown in bold. Model outputs include: random effect among-year variability (AYr) and within-year variability (WYr) in standard deviation (SD), fixed effects parameter estimates with standard error (SE; Est.±SE), and t-values. T-test significance ($P < 0.05$) designated with superscript symbols: 0.05 – 0.01 (*); 0.01 – 0.001 (**); ≤ 0.001 (***).

| Stable Isotope Ratio | Optimal Models | Random Effect (SD) | | Fixed Effects Coefficients | | | | | | | |
| | | | | Intercept | | 'South' | | DOY | | SA:DOY | |
		AYr	WYr	Est.±SE	t	Est. ± SE	t	Est.±SE	t	Est.±SE	t
δ^{15}N	a_t+**SA** (Arch.)	0.22	0.78	+13.7±0.1	t_{109}=106.23***	+13.0±0.2	t_{109}=88.38***	--	--	--	--
δ^{13}C	a_t+**SA+DOY+γ** (Arch.)	0.32	0.48	--	--	-23.5±2.4	t_{107}=-9.74***	-0.0±0.1	t_{107}=-1.39	-0.0±0.1	t_{107}=22.81**
δ^{13}C	a_t+**DOY** ('North')	0.31	0.49	-16.9±0.7	t_{54}=-23.96***	--	--	-0.0±0.1	t_{54}=-1.35	--	--
δ^{13}C	a_t+**DOY** ('South')	0.17	0.49	-29.1±2.7	t_{50}=-10.88***	--	--	+0.1±0.1	t_{50}=4.20***	--	--

Figures
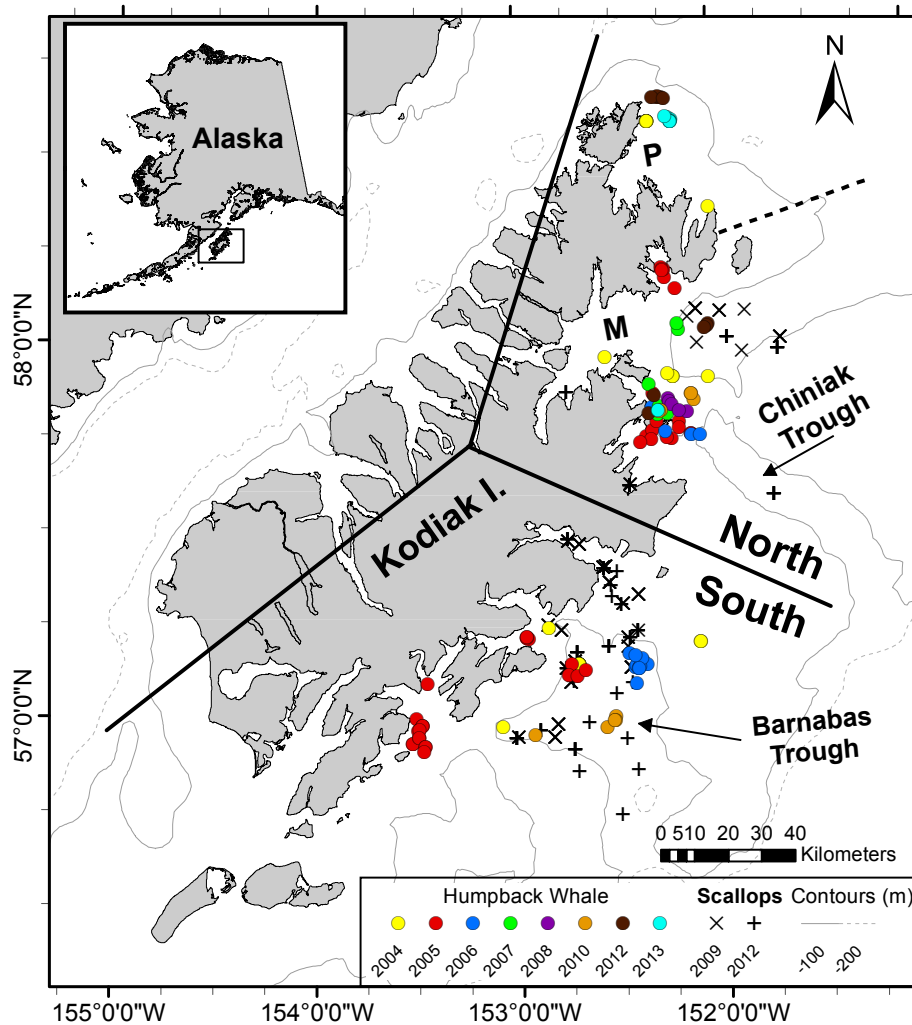
Figure 2.1. Map of the Kodiak Archipelago, AK, USA. Map includes locations of skin sample collection of free-ranging humpback whales from 2004 – 2013 (color). Also shown are collection locations of weathervane scallop samples for 2009 (X) and 2012 (+) and regional delineations (thick black lines; 'North', 'South') based on observations of humpback whale foraging events. The dashed line indicates the delineation of 'North' and 'East' regions assumed in the three-region discriminant function analysis. Letters M and P indicate Marmot and Perenosa Bay, respectively.

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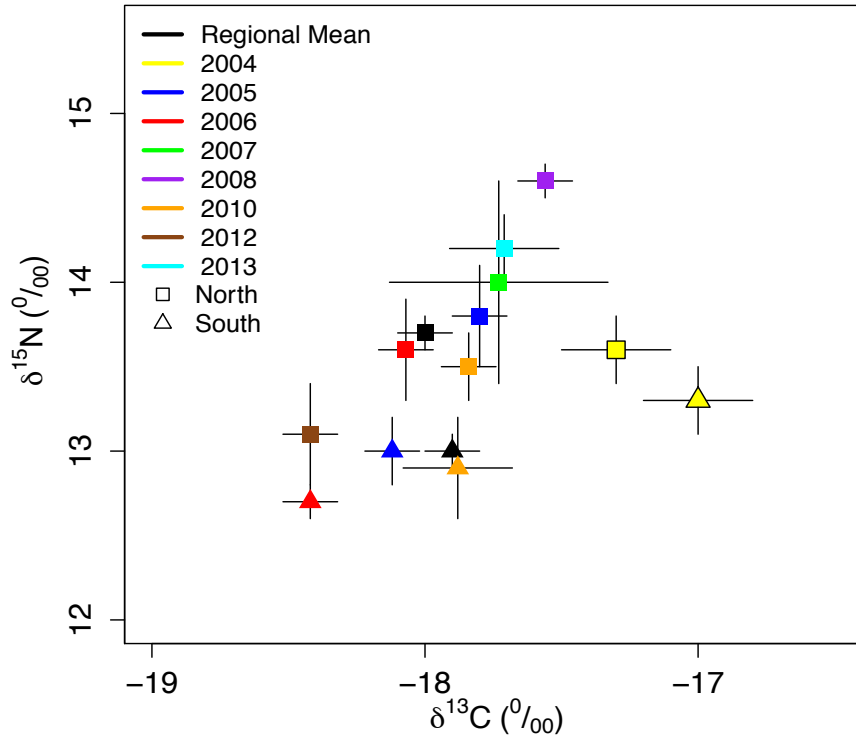
Figure 2.2. Kodiak humpback whale skin mean (± 1 SE) δ^{15}N and δ^{13}C values (‰). Stable isotope value means were computed across years (2004 – 2013; color) for two sub-aggregations along the eastern side of the Kodiak Archipelago ('North', square; 'South', triangle). Also shown are the regional mean δ^{15}N and δ^{13}C values pooled across years (black).
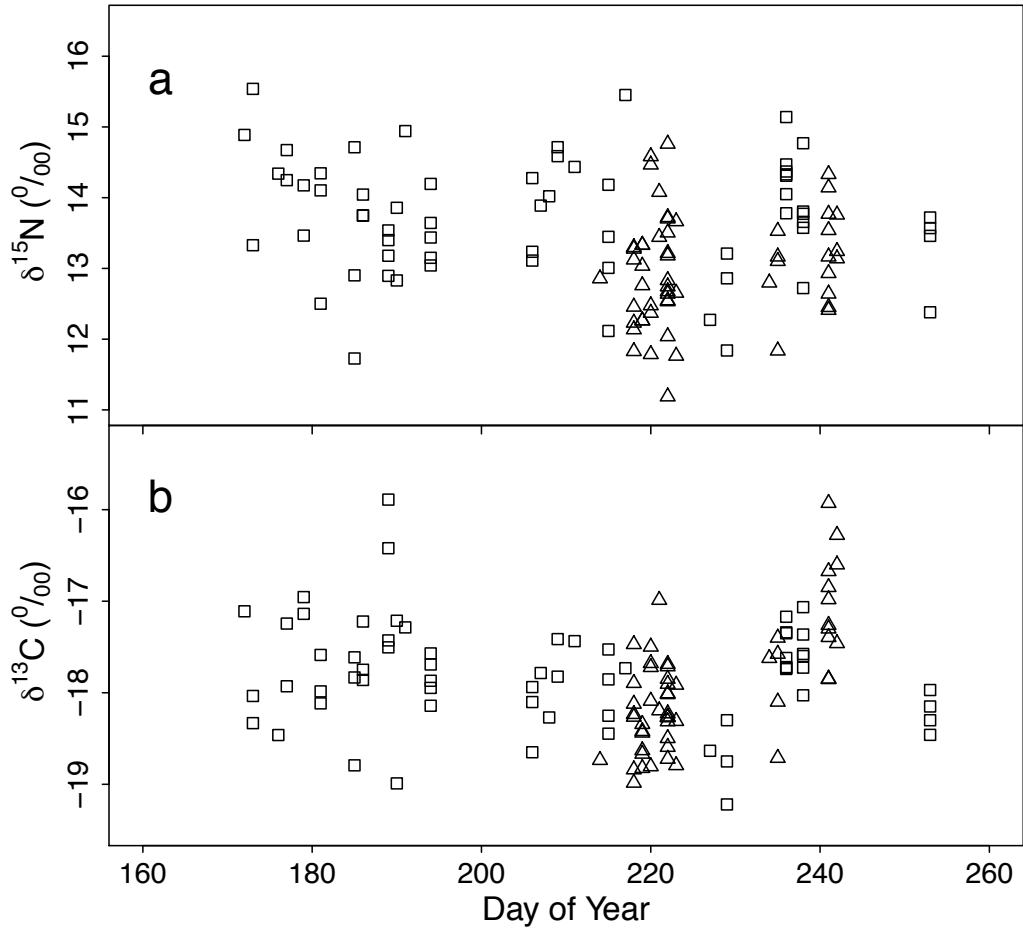
Figure 2.3. Kodiak humpback whale skin δ^{15}N (a) and δ^{13}C (b) values (‰). Stable isotope values are shown by day of year for two sub-aggregations along the eastern side of the Kodiak Archipealgo ('North', square; 'South', triangle).
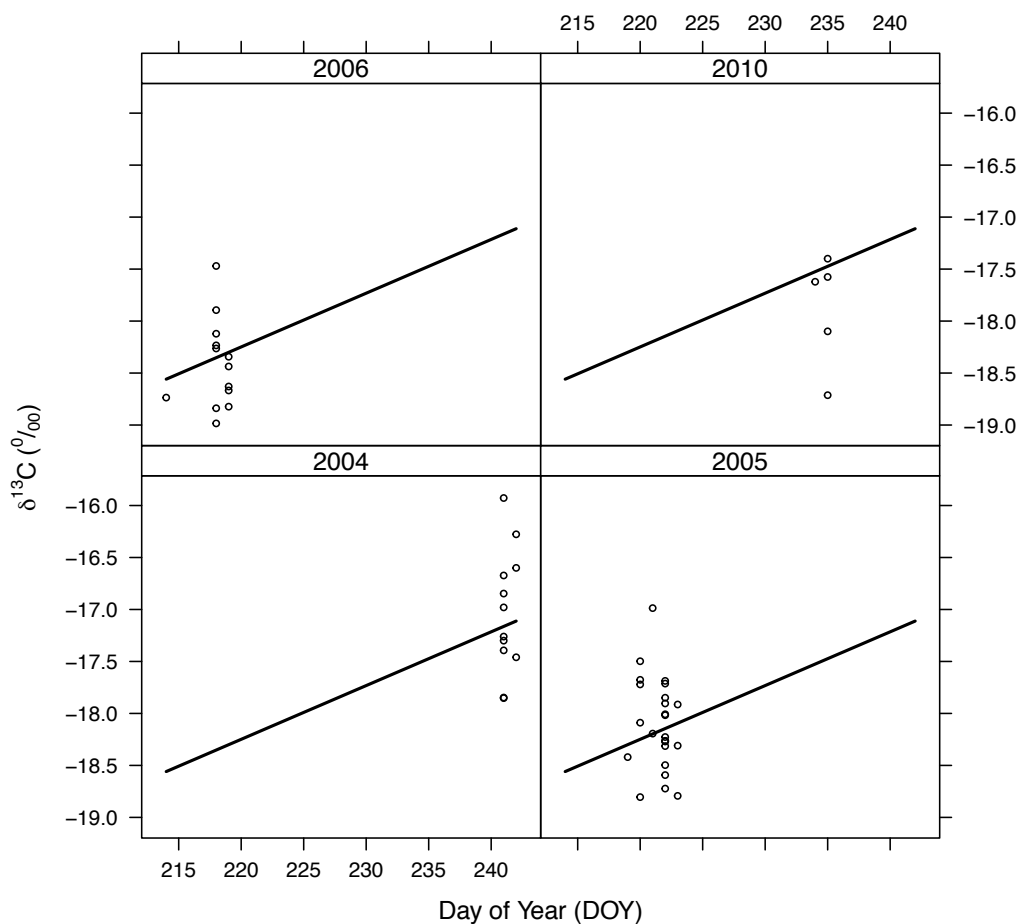
Figure 2.4. 'South' region humpback whale skin $\delta^{13}C$ values (open circles). Stable carbon isotope values shown by day of sample collection (DOY) across years (2004 – 2010). Black line indicates trend in $\delta^{13}C$ values with DOY as defined from linear mixed models.
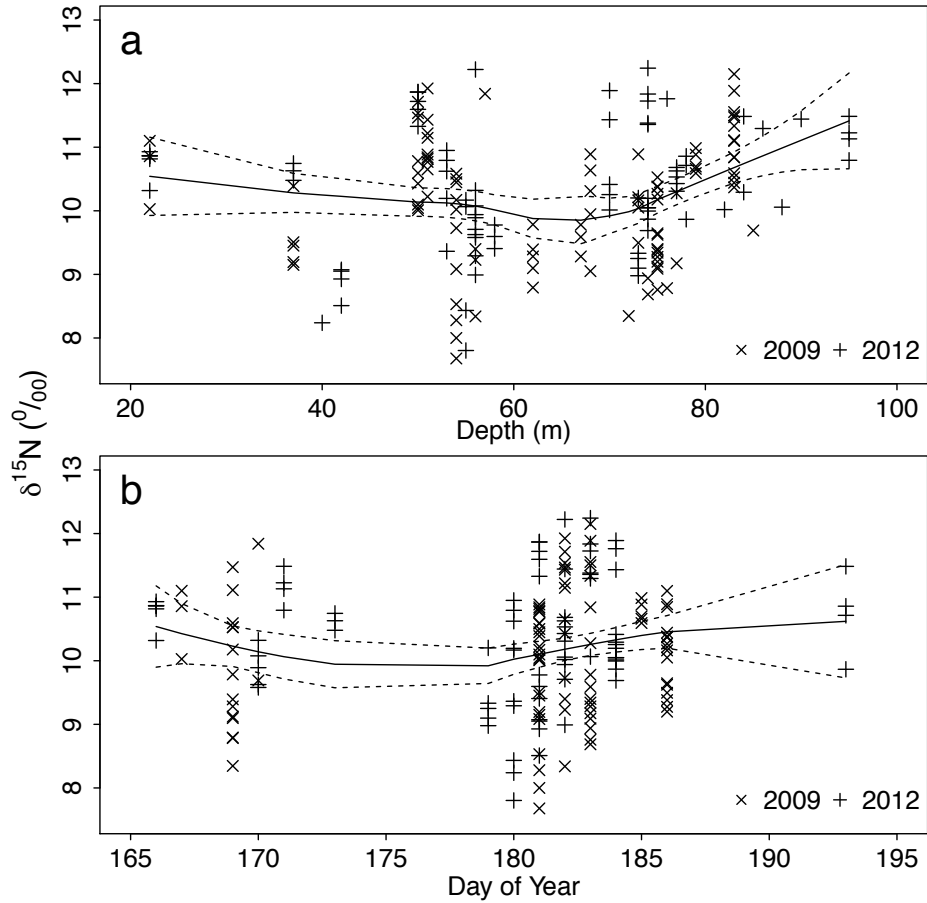
Figure 2.5. Weathervane scallop $\delta^{15}N$ values (‰). Nitrogen stable isotpoe values shown by water depth (a) and day of year (b) for samples collected in 2009 (X) and 2012 (+). Solid black lines represent LOESS predictions with span = 0.75 (R package 'stats') and 95% confidence intervals (dashed).
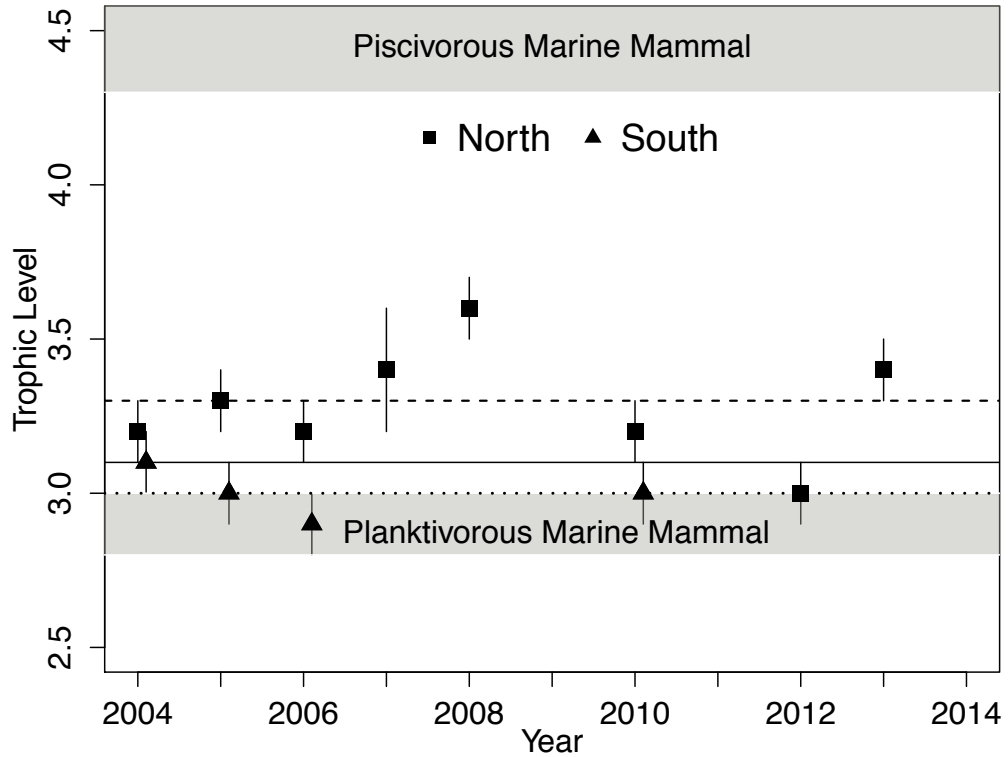
Figure 2.6. Annual mean (± 1 SE) trophic level (TL) of Kodiak humpback whales. TL estimates were computed from humpback whale skin and weathervane scallop adductor δ^{15}N values for 2004 – 2013 by sub-aggregation ('North', square; 'South' triangle; Eq. 2.4). SE < 0.05 are shown as 0.1 as this is the precision of the machinery used in stable isotope analysis. Black lines indicate mean TLs for 'North' (dashed) and 'South' (dotted) sub-aggregations and overall mean TL (solid). Shaded regions represent TLs for mainly fish-eating (piscivorous) and plankton-eating (planktivorous) cetaceans (Lesage *et al.* 2001, Hoekstra *et al.* 2002).

Chapter 3: Spatial variability in the trophic niche overlap of two recovering apex predators on the Kodiak feeding ground in the Gulf of Alaska[1]

Abstract

In the Gulf of Alaska, humpback whale (*Megaptera novaeangliae*) and Steller sea lion (SSL; *Eumetopias jubatus*) populations are recovering at varying rates (6.8 %, 1.7 %, respectively) from population decline. Separate diet studies of both predators indicate a potential for diet overlap, which may influence the recovery rate of these species depending on the available biomass of shared resources. Thus, the diet composition and degree of overlap in trophic niche of humpback whales and SSLs were compared for two regions in the Kodiak Archipelago ('North', 'South'). Potential humpback whale diet compositions were estimated using a stable isotope mixing model, and SSL diet compositions were determined as the split-sample frequency of occurrence of prey in fecal samples. Regional differences in diet composition resulted in a higher, although not biologically significant ($O_{jk} < 0.60$), degree of overlap between humpback whales and SSLs in trophic niche in the 'North' region. However, the diet of humpback whales also appears to overlap considerably with the diet of piscivorous fishes that are prominent prey of SSLs, resulting in potential indirect impacts on prey resources of SSLs. Thus, this study highlights the complexity of trophic interactions in the Kodiak ecosystem and suggests that prey consumption by Kodiak humpback whales may indirectly impact the recovery of Kodiak SSLs on a regional scale depending on composition and biomass of prey resources and growth of humpback whale numbers within each region.

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[1] Wright DL, Witteveen BH, Wynne K, Guo L, Horstmann-Dehn LA (2014) Spatial variability in the trophic niche overlap of two recovering apex predators on the Kodiak feeding ground in the Gulf of Alaska. Prepared for submission in Marine Ecology Progress Series.

Introduction

Ecological niche provides a useful conceptual basis to assess species interactions and community structures on varying spatial and temporal scales. Successful sympatric species are thought to co-exist by differentiating along various niche axes, including temporal avoidance or dietary differences (MacArthur & Pianka 1966, Siemers & Schnitzler 2004). The degree of overlap in trophic niche among sympatric species can provide insight into complex food web linkages in an ecosystem (MacArthur & Pianka 1966, Pianka 1974).

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species that migrates between high latitude summer feeding grounds to low-latitude winter breeding and birthing grounds (Clapham 2000, Calambokidis et al. 2001). Segregation of the North Pacific population to specific feeding grounds has been studied at various spatial scales. Witteveen et al. (2009) defined six distinct feeding aggregations in the North Pacific using stable isotope analysis (SIA). Through long-term (> 10 yr) photo-identification studies, researchers have described finer-scale feeding aggregations, including the Kodiak feeding ground in the Gulf of Alaska (GOA; Calambokidis et al. 1996, Waite et al. 1999, Zerbini et al. 2006, Witteveen et al. 2007). On the Kodiak feeding ground, humpback whales may further segregate into sub-aggregations that feed at different trophic levels (Wright et al. *In review*; Chapter 2).

Fine-scale variability in foraging has been observed for other predators on the Kodiak feeding ground, including the western stock of Steller sea lions (SSL; *Eumetopias jubatus*; McKenzie & Wynne 2008). Both SSLs and humpback whales are often considered generalist predators that forage based on prey abundance (Nemato 1957, Pitcher 1981). Humpback whales are mechanistic filter feeders that use baleen plates and an expandable throat sack to engulf aggregate prey (Hain et al. 1981, Dolphin 1988, Baraff et al. 1991). In contrast, SSLs use teeth to

capture individual prey items (Pitcher 1981). Such differences in morphology and foraging strategy lead to large differences in the volume of consumed prey. The Kodiak humpback whale feeding aggregation is estimated to consume 555,000 kg/prey day (Witteveen et al. 2006; GAP unpubl. data), while the non-pup central GOA SSL population only needs ~82,000 kg prey/day (Winship & Trites 2003, Fritz et al. 2013). Therefore, depending on the abundance and site fidelity of humpback whales, SSLs, and fish populations in the Kodiak ecosystem, a partial overlap in diet resources between humpback whales and SSLs may be a substantial factor in the recovery of the SSL population. Separate studies on the diets of humpback whales and SSLs around the Kodiak Archipelago suggest differences in the dominant prey species consumed (Witteveen et al. 2006, 2012, McKenzie & Wynne 2008). However, these studies also indicate potential overlap in consumption of aggregate fish species, including commercially important species (e.g., Pacific herring (*Clupea pallasii;* hereafter 'herring') and walleye pollock (*Gadus chalcogrammus*; hereafter 'pollock')). Therefore, it is of interest to investigate the degree of overlap in trophic niche between humpback whales and SSLs in the Kodiak region, especially now as both stocks recover to varying degrees from population declines.

Humpback whales in the North Pacific were commercially harvested in the early and mid-20th century resulting in a near-decimation of the population until a moratorium on whaling was instituted in 1986 (Rice 1978, Calambokidis et al. 2008). Western SSLs experienced a population decline of ~ 85 % between the early 1970's and 2000 (Loughlin 1998, Sease et al. 2001). While the cause of the humpback whale decline is clearly known, many hypotheses were developed to explain the SSL decline, including increased predation by killer whales (*Orcinus orca*), take in commercial fisheries, changes in the foraging ecology, reproduction, and survival, and many others (DeMaster & Atkinson 2002, National Research Council 2003, Trites et al.

2007). The root cause, however, remains equivocal. Following the moratorium on commercial whaling, the North Pacific humpback whale population has increased rapidly and is estimated to be near or above pre-whaling levels and still growing (Calambokidis et al. 2008, Barlow et al. 2011). In contrast, western SSL populations have recently begun to increase, but the growth has been slow and spatially variable (Fritz et al. 2013). The potential effect that the variable recovery of these predator populations will have on each other and on the Kodiak ecosystem as a whole is currently unknown.

All developed methods used to study cetacean diet have limitations. Recently, SIA has become a widely-used tool to investigate feeding habits of cetaceans (Hoekstra et al. 2002, Horstmann-Dehn et al. 2012, Witteveen et al. 2012, Browning et al. 2014a). The stable carbon and nitrogen isotope ratios in an animal's tissues reflect that of its assimilated diet (DeNiro & Epstein 1978, 1981, Rau et al. 1982, Peterson & Fry 1987) allowing for exploration of diet composition (Phillips & Gregg 2001, 2003). Thus, stable isotope signatures of predator and prey species can be used in mass-balance equations (i.e., mixing models) to estimate the proportional contribution of individual prey species to the predator's diet without requiring direct observations of feeding events (Phillips & Gregg 2003, Phillips et al. 2005, 2014).

Diet composition of SSLs is traditionally estimated from identifiable prey remains recovered from fecal (hereafter 'scat') samples collected on haul-out sites (da Silva & Neilson 1985, Murie & Lavigne 1986, Harvey 1989). Multiple indices have been created to illustrate diet composition from scat samples, including split-sample frequency of occurrence (ssFO; Olesiuk et al. 1990). The ssFO method considers the presence or absence of a prey type in a scat sample and yields equal proportions of all prey species found in the sample (Olesiuk et al. 1990). Thus, the ssFO method tends to overestimate the importance of smaller prey species (e.g., capelin

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(*Mallotus villosus)*; Laake et al. 2002, Joy et al. 2006). As a result, this diet method provides an upper range of potential diet overlap with humpback whales that target forage fish species (Nemato 1957). In addition, the ssFO method provides a measure of diet composition which sums to 100 %, theoretically allowing for a comparison of diet composition with humpback whale dietary estimates derived from stable isotope mixing models.

A difference in dietary time frame represented by stable isotope mixing models and scat collection could impact the interpretation of any diet overlap. SSL scat samples reflect diet choices hours to days prior to collection (Tollit et al. 2007), while the time frame reflected in a tissue for SIA depends on the turnover (i.e., replacement) period of that tissue (Tieszen et al. 1983). The turnover rate of humpback whale skin is unknown, but is assumed to be longer than an approximately 20 day half-life, as was estimated for δ^{13}C and δ^{15}N values of bottlenose dolphin (*Tursiops truncatus*; Newsome et al. 2010, Browning et al. 2014b). Nevertheless, sequential and repeated sampling of diet can capture temporal variability in foraging choices (McKenzie & Wynne 2008, Williams et al. 2008) and reduce the impact of different dietary time frames.

The objective of this study is to better understand trophic interactions between humpback whales and SSLs in the Kodiak region. Specifically, we are testing the validity of using the Pianka niche overlap index (Pianka 1974) to assess the degree of overlap in trophic niche between humpback whales and SSLs. Previous analyses support the existence of two sub-aggregations of humpback whales along the eastern side of the Kodiak Archipelago ('North', 'South') that feed at different TLs during the summer feeding season (Wright et al. *In review*, Chapter 2). Therefore, we hypothesize that there is a difference in the degree of overlap in trophic niche between humpback whales and SSLs in these two regions. To assess regional

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differences in diet overlap, we estimated the average summer (May – mid-September) diet composition of both predators for the 'North' and 'South' regions on the Kodiak feeding ground. The resulting diet compositions were then used in the Pianka index (Pianka 1974) to quantify the degree of overlap in trophic niche between humpback whales and SSLs for both regions.

Methods

Study area and statistical analysis

The study area encompasses the eastern side of the Kodiak Archipelago (57°48'N, 152°24'W; Fig. 3.1). Humpback whale skin and SSL scat samples were grouped based on location of sample collection into two regions 'North' and 'South', as defined in Wright et al. (*In review*, Chapter 2). All statistics were conducted using statistical packages within R 2.13.1 (R Development Core Team 2008) or PRIMER v. 6, and hypothesis tests were made with a significance level of $\alpha = 0.05$ unless otherwise stated. Values are presented as mean ± 1 standard deviation (SD) unless otherwise noted.

Humpback whale diet modeling

We tested spatial variability in the summer (May – mid-September) diet composition of Kodiak humpback whales between two sub-aggregations (i.e., 'North', 'South') using stable isotope mixing models (SIMMs). To run SIMMs, stable isotope ratios of the mixture (humpback whale) and sources (potential humpback whale prey species) are needed. We utilized stable isotope ratios from juvenile and adult humpback whale skin samples from June 21st – September 10th, 2004 – 2013 (Wright et al. *In review*, Chapter 2). Skin samples for SIA were collected from the flank of the animal using a hollow-tipped biopsy dart shot from a modified 0.22 caliber rifle. The date, location, role of individual (i.e., calf, etc.), and general behavior of the whale following biopsy were recorded at each sampling event. Identification photographs of individuals were

taken of the fluke of each biopsied whale whenever possible to avoid duplicate sampling. Individual whales were identified by the markings (e.g., pigmentation, scars) and shape of the underside of the fluke (Hammond et al. 1990).

The list of potential humpback whale prey species included in the regional models were determined from previously published diets of Kodiak humpback whales and observations of humpback whale foraging behavior in the two Kodiak regions, resulting in the following species: capelin, eulachon (*Thaleichtys pacificus*), pollock, herring, Pacific sand lance (*Ammodytes hexapterus;* hereafter 'sand lance'), Pacific sandfish (*Trichodon trichodon*; hereafter 'sandfish'), and euphausiids (Thompson 1940, Nemato 1957, Witteveen et al. 2006, 2008, 2012). The prey samples used in SIA were collected by either the Gulf Apex Predator-prey (GAP) study or the Alaska Department of Fish and Game (ADF&G). Fishes were collected for SIA during mid-water trawl and hydroacoustic surveys conducted from May 5 – August 24, 2003 – 2013. Acoustic backscatter identified prey layers, which were then sampled with a commercial mid-water trawl net with a 22-mm mesh cod-end liner for the target prey species. Species counts and individual fish lengths were recorded for each tow. Due to the mechanics of humpback whale foraging and prey ingestion, only fish < 30 cm were assumed to be potential prey of humpback whales and used in SIMMs (Nemato 1957, Goldbogen et al. 2011). Zooplankton were collected by GAP researchers from a 75-m diameter twin-ring net (500/1000 mesh) and grouped by taxa (e.g., copepod, euphausiids). Euphausiids isolated for SIA were not identified to species, although the samples are likely dominated by *Thysanoessa inermis* (Lei Guo, pers. comm. UAF GAP, Kodiak, AK). As a result, euphausiids are referred to as 'krill' in this paper. Collection effort resulted in the utilization of new (2007 – 2013) and previously published (2003 – 2006; Witteveen et al. 2012) prey samples for SIA. Sand lance were not caught in trawls but were still

assumed a potential prey type of humpback whales (Witteveen et al. 2012). Therefore, sand lance stable isotope data were obtained from a previously published study that collected tufted puffin (*Fratercula cirrhata*) bill loads in the 'North' region (Williams et al. 2008). All humpback whale and prey samples were kept on ice in the field. Humpback whale and krill samples were transferred to 1.2 mL cryogenic vials and fish were left whole in plastic bags. All samples were frozen at -80 ℃ until processing.

Humpback whale skin, whole body homogenates of fish, and individual krill samples were prepared for SIA using the protocol by Witteveen et al. (2012) and Wright et al. (*In review*, Chapter 2), which involved oven drying and defatting all samples using a Soxhlet extractor with petroleum ether (Dobush et al. 1985). Individual fish were ground using a blender before ~ 0.2 g aliquots of homogenized samples were measured into cryogenic vials for drying. Krill were placed individually in vials and dried with the other samples. Samples were defatted because lipids are depleted in ^{13}C compared with bulk diet, and thus, can skew stable carbon isotope measures (DeNiro & Epstein 1977). On the other hand, defatting samples can bias stable nitrogen isotope ratios toward higher $\delta^{15}N$ values (Dobush et al. 1985, Post et al. 2007), but all samples were defatted using the same solvent and extraction protocol to allow comparison of the new and previously published data. Calcium carbonate ($CaCO_3$) from crustacean exoskeletons can also skew $\delta^{13}C$ values as $CaCO_3$ is derived from isotopically heavy HCO_3^- ions (Søreide et al. 2006). However, Kodiak krill samples defatted with 2:1 chloroform:methanol did not differ significantly in $\delta^{13}C$ value (± 1 standard error; SE) after being fumed at saturated HCl vapors for six hours ($n = 9$; -17.7±0.1; Lorrain et al. 2005) compared with non-acid fumed samples from the same tows ($n = 10$; -17.7±0.1; $t_{17} = -0.02$, $P = 0.99$; Fig. 3.2). As a result, krill samples reported here were not acid fumed.

Humpback whale and prey samples were analyzed for stable carbon and nitrogen isotope ratios using a Costech Elemental Analyzer (ESC 4010) coupled to a Finnigan MAT Delta Plus XL stable isotope ratio mass spectrometer (IRMS) at the University of Georgia Institute of Ecology Stable Isotope Laboratory. All stable carbon and nitrogen isotope ratios were reported in δ notation as per mil (‰) as determined from:

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1000 \qquad (3.1)$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Laboratory standards (bovine liver) were used to calibrate samples to international standards, Vienna PeeDee Belemnite for carbon and atmospheric air for nitrogen. Replicate measurements of $\delta^{13}C$ and $\delta^{15}N$ values were tracked using the internal laboratory standard bovine liver and indicated a measurements error of < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values ($n = 98$).

Stable isotope ratios of humpback whale skin and potential prey species were tested for normality using the Shapiro-Wilk's test to determine what statistical analyses were possible using the data. Many pelagic fish species consume higher trophic level prey with increasing body length and mouth-gape changes (Dwyer et al. 1987, Yamamura et al. 2002). These ontogenetic changes should be reflected in the stable isotope ratios of fish tissues (Hobson 1999). Therefore, to increase the resolution of humpback whale dietary estimates, prey were separated into age-at-length classes based on fork lengths of each individual, resulting in the following classes: age-1 capelin, > age-1 capelin, ≥ age-3 eulachon, > age-1 herring, and age-0 pollock (Table 3.1; Witteveen et al. 2012; I. Benson and B Goetz, pers. comm. NOAA Seattle, WA). Sandfish were not separated into size classes due to the small sample size ($n = 9$). These combinations of prey species and classes were tested for differences in $\delta^{13}C$ and $\delta^{15}N$ values using one-way analysis of

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variance (ANOVA), and Tukey's HSD *post-hoc* tests isolated pairwise differences.

Stable isotope mixing model

Regional summer humpback whale diet compositions were computed by SIMMs *via* Bayesian inference from the R package Stable Isotope Analysis in R (SIAR; Parnell et al. 2008, 2010). Models in SIAR are fit hierarchically *via* Markov Chain Monte Carlo (MCMC) to produce parameter estimates based on both the data and the prior distribution (Parnell et al. 2010). The hierarchical structure allows for unbounded flexibility in adding complexity resulting in the ability to include unlimited sources (i.e., prey), which is beneficial when modeling the mixture (diet of a generalist predator). SIAR utilizes the Dirichlet *prior* distribution, which treats each source input (prey) independently, but forces the diet proportions to sum to 1. The modeling framework allows the *prior* parameters to be left intentionally vague to allow the source data to shape the distributions (Parnell et al. 2010). The model also allows for the propagation of uncertainty of source or stable isotope discrimination values through the model to return true probability distributions of estimated dietary proportions. The modeling framework thus derives probabilistic density estimates of proportionate dietary contributions of sources to the mixture.

To correct for shifts in stable isotope ratios between trophic levels, stable isotope discrimination values were added to source stable isotope values before modeling (Parnell et al. 2010). The stable isotope discrimination value estimated for krill to fin whale skin (*Balaenoptera physalus*; 1.3±0.4 ‰ for δ^{13}C and 2.8±0.3 ‰ for δ^{15}N; Borrell et al. 2012) was used for all prey species in this study, because this represents the only published value of skin for a rorqual whale. Region ('North', 'South') was used as a grouping factor to investigate resource preferences between regions. In each of our models, the SIAR MCMC was run for 200,000 iterations, and the first 5,000 samples were discarded to account for the fact that samples at the beginning of the

MCMC chain may not accurately represent the desired distribution. SIAR model outputs produce probability density function distributions of dietary estimates, and thus, the upper and lower credibility intervals describe the range of feasible contribution of each prey item to the predator (Parnell et al. 2010). Thus the SIAR model can provide considerably more robust quantitative measures of a generalist consumer's feeding preferences compared with previous SIMMs approaches (Inger & Bearhop 2008, Moore & Semmens 2008, Parnell et al. 2010).

Two key assumptions of the SIAR model are: (1) all sources contribute to the dietary composition of the mixture, and (2) dietary contributions of all prey species must sum to one (Parnell et al. 2010). Therefore, as the dietary proportion of one source increases, another must decrease, resulting in correlations among sources. The strength of the correlation depends on the spatial configuration of sources around the mixture. Strong negative correlations of sources that overlap in isotopic space (i.e., prey species that overlap in δ^{15}N and δ^{13}C value on the isotope bi-plot) could be indicative of the model having difficulty distinguishing one source from another (Parnell et al. 2010), consequently providing unreliable diet estimates. Therefore, to assess the model fit of diet source contributions, Pearson product pairwise correlations were calculated among isotopically similar sources for each model (Parnell et al. 2010). Correlations ≤ -0.20 were considered potentially influential to the model fit due to the high number of sources included in the model. To compare the proportion of sources within and between the two humpback whale sub-aggregations, we tested the probability of the hypothesis that one source was proportionally larger than another source *via* Bayesian inference of model parameters (M) given the *prior* data (D; Pr(M|D)), whereby larger probability values imply support of the hypothesis (Parnell et al. 2010, Ryan et al. 2012).

SSL diet composition

Identifiable prey remains from SSL scat samples collected from May 1 – August 21, 2000 – 2005 (McKenzie & Wynne 2008) were used to estimate the regional summer diet composition of SSLs. Scat samples were collected from haul-out sites in the 'North' and 'South' regions of the Kodiak Archipelago (Fig. 3.1). Individual scat samples were collected with trowels and placed in separate plastic bags in the field and then frozen at -20 ºC until processing (McKenzie & Wynne 2008). Individual SSL scats were soaked in soapy water for at least 1 d and then washed through nested sieves (1.4, 0.7, 0.5 mm). All recovered hard remains were dried and sent to Pacific Identifications (Victoria BC, Canada) for prey identification to the lowest taxonomic level possible (McKenzie & Wynne 2008).

Average summer (May – mid-September) diet compositions of SSLs in the 'North' and 'South' regions of the Kodiak Archipelago were assessed from scat samples using the split-sample frequency of occurrence (ssFO) index as follows:

$$ssFO_{jk} = \sum_{i=1}^{N}\left(Y_{ik}\Big/\sum_{k=1}^{n} Y_{ik}\right)/N_j \qquad (3.2)$$

where *n* is the number of different prey species, Y_{ik} is a binary variable to indicate presence (1) or absence (0) of the *k*th prey species in the *i*th scat sample of the *j*th collection (e.g., region), and N_j is the total number of samples in the collection (Olesiuk et al. 1990). Individually identified prey species from scat samples were pooled across sites and years by region (Table 3.2).

Niche overlap

To compare the degree of overlap in trophic niche between humpback whales and SSLs for two regions in the Kodiak ecosystem, the Pianka trophic niche overlap index was used:

$$O_{jk} = O_{kj} = \frac{\sum_i^n p_{ij} \times p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}} \qquad (3.3)$$

where $O_{jk} = O_{kj}$ is the Pianka measure of niche overlap index between predator species j (SSL) and k (humpback whale); p_i is the proportion of prey species i in relation to the total diet composition of the predator, and n is the total number of prey species (Pianka 1974). The Pianka index is symmetrical, meaning the overlap estimate is the same for both predators ($O_{jk} = O_{kj}$). The index ranges from 0 (no overlap) to 1 (full overlap; Pianka 1974). In accordance with Wallace (1981), a Pianka index value (O_{jk}) > 0.60 is considered biologically significant. Calculation of niche overlap was determined from six individual prey species hypothetically shared by both predators; capelin, eulachon, herring, pollock, sandfish and sand lance. Krill was also included as an individual prey source because of its prevalence in the humpback whale diet; all other prey species were summed as 'other'.

Average regional summer SSL ssFO proportions were used to represent the diet composition of SSLs in the trophic niche overlap index. Humpback whale summer diet compositions were expressed in the niche overlap index as mean, mode, and median values of proportional contributions of sources from SIAR SIMMs. These measures were chosen to account for variability in humpback whale diet estimates from the SIAR models. Estimates from the SIAR models for size classes of a species were summed to represent that species for the humpback whale diet in trophic niche overlap indices.

Because the difference in sampling period for SSLs and humpback whales (Table 3.1, 3.2) may limit the interpretation of the diet overlap, we tested for differences in 'North' region SSL diet composition in years that did (2004 – 2005) and did not (2000 – 2003) overlap with humpback whale sampling using nonparametric analysis of similarities (ANOSIM) on the Bray-Curtis similarities matrices (PRIMER v. 6) and 9,000 randomizations of collections. ANOSIM tests the null hypothesis that within-group similarities (2000 – 2003 and 2004 – 2005) do not

exceed between-group similarities (2000 – 2003 vs. 2004 – 2005). The value of the test statistic

R was used to assess between-group differences where R ranges from -1 to 1, and 0 represents

the null hypothesis of no between-group difference (Clarke & Warwick 2001). ANOSIM tests

were computed using ssFO values of the six individual prey species hypothetically shared by

both predators; capelin, eulachon, herring, pollock, sandfish and sand lance. Arrowtooth flounder

(ATF; *Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus

stenolepis*), and various salmon species (*Oncorhynchus* spp.) were also included as individual

prey species due to their historical prevalence in Kodiak SSL diets (Sinclair & Zeppelin 2002,

McKenzie & Wynne 2008); all other prey species were summed as 'other'. Ordination of

samples was carried out using non-metric multidimensional scaling (MDS) and presented in two

dimensions. Stress values were calculated to measure how well the two-dimensional plots

represent the true ordination, with values < 0.1 considered good representations and values < 0.2

still useful (Kruskal & Wish 1981).

ANOSIM tests revealed SSL diet composition was similar for years that did (2004 –

2005) and did not overlap (2000 – 2003) with humpback sample collection years (R = 0.05, P =

0.01; Fig 3.3). In addition, humpback whale samples did not differ significantly in annual mean

δ^{15}N value (Wright et al. *In review*, Chapter 2) suggesting forage fish availability was similar

from 2004 – 2013. Therefore, we proceeded to compare the diet overlap of humpback whales

and SSLs for the two regions, 'North' and 'South'.

Results

On the Kodiak feeding ground, 118 humpback whale skin samples collected from 2004 –

2013 were used in analyses: 55 from the 'North' and 63 from the 'South' region (Table 3.1;

Wright et al. *In review*, Chapter 2). Humpback whale δ^{13}C and δ^{15}N values were normally

distributed (δ^{13}C: W = 0.98, P = 0.06; δ^{15}N: W = 0.99, P = 0.92).

A total of 151 prey samples collected on the Kodiak feeding ground were used to compute prey species mean (± 1 SD) δ^{13}C and δ^{15}N values for SIAR modeling (Table 3.1). Samples sizes ranged from nine (age-1 pollock, sandfish, and age-0 pollock) to 42 samples (> age-1 capelin; Table 3.1). Only capelin grouped into more than one age class based on the lengths of samples collected (Table 3.1; Fig. 3.4). Smaller age-classes of pollock, eulachon, and herring were not collected in trawls and thus, were not included in SIA and modeling (Table 3.1; Fig. 3.4).

Mean δ^{13}C and δ^{15}N values varied for potential humpback whale prey (Table 3.1; Fig. 3.5). Mean δ^{13}C values ranged from a high of -17.7±0.7 ‰ for sandfish to a low of -19.6±0.7 ‰ for krill. Similarly, mean δ^{15}N values ranged from the maximum +13.9±0.9 ‰ for sandfish to the minimum of +9.5±0.3 ‰ for krill (Table 3.1; Fig. 3.5). Normality results for prey species were mixed. ANOVA and Tukey *post-hoc* tests were used to assess isotopic similarity among prey species and size classes. Both δ^{13}C and δ^{15}N values varied significantly among sources ($F_{6,130}$ = 12.43; P < 0.001 for δ^{13}C; $F_{6,130}$ = 146.80; P < 0.001 for δ^{15}N). *Post-hoc* tests of δ^{13}C values revealed no prey type was significantly different from all others (Table 3.1). In contrast, mean δ^{15}N values of prey distributed into three subsets: (1) krill, (2) age-1, > age-1 capelin, and age-0 pollock, and (3) ≥ age-3 eulachon, > age-1 herring, and sandfish (Table 3.1; Fig. 3.5).

Humpback whale diet modeling

Pairwise correlations were computed to assess whether the SIAR model fit of individual source contributions are reliable for isotopically similar sources. Negative pairwise correlations ranged from a minimum of -0.23 to a maximum of -0.18 for > age-1 capelin, sand lance, and age-0 pollock. Weaker negative pairwise correlations occurred among > age-1 herring, ≥ age-3

eulachon, and sandfish, ranging from a minimum of -0.17 to a maximum of -0.11. The negative correlations indicate the model may have had difficulty in differentiating among certain isotopically similar sources (Fig. 3.5). As a result, the isotopically similar sources were combined into groups and the resulting model (Grouped Sources (GS) model) was run for comparison with the individual prey model (IP; Fig. 3.6) to explore how grouping isotopically similar sources may impact the posterior probability distributions. To compute the mean and SD of the group involving sand lance, 14 normally distributed random numbers were synthesized (package 'stats') with the mean and SD of sand lance from Williams et al. (2008). The resulting stable isotope values were used with the > age-1 capelin and age-0 pollock stable isotope data to compute the group mean and SD.

Dietary estimates of humpback whales in the two Kodiak sub-aggregations were computed in SIAR (Parnell et al. 2010). Results from both the IP and GS models support dietary differences between the two sub-aggregations (Fig. 3.5). For IP models, krill was a dominant (mean, 95% credibility intervals) diet component of both sub-aggregations ('North': 38.6 %, 22.9–54.3; 'South': 66.1 %, 55.1–76.7; Fig. 3.6A1, B1). The dominance of krill to the diet was similar in the GS models ('North': 39.1 %, 21.6–59.2; 'South': 68.0 %, 55.7–80.4; Fig. 3.6A2, B2). Krill comprised a greater proportion of the diet of humpback whales in the 'South' sub-aggregation compared with the 'North' for both models (Pr(D|M)=1.00). Fishes were more important to the 'North' sub-aggregation diet than the 'South' for both IP and GS models (Fig. 3.6). For the 'North' sub-aggregation of the IP model, age-1 capelin (15.5 %, 1.1–28.9) composed the greatest proportion of the fish sources followed by age-0 pollock (11.8 %, 0.0–28.2), > age-1 capelin (10.7 %, 0.0–26.5), and sand lance (9.3 %, 0.0–23.2; Fig. 3.6A1). For the GS model, the group including > age-1 capelin, age-0 pollock, and sand lance was the second

most important prey source for both sub-aggregations ('North': 31.0 %, 2.7–54.7; 'South': 18.8 %, 0.6–35.0; Fig. 3.6A2, B2). This group constituted more of the diet in the 'North' sub-aggregation (Pr(D|M)=0.74). Age-1 capelin composed a greater proportion of the 'North' sub-aggregation diet in the GS models compared with the 'South' (Pr(D|M)=0.84). In contrast, IP model mean fish sources for the 'South' sub-aggregation each comprised < 7.5 % of the diet composition (Fig. 3.6B1). Sandfish, $\geq$ age-3 eulachon, and > age-1 herring were the least important sources to the diet as individual sources (< 6.0 %; Fig. 3.6A2, A2) and grouped ('North': 13.6 %, 0.0–28.3; 'South': 7.1 %, 0.0–15.8; Fig. 3.6A2, B2) for each humpback whale sub-aggregation, but the sources were left in both models to account for the upper range of humpback whale $\delta^{13}C$ and $\delta^{15}N$ values in isotopic space (Fig. 3.5).

SSL diet modeling

A total of 656 SSL scat samples containing identifiable prey remains were collected from haul-out sites for the ssFO diet estimation method: 530 from the 'North' and 126 from the 'South' region (Table 3.2). Scat samples were collected in more months and years in the 'North' region compared with the 'South' (Table 3.2). The regional difference in sample size and sampling months and years (Table 3.2) was primarily due to sampling constraints. Out of the six prey species shared with humpback whales, capelin and herring comprised proportionally more of the SSL diet in the 'North', whereas pollock was more important in the 'South' (Fig. 3.7). The proportion of sand lance in the diet was similar between regions (9.2 % 'North', 8.8 % 'South'; Fig. 3.7). Contribution of eulachon and sandfish were minimal (< 1 %) to SSL diet of both regions (Fig. 3.7). The 'other' category comprised the majority of the SSL diet for each region, but it was smaller in the 'North' region (55.2 % 'North', 66.3 % 'South'; Fig. 3.7). Within the 'other' category, ATF and salmon species were the dominant prey of both regions (Fig. 3.7)

Niche overlap

The trophic niche overlap index between Kodiak humpback whales and SSLs was less than the biologically significant value of 0.60 (Wallace 1981) for all diet composition indices in both regions, regardless of SIAR model (IP and GS; Table 3.3). However, the 'North' region indices were higher than the 'South' for both models, and the regional difference was larger for the GS model. The niche overlap indices computed from IP SIMMs ranged from 0.02 (SIMM mode) to 0.09 (SIMM mean) for the 'South' region and 0.09 (SIMM mode) to 0.16 (SIMM mean) for the 'North' region (Table 3.3). The 'North' region overlap indices computed from GS SIMMs were much larger (0.43 mode; 0.44 mean and median) compared with the 'South' region (0.14 mode; 0.15 mean and median; Table 3.3).

Discussion

Diet compositions

As generalist consumers, differences in diet composition between 'North' and 'South' regions for humpback whales and SSLs may reflect variability in prey biomass along the eastern side of the archipelago. The waters of this region consist of distinct water masses (*e.g.*, Alaska Coastal Current, Kodiak coastal water, Alaska Stream) that interact at varying spatial and temporal scales due to complex bathymetric features, including several troughs, such as Chiniak Trough in the 'North' and Barnabas Trough in the 'South' region (Fig. 3.1; Kendall et al. 1980, Stabeno et al. 2004, Hollowed et al. 2007). Oceanographic conditions within and around troughs during summer months (May – mid-September) have been linked to spatial differences in prey assemblages (Hollowed et al. 2007). Capelin biomass appears to be influenced by frontal systems, which may explain their observed homogenous distribution over Chiniak Trough in the 'North region', and aggregation on the ocean-side of the mid-trough frontal zone over Barnabas

Trough in the 'South' (Wilson et al. 2003, Guttormsen & Yasenak 2007, Hollowed et al. 2007).

Capelin also frequently occur during summer off the northeast tip of the Kodiak Archipelago

(Guttormsen & Yasenak 2007). Similar to capelin, pollock have appeared homogeneously

distributed within Chiniak Trough, but in contrast to capelin have been observed aggregating on

the coastal side of the Barnabas mid-trough frontal zone (Spalinger 2003, 2006, 2012,

Guttormsen & Yasenak 2007, Hollowed et al. 2007). Sandfish and herring occur in lower

biomass in both regions of this study compared with other forage fish species (Jackson 2005,

2006, 2007). Baleen whales feed on aggregate prey above a threshold density to ensure positive

net energy gain from a feeding event (Piatt & Methven 1990, Hazen et al. 2009, Goldbogen et al.

2011). Therefore, sandfish and herring may not be favorable prey for humpback whales along the

eastern side of the archipelago because of their low biomass in the region. Eulachon occur in

patches in summer months in both Kodiak regions (Jackson 2005, 2006) and have the highest

wet and dry energy density of all GOA forage fishes (Anthony et al. 2000). The lack of eulachon

in the diet of humpback whales appears to be due to eulachon occurring at depths deeper than

humpback whales tend to dive (Witteveen et al. 2008). Alternatively, humpback whales may be

feeding on eulachon size classes that were not captured in our sampling (Table 3.1, Fig. 3.3).

Depth of Kodiak eulachon may also explain why eulachon is not a prominent prey of Kodiak

SSLs. Southeast SSLs target eulachon in high abundance in summer months, but do so while

eulachon aggregate nearshore in early summer (April-May) before traveling in rivers to spawn

(Sigler et al. 2004, Womble & Sigler 2006). The lack of eulachon in Kodiak SSL diets may also

be influenced by the sampling method (scat samples). Captive feeding studies with California sea

lions (*Zalophus californianus*) showed an average recovery rate of eulachon otoliths of

46.5±13.7% (Orr & Harvey 2001), suggesting eulachon may be underestimated in the diet of

SSLs when scat samples are used. Preliminary analysis of hydroacoustic backscatter collected during mid-summer (2005, 2011, 2013) suggests krill biomass peaks over Barnabas Trough (K. Simonsen, pers. comm. NOAA Seattle, WA). Little distribution data are available for sand lance, but adult fish start aggregate spawning in August in the intertidal zone of bays (Robards et al. 1999). Humpback whales and SSLs fed more on capelin in the 'North' region, whereas humpback whales in the 'South' consumed more krill and SSLs ate more pollock (Fig. 3.5, 3.6). Therefore, the diet compositions of humpback whales and SSLs in the 'North' and 'South' regions of the archipelago appear to reflect opportunistic consumption of nearshore prey assemblages.

The humpback whale diet composition findings are consistent with Wright et al. (*In review*, Chapter 2) that concluded humpback whales in the 'North' region foraged on higher TL prey than whales in the 'South' region. The range of feasible contributions of the humpback whale GS model including > age-1 capelin, age-0 pollock, and sand lance may be more reasonable than the IP model estimates of individual sources due to the overlap in stable isotope values for these sources (Fig. 3.4). However, it is not possible to discern how much of each of these prey sources contributed to the GS range based on our data. Capelin and age-0 pollock often co-occur spatially in the water column (Hollowed et al. 2007), yet, tagged whales in the 'North' region have been shown to preferentially forage on capelin over age-0 pollock when both species are present (Witteveen et al. 2008). Humpback whales may target capelin because they have a higher energy density per gram compared with pollock (Anthony et al. 2000). Sand lance have similar energy densities to capelin (Anthony et al. 2000) and are thought to be able to tolerate wider ranges of water temperature, thus allowing them to occupy broader habitat ranges than other forage fish species (e.g., herring; Abookire & Piatt 2005). Therefore, depending on

abundance and oceanographic conditions, humpback whales may be more likely to feed on capelin and sand lance than age-0 pollock.

The diet diversity of SSLs included demersal, semi-pelagic, and pelagic species, supporting their opportunistic feeding strategy as central place foragers (Fig. 3.6; Orians & Pearson 1979). It should be noted that the regional difference in SSL diet composition might be influenced by the difference in months sampled between regions (Table 3.2). MDS plots of Kodiak SSL scat grouped Kodiak SSL diet composition into May-June and July-August diets (GAP unpubl. data), which suggest prey availability and diet choice may vary within the summer feeding season. Collecting SSL scat samples in early summer is difficult due to the aggressive behavior of the bulls. However, early summer samples are needed in the 'South' region to accurately compare regional SSL diet composition.

There are limitations to the use of hard remains in scats to reconstruct diet. The predominant bias being the differential rates of digestion and recovery of diagnostic structures between and within prey species (Cottrell & Trites 2002, Tollit et al. 2003, Joy et al. 2006). More robust bones from species such as pollock may have greater recovery rates compared with fragile structures of smaller species, such as capelin and sand lance (Tollit et al. 2003, 2007), which could lead to an underrepresentation of forage fishes in this study. However, as stated previously, ssFO tends to overestimate the importance of smaller prey species (Laake et al. 2002), and thus this method may have provided a realistic diet composition of Kodiak SSLs.

Niche overlap

Strict interpretation of the trophic niche overlap indices may be limited due to the lack of direct temporal overlap between predator diets and differences in diet estimation (Table 3.1, 3.2). However, the 'North' region SSL diet was similar between the years that did (2004 – 2005) and

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did not (2000 – 2003) overlap with humpback whale sampling (Fig. 3.3). In addition, consistency of humpback whale skin δ^{15}N values from 2004 – 2013 (Wright et al. *in Review*, Chapter 2) suggests similar forage fish availability among sampling years. Little biomass data are available for forage fish species, and therefore, we cannot determine whether biomass of forage fishes varied within the study period (2000 – 2013). On the other hand, bottom trawls conducted by ADF&G suggest ATF, pollock, and cod stocks have increased in abundance in both regions between 2002 (start of trawl sampling period) and present (Spalinger 2003, 2006, 2012). Thus, our SSL diet composition estimates likely reflect lower contributions of piscivorous fishes compared with more recent samples, and our results may overestimate the diet overlap between humpback whales and SSLs. Concurrent sampling of SSL and humpback whale diets are needed to provide more accurate diet overlap indices.

The difference in time frame reflected by the sample collection methods (scat versus SIA) remains a limitation of the study. Obtaining scat samples from haul-out sites has been the predominant method to study SSL diets (da Silva & Neilson 1985, Murie & Lavigne 1986, Harvey 1989, Tollit et al. 2006), and obtaining scat samples from cetaceans is opportunistic and time intensive (Parsons et al. 1999). Both predator datasets span the summer season (Table 3.2; Wright et al. *In review*, Chapter 2), and thus, the datasets likely overlap, at least partially, in reflected dietary time frame within the summer feeding season. However, as stated, SSL scat samples were not collected in early summer in the 'South' region (Table 3.2). As a result, the diet overlap indices presented in this study should be interpreted cautiously and treated only as a first approximation.

Humpback whale and SSLs diet did not overlap significantly for either region. However, the higher trophic niche overlap in the 'North' region reflects the importance of forage fishes to

the 'North' sub-aggregation humpback whale diet and capelin to the 'North' SSL diet. In regions where predators consume the same forage species, it is possible that prey competition exists if resources are limited (Connell 1961). The biomass of forage fishes around the Kodiak Archipelago remains poorly understood, but this information is crucial to ascertain if prey resources are limiting or approaching limited numbers. Capelin comprised more of the 'North' region SSL diet than any other prey species (Fig. 3.7) and are themselves prey for multiple piscivorous fishes that are consumed by SSLs (Knoth & Foy 2008, McKenzie & Wynne 2008, Urban 2012). An average Kodiak humpback whale consumes 370 kg prey/day (Witteveen et al. 2006), and there is an estimated 1,500 individuals in the Kodiak Archipelago population (GAP, unpubl. data). Therefore, humpback whales have the potential to annually remove large volumes of prey from Kodiak waters (~555,000 kg prey/day) and, in turn, impact available prey biomass for other species. Thus, a partial diet overlap between humpback whales and SSLs may directly impact the recovery of the Kodiak SSL population depending on the humpback whale population size and biomass of available prey species. It is unlikely that a major decline in any single prey species would negatively affect SSLs due to their adaptive feeding strategy as opportunistic central place foragers (Orians & Pearson 1979). However, forage fishes and krill are critical links between primary production and higher trophic level predators in the Kodiak region. Consumption by a growing humpback whale population on forage fishes and krill may affect multiple trophic levels in the system, which could impact the population growth of various generalist predators, including SSLs.

Proximity of humpback whale foraging to SSL haul-out and rookery sites may also impact SSL populations. SSL foraging behavior appears to depend on the predictable patterns of their prey, specifically targeting nearshore and densely schooled prey aggregations (Sinclair &

Zeppelin 2002). It has been suggested that regional foraging strategies of SSL females are learned near their natal rookery sites (Sinclair & Zeppelin 2002), and most GOA pups and juvenile SSLs make short foraging trips ($\leq$ 15 km, < 20 h; Raum-Suryan et al. 2004). In addition, juvenile SSLs are often inexperienced foragers, and thus, may not be able to behaviorally adapt to prey switches on short temporal scales (Merrick 1995). Also, high energy demands of pregnancy and lactation (Charnov 1976) could affect reproductive females' energy budget and physiological condition if increased travel is needed to secure adequate prey resources. Under these conditions, seasonal shifts in prey composition near rookeries or haul-out sites due to consumption by humpback whales could impact the foraging success of females and young SSLs. This is especially pertinent as both Kodiak Archipelago SSL rookeries (Marmot and Sugarloaf) are located in the 'North' region (Wynne et al. 2012), where the trophic niche overlap is higher.

Movement by individual SSLs to areas with adequate prey abundance could potentially mitigate any localized shifts in prey assemblages. Through tagging studies, researchers have shown that SSLs can move great distances (> 1,000 km) from their natal rookeries depending on their life stage (Raum-Suryan et al. 2002, Jemison et al. 2013). Brand resights of SSLs in the Kodiak region have documented individuals occupying multiple haulout/rookery sites throughout their lifetime (Wynne et al. 2012). However, most Kodiak young-of-the-year SSLs do not appear to travel far from rookery sites (Wynne et al. 2012). Also, as stated previously, increased travel time for nursing or pregnant females among sites would likely impact the energy budget of individuals and may alter physiological condition. Thus, a seasonal reduction in the availability of predictable prey species from consumption by humpback whales around rookery or haul-out sites could impact the success of reproductive females and juvenile SSLs.

Forage fishes as a whole comprise only a fraction of the diet of SSLs as highlighted by the 'other' category of the ssFO pie chart (Fig. 3.7). At least 50% of the SSL diet of both regions was comprised of prey species other than forage fishes. The most prominent prey type in the 'other' category was piscivorous fishes, which appear to overlap considerably with the diet composition of Kodiak humpback whales. For example, ATF was the most abundant prey species of the 'other' category (14.5 % 'North', 25.3 % 'South'; Fig. 3.7), and during summer, ATF in Kodiak waters consume krill, age-0 pollock, sand lance, and capelin in addition to shrimp (Knoth et al. 2008). Pink (*Oncorhynchus gorbuscha*) and red salmon (*Oncorhynchus nerka*) in the GOA consume krill at multiple life stages (Kaeriyama et al. 2000, Armstrong et al. 2005), and salmon is the second most abundant piscivorous fish in the SSL diet of both regions ('North' 15.2 %; 'South' 21.6 %; Fig. 3.7). Adult pollock consume krill in high abundance and supplement with forage fishes, including sand lance and capelin (Urban 2012). Therefore, humpback whale diet appears to overlap substantially with multiple piscivorous fish species that are prey of SSLs. This overlap may have a more detrimental indirect impact to the recovery of SSL populations than a direct overlap of forage fish consumption between humpback whales and SSLs. Thus, predominant consumption of krill by humpback whales in the 'South' region may result in stronger indirect impacts on SSL prey resources than the higher direct diet overlap seen in the 'North' region. As a result, our diet overlap index may not be the most appropriate tool to assess the extent of potential effects of diet overlap among sympatric marine mammals in the Kodiak region due to complexity of multi-species trophic interactions. Future studies that compare the trophic level and diet overlap of humpback whales and piscivorous fishes are needed to better elucidate potential impacts of humpback whale consumption to SSL populations. These data could be used with diet data of other predators in ecosystem models to

better understand multi-species interactions and annual fish removal. Thus, our study highlights the trophic complexity of the dynamic Kodiak Archipelago ecosystem and supports the potential for regional differences in diet overlap among sympatric marine mammals on a feeding ground.

Acknowledgements

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whales off Western Alaska and the central Aleutian Islands. Deep Sea Research Part I

53:1772-1790

Tables

Table 3.1. Humpback whale and potential prey species stable isotope data. Table includes mean (± 1 SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) of prey species and humpback whales used in SIAR Bayesian mixing models. Also shown are sample sizes and size ranges (fork length; cm) for age classes of prey species. Letters (*a, b, c*) indicate groupings for prey species in which $\delta^{13}C$ values were not significantly different, and Roman numerals (*i, ii, iii*) indicate prey species in which mean $\delta^{15}N$ values were not significantly different as shown by *post hoc* tests. Asterisks (*) indicate significantly different ($P < 0.05$) stable isotope signatures of humpback whale sub-aggregations as defined by a Student's t-test in Wright et al. (*In Review*; Chapter 2). Sand lance stable isotope values were collected from the 'North' region of this study by Williams et al. 2008 and were not included in variance testing.

Species	n	Class	Size range [cm]	$\delta^{13}C$ [‰]	$\delta^{15}N$ [‰]
Capelin	9	Age-1	< 10	-19.8 ± 0.9^c	11.3 ± 0.5^{ii}
Capelin	42	> Age-1	≥ 10	-18.6 ± 0.6^b	11.5 ± 0.6^{ii}
Eulachon	40	≥ Age-3	≥ 10	-18.1 ± 1.0^{ab}	13.5 ± 0.5^i
Euphausiids (krill)	14	All	n/a	-19.6 ± 0.7^c	9.5 ± 0.3^{iii}
Pacific herring	14	> Age-1	≥ 14	-17.9 ± 0.6^{ab}	13.7 ± 0.3^i
Pacific sandfish	9	All	9-24	-17.7 ± 0.7^a	13.9 ± 0.9^i
Pacific sand lance	14	All	< 6	-18.4 ± 0.6	11.5 ± 0.7
Pollock	9	Age-0	< 10	-18.7 ± 0.8^{bc}	11.3 ± 0.3^{ii}
Humpback whale; 'North'	55	n/a	n/a	-18.0 ± 0.6	$13.7 \pm 0.8*$
Humpback whale; 'South'	63	n/a	n/a	-17.9 ± 0.7	$13.0 \pm 0.8*$

Table 3.2. Steller sea lion fecal (scat) data. Table includes scat sample size (*n*), number of haul-out sites sampled, months with samples collected (X), and collection years of scats used in split-sample frequency of occurrence diet composition calculations (Eq. 3.2) for the 'North' and 'South' regions of the Kodiak Archipelago.

Region	*n*	# Sites	Months				Years
			May	June	July	Aug.	
'North'	530	6	X	X	X	X	2000 - 2005
'South'	126	2			X	X	2000 - 2003

Table 3.3. Pianka's trophic niche overlap index O_{jk}. Degree of overlap in trophic niche of Steller sea lion (SSL) and humpback whale summer diet composition in the 'North' and 'South' regions of the Kodiak Archipelago (Eq. 3.3). The Pianka index is symmetrical, meaning the overlap estimate is the same for both predators. The index ranges from 0 (no overlap) to 1 (full overlap) and a value of > 0.60 is considered biologically significant (Wallace 1981). SSL diet compositions were expressed from scat samples as split-sample frequency of occurrence as the proportion of the overall diet made up of six fish species hypothesized in the diet of Kodiak humpback whales; capelin, eulachon, herring, pollock, sandfish, and sand lance. All other SSL prey species in the scat sample were summed into an 'other' category. Humpback whale diet compositions were expressed as mean, mode, and median proportional contributions of sources from SIAR stable isotope mixing models. The first SIAR model included all individual prey species and size classes (IP) and the second model included isotopically similar sources (GS) grouped.

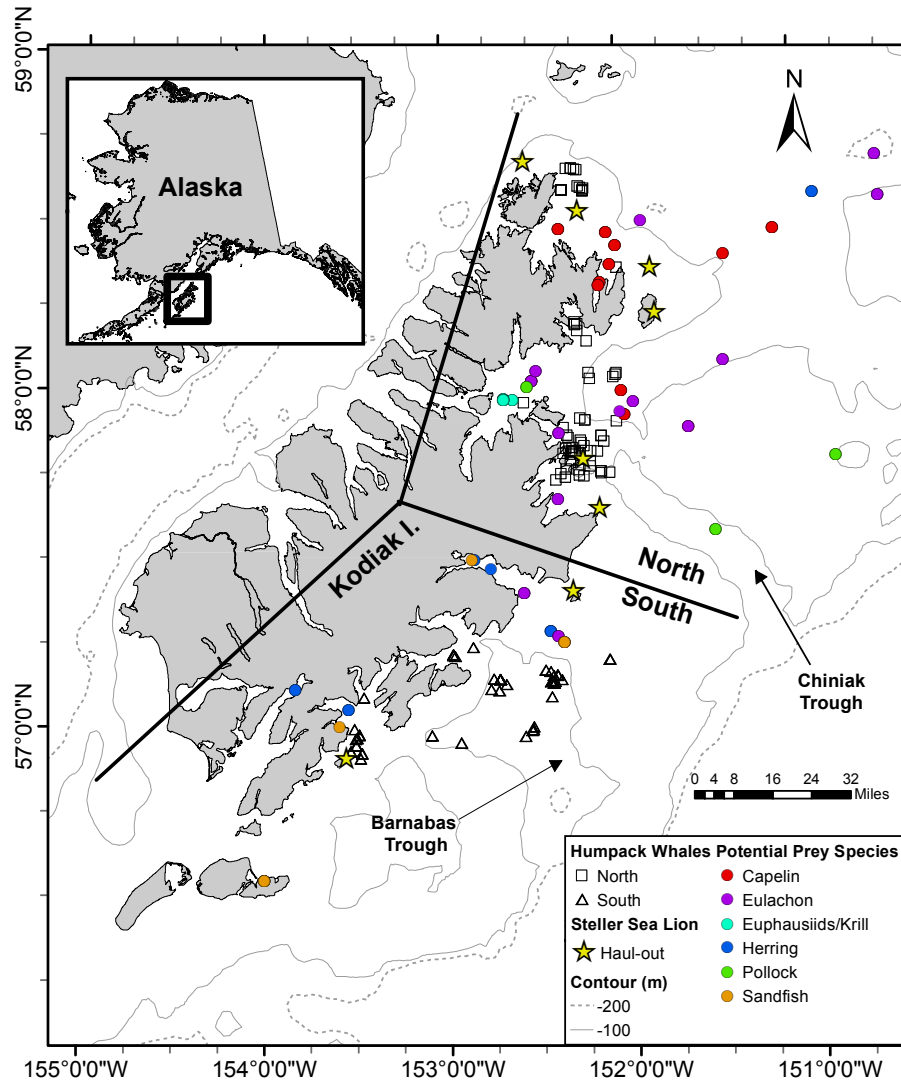| Model	Diet Compositions	'North'	'South'
IP	SSL + Humpback whale Mean	0.16	0.09
IP	SSL + Humpback whale Mode	0.09	0.02
IP	SSL + Humpback whale Median	0.15	0.07
GS	SSL + Humpback whale Mean	0.43	0.15
GS	SSL + Humpback whale Mode	0.44	0.14
GS	SSL + Humpback whale Median	0.43	0.15

Figures

Figure 3.1. Map of the Kodiak Archipelago, AK, USA. Map includes locations of skin sample collection of free-ranging humpback whales by sub-aggregation ('North', black open square; 'South', black open triangle). Also shown are Steller sea lion haul-out/scat collection sites (yellow star) and collection locations of prey species from mid-water trawls and bongo-net tows (colored circles).
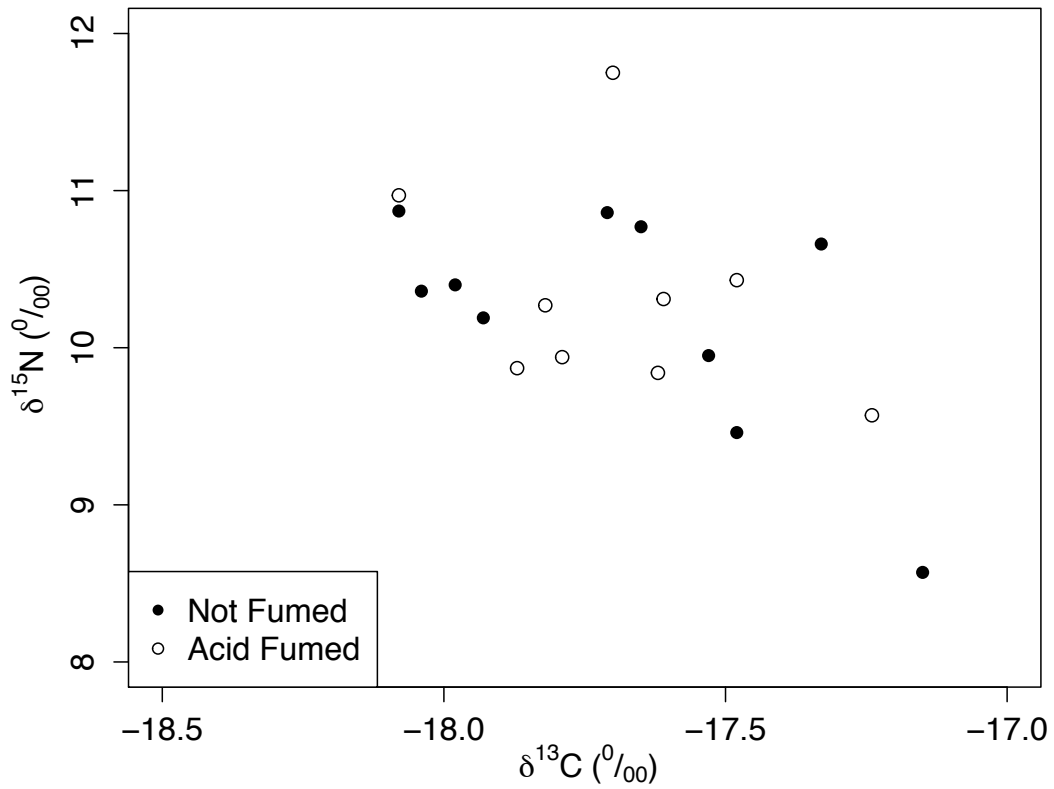
Figure 3.2. Stable carbon and nitrogen isotope ratios of individual adult krill. Krill were sampled from twin-ring bongo net tows in Kodiak waters. All samples were defatted using 2:1 chloroform:methanol washes. Open circles indicate krill that were fumed at saturated HCl vapors for six hours ($n = 9$) to remove $CaCO_3$ exoskeletons and closed circles indicate non-acid fumed samples ($n = 10$).
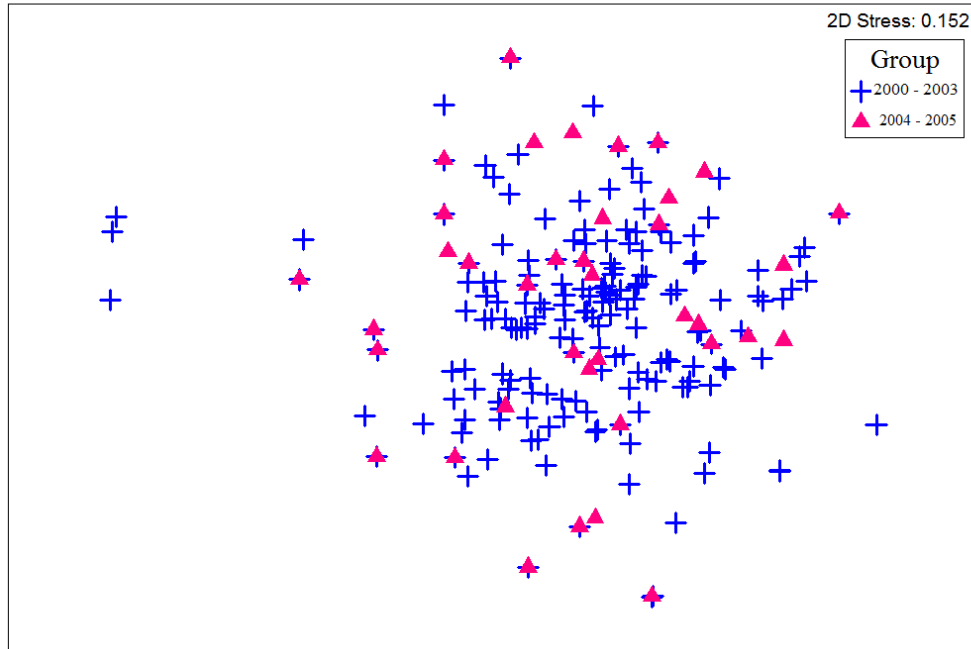
Figure 3.3. MDS ordination of Steller sea lion (SSL) diet composition. Diet composition was defined as the split-sample frequency of occurrence (ssFO) of identifiable prey remains in scat samples ($n = 530$) sampled from haul-out sites in the 'North' region of the Kodiak Archipelago, AK. Samples are separated into time periods that did (2004 – 2005; pink triangle) and did not (2000 – 2003; blue cross) overlap with humpback whale sampling (2004 – 2013). Prey species of the ssFO include the 6 prey types hypothetically shared between humpback whales and SSLs and piscivorous fish species that were historically prevalent in Kodiak SSL diets (Sinclair & Zeppelin 2002); all other prey types were summed into 'other'.
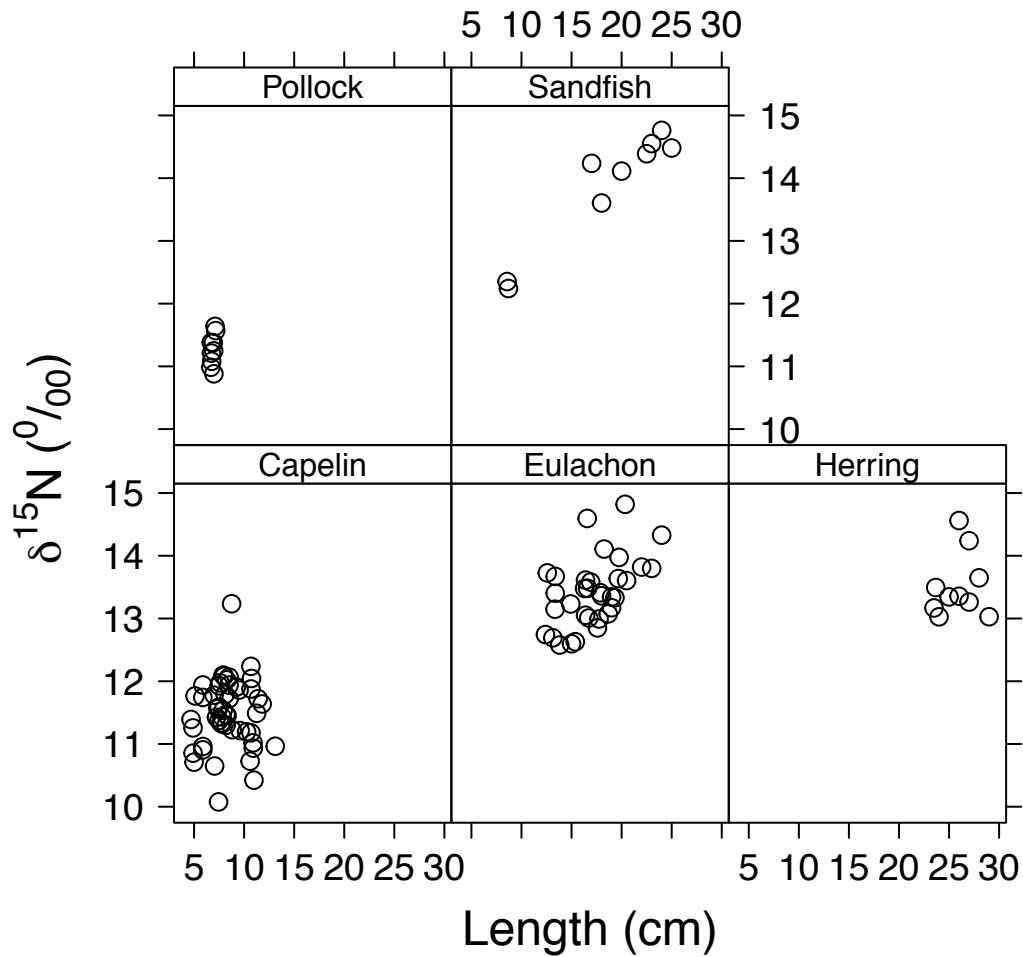
Figure 3.4. Potential humpback whale fish prey δ^{15}N values (‰) by fork length (cm). Fishes were collected from mid-water trawls on the eastern side of the Kodiak Archipelago. Dashed lines indicate regional age-at-length class divisions with the left of the line representing the age class, and the right of the line signifying 'greater than' the age class, from bottom left to top right: age-1 capelin, age-3 eulachon, age-1 herring, and age-0 pollock. Sandfish δ^{15}N values were not separated into age classes due to small ($n < 10$) sample size.
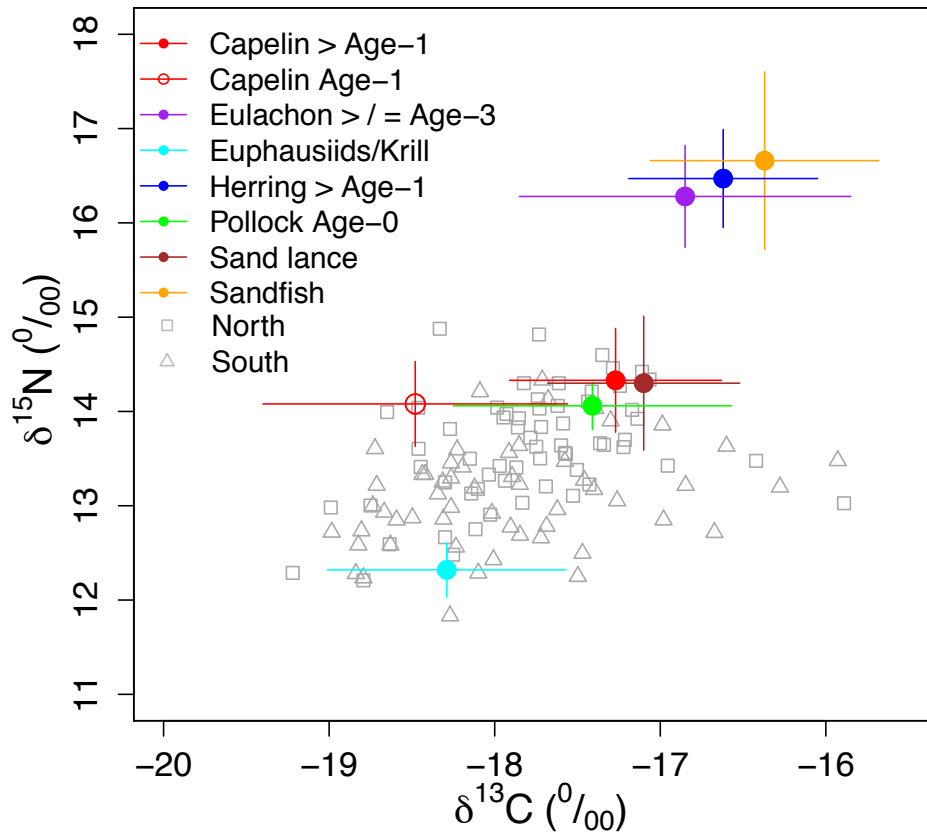
Figure 3.5. Mean (± 1 SD) potential humpback whale prey δ^{13}C and δ^{15}N values (‰) after the stable isotope discrimination value for fin whale skin (1.3 ‰ for δ^{13}C; 2.8 ‰ for δ^{15}N; Borrell et al. (2012)) was applied. Prey species are defined by colored circle. The open red circle represents the smaller size class of capelin (age-1), and the solid red is the larger size class (> age-1). Prey were collected from mid-water trawls and bongo-net tows in waters of the eastern Kodiak Archipelago Also shown are δ^{13}C and δ^{15}N values of humpback whale skin by sub-aggregation ('North', gray open square; 'South', gray open triangle).
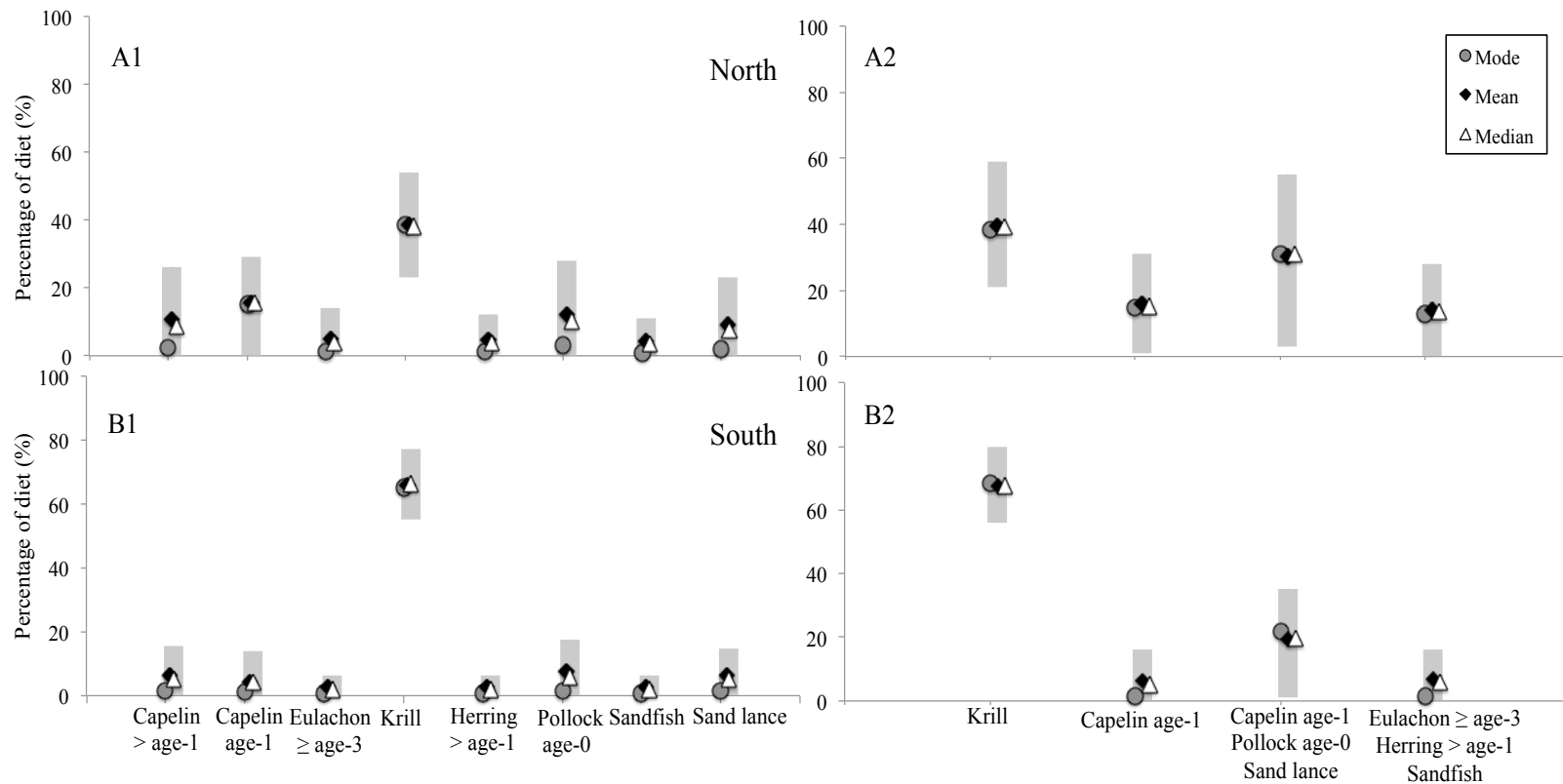
Figure 3.6. Humpback whale regional summer diet composition. Differential proportional contributions of prey sources in modeled summer (May – mid-September) diet solutions of humpback whales from the 'North' (A1, A2) and 'South' (B1, B2) sub-aggregations on the Kodiak feeding ground as mode (gray circle), mean (black diamond), and median (white triangle) values with 95% credibility intervals (gray bars). Left panels (A1, B1) indicate SIAR models computed using all individual prey sources and size classes (IP), whereas the right panels (A2, B2) show SIAR models computed with isotopically similar prey sources (GS) grouped.
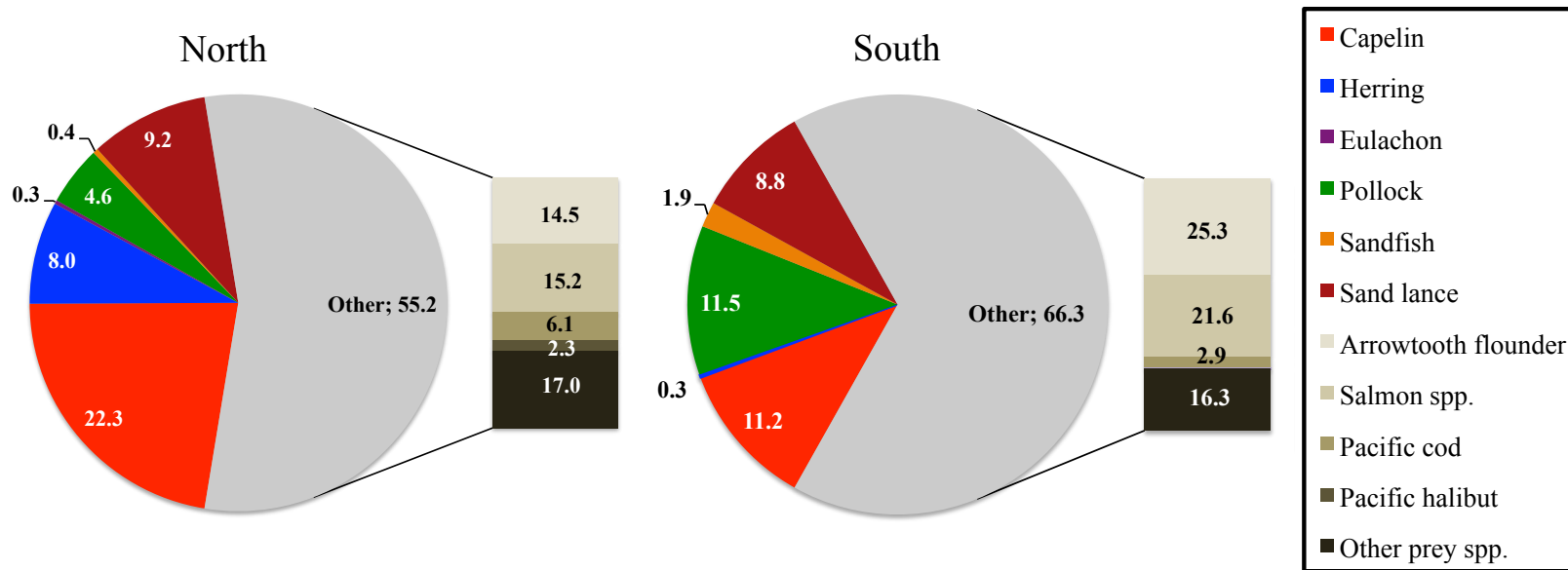
Figure 3.7. Kodiak Steller sea lion (SSL) regional summer diet composition. Diet composition was computed from scat samples collected from the 'North' ($n = 530$; left) and 'South' ($n = 126$; right) regions of the Kodiak Archipelago, and is expressed in the pie chart as split-sample frequency of occurrence (Eq. 3.2) as the proportion (%) of the overall diet made up of 6 fish species hypothesized to be in the diet of Kodiak humpback whales, with all other prey species in the scat sample summed into an 'other' category (gray slice). The dominant species that comprised the 'other' category are shown in the adjacent gold-stacked bar chart.

Appendix
Permission of Chapter 3 manuscript, Dr. Lei Guo

Marine Advisory Program
School of Fisheries and Ocean Sciences
University of Alaska Fairbanks

Kodiak Seafood and Marine Science Center
118 Trident Way, Kodiak, AK 99615
907.486.1503 (phone) 907.486.1540 (fax)
lei.kodiak@gmail.com

Dana L. Wright
Graduate Student | Research Assistant
School of Fisheries and Ocean Sciences
University of Alaska Fairbanks

Kodiak Seafood and Marine Science Center
118 Trident Way, Kodiak, AK 99615

August 8th, 2014

Dear Dana Wright,

You have my permission to include any manuscript we have been or will be working

together in your master thesis.

Leo Guo   *August 8th, 2014*

Dr. Lei Guo
Post-Doctoral Fellow
Marine Advisory Program
School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
lguo2@alaska.edu
(907) 486-1503

www.marineadvisory.org

Anchorage • Bethel • Cordova • Dillingham • Juneau • Ketchikan • Kodiak • Nome • Petersburg • Unalaska

Chapter 4: Conclusions

The chapters of this thesis contribute to the understanding of variability in foraging by humpback whales (*Megaptera novaeangliae*) along the eastern side of the Kodiak Archipelago using stable isotope analysis (SIA). In addition to increasing our understanding of humpback whale foraging ecology, analyses and results from this thesis provide evidence that increasing humpback whale populations may have the potential to indirectly impact the recovery of Steller sea lions (SSLs; *Eumetopias jubatus*) on a regional scale through increased consumption of shared prey resources. Using different approaches utilizing stable isotope data, the results of Chapters 2 and 3 show that Kodiak humpback whales sampled from the 'North' region (Fig. 4.1) fed on a mixed diet of euphausiids (hereafter, 'krill') and forage fishes (higher trophic level; TL), while 'South' region whales fed predominantly on krill (lower TL) throughout the study period ($n = 118$, 2004-2013; Fig. 4.1). Chapter 3 also presents evidence of spatial variability in the diet composition of SSLs for the two regions defined in Chapter 2 ('North', 'South') using fecal samples ($n = 656$, 2000 – 2005) and the split-sample frequency of occurrence diet estimation method (Olesiuk *et al.* 1990). Chapter 3 indicates greater overlap in prey resources, although not biologically significant, between humpback whales and SSLs in the 'North' region compared with the 'South', primarily due to the consumption of capelin (*Mallotus villosus*) by both predators. The chapters of this thesis suggest that at least two sub-aggregations of humpback whales occur within the Kodiak feeding ground, and that foraging by these sub-aggregations may impact available prey resources for sympatric predators in the Kodiak ecosystem on a regional scale.

Diet overlap among apex predators for limited prey resources have been documented in other ocean systems. In the northwest Atlantic, predation by grey seals (*Halichoerus grypus*) on

Atlantic cod (*Gadus morhua*) increased due to a reduction in seal hunts (Mohn and Bowen 1996). This increased consumption exacerbated the rate of depletion of Atlantic cod triggered by commercial over-harvest, which ultimately resulted in the collapse of the Atlantic cod stock and fishery (Mohn and Bowen 1996, Myers *et al.* 1997, Harris 1998). Ramifications of the cod stock collapse include trophic cascades that impacted prey abundance and the success of predator populations (Regehr and Montevecchi 1997, Tasker *et al.* 2000, Frank *et al.* 2005). For example, reduced and delayed availability of capelin from the trophic cascade in the northwest Atlantic led to nutritional stress in black legged kittiwakes (*Rissa tridactyla*) resulting in decreased breeding success (Regehr and Montevecchi 1997). In addition, food-stress increased predation of kittiwake egg clutches by common gulls (*Larus canus*; Regehr and Montevecchi 1997).

A second example of diet overlap for limited resources occurs in the South Georgia ecosystem off Antarctica. Antarctic krill (*Euphausia superba*) remain a prominent prey source for multiple predators in the Antarctic ecosystems, including marine birds, seals, and whales (Laws 1977, Hempel 1985). The biomass of Antarctic krill has been declining over the last half-century, which is thought to be the result of changing oceanographic conditions (Murphy and Reid 2001, Atkinson *et al.* 2004). However, Antarctic balaenopterid populations, which forage predominantly on krill, are increasing in Antarctic waters following their severe exploitation in the 20th century (Paterson *et al.* 1994, Clapham *et al.* 1999, Branch *et al.* 2004). The recovery of balaenopterids in Antarctic waters may impact the available krill biomass. Limited krill biomass has been linked to reduced breeding success of various Antarctic seabirds and seals (Croxall *et al.* 1988, Weimerskirch *et al.* 2003). Thus, competition among predator species, including seabirds, seals, and increasing baleen whale populations, for limited krill biomass may result in population fluctuations of Antarctic predators depending on their foraging strategy and affiliation

with sea ice (Loeb *et al.* 1997, Barlow *et al.* 2002, Croxall *et al.* 2002, Lynnes *et al.* 2004). Both ecosystems demonstrate that diet overlap among apex predators for limited prey may alter ecosystem dynamics. Thus, a better understanding of variability in foraging of predator populations is needed to predict potential impacts of competition among predators in an ecosystem.

Results from this thesis can be used to further our understanding of the importance of humpback whales in the Kodiak ecosystem. The humpback whale diet composition estimates of Chapter 3 could be used with a current abundance estimate of the Kodiak humpback whale feeding aggregation to update annual estimates of prey removal by Kodiak humpback whales and provide a more accurate estimate of predation mortality for various fish species. These estimates could then be utilized in multi-species ecosystem models to increase the resolution of multi-species interactions in the Kodiak region. In addition, the humpback whale stable isotope time series (2004 – 2013) provides a contemporary baseline of foraging data, which could be combined with future stable isotope data to track potential changes in humpback whale diet associated with changing oceanographic conditions. For example, sightings of bowhead whales (*Balaena mysticetus*) off Barrow, AK, coincided with wind and oceanographic conditions that promote frontal formations, which are thought to aggregate and retain zooplankton on the western Beaufort Sea Shelf (Okkonen *et al.* 2011). In the Gulf of Alaska, sand lance (*Ammodytes hexapterus*), a prey species of humpback whales, SSLs, and multiple seabirds (Anderson *et al.* 1997, Chapter 3), can tolerate wider temperature ranges than other forage fishes (*e.g.*, Pacific herring (*Clupea pallasii*); Abookire and Piatt 2005). Global ocean temperatures have been increasing at 0.11 ºC decade^{-1} in the upper 75 m of the water column from 1971 – 2010 (Stocker

et al. 2013). Thus, the composition of prey assemblage for predators in the Kodiak ecosystem may change with increasing ocean temperatures.

The methods used in the chapters of this thesis could be applied to other Kodiak predators to further enhance our understanding of trophic interactions and trophic cascades around the Kodiak Archipelago. Similar to humpback whales, fin whales (*Balaenoptera physalus*) underwent a marked population decline in the North Pacific from commercial harvest until a moratorium was placed in 1986 (Reeves *et al.* 1985, Klinowska 1991). Little is known about the recovery of fin whale populations in the North Pacific following the moratorium, but the abundance of fin whales has increased in the 'North' region of this study since observations began in 2000 (Gulf Apex Predator-prey (GAP) study, Kodiak, AK, unpubl. data). Fin whales are filter feeders that are thought to consume predominantly krill (Nemato 1957, Flinn *et al.* 2002), and stable isotope data from the Kodiak 'North' region suggest fin whales feed on lower trophic level prey than humpback whales (Wynne and Witteveen 2008). Thus, fin and humpback whales may partition prey resources in the 'North' region. However, humpback whales in the 'South' region are estimated to consume predominantly krill (Chapter 3), and thus, movement and foraging of fin whales in the 'South' region may lead to a substantial overlap in diet composition. Removal of krill by two large balaenopterid species could impact food web linkages between primary producers and upper trophic levels, in turn impacting the available prey resources of consumers at multiple trophic levels.

This study concluded that humpback whales forage at a consistent trophic level throughout the foraging season. However, this consistency may be an artifact of using humpback whale skin tissue for SIA considering the turnover rate of humpback whale skin is unknown, but is estimated to be longer than a 20-day half-life as was estimated for bottlenose dolphin

(*Tursiops truncatus*) skin (Newsome *et al.* 2010, Browning *et al.* 2014). The turnover rate of humpback whale skin may never be empirically tested for logistical reasons. Despite this, the metabolic rate of a larger animal is lower per unit weight compared with a smaller animal (Kleiber 1947). This results in a slower turnover of tissues in an adult animal within its class (*e.g.*, bird, mammal) with the greater body mass (MacAvoy *et al.* 2005, Martínez del Rio *et al.* 2009). Therefore, further studies on the skin stable isotope turnover rate of mammals of varying mass could be used to estimate the tissue turnover rate of humpback whales, as was done for muscle tissue of ice seals and walruses (*Odobenus rosmarus*; Carroll 2012, Seymour *et al.* 2014). However, the metabolic rate of a species may deviate from the expected value, and thus, accurate mass-specific metabolic rate estimates of large whales are also needed to approximate the turnover rate of an animal using body mass. For example, the metabolic rate of the bowhead whale is ~ 1/3 lower than expected based on the Kleiber line (George 2009). Until further information becomes available on the turnover rate of humpback whale skin, stable isotopes may not be the ideal tool to answer questions on seasonal diet changes of humpback whales. To further test if humpback whales are changing their diet within the foraging period, acoustic time-depth transmitters can be placed on individual humpback whales and used in combination with fish acoustic surveys and mid-water trawls to provide short-term (*i.e.*, hours to days) data on humpback whale foraging (Witteveen *et al.* 2008). Alternatively, detection dogs could be utilized to locate cetacean fecal plumes (Rolland *et al.* 2006), or stable isotopes from the baleen of stranded individuals could be analyzed in increments to look for short-term diet shifts (Schell and Saupe 1993).

This study found evidence for the existence of two sub-aggregations of humpback whales on the Kodiak feeding ground. Humpback whales could easily travel and forage within both

study regions to obtain specific prey species. Therefore, it is of interest to investigate the fluidity of the sub-aggregations across the feeding season to better understand prey preference of individuals. Incorporation of photo-identification effort could help to determine the degree of site fidelity of individual whales to these two assumed feeding sub-aggregations. Humpback whales are known for their high site fidelity to feeding aggregations, as migratory paths are transmitted from mother to calf during the calf's early life history (Baker *et al.* 1990, 1994). Hence, it is possible that foraging strategies and prey preferences in addition to foraging location may be culturally transmitted to offspring, as has been observed for killer whales (*Orcinus orca*; Bigg *et al.* 1987, Hoelzel 1989, Yurk *et al.* 2002) and bottlenose dolphins (Sargeant and Mann 2009). Maternal transmission of foraging behavior could then result in segregation of animals into regional feeding sub-aggregations based on composition of prey assemblages. Future studies focusing on fine-scale foraging choices of humpback whale mothers and offspring may shed light on this.

The overlap of some humpback whale prey species in isotopic space (Chapter 3) suggests that the exact diet of humpback whales cannot be distinctly identified using only stable carbon and nitrogen isotopes. Additional chemical tracers (*e.g.*, sulfur or oxygen stable isotopes, fatty acids, compound specific stable isotope analysis) could be used in concert with SIA of δ^{13}C and δ^{15}N values to differentiate individual prey species and size classes (Budge *et al.* 2006, 2008, Iverson 2009). For example, variability in the proportion of specific fatty acids among prey species could be utilized in quantitative fatty acid signature analysis models (QFASA; Iverson *et al.* 2004) to estimate the diet of humpback whales using metabolically active adipose tissue (*e.g.*, blubber). While none of these dietary methods are adequate in describing feeding ecology of large whales, a combination of techniques might prove most useful (Bryan 2014).

This thesis provides evidence for the existence of spatial variability in the diet of two recovering generalist predators on the Kodiak feeding ground, the humpback whale and SSL. Fine-scale spatial variability in diet composition of humpback whales on feeding grounds may have direct and indirect impacts on prey availability for sympatric apex predators depending on the growth rate of each species and available prey biomass in the regions. Ultimately, fine-scale variability in foraging by a growing population of humpback whales on feeding grounds in the GOA may have wide-reaching implications involving trophic interactions among sympatric consumers of marine resources, including marine mammals, fishes, and commercial fisheries.

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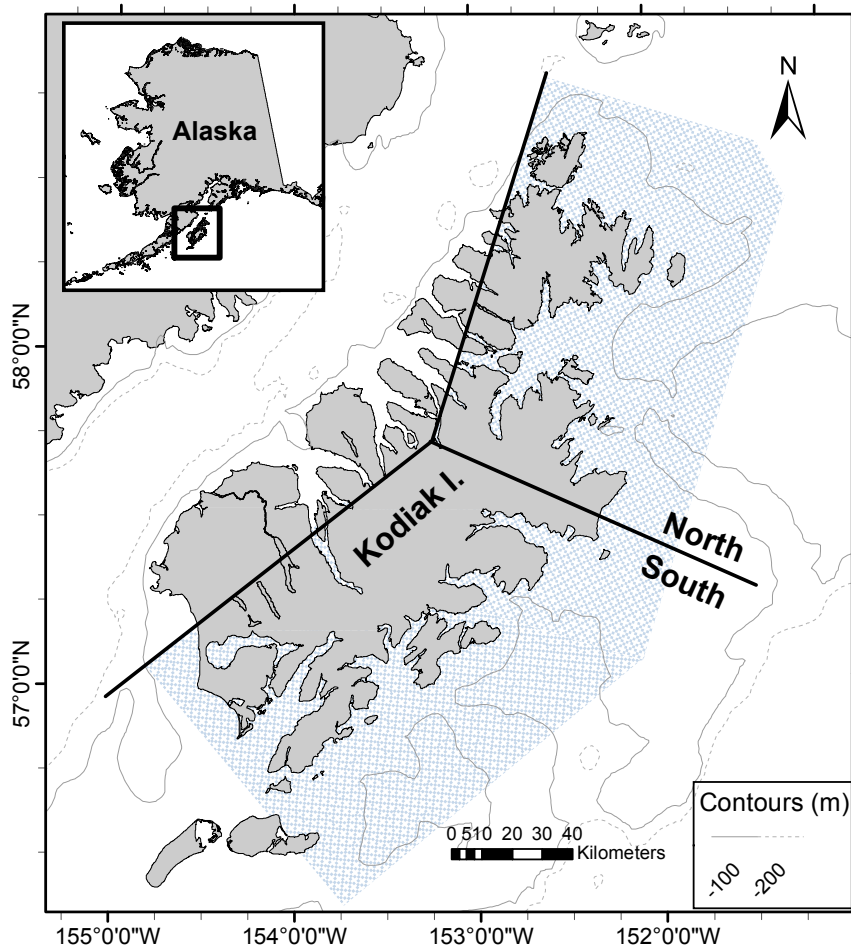
Figure

Figure 4.1 Map of the Kodiak Archipelago including the study area (blue crosshatch.) Also shown are the regional delineations 'North' and 'South' (solid black lines).

Appendix
IACUC Approval

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UNIVERSITY OF
ALASKA
FAIRBANKS

(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

March 7, 2014

To: Kate Wynne
            Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [140171-8] Whale Abundance and Feeding Ecology in Kodiak, Alaska

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	March 4, 2014
Initial Approval Date:	April 29, 2009
Effective Date:	March 7, 2014
Expiration Date:	April 29, 2015

This action is included on the March 13, 2014 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 detailed in the form 005 "Reporting Concerns".*