Spring 2013

Spatiotemporal Patterns in Diet and Habitat Use of Black-legged Kittiwakes (*Rissa tridactyla*) and Thick-billed Murres (*Uria lomvia*) in the Bering Sea

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DOI: <https://doi.org/10.31979/etd.zyb3-fg2t>
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SPATIOTEMPORAL PATTERNS IN DIET AND HABITAT USE OF BLACK-
LEGGED KITTIWAKES (*Rissa tridactyla*) AND THICK-BILLED MURRES (*Uria*
lomvia) IN THE BERING SEA

A Thesis

Presented to the faculty of

Moss Landing Marine Laboratories

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

By

Nathan M. Jones

May 2013

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The Designated Thesis Committee Approves the Thesis Titled

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ABSTRACT

SPATIOTEMPORAL PATTERNS IN DIET AND HABITAT USE OF BLACK- LEGGED KITTIWAKES (*Rissa tridactyla*) AND THICK-BILLED MURRES (*Uria lomvia*) IN THE BERING SEA

By Nathan M. Jones

This study quantified the multi-trophic influence and spatial structure of a cross-shelf $\delta^{15}\text{N}$ gradient in the Bering Sea and used it to contrast foraging patterns and seasonal changes in niche width between thick-billed murres and black-legged kittiwakes during July and August, 2008 and 2009. Gut contents of collected seabirds were characterized and stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) were conducted on whole prey tissues and seabird cheek feathers, pectoral muscle, and liver tissues. Gut contents of both seabird species were spatially auto correlated and varied with habitat type. Feather and muscle tissues indicated that murres underwent a trophic niche contraction with the onset of the breeding season, whereas kittiwakes did not. Significant geospatial structure was detected between stomach contents and isotope values from liver and muscle in murres, whereas little was observed in kittiwakes. A geospatial analysis of $\delta^{15}\text{N}$ values in prey items identified a cross-continental shelf gradient in baseline isotopic enrichment that was clearly propagated to seabird tissues. Patterns in stomach contents and isotope values indicated that murres foraged locally with more consistency than did kittiwakes and that foraging habitat partitioning was greater among murres during the breeding season in the southern Bering Sea.

ACKNOWLEDGEMENTS

This project was part of the Patch Dynamics Study, a component of the Bering Sea Integrated Ecosystems Research Project funded by the North Pacific Research Board (projects B67, B77; <http://bsierp.nprb.org/focal/index.html>). In addition, I was generously funded with an NPRB Graduate Student Fellowship during lab work, data analyses and writing in the year 2010. I thank the captains and crew of the *F/V Frosti* and *F/V Gold Rush* for their expert seamanship, commitment to safety, enthusiasm for science, and tireless efforts in support of the data collected at sea. In the laboratory, Norma Haubenstock (UAF), Tim Howe (UAF), and Rick Doucett (NAU) were exceedingly generous with their time and equipment in assisting me with isotope analyses and interpretations. I thank Larry Boyle (AK Fish and Game), David Irons (USFWS), and Dan Roby (OSU) for consultations on seabird collection techniques and for some quality time at the range in preparation, and Kathy Turco (Alaska's Spirit Speaks: Sound & Science) for her expert prey identification. Thanks also to Michelle St. Peters (USFWS) for logistics support, Larry Young for IACUC consulting at SJSU, Jim Harvey (MLML) and Kathy Kuletz (USFWS) for time to review initial drafts of this manuscript, Hannah Nevins and California Fish and Game for providing seabird processing facilities, and the students and technicians at Moss Landing Marine Labs and OSU for their time in processing collected seabirds. A special mention of thanks goes to fellow students and field crew members Brian A. Hoover (MLML) and Luke D. Whitman (OSU), without whom the size of my collections and the quality of my manuscripts would have been greatly diminished. These men remained committed and convivial under conditions

harsh enough to warrant the need for spotlights, night-vision equipment, lanyards (one of which snapped as it froze), and life vests, while balanced on the decks of ships on the open Bering Sea. They enabled a sizeable portion of the work presented here. Thanks also to Simon Brown, who helped with programming problems and shared with me a fascination with isotope ecology and love of carbonated adult beverages.

My heartfelt thanks go to my parents, who instilled in me an appreciation for the outdoors and a curiosity and enthusiasm for learning, which ultimately evolved into a professional calling. I thank here my friends and colleagues J. Peter Woodman, Mercy Vaughn, William Boarman, Gerald Monks, and J. Brooks Hart, for aggressively pursuing quality and doggedly retaining integrity in the sometimes murky field of environmental consulting. They kept me gainfully employed and, therefore, enabled my continued studies during my time at Moss Landing. I thank Kathy Kuletz (USFWS) and David Irons (USFWS) personally, both of whom opened their homes to me and many, many other field technicians during summer seasonal work in Alaska. In the “lower 48”, I also thank Dan Hankins, good friend and philosopher, who quite literally maintained an open door for me during my many times of transition between Alaskan seas, desert dunes, and CA central coast living. Great thanks also to Bill Harp for procuring student copies of ArcGIS, and passing along his enthusiasm for spatial analyses. And, lastly and most importantly: Thank you Liana Harp for sharing with me a sharp intellect and a profound capacity for commitment and engagement in the love of life and one another.

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THESIS INTRODUCTION

The Bering Sea spans a region between cold, dry Arctic air masses to the north, and relatively moist, warm Pacific air masses to the south. Like the eastern North Atlantic, it has been characterized as a transition zone between Arctic and sub-Arctic marine ecosystems, and particularly sensitive to climatic fluctuations (Overland et al. 2004; Barnett et al. 2005). Bering Sea animal communities are experiencing a prolonged northward biogeographical shift in response to climate changes (Grebmeier et al. 2006, Mueter and Litzow 2008). Current warming trends are predicted to continue, and the most rapid changes are expected to occur in northerly latitudes (Barnett et al. 2005, Wang et al. 2012). The Bering Sea currently provides 47% of the U.S. fishery biomass, and supports 80% of the U.S. seabird population, 95% of northern fur seals, and large populations of sea lions, walrus, and whales; and a biogeographical shift would have profound ramifications for commercial and subsistence fisheries (Overland and Stabenow 2004, Mueter et al. 2011). Marine birds are conspicuous and abundant top-tier predators that can be viewed in an ecological context as “indicator species” whose foraging dynamics, diet, and reproductive success are responsive to changes in relationships within the food web below them (Furness et al. 1997, Piatt et al. 2007). In this capacity, seabirds have yielded insights into the health and structure of a prey base that is shared with human fisheries (Sinclair et al. 2008, Wagner and Boersma 2011), and their demographics have been correlated with fluctuations in environmental parameters in the Bering Sea (Kitaysky et al. 2000, Hunt et al. 2002, Byrd et al. 2008).

Among Bering Sea birds, black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) are useful model organisms because they represent contrasting feeding guilds (plunging surface-feeders and pursuit-divers, respectively). As pursuit-divers, murres have greater field metabolic rates than surface-feeding kittiwakes (Gabrielsen et al. 1988; Croll and McLaren 1993; Kitaysky et al. 2000). The differences reflect the greater energy demands of a sub-surface foraging strategy (e.g., immersion in cold water, periodic oxygen deprivation), and the flight costs of morphological adaptation to diving (greater body mass and small, stiff wings) that contribute to heavier wing-loading in murres than in kittiwakes. Kittiwakes, therefore, are likely capable of foraging more widely in search of more dispersed prey (Sigler et al. 2012). During summer, both of these species function as central place foragers, whose foraging time and trip length are constrained by the need to return repeatedly to a nesting site at a central colony location (Weimerskirch 2007). Given such constraints, central place foragers can be especially sensitive to the distribution, abundance, and density of local food supplies that surround their island breeding colonies (Anderson and Piatt 1999, Kitaysky et al. 2000, Pichegru et al. 2010, Wolf et al. 2010).

In the Bering Sea, the Pribilof Islands of St. Paul (57.19°N, 170.26°W) and St. George (56.60°N, 169.58°W) are valuable breeding habitats for colonial seabirds because they are positioned near the average southern extent of seasonal ice cover on the Bering Sea shelf, and they are in a productive transition zone between deep-basin and shallow-shelf habitats (Hunt et al. 2002, Byrd et al. 2008, Hunt et al. 2008). In addition, the islands are the only land mass for a radius of > 300 km in any direction, and as such

represent a unique breeding habitat for seabirds in the region. Murre and kittiwake populations breeding on the relatively remote Pribilofs, therefore, could be disproportionately affected by fluctuations in climate conditions that fundamentally change prey patch dynamics in the central and southern Bering Sea (Hunt et al. 2002, Grebmeier et al. 2006, Mueter and Litzow 2008, Wang et al. 2012). During the 1990s and early 2000s the numbers of breeding piscivorous birds on St. Paul Island decreased in a trend concurrent with a northward retreat of winter sea ice, and those on St. George remained unchanged (Byrd et al. 2008); whereas many colonies in the Aleutian Archipelago to the south increased, and exhibited strong reproductive success (Byrd et al. 2005). Studies of seabirds in the Pribilofs indicated that these trends reflected regional differences in seabird foraging dynamics and prey base characteristics (Kitaysky et al. 2000, Byrd et al. 2008).

The study reported here was part of a Bering Sea ecosystem investigation sponsored by the North Pacific Research Board (<http://bsierp.nprb.org/>), which had the overarching goal of increasing the understanding of the impacts that climate change will have on the physical and biological components of the marine system. This study quantified the diet and foraging habitat use of two seabird species, black-legged kittiwakes and thick-billed murres, during the breeding seasons (July and August) of 2008 and 2009 in areas surrounding the Pribilof Islands and extending southward to Bogoslof Island (53.93°N, 168.03°W). It was expected that there would be differences between surface-feeding kittiwakes and pursuit-diving murres. Specifically,

- i) Seabird diet would differ between the two focal species. Thick-billed Murres are known to consume greater proportions of invertebrate euphausiids and squid than do kittiwakes.
- ii) Central place foraging constraints could result in measureable trophic niche width contractions of either or both species after the onset of breeding activity.
- iii) Spatiotemporal patterns in diet and isotope signals might be evident in one or both seabird species, and could be more pronounced at local scales in murres because kittiwakes range more widely when foraging.

In this study, a combination of gut contents and stable isotope analyses were used to explore the influence of central place foraging constraints on trophic niche widths and foraging habitat use in two seabird species. This study quantified geospatial patterns in seabird gut contents and stable isotope signatures of feather, muscle, and liver tissues and compared them with prey isotope values. Chapter I of this thesis quantifies seasonal changes in trophic niche widths within and among seabird species, contrasts immediate diet (stomach contents) composition between species and years, and explores the spatiotemporal patterns in diet and isotopic enrichment of seabird tissues to infer the locations and persistence of seabird foraging areas. Chapter II uses isoscape mapping of two prey isotope baselines to quantify the strength and structure of the geospatial linkage between birds and their prey.

Chapter I

Stomach contents and stable isotope analyses indicate contrasting foraging habitat use between thick-billed murres and black-legged kittiwakes in the Bering Sea

ABSTRACT

Seabirds are wide ranging predators that become central place foragers during the breeding season, and differences in diet or foraging habitat often occur between pre-breeding to breeding seasons. Thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*) were collected at sea in the central and southern Bering Sea during the chick rearing period (July through August), in 2008 and 2009. Stomach contents were characterized and isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) were analyzed in cheek feathers, pectoral muscle, and liver tissues, the values of which represent an isotopic signal of bird diet integrated through the time of tissue synthesis (months, weeks, and days, respectively). Comparisons of feather and muscle tissues indicated that murres underwent a niche width contraction with the onset of the breeding season and central place foraging constraints, whereas kittiwakes did not. There were no differences in breeding season niche widths between species; however, greater proportions of invertebrates in murre diets were reflected in small but significant differences between murres and kittiwakes in relative trophic niche levels. Stomach contents in both species were spatially auto correlated, and species composition of contents varied with habitat type, indicating patchiness in prey availability, specificity in foraging effort, or both. Among murres, stomach contents were correlated with liver isotope values, and significant geospatial structure was detected in isotope values of liver and muscle tissues, but such patterns were not evident among kittiwakes. These results indicated that murres foraged in specific areas with more consistency, and for greater periods of time, than kittiwakes.

INTRODUCTION

The foraging efforts of animals as diverse as beavers, bats, bees, and boobies are influenced by a central place foraging (CPF) regime when their foraging time and trip length are constrained by a need to return repeatedly to a central location such as a den (Haarberg and Rosell 2006), a roost (Daniel et al. 2008), a hive (Cresswell et al. 2000), or a nesting site (Young et al. 2010, Kappes et al. 2011). Central place foraging can be a significant constraint that defines an organism's niche and life history patterns (Orians and Pearson 1977, Costa 1991, Ydenberg and Davies 2010). Among seabirds, central place constraints have been expressed in niche segregation through the differential use of space (Navarro et al. 2009, Kappes et al. 2010), time (Rayner et al. 2010) and prey resources (Young et al. 2010, Barger and Kitaysky 2011, Kappes et al. 2011). The present study used a combination of stable isotope and gut contents analyses to explore the influence of CPF constraints on trophic niche width (Bearhop et al. 2004, Newsome et al. 2007) in two seabird species, to quantify geospatial patterns in seabird diet, and to determine if there were persistent patterns in seabird foraging areas in the southern Bering Sea.

Niche theory has been used to describe the ecological relationships among organisms, and has recently seen a resurgence of interest in the ecological literature (Grinnell 1917, Hutchinson 1978, Ackerly et al. 2006, Leibold 2007). Ecologists have most often quantified an organism's niche in terms of its location occupied in a multi-dimensional space, the axes of which represent relationships to environmental (abiotic)

and biological (biotic) factors influencing its life history (Hutchinson 1978). Stable isotope analyses have increasingly been used as powerful tools to describe niches in bivariate space, most frequently depicting measurements of $\delta^{13}\text{C}$ on the X axis, and $\delta^{15}\text{N}$ on the Y axis (Bearhop et al. 2004, Layman et al. 2007, Newsome et al. 2007). This orientation makes intuitive sense when approached from a food web perspective because $\delta^{15}\text{N}$ values are more sensitive to relative trophic relationships, and $\delta^{13}\text{C}$ values are commonly related to habitat baselines influenced by geochemical processes, nutrient cycling, and plant photosynthesis (Kelly 2000, Post 2002, Inger and Bearhop 2008, Flaherty and Ben-David 2010).

Stable light isotopes are useful tools in ecological studies because physical and geochemical processes affect their concentrations in predictable ways, and biophysical processes cause their differential accumulation in the tissues of plants and animals that feed and grow within specific environments (Kelly 2000, Post 2002). In animals, different tissues are synthesized at different rates. Therefore, stable isotope signatures of a given tissue can provide a record that reflects the integration of an animal's diet during the period of tissue synthesis (Dalerum and Angerbjorn 2005). For example, among marine birds, blood plasma and liver cellular turnover rates are quite rapid, representing tissue synthesis periods of a week or less, whereas muscle and red blood cell tissue turnover rates are perhaps three to five weeks (Hobson and Clark 1992a, Bearhop et al. 2002, Ogden et al. 2004, Cherel et al. 2005). Tissues that are metabolically inert after formation, such as feathers, will preserve an isotopic record indefinitely (Becker and Beissinger 2006, Jaeger and Cherel 2011).

Stable isotope analysis, therefore, has become a powerful tool in seabird niche studies detailing differences in diet, foraging habitat use, and relative trophic relationships of seabirds, between sexes within a species (Awkerman et al. 2007, Phillips et al. 2011), among members of a single species (Fort et al. 2010, Votier et al. 2011), and among species assemblages (Hobson et al. 2002, Forero et al. 2004, Quillfeldt et al. 2005, Young et al. 2010, Roscales et al. 2011). To date, however, most researchers have investigated high latitude Atlantic and Indian Ocean species (Forero et al. 2004, Quillfeldt et al. 2005, Bearhop et al. 2006, Jaeger et al. 2010a,b, Roscales et al. 2011), and few have linked seabird diet and isotopic data to investigate fine scale habitat use (Moreno et al. 2011). Considering stomach contents and isotopes in tandem can greatly increase the scope of inference for niche studies because the two datasets are complimentary measures providing both instantaneous and time-integrated indicators of an animal's diet (Dalerum and Angerbjorn 2005, Barrett et al. 2007, Inger and Bearhop 2008). This study used stable isotope analyses and stomach contents to explore trophic niche differentiation and contrasted diet and foraging habitat use on a fine scale (<100 km) between two wide-ranging, pelagic seabirds: Thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*).

Thick-billed murres and black-legged kittiwakes represent contrasting seabird feeding guilds (pursuit-divers and plunging surface-feeders, respectively), and these two foraging strategies are widely used by seabirds throughout the world. In the central and southern Bering Sea, individuals of these species become obligate central place foragers during their breeding season, which encompasses territorial defense, egg incubation (~

May-June), and the raising of young (~ July-August). Isotopic niches in either (or both) species are likely influenced by CPF constraints, however, the pursuit-diving strategy of murres necessitates a greater commitment to discrete foraging locations. Therefore, I hypothesized that if breeding birds foraged preferentially and repeatedly in specific regions within the vicinity of their breeding colonies, then I should detect a coherent geospatial structure among isotopic signatures within a given taxon, and that such a phenomenon would be more pronounced among murres than among kittiwakes. Greater isotopic niche widths can be associated with more extensive foraging ranges (Bearhop et al. 2004, 2006, Quillfeldt et al. 2005, Navarro et al. 2009); therefore, I further expected that isotope signatures among breeding kittiwake would be more variable than those of murres, and that both species might exhibit some amount of niche width contraction as seasons progressed and CPF constraints dictated shorter, more localized foraging trips.

METHODS

Study Area

Seabirds were collected in waters within 200 kilometers of the Pribilof Islands, St. George (56.60°N, 169.58°W) and St. Paul (57.19°N, 170.26°W) and extending southeastward to Bogoslof Island (53.93°N, 168.03°W; Figure 1).

Figure 1. Seabird collection locations and study area. Ship survey tracks are shown within the 200 kilometer radius of St. Paul Island (2008, 2009), and extending south to within 200 km of Bogoslof Island, near the Aleutians (2009). No more than 3 individuals of a given bird species were collected from any one location (within 500m of first collection point). Birds were collected between the hours of 0300 and 2340 AST, while foraging, or associated with foraging activity, wherever they were encountered.

The marine environment in the central Bering Sea has dramatically contrasting habitat types, including a shallow shelf (< 200 m depth), deep basin (> 2000 m depth), and inter-oceanic Aleutian Island passes (Hunt and Stabeno 2005, Hunt et al. 2008). The two Pribilof Islands are located at the edge of the Bering Sea continental shelf and host large seabird breeding colonies that are functionally isolated (> 300 km to nearest neighboring colonies) during the summer breeding season (Kitaysky et al. 2000, Byrd et al. 2008, Jahnke et al. 2008). Bogoslof Island waters have a stronger Pacific influence than do the Pribilofs (Hunt and Stabeno 2005). Based on previous studies, I considered the 200 km radius appropriate for characterizing the foraging activity of locally breeding murres and kittiwakes (Kitaysky et al. 2000, Hunt et al. 2008, Jahnke et al. 2008).

Sample Collection

A lethal take of adult birds was necessary to characterize stomach contents and obtain organ tissue samples of foraging birds on the open ocean. Large (150-225') research vessels are too imposing and slow to approach foraging birds for live capture, and the rough ocean conditions prevalent in the Bering Sea precluded the deployment of small skiffs. Birds were collected with a shotgun, under the auspices of the US Fish and Wildlife Service (USFWS/Migratory Bird collection permit #MB08537-1) and Alaska Department of Fish and Game (Fish and Game #08-134). Concerns for ethical treatment were ascertained before sample collections by reviews and permits from San José State University Animal Care and Use (IACUC Harvey#926), and US Fish and Wildlife Care

and Use permits (IACUC #2008013). Birds were collected as they engaged in foraging activity in the open ocean (Figure 1). A total of 47 murres and 39 kittiwakes were collected in 2008, and 78 murres and 66 kittiwakes in 2009. Collection locations were associated with randomly distributed net tow sampling and strip transects which were stratified to include all potential habitat types, in each week of data collection, for the duration of the study periods. Birds were collected between the hours of 0300 and 2340 hrs, Alaska Standard Time (AST). Based on personal shooting experience, personal communications with professional instructors, and current literature, it was estimated that an average of four shots would be needed for each successful take, and in fact the average was three (pers. comm. D. Irons, L. Boyle, D. Roby, L. Rogers; Noer et al. 2007). This study preferentially targeted foraging birds that were within 25 m range and on the water surface rather than in flight, because on-water birds could be linked more confidently to the specified collection location, and because on-water birds were more likely to contain identifiable prey remains (Duffy and Jackson 1986). However, both species are capable of traversing the entire study area in hours; thus the length of time a bird had spent at a given location was unknown (Hatch et al. 2000). Shooters attempted to collect two birds within a 500m radius at each location in order to account for anticipated “empty” stomachs and therefore ensure the collection of usable stomach contents. This was not always possible, and in some cases only one bird was taken. However, to minimize sampling bias, shooters never took more than three birds from a given location (within a maximum 500 m radius of initial take).

Birds were shot with a RemingtonTM brand, model 870, 12-gauge shotgun, firing steel 4-shot. Shooters were experienced, and in preparation for collection also completed a comprehensive firearms safety course, and underwent approximately ten hours of live-fire target practice under professional supervision by a licensed instructor. The target distance in this study (< 25 m) was substantially closer than average sport hunting distances (42.4 m; Anderson and Sanderson 1979, 33.4 m; Humburg et al. 1982). The extensive field sampling by Humburg and colleagues (4,219 hunting attempts, 10,587 shots fired) indicated that sport hunters crippled flying waterfowl at a rate of 11.9%; however, murres and kittiwakes were targeted at close range and on the water surface whenever possible, and these were relatively stationary, so a crippling rate of less than 5% was achieved in this study (Humburg et al. 1982, Noer et al. 2007). All crippled birds were shot immediately a second time to limit suffering and expedite retrieval. The birds were retrieved from the water using a long-handled dip net and then frozen (-20°F) immediately on the ship for preservation (Barrett et al. 2007; Bugoni et al. 2008). The few birds that were still alive upon immediate retrieval were killed quickly by cervical dislocation (Gaunt et al. 1997). It was expected that few wounded birds would escape, because they were exposed on the open ocean surface and unable to dive or fly once crippled. In practice, only two murres were lost (< 1% of all birds targeted); one disappeared in rough seas after being killed, and another in a dive immediately after being wounded.

Upon return to laboratories (University of Oregon; 2008, California Fish and Game; 2009), tissue samples of cheek feather, muscle, and liver were removed for stable

isotope analyses, and whole stomachs were sent frozen to University of Alaska Fairbanks for identification of hard parts and soft material to the lowest possible taxonomic level. In the process, wet material was weighed and hard parts (otoliths, carapaces, squid beaks) were enumerated to determine minimum number of individuals represented in each stomach. In all cases, the carcasses were re-frozen immediately after organ and feather tissue removal, and stored at Moss Landing Marine Laboratories for further studies.

Stable Isotope Measurements

Before testing, all samples were dried at 40°C for 48 h, then ground into a fine powder. Muscle and liver samples were lipid-extracted using a methanol-chloroform mixture (Doucette et al. 2010, Hoffman and Sutton 2010). Isotope values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured using continuous-flow isotope-ratio mass spectrometry, using a Thermo-Electron Deltaplus Advantage gas isotope-ratio mass spectrometer interfaced with a Costech Analytical ECS4010 elemental analyzer at the University of Alaska, Fairbanks. Data were normalized using four internationally-accepted isotope standards (IAEA CH6, CH7, N1, and N2). The main working standard was peach leaves (NIST 1547). Calibration runs were conducted frequently to check for run drift and linearity. External precision on standards was $\pm 0.10\text{‰}$ or better for $\delta^{13}\text{C}$ and $\pm 0.20\text{‰}$ or better for $\delta^{15}\text{N}$. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ concentrations are expressed relative to Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon, and to air for nitrogen. Stable isotope measurements are based on differences in the relative abundance of heavy to light forms, and are standardized to an international reference and expressed in the delta (δ) notation.

In this way $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is the isotope in question (^{15}N or ^{13}C in our case) and R_{sample} and R_{standard} are the ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in the sample and an international standard to which it is compared. One is then subtracted from this $R_{\text{sample}}/R_{\text{standard}}$ fraction, and that number multiplied by 1000, to facilitate comparisons of values in units of parts per thousand (‰). The end result is that samples with a lesser ratio of heavy isotopes than the standard have negative values, and samples with greater ratios of heavy isotopes than the standard have positive values (Fry 2006). In general, a predator's physiological processes result in the preferential retention of the heavier (^{15}N or ^{13}C) isotope over the lighter (^{14}N or ^{12}C) one in its diet, with each trophic level accounting for an approximate enrichment of +3.2 - 3.4 ‰ in N and ± 1.0 ‰ in C, relative to that of its prey (Kelly 2000, Post 2002).

Data Analyses

Isotopic niche differentiation – I assessed inter-specific and inter-annual differences in niche width and relative trophic level by comparing isotopic signals within and among three tissue types, each of which served as a time-integrated proxy for seabird diet: cheek feathers (approximately 2-3 months, molted in late winter and spring before breeding); pectoral muscle (approximately 3-5 weeks, during sampling period; Hobson and Clark 1992a); and liver tissue (approximately 5-7 days, during sampling period; Hobson and Clark 1992a). This study did not attempt to calculate specific trophic levels of birds or prey, however, to facilitate inter-seasonal comparisons of relative trophic niche space,

muscle and liver tissue values were standardized to those of feathers, to account for differential isotopic discrimination among tissues. Adjustments were based on overall averages reported by Caut et al. (2009) in their review of 52 controlled fractionation experiments in avian tissues. The average discrimination factors of Caut et al. (2009) for liver, muscle, and feather appeared similar to values reported by Hobson and Clark (1992b) specifically for gull tissues. It was expected that CPF demands might cause changes in isotopic niche metrics among feather and muscle tissues, because these two tissues represent pre-breeding (feathers grown during late winter) and breeding (muscle turnover time ~30 days) periods. Scatter plots were used in assessing niches because these can be more informative than traditional box plots when describing an isotopic niche (Forero et al. 2004, Bearhop et al. 2004). Measurements of niche width space therefore were expressed in bivariate space, with measurements of $\delta^{13}\text{C}$ on the X axis, and $\delta^{15}\text{N}$ on the Y axis (Bearhop et al. 2004, Layman et al. 2007, Newsome et al. 2007). Examinations of the spread (dispersion) among individual data points can more readily depict the true spatial extent of the niche(s) in question (Bearhop et al. 2004, Forero et al. 2004, Layman et al. 2007, Jackson et al. 2011). For example in a study of Patagonian seabird trophic relationships, Forero et al. (2004) demonstrated that although there were significant differences in the mean values among species, an extensive amount of niche overlap was in effect hidden when results were depicted as traditional bivariate box plots. Therefore statistical tests of niche widths were based on measures of relative dispersion (variance in bivariate space) instead of simple convex hull comparisons, because these measures are less sensitive to distortion from extreme outliers and differences in sample

size (Layman et al. 2007, Jackson et al. 2011). The Vegan package of the statistical program R 2.11.0 (Dixon 2003) was used to perform the analyses. Permutation testing (analogous to ANOVA F-tests) was used to detect significant within-year, intra-species changes in niche width (variance, or dispersion of points in bivariate space) between feather (pre-breeding season) and muscle (breeding season) tissues. I also compared simple arithmetic differences in niche metrics expressed in feather and muscle tissues: convex hull areas, mean dispersions, standard ellipse areas, and standard deviation among nearest neighbor distances (Layman et al. 2007, Jackson et al. 2011). Predator isotope signals are heavily influenced by variation in the trophic level of prey species present in the diet, therefore, nitrogen signatures were more variable, because $\delta^{15}\text{N}$ tends toward an average enrichment of 3.2-3.4‰ with each increase in trophic level, whereas $\delta^{13}\text{C}$ concentrations change little with increasing trophic level, and are often less variable (approximately 1‰ with each level; Kelly 2000, Post 2002). Parametric ANOVA testing was therefore used to infer differences in relative trophic levels ($\delta^{15}\text{N}$) expressed in a given tissue type between species within a given year.

Stomach contents -- Seabird digestion is thorough and rapid. Mean retention times of wet fish biomass in kittiwakes and murrelets are at most 6-7 hours (Hilton et al. 2000), and freshly ingested prey items are rendered unidentifiable in much less time. Hard parts of prey may persist for some days thereafter; however, little work has been done to measure gut retention times of such vestigial remains. I explored the spatial relationships of

seabird gut contents and isotopic signatures in muscle and liver tissues, however, liver tissue turnover rates likely average several days, and muscle tissues average three to five weeks, whereas wet stomach contents persist for fewer than 6 hours. Due to this mismatch in temporal scales, I chose a broadly inclusive approach for summarizing diets based on stomach contents, and considered both wet biomass and hard parts as evidence of most recent diet. In this way I attempted to leverage stomach content data to include a maximum number of usable samples and capture as broad a temporal scale as possible. Samples were pooled by taxonomic families, and then summarized in bar graphs with percent Frequency of Occurrence of presence of prey items (wet or hard) on the vertical axes, and percent Wet Biomass as the relative width of bars on the horizontal axes. Data were then analyzed as presence/absence matrices (counting the occurrence of wet biomass, hard parts, or both, as “presence”). Using the presence/absence method might have resulted in an over-weighting of some rare species, and an over-estimation of the occurrence of fish and squid, because these taxa possess hard parts (e.g., otoliths and beaks) that may persist for many days beyond initial consumption. It also may have under-weighted the importance of certain dominant prey species as measured in terms of wet biomass (Barrett 2007). But, considering the rapid digestion rates in the study species, I determined this to be an inclusive method for assessing short term (<10 days) seabird diet in a spatial context.

Geospatial patterns in isotopes and stomach contents – Traditionally, $\delta^{15}\text{N}$ has been used in food web studies to place animals in trophic context, whereas $\delta^{13}\text{C}$ has more often been used to infer habitat use (Kelly 2000, Post 2002, Inger and Bearhop 2008). Therefore, a consideration of the two signals in tandem can take into account the simultaneous influences of diet and location, and offers a way for ecologists to evaluate animal diets in the context of their movement patterns (Hobson 2005, Phillips et al. 2009, Jaeger et al. 2010b, Olson et al. 2010). Samples were taken extensively throughout an area comprising dramatic contrasts among potential foraging areas over the shallow (< 200 m) North American continental shelf, the shelf break, and deep (>2000 m) Aleutian basin and island pass habitats. In the marine environment, bathymetric gradients in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been referenced to distinguish seabird habitat use between deep basin or pelagic systems and shallow, nearshore shelf systems (Sydeman et al. 1997, Quillfeldt et al. 2005, Phillips et al. 2009, Jaeger et al. 2010a). The stepwise, trophic enrichment of $\delta^{15}\text{N}$, and to a lesser extent $\delta^{13}\text{C}$, often leads to a linear, positive correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the tissues of seabirds that routinely forage across shelf-pelagic boundaries (Forero et al. 2004, Quillfeldt et al. 2005, Navarro et al. 2009, Phillips et al. 2009, Jaeger et al. 2010b). I suspected, therefore, that enrichment in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ could be quantified to reflect diet and habitat use, and so yield information about patterns in the foraging effort of seabirds in the study system. A two-step method was used for quantifying dual patterns in enrichment in the system.

In a first step, liver and muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were combined in a Principal Components Analyses, and axis_1 scores were use as a proxy for the joint enrichment in

the positively correlated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in liver and muscle tissues within this system. These scores accounted for 82-92% of the joint carbon and nitrogen variability, and thus were considered to be a robust parameter for use in the analyses. In the second step, I compared the degree of geospatial similarity in stomach contents, and in isotopic enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between species and years. Universal Transverse Mercator units were used in mapping to avoid distortions at high latitude. Data sets were standardized to Z-scores to account for the differences in scale between isotope values and distance measurements, and Jaccard's distances were used in the preparation of stomach contents presence/absence data, because this measure is more appropriate when working with zero-inflated data (>90% of stomachs contained fewer than four of 10 possible prey items; Legendre and Legendre 1998, Fortin and Dale 2005). I tested and quantified geospatial structure (autocorrelation) among isotope signatures, among bird stomach contents, and between stomach contents and isotope signatures using Mantel's testing in the Vegan package of the statistical program R 2.11.0 (Mantel 1967, Legendre and Legendre 1998, Dixon 2003).

Mantel's test determines the relationship between two dissimilarity (distance) matrices, in this case: (i) isotopic signatures and, (ii) physical locations. The significance of the Mantel coefficient (r_M) is evaluated by comparison with a distribution of equivalent values obtained by repeated random permutations of the rows and columns of one of the distance matrices. With each reshuffling (permutation), a correlation coefficient (Pearson Product Moment Correlation) is recalculated, and in aggregate ($n=10000$) this process generates a theoretical distribution of possible relationships. The test yields the

standardized Mantel's co-efficient, r_M , which is analogous to Pearson's r , bounded by -1 to $+1$, and representing the proportion of the matrix permutations that lead to a correlation coefficient greater than zero. The null hypothesis, that there would be no relation between the two matrices, assumes that permuting the rows and columns of a matrix should be equally likely to produce a larger or a smaller coefficient, which would then result in a coefficient (r_M) of zero. In the context of the data, positive r_M values indicate that tissues that were more similar in terms of isotopic signature (the isotope dissimilarity matrix) were also in closer physical proximity to one another (the distance dissimilarity matrix), with larger positive values indicating a stronger relationship between the matrices. When applied to a given dataset, a Mantel's test will in general return a lesser coefficient (r_M) value than traditional correlation and regression techniques. Recent simulations have indicated that the power of linear correlation, regression, and canonical analyses are greater than that of the Mantel's test, but that the Mantel's remains superior and most appropriate when testing for patterns that are explicitly spatial in nature (Gilbert and Bennett 2010, Legendre and Fortin 2010).

Finally, muscle and liver enrichment scores were tested for correlation within a given species and year, and the magnitude and statistical significance was assessed in Pearson's r value as an indication of continuity in seabird foraging patterns through time. Available literature indicates that the isotopic signature of muscle tissue would represent a bird's diet integrated over a period of approximately 30 days, whereas liver tissue would represent approximately 5 days. Therefore, given that I sampled continuously throughout a 30-day period, the strength in spatial structure and any correlation of

enrichment values between tissue types would be indicative of corresponding spatiotemporal similarities in the diet of the birds.

RESULTS

Trophic Niche Width Comparisons Among Seasons, Years, and Species

Niche differentiation with onset of breeding season - Comparisons of trophic niche width (variance) in isotopic signatures of cheek feathers and pectoral muscle tissue indicated that kittiwakes demonstrated a slight niche width expansion after the onset of a central place foraging (CPF) regime, whereas murres underwent a marked trophic niche-width contraction (Figure 2, Table 1).

Figure 2. Contrasting pre-breeding and breeding season isotopic niche widths in black-legged kittiwakes (blue) and thick-billed murre (red). Birds were collected during July-August, 2008 and 2009, on the southern Bering Sea, Alaska. Dashed lines are 95% confidence ellipsoids (niche width areas) for cheek feather samples, the values of which represent an isotopic signal of bird diet integrated through the time of tissue synthesis (2-4 months) before the breeding season. Solid lines represent 95% confidence ellipsoids (niche width areas) for pectoral muscle tissue samples, the values of which represent an isotopic signal of bird diet integrated throughout tissue synthesis (~30 day period) during the breeding season. Muscle values were calibrated to those of feathers using discrimination values from Caut et al. (2009).

In 2008 the metrics of convex hull area, standard ellipse area, and standard deviation of distance to nearest neighbors among kittiwakes were all greater in muscle tissues than in

feather tissues, although mean distance to centroid measures remained equal; in 2009, kittiwakes had an increase in all niche width metrics (Table 1).

Table 1. Intra-annual changes in isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) niche widths among black-legged kittiwakes and among thick-billed murres. Samples of cheek feathers grown in late winter are contrasted with pectoral muscle synthesized during the summer breeding season. Negative values indicate contraction in a given niche width metric from pre-breeding to breeding seasons. Statistical tests of niche width (bivariate dispersion) used parametric ANOVAs based on euclidean distances to centroids. Bold font indicates statistical significance. Birds were collected during July-August, 2008 and 2009, on southern Bering Sea, Alaska.

Change in isotopic niche-width metrics: Feather tissue to Muscle tissue							
Species	Year	Convex Hull area	Standard Ellipse area	Std.Dev. Dist. Nearest Neighbor	Mean Distance to Centroid	Dispersion (variance) Test Statistic	Dispersion (variance) Test p-value:
Kittiwakes	2008	+ 2.91	+ 0.33	+ 0.30	0	$F_{1,76}=1.460$	0.2300
Murres	2008	- 3.28	- 0.63	- 0.05	- 0.37	$F_{1,92}=15.135$	0.0002
Kittiwakes	2009	+ 4.33	+ 0.49	+ 0.08	+ 0.06	$F_{1,130}=0.311$	0.5800
Murres	2009	- 6.53	- 0.71	- 0.11	- 0.20	$F_{1,154}=3.450$	0.0700

There were no significant differences in dispersion between feather and muscle data in either year, although there were arithmetic differences in niche width in both years. This indicates that differences in trophic niche width between pre-breeding (feather) and breeding (muscle) seasons were relatively minor among kittiwakes (Table 1). Among

murres in 2008, niche width changes from feather to muscle tissues indicated a decrease in all measures and, overall, niche width in muscle (breeding period) tissue was significantly less than in feather tissues (pre-breeding period; Table 1). In 2009 there again were marked arithmetic decreases in niche width among murres and the overall decrease was marginally significant (Table 1). Overall, there was a great degree of inter-seasonal niche width overlap between pre-breeding and breeding seasons in kittiwakes, but not in murres, where the differentiating factor was $\delta^{13}\text{C}$. In contrast, $\delta^{15}\text{N}$ values remained constant in feathers and muscle tissues of both species, and $\delta^{13}\text{C}$ values were relatively enriched in muscle tissues, especially in murres (Figure 2).

Relative niche widths and trophic positions in pre-breeding and breeding seasons -

Overall, trophic niche widths in murres were slightly greater than in kittiwakes in both years during the pre-breeding seasons (feather tissues), and slightly lesser during the breeding period (muscle and liver tissues; Table 2).

Table 2. Intra-annual differences in isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) niche widths between black-legged kittiwakes and thick-billed murres. Tissues values represent an isotopic signal of bird diet integrated through the time of tissue synthesis; feathers in late winter (2-4 months before the breeding season), and muscle (~30 day period) and liver (~5-7 day period) throughout the breeding season. Negative values indicate the metric in question is smaller by the given amount in murres than in kittiwakes. Statistical tests of differences in niche width (bivariate dispersion) accomplished using permutation ANOVA (Vegan package of statistical program R). Bold font indicates statistical significance. Birds were collected during July-August, 2008 and 2009, on the southern Bering Sea, Alaska.

Differences in isotopic niche-width metrics: Murres – Kittiwakes							
Tissue Type	Year	Convex Hull area	Standard Ellipse area	Std.Dev. Dist. Nearest Neighbor	Mean Distance to Centroid	Dispersion (variance) Test Statistic	Dispersion (variance) p-value:
Feather	2008	2.88	0.40	0.06	0.23	$F_{1,84} = 5.42$	0.02
Muscle	2008	-0.51	-0.11	-0.10	-0.02	$F_{1,84} = 0.10$	0.75
Liver	2008	-0.67	-0.06	0.03	-0.05	$F_{1,84} = 0.29$	0.59
Feather	2009	6.85	0.66	0.08	0.11	$F_{1,142} = 0.83$	0.36
Muscle	2009	-4.01	-0.55	-0.11	-0.15	$F_{1,142} = 2.19$	0.14
Liver	2009	-2.49	-0.35	-0.07	-0.08	$F_{1,142} = 0.65$	0.42

However, these arithmetic differences were significant only among 2008 feather tissues, which indicated kittiwakes occupied a significantly smaller niche width than murres during the pre-breeding season of that year (Table 2). Significant results of parametric

ANOVA testing of $\delta^{15}\text{N}$ values of muscle and liver tissues indicated that during 2008 and 2009 breeding seasons murre were feeding at slightly lower trophic levels than were kittiwakes, however the differences were small, amounting to $\pm 0.5\text{-}1\text{‰}$ (Table 3).

Table 3. Parametric ANOVA testing of differences among mean $\delta^{15}\text{N}$ Nitrogen values in tissues of black-legged kittiwakes and thick-billed murre collected during July-August, 2008 and 2009 in the southern Bering Sea, Alaska. Superscripted letters indicate similarity among groups.

Tissue type	Test statistic	p-value	Kittiwakes	Kittiwakes	Murres	Murres
			2008 (n=39)	2009 (n=66)	2008 (n=47)	2009 (n=78)
Feather	$F_{3,226} = 8.24$	< 0.001	14.74 ^A ± 0.11	14.79 ^A ± 0.12	14.94 ^A ± 0.14	14.18 ^B ± 0.12
Muscle	$F_{3,226} = 23.77$	< 0.001	12.76 ^A ± 0.09	13.16 ^A ± 0.13	12.24 ^B ± 0.08	12.13 ^B ± 0.09
Liver	$F_{3,226} = 42.31$	< 0.001	14.60 ^A ± 0.11	14.83 ^A ± 0.12	13.35 ^B ± 0.09	13.70 ^B ± 0.09

In general, a large amount of trophic niche width overlap occurred between kittiwakes and murre during the pre-breeding and breeding seasons in 2008 and 2009 (Figure 3).

Figure 3. Pre-breeding and breeding season isotopic niche widths among black-legged kittiwakes (blue circles) and among thick-billed murres (red circles). Birds were collected during July-August, 2008 and 2009, in the southern Bering Sea, Alaska. Lines represent 95% confidence ellipsoids (niche width areas) for cheek feather, pectoral muscle, and liver samples, the values of which represent an isotopic signal ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of bird diet integrated through the time of tissue synthesis; feathers at 2-4 months before the breeding season, muscle (~30 day period) and liver (~5-7 day period) during the breeding season. Muscle and liver values were calibrated to those of feathers using discrimination values from Caut et al. (2009).

Breeding Season Diet and Foraging Habitat Use

Short term diet: stomach contents - Geospatial patterns in the stomach contents of murres and kittiwakes exhibited highly significant spatial structure (autocorrelation) in both years, indicating a great degree of similarity in the immediate diet of those birds of a given species that were collected in close proximity to one another. Mantel's testing

revealed highly significant spatial structure ($p \leq 0.002$) among stomach contents of both species in each year (Table 4).

Table 4. Geospatial autocorrelation in the diet (presence/absence species composition of prey items in stomachs) of black-legged kittiwakes and thick-billed murres. Birds were collected during July-August, 2008 and 2009 in the southern Bering Sea, Alaska. Bold indicates significance at $p < 0.0125$ after Bonferonni corrections were applied for multiple testing.

Species	Year	Mantel's r	p-value
Kittiwakes	2008	0.32	< 0.001
Murres	2008	0.22	< 0.001
Kittiwakes	2009	0.17	0.002
Murres	2009	0.22	< 0.001

Stomach contents show that kittiwakes foraged predominantly on fish in both years (Figure 4). Kittiwake diets in 2008 were heavily dominated by myctophid fish (lanternfish; *Stenobrachius leucopsarus*) throughout the study area, although birds collected over the shelf break and Pribilof Canyon contained some smaller amounts of squid (family: Gonatidae), krill (*Thysanoessa* spp; family Euphausiidae) and amphipods (*Themisto* spp; family Hyperidae). Gonatid squid were not a large proportion of kittiwake stomach contents, and squid consumption was associated with birds collected near continental shelf break habitat. The great majority of kittiwakes collected in 2008 had only one or two unique prey taxa (hard or soft parts) represented in their stomachs.

In 2009, kittiwake diet varied more overall. Kittiwake diets collected from the northwest of St. Paul Island contained primarily Walleye Pollock (*Theragra chalcogramma*; family Gadidae); birds collected from the outer continental shelf and break contained primarily myctophids, and some squid, pollock, and euphausiids; birds collected over deeper basin and Aleutian shelf waters contained fishes commonly associated with deep pelagic habitats (primarily myctophids, but also some bathylagids, zoarcids, and gonatid squid). Only one kittiwake collected in 2009 over the inner shelf to the north of St. Paul Island had any evidence of squid remains. In 2009, most kittiwake stomachs contained evidence of only one or two unique prey taxa, and the expansion of the study area that year to include Aleutian shelf habitat did not result in the addition of any new prey taxa beyond those already recorded elsewhere in 2008 in the study area surrounding the Pribilof Islands (Figure 4).

Figure 4. Seabird wet stomach contents, by year, listed by taxonomic family in %Weight (relative widths on horizontal axes) and % Frequency of Occurrence Presence/Absence (relative heights on vertical axes). Fish families (black bars) include, from left to right: Myctophidae (Lanternfish; *Stenobrachius leucopsarus*), Bathylagidae (Smoothtongue; *Leuroglossus schmidtii*), Gadidae (Pollock; *Theragra chalcogramma*), Zoarcidae (Eelpout; *Lycotes brevipes*), Stichaeidae (Eelblenny; *Lumpenus fabricii*), Ammodytidae (Sandlance; *Ammodytes hexapterus*); Invertebrate families (gray bars) include, from left to right: Gonatidae (Squid; Unk. Spp.), Pandalidae (Shrimp; Unknown Species), Euphausiidae (Krill; *Thysanoessa* spp.), Hyperiididae (Amphipods; *Themisto libellula*).

Murre stomach contents indicated a more varied diet of fish and invertebrates in both years (Figure 4). Murre stomachs in 2008 contained almost exclusively krill and gonatid squid. Amphipods were not present in murre stomachs in 2008, and only one murre collected in 2008 over inner shelf waters to the north of St. Paul Island had any evidence of squid. In 2008 most (> 90%) murre stomachs contained evidence of only one or two unique prey taxa. Murre stomach contents were more diverse in 2009 than in 2008, and seemed to vary regionally to a greater extent. Murres collected from the north and west of St. Paul contained primarily pollock, krill, and amphipods, and lesser amounts of bathylagid (Smoothtongue; *Leuroglossus schmidtii*) and zoarcid (Eelpout; *Lycotes brevipes*) fishes, but none of them contained any evidence of squid. Murres collected in 2009 over deeper pelagic and Aleutian shelf habitats contained primarily fishes (gadids and bathylagids) and gonatid squid. In 2009, individual murres generally contained evidence of one, two, and three unique prey taxa in their stomachs, and the expansion of the study area in 2009 to include Aleutian shelf habitat did not result in the addition of any new prey taxa beyond those already recorded elsewhere in 2008 in the study area surrounding the Pribilof Islands.

Time-integrated diet: Geospatial patterns in stomach contents and isotope values -

Geospatial patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in liver and muscle tissues were similar to patterns in stomach contents data. Isotope values were autocorrelated ($p \leq 0.001$) in murres in

both years, indicating that birds collected in close proximity also were similar to one another in isotopic enrichment (Table 5).

Table 5. Geospatial structure among $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in muscle and liver tissues from black-legged kittiwakes and thick-billed murres. Birds were collected during July-August 2008 and 2009, in the southern Bering Sea, Alaska. Bold indicates significance in Mantel's statistic at $p < 0.006$ after Bonferonni corrections were applied for multiple testing.

Species	Tissue	Year	Mantel's r	p-value
Kittiwake	Liver	2008	0.16	0.04
Kittiwake	Muscle	2008	0.16	0.04
Murre	Liver	2008	0.33	< 0.001
Murre	Muscle	2008	0.42	< 0.001
Kittiwake	Liver	2009	-0.01	0.50
Kittiwake	Muscle	2009	-0.02	0.62
Murre	Liver	2009	0.43	< 0.001
Murre	Muscle	2009	0.35	< 0.001

Carbon and nitrogen isotope values were positively correlated in liver and muscle tissues of both species in each year, and principle component analyses yielded axis_1 scores that accounted for 82-92% of the variation in liver enrichment, and 84-90% in muscle enrichment.

In both years enrichment in murre liver (Fig. 5) and muscle (Fig. 6) tissues was greatest in birds collected in relatively shallow water (< 200 m) over the continental shelf to the north and west of St. Paul Island, and enrichment was least in birds collected over deeper (> 2000 m) continental shelf-break, Pribilof Canyon, and Aleutian shelf habitats.

Figure 5. Inverse Distance² weighted interpolation mapping of isotopic enrichment (PCA axis_1 scores; $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in liver tissues of black-legged kittiwakes and thick-billed murres collected in the southern Bering Sea, in July and August, 2008 and 2009.

Figure 6. Inverse Distance² weighted interpolation mapping of isotopic enrichment (PCA axis_1 scores; $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in muscle tissues of black-legged kittiwakes and thick-billed murres collected in the southern Bering Sea, in July and August, 2008 and 2009.

Isotopic patterns among kittiwake tissues indicated fewer distinct spatial patterns. In 2008, kittiwake liver (Fig. 5) and muscle (Fig. 6) tissues had a weak ($p = 0.04$) spatial pattern, but virtually no structure whatsoever was detected among kittiwake tissues in 2009, and these weaker relationships were discounted after Bonferonni's statistical correction for multiple testing (Table 5). Liver and muscle enrichment levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (axis_1 scores) in individual birds were significantly ($p < 0.001$) correlated in murres and kittiwakes in both years. The correlation in tissue values was greater in both species in 2008, but murres had a stronger correlation than kittiwakes in both years (Table 6).

Table 6. Correlation between relative $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment (PCA axis_1 scores, representing the covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) of muscle and liver tissues in black-legged kittiwakes and thick-billed murres. Bold font indicates statistical significance. Birds were collected during July-August 2008 and 2009, in the southern Bering Sea, Alaska. Isotopic enrichment values are PCA axis_1 scores from positively correlated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data.

Species	Year	Test statistic	Pearson's r	p-value
Kittiwake	2008	$t_{22}=4.01$	0.65	< 0.001
Murre	2008	$t_{36}=10.38$	0.87	< 0.001
Kittiwake	2009	$t_{49}=4.51$	0.54	< 0.001
Murre	2009	$t_{61}=8.59$	0.74	< 0.001

In addition, stomach contents (prey taxa presence / absence) were more tightly coupled (highly correlated) with isotope values among murres, than among kittiwakes (Table 7).

Table 7. Correlation of diet (presence/absence species composition of prey items in stomachs) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of liver tissues in black-legged kittiwakes and thick-billed murres. Birds were collected during July-August, 2008 and 2009 in the southern Bering Sea, Alaska. Bold indicates significance at $p < 0.0125$ after Bonferonni corrections were applied for multiple testing.

Species	Year	Mantel's r	p-value
Kittiwake	2008	0.22	0.073
Kittiwake	2009	0.11	0.045
Murre	2008	0.16	< 0.001
Murre	2009	0.23	< 0.001

DISCUSSION

Trophic Niche Width Comparisons Among Seasons, Years, and Species

With the onset of the breeding season and associated central place foraging constraints, murres experienced a greater niche width contraction in both years than did kittiwakes. These findings are consistent with expectations, given the greater energetic cost of flight for pursuit-diving murres in contrast to surface-feeding kittiwakes (Croll et al. 1992, Gabrielsen et al. 1988). Inter-seasonal niche width changes have recently been shown in Leach's Storm Petrels (*Oceanodroma leucorhoa*; Hedd and Montevecchi 2006), Atlantic Puffins (*Fratercula arctica*; Hedd et al. 2010), and two subspecies of the Cory's Shearwater (*Calonectris* spp.; Navarro et al. 2009), all of which demonstrated contractions in isotopic dispersion metrics from wintering to breeding seasons. Broader isotopic niche widths may reflect a greater variation in predator diet (Willson et al. 2010, Polito et al. 2011) or a greater range in foraging habitats (Darimont et al. 2008, Martinez del-Rio et al. 2009, Flaherty and Ben-David 2010). Niche widths of wide ranging seabirds, however, are likely influenced by a combination of both of these factors because prey are often dispersed, ephemeral, and patchily distributed (Weimerskirch 2008, Navarro et al. 2009, Hedd et al. 2010, Wiley et al. 2012).

Traditionally, $\delta^{13}\text{C}$ has been used as a diagnostic marker to infer patterns in habitat use and to distinguish between use of shallow, continental shelf and deeper, pelagic foraging areas (Hobson et al. 1994, Sydeman et al. 1997). The $\delta^{13}\text{C}$ values in kittiwake and murre muscle tissues were enriched relative to those in feather tissues and

in murres the variance decreased from pre-breeding to breeding seasons. This is likely to be a signal marking a transition from late winter foraging areas throughout the deep, pelagic habitat of the southwest Bering Sea (in the case of murres) and northern Pacific Ocean (for kittiwakes), to more restricted central place foraging patterns associated with their breeding colonies located in shallow continental shelf waters. Typically, $\delta^{15}\text{N}$ gives greatest insight into the species composition of predator diet because of its greater association with protein synthesis (Kelly 2000, Caut et al. 2009). In this system no differences were found in mean $\delta^{15}\text{N}$ between pre-breeding and breeding season diets in murres or kittiwakes, but variance in $\delta^{15}\text{N}$ values decreased in murres. Such patterns indicated that murres may become more restricted and focused in their foraging efforts while under CPF constraints, either in terms of habitat use, prey species consumed, or both. Differences in isotopic baselines among habitats have been recognized as being fundamental to inferences about foraging locations for seabirds in the Pacific (Wiley et al. 2012), Atlantic (Moreno et al. 2011), and Indian (Jaeger et al. 2010 a,b) Oceans. There are strong indications of a cross-shelf gradient in isotopic baseline in the central Bering Sea (Schell et al. 1998, Granger et al. 2011). To the extent that such a cross-shelf gradient might exist, it would likely have increased the geospatial variability among isotope values in prey species whose distribution spanned the continental shelf. This would have produced correspondingly greater values marking aggregations of individuals that feed and grow over the inner shelf areas, and lesser values in those from deeper basin and Aleutian shelf habitats. Such a signal would likely propagate upwards through the food web to top-tier predators such as seabirds, as has been noted in other ocean systems

of the world (Jaeger et al. 2010a,b, Moreno et al. 2011, Wiley et al. 2012). In this study system, with its abrupt change in depth from basin to shelf waters, a cross-shelf baseline gradient resulted in clear geospatial isotopic signals. This increased the differences among groups of birds foraging in separate locations, even if they were feeding on similar prey species, and led to the presence of geospatial structure among the isotope values of birds collected at sea, as repeat foragers in each area acquired a distinctive, corresponding isotopic signal.

Under CPF constraints, kittiwakes and murres contract their foraging range during the breeding season, theoretically remaining closer to their breeding colonies. However, kittiwakes forage more widely than murres even during the breeding season (Sigler et al. 2012), and therefore should acquire more variation in their isotopic signal as they consume prey from contrasting habitat types. Greater variability among kittiwake isotope values could lead to less pronounced changes in niche width measurements and lesser niche width contraction from pre-breeding to breeding seasons than in murres. Muscle and liver tissues indicated that there were no significant differences in niche widths between species during the breeding seasons in either year, although murre $\delta^{15}\text{N}$ values in both tissues were slightly less than those in kittiwakes, which indicates that murres may have been feeding at a slightly lower trophic level. Indeed, stomach contents of murres contained greater proportions of invertebrates than did those of kittiwakes.

Short Term Diet: Stomach Contents

An examination of diet presence/absence data within a spatial context indicated that seabird prey consumption was patchy. Mantel's testing revealed highly significant spatial structure ($p \leq 0.002$) among stomach contents of both species in each year.

Individual stomachs of both seabird species rarely contained more than two unique prey taxa, regardless of location of collection, indicating that birds were restricting their foraging efforts within prey patches, or that the patches encountered were dominated by relatively few species. The results indicate that prey patchiness may persist during the breeding season. For example, there were no intra-annual changes in diet composition among birds collected sequentially within any specific areas. Rather, stomach contents indicated that localized prey availability was generally consistent during summer in both years. Furthermore, squid was nearly absent in any of the kittiwakes sampled over the inner shelf, and among murrelets the presence of squid and smoothtongue was more widespread over deeper shelf break, basin, and Aleutian shelf waters. Squid beaks and fish otoliths are resistant to seabird digestion, and thus likely persist longer in the guts of birds than other prey remains, probably for several days or more. The absence of deep-water prey remains in birds sampled over the shallow inner shelf, when contrasted with the prevalence of such remains in stomachs from deeper water, is consistent with the concept that seabirds taken in shallower continental shelf habitat had been foraging there for periods of at least several days.

Murre stomach contents were more varied than those of kittiwakes. In 2009 murre began consuming large amounts of *Themisto libellula* amphipods, a species often associated with cooler ocean conditions and rarely recorded in Pribilof Island seabird diets during the chick-rearing season since the 1970s (Renner et al. 2012). The 1970s were a period of cooler oceanographic conditions overall, and the study years also were cooler than the average between 1980's and 2000's (Overland et al., *in press*). Long term diet data have confirmed that pollock has been a major component in the diet of breeding murre and kittiwakes on the Pribilof Islands (Sinclair et al. 2008), but it was not prevalent in stomachs of either species collected in 2008. In 2009, however, pollock was a more common food source, and occurred in stomachs of both bird species collected to the north and west of St. Paul Island over shallow water. Pollock also was recorded in murre collected from throughout the deeper shelf break, basin, and Aleutian shelf habitats, which indicates that pollock patches in these regions could have occurred at greater depths not accessible to surface-feeding kittiwakes (Benoit-Bird et al. 2011).

It is evident from stomach samples that euphausiids and amphipods were far more prevalent in the diet of murre than in kittiwakes, as measured in terms of percent frequency of presence in the diet and percent total wet biomass consumed. Stable isotope values reflect this pattern, as murre muscle and liver tissues were less enriched in $\delta^{15}\text{N}$ than those of kittiwakes, implying murre were consuming prey items at a lower trophic level in the food chain. These results contrast with a 25+ year data set from the Pribilof Islands summarized by Sinclair et al. (2008), which indicated that kittiwakes consumed euphausiids and amphipods at a similar or perhaps greater rate than murre. Data from

the study presented here also differ from those of contemporaneous, non-lethal (lavage and regurgitations) stomach content samples taken from adult birds on the Pribilof Island colonies, which showed that murrelets ate less than half as much of these invertebrate prey items as kittiwakes (Renner et al. 2012). Seabird digestion is rapid and efficient, and the marine environment presents a dynamic foraging arena, making it challenging to quantify and contextualize seabird stomach contents data (Barrett 2007). In the present study, however, individuals of each species were collected on a near daily basis, spanning hours between 0300 and 2340 AST, and sampled in each potential habitat type several times during a ~30 day collection period. The data presented here could therefore be considered a reasonable and unbiased representation of adult diet during the chick-rearing periods in July-August, 2008 and 2009.

Breeding adults will often eat different prey than what they deliver to their chicks (Wilson et al. 2004), which is one explanation for the differences between birds I collected at sea and the colony-based sampling (Renner et al. 2012). Additionally, it is likely that on-colony sampling of adult birds returning from foraging trips might fail to adequately detect prey taxa that had been digested quickly while birds were still at sea (Tierney et al. 2008, Polito et al. 2010). Because birds in this study were collected while they foraged at sea, these data increase our understanding of patterns in foraging effort and diet in adult seabirds in the southern Bering Sea. In contrast, nearly all previous data were based on samples collected on colonies as adults returned from foraging trips to attend nesting sites and feed chicks.

Implications of Geospatial Patterns in Stomach Contents and Isotope Values

Tissue turnover time in murre and kittiwake pectoral muscle is approximately 3-5 weeks, whereas that of liver is less than 10 days (Hobson and Clark 1992a, Bearhop et al. 2002, Ogden et al. 2004, Cherel et al. 2005). I measured a significant spatial structure in the immediate diet (stomach contents) of both species in both years. Therefore, given tissue turnover rates, and a sampling period of approximately 30 days, it can be inferred that a consideration of the magnitude in spatial structure (Mantel's r), and liver to muscle correlations (Pearson's r), would indicate the extent to which birds were foraging repeatedly in specific areas for periods of more than 30 days during the breeding season. Among thick-billed murres there was highly significant geospatial structure in the isotopic enrichment of liver and muscle tissues, and in immediate diet (stomach contents), in both years. Patterns in isotopic enrichment of liver and muscle tissues appeared to be similar in both years: birds foraging over shallow continental shelf waters, especially those to the north and west of St. Paul Island, tended to be enriched relative to the mean of the given year, whereas birds foraging over deeper basin and Aleutian waters tended to be depleted relative to the mean (Figures 5,6). In addition, stomach contents were highly correlated with liver isotope values (Table 7), indicating that those birds containing similar prey taxa were also similar in isotopic signatures of carbon and nitrogen. Murre liver and muscle enrichment levels were strongly correlated in both years, and this relationship indicates a consistency in diet through a time period roughly equivalent to tissue turnover rates. It is likely, therefore, that spatial structure in murre

diet is closely related to similar patterns in isotopic enrichment, and that murrelets foraged in specific regions during their breeding periods in both years.

Foraging patterns among black-legged kittiwake were more variable than murrelets. Strong geospatial structure in the stomach contents of kittiwakes in both years indicated a localized specificity in their immediate diet. There was less structure, however, detected among isotope values of kittiwake tissues. In 2008, marginally significant spatial autocorrelation was measured among kittiwake liver and muscle isotope values, indicating that kittiwakes in 2008 were perhaps varying their use of foraging areas over periods of days, and that foraging patterns were not consistent enough over periods of weeks to acquire any distinct spatially variable isotopic signals. In 2009, there was no geospatial structure among isotope values of kittiwake liver or muscle tissues, despite the spatial autocorrelation detected amongst their stomach contents. Furthermore, there were no significant relationships between kittiwake stomach contents and liver isotope values in either year. Together, these results indicate that kittiwakes ranged more widely throughout the study area during 2009, without returning to any one region often enough to develop a detectable pattern in isotopic enrichment.

I used PCA axis_1 scores as integrative measures of changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to identify significant spatial patterns among enrichment values of seabird tissues collected in waters spanning the continental shelf in the central and southern Bering Sea. This application of principle components analysis was chosen because, in addition to well established trophic fractionation patterns that result in stepwise enrichment of both

isotopes, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines can vary regionally with bathymetry and distance from nearest shore (Schell et al. 1998, Miller et al. 2008). In this study area there is evidence of a cross-shelf gradient in isotopic enrichment associated with the dramatic differences in depth between Aleutian Basin and continental shelf habitats (Schell et al. 1998, Granger et al. 2011). Therefore, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vary in tandem to a great extent in the study area. However, this use of PCA axis_1 scores to describe the dual enrichment of carbon and nitrogen is likely not appropriate for all systems, especially those characterized by more subtle differences among habitats, or studies conducted at finer spatial scales, because such systems likely would have less variation among isotopic baselines and prey patch community composition. In addition, it is likely that reliance on a proxy measure such as PCA axis_1 scores is a less powerful approach in cases where variability is influenced primarily by underlying patterns in just one of the two isotopes being measured.

Differences in foraging habitat use between murres and kittiwakes likely reflect physiological and morphological adaptations that accommodate their contrasting foraging strategies. Pursuit-diving murres exhibit greater field metabolic rates than surface-feeding kittiwakes (Gabrielsen et al. 1988, Croll and McLaren 1993, Kitaysky et al. 2000), because of the greater energy demands of a sub-surface foraging strategy (e.g., immersion in cold water, periodic oxygen deprivation), and the increased flight costs of their adaptation to diving (greater body mass and small wings) that contribute to heavy wing-loading. With greater flight costs, murres should be more selective in their foraging effort and therefore might return more consistently to specific areas where prey are

encountered more consistently or in greater abundance or density. In doing so they could acquire a more distinct local isotopic signal, as was supported by the results of my study. Some studies in the Bering Sea have indicated that sub-surface foragers, such as murres, may require more consistency in prey patch density, abundance, or persistence than surface-feeders such as kittiwakes, and this could explain the more dispersed distribution patterns of kittiwakes foraging at sea (Lovvorn et al. 2001, Hunt et al. 2005; Benoit-Bird et al. 2011, Sigler et al 2012), as well as the minimal isotopic spatial structure found in kittiwakes.

The persistence of spatial structure among murre isotopic signals indicates that murres might have been partitioning the available habitat by foraging repeatedly in distinctly separate areas. The geospatial stratification among thick-billed murre isotope values coincided in latitude with three colonies (St. Paul, St. George, and Bogoslof; Figures 5,6), indicating foraging habitat partitioning among them, despite the close proximity of St. Paul to St. George (< 75 km). Among Alaskan seabirds, intra-specific habitat partitioning was described in kittiwakes in Prince William Sound, Alaska, when Ainley et al. (2003) noted that there was little overlap among the foraging areas used by neighboring black-legged kittiwake colonies, and that the largest colonies of black-legged kittiwakes were located as far apart from one another as geography allowed. Also, in the Bering Sea, intra-specific foraging site fidelity was inferred through analyses of stomach contents and stable isotope values in short-tailed shearwater (*Puffinus tenuirostris*) tissues (Baduini et al. 2006). The shearwaters were collected while foraging in several locations throughout Bristol Bay and the Eastern Bering Sea. Stable isotope signatures of organs

indicated that groups of shearwaters were likely feeding for multiple weeks at a time in specific locations, even though they were theoretically free to forage freely because they were not breeding on a colony. Elsewhere, off the coast of South Africa, Gremillet et al. (2004) demonstrated that foraging areas of cape gannets (*Morus capensis*) from two neighboring colonies overlapped little, even though the two study colonies were well within (65-85%) the theoretical foraging range of one another. In South Georgia Wanless and Harris (1993) recorded habitat partitioning among blue-eyed shags (*Phalacrocorax atriceps*), and in the central Pacific Wiley et al. (2012) inferred habitat partitioning between two colonies of Hawaiian petrels (*Pterodroma sandwichensis*) in the Hawaiian Islands. The results of this current study, therefore, contribute to the body of evidence that indicates habitat partitioning among conspecific marine birds can be an influential force in the delineation of a seasonal isotopic niche that can be influenced as much by variations in the spatial patterns in foraging effort as by differences in diet (Bearhop et al. 2004, Newsome et al. 2007, Flaherty and Ben-David 2010).

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Chapter II:

Stable Isotope Values of Krill and Pollock Reflect a Cross-shelf Gradient that Indicates Seabird Foraging Patterns in the Bering Sea

ABSTRACT

Differences among stable isotope baselines of invertebrate prey species can exist between shallow, near-shore areas and deep, off-shore habitats in the marine environment. Such differences have been used to infer top predator diet and habitat use on broad scales of 100's to 1000's of kilometers, however, few studies have investigated how isotope baselines might directly influence measurements in marine predators and prey at fine scales. This study quantified the multi-trophic influence and spatial structure of a cross-shelf $\delta^{15}\text{N}$ nitrogen gradient in the central and southern Bering Sea, and used it to delineate and contrast fine scale foraging patterns of thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*) on the open ocean. Seabird liver and muscle $\delta^{15}\text{N}$ values were compared with those of krill (*Thysanoessa* spp) and walleye pollock (*Theragra chalcogramma*) tissues sampled concurrently throughout the study area in 2008 and 2009. Both krill and pollock are known to be common and abundant constituents of murre and kittiwake diets. Krill, pollock, and murre tissues from northern, shallow shelf habitat (< 200m) were enriched 1-2‰ relative to samples taken from much deeper habitats (> 2000m) to the south and west, and krill $\delta^{15}\text{N}$ Nitrogen baseline values predicted 35-42% of the variability in murre tissue values. Patterns between kittiwakes and prey were less coherent. The persistence of strong spatial autocorrelation and tight coupling of $\delta^{15}\text{N}$ Nitrogen in murre and prey tissues indicated that the birds were foraging repeatedly in distinct areas. Geospatial stratification among murre isotope values coincided with three island colonies, St. Paul, St. George, and Bogoslof, which indicated some degree of foraging habitat partitioning among island

colonies. Measurements at three trophic levels demonstrated that baseline signals of a cross-shelf gradient can be propagated through a marine food web to top-tier predators, and can inform the delineation of foraging areas at local scales. In turn, habitat partitioning among conspecific marine birds can become an influential force affecting the characterization of a seasonal isotopic niche.

INTRODUCTION

Stable light isotopes are useful tools in ecological studies because physical and geochemical processes affect their concentrations in predictable ways, and biophysical processes lead to their differential accumulation in the tissues of plants and animals that feed and grow within specific environments (Kelly 2000, Post 2002). Isotopic signatures of new tissues reflect the diet and habitat use of an animal at the time of tissue synthesis. For example, among birds, blood plasma and liver cellular turnover rates are quite rapid, representing tissue synthesis periods of a week or less, whereas muscle and red blood cell tissue turnover rates range from three to five weeks (Hobson and Clark 1992, Bearhop et al. 2002, Ogden et al. 2004). Therefore, it is possible to infer a bird's diet or habitat preference over a range of temporal and spatial scales by sampling specific tissue types at specific times (Inger and Bearhop 2008). Indeed, recent studies of captive and wild seabirds have indicated that isotopic signatures in blood, feather, and internal organ tissues can be used to infer long distance migratory movements, identify likely foraging habitat use, and elucidate trophic relationships among birds and their prey (Hobson et al. 2002, Phillips et al. 2009, Quillfeldt et al. 2010, Roscales et al. 2011, Moreno et al. 2012). Some of the most recent studies have made use of predictive isoscape techniques.

Predictive isoscape maps are theoretical isotopic landscapes to which researchers can compare focal species samples and infer movement patterns or assign a place of likely origin based on isotopic signatures (Hobson et al. 2007, Barnes et al. 2009, Bowen 2010, Quillfeldt et al. 2010). The development of isoscapes began in the terrestrial environment (Amundson et al. 2003, West et al. 2008). Until recently, isoscape mapping

techniques have been less frequently applied in the marine environment, although many marine animals such as seabirds, mammals, turtles, and some fish routinely move long distances for migration or foraging, making them good candidates for the application of isoscape analytical techniques (Valenzuela et al. 2009, Olson et al. 2010, Reich et al. 2010). Much isoscape work within the marine environment is based on coherent, cross-shelf patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baseline concentrations among shallow nearshore (shelf), and deep offshore (pelagic) systems (Goericke and Fry 1994, Schell et al. 1998, Miller et al. 2008, Barnes et al. 2009, Kline 2009, Quillfeldt et al. 2010). For example in broad scale studies of the Bering Sea, Schell et al. (1998) found that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in euphausiids and copepods decreased from east (onshore, shallow, shelf system) to west (offshore, deep, pelagic system). More recently, Granger et al. (2011) measured a large cross-shelf gradient of $\pm 5\text{‰}$ in $\delta^{15}\text{N}$ of surface sediments, with greatest values measured to the north and east over shallow, shelf waters. In addition, Kline (2009) measured a similar cross-shelf gradient in signatures of copepods in the Gulf of Alaska, and Moreno et al. (2011) measured significant differences in $\delta^{15}\text{N}$ between pelagic and coastal fish species in the diet of the European shag (*Phalacrocorax aristotelis*). Such patterns result from differences in the source pools of nutrients, the extent of vertical mixing, the length of the food chain, and the products of phytoplankton physiology that result in differential uptake of nutrients between shelf and pelagic systems of the North Pacific and Bering Sea (Schell et al. 1998, Smith et al. 2002, Guo et al. 2004, Kline 2009, Granger et al. 2011). Cross-shelf contrasts in trophic baselines can be used to infer the movement patterns of animals that routinely forage across pelagic/shelf boundaries. In general,

however, cross-shelf patterns have proven most useful for inferring movement across large distances (> 100 's km); finer scale studies are less common because open ocean baseline sampling is often lacking or, at best, of limited resolution (Schell et al. 1998, Phillips et al. 2009, Jaeger et al. 2010, Quillfeldt et al. 2010). Fewer researchers have used marine isoscapes and GIS techniques to characterize food web linkages that describe foraging arenas of ocean predators at fine to medium (< 100 km) scales (Barnes et al. 2009), and none have tested the multi-trophic influence of the apparent cross-shelf gradient in the Bering Sea.

The present study quantified the multi-trophic strength and spatial structure of a cross-shelf $\delta^{15}\text{N}$ isotopic gradient in the central and southern Bering Sea, and used it to delineate fine-scale foraging areas and contrast the foraging patterns of two wide-ranging, pelagic seabirds, thick-billed murre (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*). Measurements were developed from comparisons of nitrogen isotope signatures in seabird liver and muscle tissues to baseline krill and pollock signatures obtained from predictive isoscape mapping techniques. Based on Schell et al.'s (1998) work that suggested a shelf / pelagic contrast in isotopic signatures of euphausiids and copepods, I hypothesized that if breeding seabirds foraged preferentially and repeatedly in specific regions within the vicinity of their breeding colonies, they would acquire an isotopic signature positively correlated with that of basal prey species present in the same region. Such a phenomenon would lead to coherent spatial structure among isotopic signatures within a given taxon, yielding related patterns in predator and prey isotopic signatures (Kelly 2000, Post 2002, Bowen 2010, Kline 2010, Olson et al. 2010).

I expected that fine-scale patterns in isotopic signatures of predators would be heavily influenced by variation in the trophic level of prey species present in predator diet. Nitrogen signatures, therefore, could be pronounced, because $\delta^{15}\text{N}$ tends to have an average enrichment of 3.2-3.4‰ with each increase in trophic level, whereas $\delta^{13}\text{C}$ concentrations change little with increasing trophic level, and are often less variable (approximately 1‰ with each level; (Kelly 2000, Post 2002). Characterizing the $\delta^{15}\text{N}$ signal of primary producers at the biological base of an aquatic food web can be challenging because phytoplankton have short life spans, and individual generations can respond rapidly to transient conditions (Laws et al. 1995, Burkhardt et al. 1999, Rolff 2000, Tamelander et al. 2009). Euphausiids (krill: *Thysanoessa* spp.) and walleye pollock (pollock: *Theragra chalcogramma*) were therefore chosen for sampling to measure the prey base. Such prey species integrate the more variable isotopic signal from phytoplankton, in effect averaging short-term conditions and reducing uncertainty in the estimation of the trophic position of consumers located higher in a given food web (Post 2002, Barnes et al. 2009). These prey species occur throughout the study region, they are among the dominant taxa of the eastern Bering Sea shelf in terms of biomass (Aydin et al. 2007), and they are commonly consumed by the focal seabird study species, thick-billed murres and black-legged kittiwakes (Sinclair et al. 2008, Renner et al. 2012).

Thick-billed murres and black-legged kittiwakes represent contrasting seabird feeding guilds (pursuit-divers and plunging surface-feeders, respectively), and these two foraging strategies are widely used by seabirds throughout the world, thus making them ideal candidates that represent typical foraging patterns. In the central and southern

Bering Sea, the breeding season for both species spans the period May – August (Byrd et al. 2008). During the breeding season these species function as central place foragers because both parents participate in territorial defense, egg incubation (~ May-June), and the raising of young (~ July-August), therefore, their foraging time and trip length are constrained by the need to return repeatedly to a nesting site at a central colony location (Weimerskirch 2007). Given such constraints, central place foraging seabirds are sensitive to local food availability (distribution, abundance, density), and often demonstrate a specific diet or choice of foraging location that can appear as signals in isotopic measurements (Quillfeldt et al. 2005, Roscales et al. 2011). Isotopic signals in either (or both) species are likely influenced by diet specificity, however, the pursuit-diving strategy of murres necessitates a greater commitment to discrete foraging locations, so their isotopic signal could be more noticeably enhanced by a local geospatial influence. I expected, therefore, that any isotopic coupling between prey base and predator would be stronger in murres than in the more widely-ranging kittiwakes. In this context this study expanded on the spatiotemporal extent to which isotopic analysis can successfully inform foraging studies that link mobile marine predators to their dynamic prey base.

METHODS

Study Area

Fine scale, synoptic sampling of seabirds and their prey occurred in waters within 200 kilometers of the Pribilof Islands, St. George (56.60°N, 169.58°W) and St. Paul (57.19°N, 170.26°W), and extending southeastward to Bogoslof Island (53.93°N, 168.03°W; Figure 1). The marine environment in the central and southern Bering Sea is characterized by three abrupt and dramatically contrasting habitat types: shallow shelf (< 200 m depth), deep basin (> 1000 m depth), and inter-oceanic Aleutian island passes (Hunt and Stabeno 2005, Hunt et al. 2008). The two Pribilof islands host large, remote seabird breeding colonies that are functionally isolated (> 300 km to nearest neighboring colonies) during the summer breeding season, making them ideal for fine scale studies of foraging dynamics in marine birds because animals sampled near the islands would likely have been using the area specifically for foraging and breeding, and were unlikely to be associated with more distant colonies (Kitaysky et al. 2000, Byrd et al. 2008, Jahnke et al. 2008). Pacific-influenced waters near Bogoslof Island provided a clear contrast in habitats (Hunt and Stabeno 2005). Based on data in the literature it was determined that the 200 km radius was appropriate for characterizing the foraging activity of locally breeding murre and kittiwakes (Kitaysky et al. 2000, Hunt et al. 2008, Jahnke et al. 2008).

Sample Collection

Prey collections - Prey sampling locations were associated with pre-determined, stratified, randomly chosen transect surveys (90%), as well as adaptive transects (10%) that targeted prey patches discovered through acoustic measurements (Figure 1).

Figure 1. Prey species sampling locations for euphausiids (*Thysanoessa* spp) and age-0 walleye pollock (*Theragra chalcogramma*) that were sampled in randomly placed net tows during July-August, 2008 and 2009. Study area with ship survey tracks is shown within the 200 km radius of St. Paul Island (2008, 2009) and extending south to within 200 km of Bogoslof Island, Aleutians (2009).

In each location, prey specimens of age-0 pollock and the dominant krill species (*Thysanoessa* spp) were collected using modified Marinovich trawls and Neuston nets targeted at prey patches that had been located with split-beam echo-sounders (38, 70, 120, and 200 kHz). Subsamples from net tows were collected, identified, and immediately frozen (-20° F). Subsequent inter-year statistical analyses of isotopic signatures revealed no deviations from normality and no statistical differences between means within a given prey taxon, so data from both years were pooled for each taxon to create homogeneous prey baseline datasets for krill and pollock. Repeat sampling effort at a given location was averaged to generate a single value for each prey species at each location. The resulting datasets consisted of 33 sample locations for krill and 46 locations for pollock (Figure 1).

Seabird collection - Thick-billed murres and black-legged kittiwakes were collected with a shotgun as they engaged in foraging activity on the open ocean (Figure 2).

Figure 2. Seabird collection locations. Study area with ship survey tracks shown within the 200 km radius of St. Paul Island (2008, 2009), and extending south to within 200 km of Bogoslof Island, Aleutians (2009). No more than 3 individuals of a given bird species were collected from the same location (within 500m of first collection point). Birds were collected between the hours of 0300 and 2340 AST, while foraging, or associated with foraging activity, wherever they were encountered.

Collections totaled 47 murres and 39 kittiwakes in 2008, and 78 murres and 66 kittiwakes in 2009. Collection locations were associated with randomly distributed net tow sampling and strip transects undertaken concurrently by the research vessel, therefore, a thorough stratification of sampling was achieved to include all potential habitat types, in each week of data collection, for the duration of both periods. Birds were collected at all times of day between the hours of 0300 and 2340 hrs, AST. Shooters preferentially targeted foraging birds that were within 25 m range and on the water surface, rather than in flight, because on-water birds could be linked directly to synoptic prey base measurements and could be linked more confidently to the specified collection location. However, kittiwakes in particular are accomplished fliers and both species are theoretically capable of traversing the entire study area in a single afternoon, so it was not possible to know how long a particular bird had spent at a given location as it was targeted for collection (Hatch et al. 2000). No more than 3 birds were collected from a given location (within 500m radius of initial take), and the birds were retrieved from the water using a long-handled dip net, and then frozen (-20°F) immediately on the ship for preservation (Barrett et al. 2007, Bugoni et al. 2008). Upon return, samples of liver and muscle were removed for stable isotope analyses. All seabirds were examined during tissue removal to ensure their status as adult breeders (presence of a brood patch), and to ascertain that all were in good health (subcutaneous fat and pectoral muscle condition) at the time of collection.

Ethics Statement – A lethal take of 230 seabirds was necessary for the sampling of foraging birds on the open ocean. Large (150-225') research vessels are too imposing

and slow to approach foraging birds for live capture, and the rough ocean conditions prevalent in the Bering Sea precluded the deployment of small skiffs. Birds were collected with a shotgun, under the auspices of the US Fish and Wildlife Service (USFWS/Migratory Bird collection permit #MB08537-1) and Alaska Department of Fish and Game (Fish and Game #08-134). Concerns for ethical treatment of birds were ascertained by reviews and permits from San Jose State University Animal Care and Use (IACUC Harvey#926), and US Fish and Wildlife Care and Use permits (IACUC #2008013). Ethical prey sampling was approved with reviews by Oregon State University Animal Care and Use (Protocol #3659), and was accomplished with permitting from Alaska Department of Fish and Game (Fish and Game #CF-09-094).

Stable Isotope Analyses

Before testing, all samples were dried at 40°C for 48 h, then ground into a fine powder and lipid-extracted using a methanol-chloroform mixture (Doucette et al. 2010, Hoffman and Sutton 2010). Seabird tissues were analyzed at the University of Alaska, Fairbanks. Fish and euphausiid tissues were analyzed at Northern Arizona University. Isotope values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured using continuous-flow isotope-ratio mass spectrometry, using a Thermo-Electron Deltaplus Advantage gas isotope-ratio mass spectrometer interfaced with a Costech Analytical ECS4010 elemental analyzer. Data were normalized using 4 internationally-accepted isotope standards (IAEA CH6, CH7, N1, and N2). The main working standard was peach leaves (NIST 1547). Calibration

runs were conducted frequently to check for run drift and linearity. External precision on standards was $\pm 0.10\text{‰}$ or better for $\delta^{13}\text{C}$ and $\pm 0.20\text{‰}$ or better for $\delta^{15}\text{N}$. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ concentrations are expressed relative to Vienna-Pee Dee Belemnite limestone V-PDB for carbon, and to air for nitrogen. Stable isotopes are reported here in δ notation as the deviation from standards, in parts per thousand (‰), according to the following equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ where X is the isotope in question (^{15}N or ^{13}C) and R is the ratio of the heavier (e.g., ^{15}N) to the lighter (e.g., ^{14}N) isotope of the element (Fry 2005). In general, a predator's physiological processes result in the preferential retention of the heavier (^{15}N or ^{13}C) isotope over the lighter (^{14}N or ^{12}C) one in its diet, with each trophic level accounting for an approximate enrichment of $+3.2 - 3.4\text{‰}$ in $\delta^{15}\text{N}$ and $\pm 1.0\text{‰}$ in $\delta^{13}\text{C}$, relative to that of its prey (Kelly 2000, Post 2002).

Data Analyses

Spatial Structure among isotope values of samples collected at sea - Literature detailing controlled studies of avian tissue turnover times indicates that the isotopic signature of muscle tissue would represent a bird's diet integrated over a period of approximately 30 days, whereas liver tissue would represent approximately 5 to 10 days. Therefore, given collections throughout a 30 day sampling period, it can be considered that the strength of any spatial structure in isotopic signatures, coupled with the strength of a correlation between muscle and liver values, would be indicative of corresponding spatiotemporal similarities in the diet of the birds. Data sets were standardized to Z-scores to account for the large differences in scale between isotope values and distance measurements, and

then spatial structure (autocorrelation) was assessed using the Moran's I statistic in the statistical program R 2.11.0 (Moran 1950, Legendre and Legendre 1998). The temporal persistence of spatial structure was inferred using the Pearson's r correlation statistic, which compared the strength and significance of similarities between muscle and liver tissue isotope signals.

Isoscape mapping and patterns in trophic relationships among taxa - Mapping and visualization were accomplished using ArcGIS v.9.3 (ESRI Corporation, Redlands, CA). To examine basic patterns in isotopic signatures across the study region, Inverse Distance² Weighted interpolations were used to generate a simple contour map of each isotopic dataset ($\delta^{15}\text{N}$ for tissues: krill, pollock, seabird liver, seabird muscle; Fortin and Dale 2005). The resultant cross-shelf contrast evident among isotopic signatures of prey and predators was then smoothed and modeled using a Local Polynomial Interpolation function in the Geostatistical Analyst toolkit of ArcGIS. In this process, the software generated isoscape surfaces by repeatedly fitting a first-order polynomial through prey sampling points ($\delta^{15}\text{N}$ of prey items captured in net tows) that fell within a pre-defined search neighborhood as it was passed across the entire study region. The search neighborhood parameters that were applied in the calculation (the shape, size, orientation, number of points included, and directional bias) were determined through an iterative process of variogram analysis and cross validation (ArcGIS v.9.3). The Local Polynomial Interpolation created two smoothed surfaces, one krill and one pollock, that were then used in effect as predictive templates to which seabird sample values were

compared at their points of collection. This process yielded sets of values in triplicate (seabird tissue, predicted pollock tissue, predicted krill tissue), and enabled the comparison of measured $\delta^{15}\text{N}$ signatures in seabird tissues to theoretical prey base $\delta^{15}\text{N}$ values that were derived from actual prey items sampled contemporaneously in net tows throughout the study area. Pearson's correlation statistics were used to assess the strength of the relationship between krill and pollock baselines, and then linear regression was used to test for a multi-trophic influence of krill prey baseline signatures on seabird $\delta^{15}\text{N}$ muscle and liver values. Dependent variables were seabird values, with krill baseline $\delta^{15}\text{N}$ values as predictors (statistical program R 2.11.0). Finally, Pearson's correlation statistics were applied to quantify similarities in $\delta^{15}\text{N}$ enrichment patterns of liver and muscle, to infer the temporal persistence of the phenomenon.

RESULTS

Spatial Structure Among Isotope Values of Predators and Prey Collected at Sea

Spatial structure (autocorrelation) was detected among $\delta^{15}\text{N}$ signatures of both krill ($p = 0.017$) and pollock ($p < 0.001$; Figure 3).

Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
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Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
----	----	----	----

Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
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Figure 3. Spatial autocorrelation patterns and predictive isoscape modeling of $\delta^{15}\text{N}$ in seabird prey tissues. Spatial autocorrelation was mapped using Inverse Distance² Weighted interpolations (ArcGIS 9.3) of relative $\delta^{15}\text{N}$ in seabird prey species, and the corresponding predictive isoscape model was generated with Local Polynomial Interpolation smoothing. In the isoscape maps on the left side, red-filled contours represent areas containing prey samples that were enriched relative to mean values, whereas blue-filled contours contained samples that were relatively depleted. In the isoscape maps on the right side, enrichment increases as colors lighten, with lightest colors representing samples enriched in $\delta^{15}\text{N}$ to +2 standard deviations above mean values, and darkest colors were relatively depleted -2 standard deviations below the means.

Kittiwakes had no spatial structure ($p > 0.20$) in $\delta^{15}\text{N}$ signatures of muscle and liver tissues in either year (Figures 4 and 5). In contrast, throughout the study area the $\delta^{15}\text{N}$ values of murres collected in close proximity were more similar to one another than to those collected at greater distances ($p < 0.001$ in all tissues in both years; Figures 4 and 5).

Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
----	----	----	----

Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
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Figure 4. Patterns in spatial autocorrelation of $\delta^{15}\text{N}$ values in seabird muscle tissues. Inverse Distance² weighted interpolation (ArcGIS 9.3) was applied to $\delta^{15}\text{N}$ values measured in black-legged kittiwake and thick-billed murre muscle tissues. Results were mapped as $\pm$ standard deviations from the mean of a given species in a given year to facilitate comparisons. In the isoscape maps, red-filled contours represent areas containing seabird samples that were enriched relative to their mean, whereas blue-filled contours contained samples that were relatively depleted.

Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
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Relative Enrichment:
Standard Deviation

-2	-1	+1	+2
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Figure 5. Patterns in spatial autocorrelation of $\delta^{15}\text{N}$ values in seabird liver tissues. Inverse Distance² weighted interpolation (ArcGIS 9.3) was applied to $\delta^{15}\text{N}$ values measured in black-legged kittiwake and thick-billed murre liver tissues. Results were mapped as $\pm$ standard deviations from the mean of a given species in a given year to facilitate comparisons. In the isoscape maps, red-filled contours represent areas containing seabird samples that were enriched relative to their mean, whereas blue-filled contours contained samples that were relatively depleted. No structure was detected among kittiwakes (Moran's I ; $p > 0.3$); in murre there was strong spatial autocorrelation in both years (Moran's I ; $p \leq 0.001$).

Isoscape Mapping

Inverse Distance² weighted (IDW) mapping of $\delta^{15}\text{N}$ signatures in thick-billed murre and their prey yielded similar patterns that indicated there were fundamental differences between shallow, continental shelf habitat and deeper Aleutian Basin and Aleutian Pass habitats. More specifically, it appeared that the average enrichment in the tissues of murre and their prey base increased with increasing latitude (north of St. Paul Island), and decreasing depth (inner shelf; Figures 3, 4, and 5). Kittiwake values exhibited no coherence in 2008, but demonstrated scattered clustering of like values in 2009 that provided some suggestion of a basin-shelf dichotomy (Figures 4, and 5). Subsequent Local Polynomial Interpolation mapping effectively smoothed the prey data and generated krill and pollock predictive isoscapes that were both characterized by distinct, cross-shelf gradients in $\delta^{15}\text{N}$ values. In fact, krill and pollock tissue sampled over northern, shallow shelf habitat were enriched 1-2‰ relative to those in samples taken over deeper Aleutian Basin and Pass habitats to the south, at distances of less than 100 km (Figure 3). In addition, values of krill and pollock at seabird collection locations were positively correlated with one another in both years ($r \geq 0.95$, $p \leq 0.001$).

Patterns in Trophic Relationships Among Taxa

Black-legged kittiwakes - Kittiwake muscle $\delta^{15}\text{N}$ values were not consistent with krill and pollock $\delta^{15}\text{N}$ baselines in 2008 (Figure 6), however, liver values were weakly correlated with those of the prey base (Figure 7). The prey base models had a weak but significant predictive influence, which indicated a consistent average enrichment pattern in all taxa across the study area in 2008 ($r^2 < 0.12$; Table 1).

Table 1. Regression of $\delta^{15}\text{N}$ values in seabird liver and muscle tissues with those of predicted krill (*Thysanoessa* spp.) baseline tissues. Bold indicates significance at $p < 0.006$ after Bonferonni corrections were applied for multiple testing.

Seabird Species	Year	Tissue	β	Test statistic	R^2	Test statistic	p-value
Black-legged Kittiwake	2008	Muscle	0.06	$t_{37} = 0.27$	0.00	$F_{1,37} = 0.07$	0.7910
Black-legged Kittiwake	2008	Liver	0.45	$t_{36} = 2.18$	0.12	$F_{1,36} = 4.74$	0.0360
Black-legged Kittiwake	2009	Muscle	0.29	$t_{64} = 2.09$	0.06	$F_{1,64} = 4.36$	0.0410
Black-legged Kittiwake	2009	Liver	0.50	$t_{64} = 3.91$	0.19	$F_{1,64} = 15.30$	0.0002
Thick-billed Murre	2008	Muscle	0.55	$t_{45} = 5.71$	0.42	$F_{1,45} = 32.63$	0.0001
Thick-billed Murre	2008	Liver	0.63	$t_{45} = 5.95$	0.44	$F_{1,45} = 35.37$	0.0001
Thick-billed Murre	2009	Muscle	0.64	$t_{76} = 6.34$	0.35	$F_{1,76} = 40.22$	0.0001
Thick-billed Murre	2009	Liver	0.81	$t_{76} = 8.70$	0.50	$F_{1,76} = 75.75$	0.0001

Figure 6. Comparisons of $\delta^{15}\text{N}$ values in seabird muscle tissue and two measures of their prey base. Prey base values were obtained from predictive isoscape maps generated through local polynomial interpolation (ArcGIS 9.3) of $\delta^{15}\text{N}$ values measured in actual prey items sampled concurrently from randomly placed net tows conducted during July 15th – August 15th, 2008 and 2009. Overlaying seabird values at their points of intersection with prey isoscapes yielded food web values for euphausiids (*Thysanoessa* spp.), walleye pollock (*Theragra chalcogramma*), and seabirds at each collection location. Krill values were chosen to represent the baseline (1:1 slope) of the food web, and in all cases were tightly coupled (Pearson's $r \geq 0.95$; $p < 0.001$) to pollock values in a given year.

Figure 7. Comparisons of $\delta^{15}\text{N}$ values in seabird liver tissue and two measures of their prey base. Prey base values were obtained from predictive isoscape maps generated through local polynomial interpolation (ArcGIS 9.3) of $\delta^{15}\text{N}$ values measured in actual prey items sampled concurrently from randomly placed net tows conducted during July 15th – August 15th, 2008 and 2009. Overlaying seabird values at their points of intersection with prey isoscapes yielded food web values for euphausiids (*Thysanoessa* spp.), walleye pollock (*Theragra chalcogramma*), and seabirds at each collection location. Krill values were chosen to represent the baseline (1:1 slope) of the food web, and in all cases were tightly coupled (Pearson's $r \geq 0.95$; $p < 0.001$) to pollock values in a given year.

In 2009, kittiwake muscle $\delta^{15}\text{N}$ values were not consistent with prey $\delta^{15}\text{N}$ baselines (Figure 6), and although there were weak significant relationships between 2009 kittiwake muscle signatures and those of krill baselines, the prey base values had little predictive influence ($r^2 < 0.06$; Table 1). In 2009, kittiwake liver $\delta^{15}\text{N}$ signatures tracked

both krill and pollock $\delta^{15}\text{N}$ baselines more closely (Figure 7), although krill did not account for more than 19% of the variability in kittiwake liver signatures (Table 1). Kittiwake liver and muscle values were correlated in both years, indicating a temporal consistency of several weeks in diet composition, foraging locations, or both (Table 2).

Table 2. Correlation between $\delta^{15}\text{N}$ values in muscle and liver tissues among black-legged kittiwakes and among thick-billed murres. Bold indicates significance at $p < 0.013$ after Bonferonni corrections were applied for multiple testing.

Species	Year	Test statistic	Pearson's r	p-value
Kittiwakes	2008	$T_{35}=5.13$	0.66	< 0.001
Murres	2008	$T_{45}=10.39$	0.84	< 0.001
Kittiwakes	2009	$T_{64}=8.00$	0.71	< 0.001
Murres	2009	$T_{76}=10.71$	0.78	< 0.001

Thick-billed Murres - Thick-billed murre muscle $\delta^{15}\text{N}$ signatures were correlated with krill and pollock $\delta^{15}\text{N}$ baselines in both years (Figure 6). Krill baseline values predicted a sizeable proportion of the variability (35-42%; Table 1), and all trophic levels exhibited a cross-shelf enrichment pattern that indicated $\delta^{15}\text{N}$ in murre muscle tissue was closely coupled to $\delta^{15}\text{N}$ in krill and pollock tissues throughout the study area. These results reflect the concordance of strong spatial structure in $\delta^{15}\text{N}$ signatures of krill, pollock, and murre muscle tissue in both years, as demonstrated visually through Inverse Distance² Weighted mapping (Figures 3 and 4), and quantitatively through Moran's I

autocorrelation (Figure 4) and predator-prey regression results (Figure 6; Table 1).

Thick-billed murre liver signatures were tightly coupled to krill and Pollock baselines in both years. Krill baseline models accounted for 44% (in 2008) and 50% (in 2009) of the variability in murre liver signatures ($p < 0.0001$ in all cases; Table 1). The Inverse

Distance² weighted maps (Figures 3 and 5) and the regression plots (Figure 7)

demonstrate a strong basin-shelf trend of increasing $\delta^{15}\text{N}$ values in murre tissues and their prey, with greatest enrichment occurring N-NW of St. Paul Island over shallow shelf

waters. Murre liver and muscle values were highly correlated in both years, implying a temporal persistence of the phenomenon (Table 2).

DISCUSSION

Tissue turnover time in murre and kittiwake pectoral muscle is 3-5 weeks, whereas that of liver is relatively rapid and certainly less than a week (Hobson and Clark 1992, Bearhop et al. 2002, Ogden et al. 2004, Cherel et al. 2005). Therefore, isotope values in muscle tissue represent a diet integrated over approximately 30 days, and liver tissue perhaps 5 days. Given these turnover rates and a sampling period spanning ~ 30 days, it can be inferred that an evaluation of the degree of spatial structure (significance of Moran's I statistic), coupled with the strength of prey-predator linkage (magnitude and significance of regression r^2), likely represents the degree to which birds were foraging repeatedly in a given area over periods of 30-60 days during the breeding season. Nitrogen signatures in thick-billed murre muscle and liver tissues yielded highly significant spatial structure in both years. Regression results indicated that prey baselines and murre tissue $\delta^{15}\text{N}$ signatures were tightly coupled throughout the study area in both years, implying regional specificity, as well as intra-seasonal and inter-annual consistency, in their choice of foraging areas during their breeding period. Patterns among black-legged kittiwake tissues, however, were much less coherent. Differences between the bird species reflect, in part, the physiological and morphological adaptations that accommodate the contrasting foraging strategies of pursuit-divers (murres) and surface-feeding plungers (kittiwakes).

Pursuit-diving murres have greater caloric needs (field metabolic rates) than surface-feeding kittiwakes (Gabrielsen et al. 1998, Croll and McLaren 1993, Kitaysky et

al. 2000), reflecting the greater energy demands of a sub-surface foraging strategy (e.g., immersion in cold water, periodic oxygen deprivation) and the increased flight costs of morphological adaptation to diving (greater body mass, increased fat layer, and small, stiff wings) that contribute to heavy wing-loading. Therefore, with greater flight costs murres might have been more selective or consistent in their foraging effort in specific areas where prey species were encountered with more frequency or in greater abundance or density. In doing so, I would expect to see a more distinct local isotopic signal (if one existed); other studies in the Bering Sea have indicated that sub-surface foragers, such as murres, may require prey patches of greater density and persistence than do surface-feeders such as kittiwakes, and that kittiwakes are indeed more widely dispersed at sea (Lovvorn et al. 2001, Hunt et al. 2005, Sigler et al. 2012).

In contrast to murres, spatial structure and predator-prey associations in the $\delta^{15}\text{N}$ signatures of kittiwakes were much weaker, which indicated that individual kittiwakes were perhaps foraging more widely and consuming prey from both shelf and basin habitats (Sigler et al. 2012). Kittiwakes in the Gulf of Alaska and Bering Sea differ from murres in their diet and often consume larger proportions of myctophid fishes, the isotopic signatures of which might differ substantially from that of pollock (Sinclair et al. 2008, Renner et al. 2012). It is also likely there are differences in species composition among euphausiid communities between shelf / basin environments, although species-specific differences in isotopic signatures have not been thoroughly examined to date. A greater breadth in foraging locations, coupled with differences in diet, could therefore

result in a more variable or diluted isotopic signal in kittiwake tissues, and weaker coupling to krill or pollock specifically.

The persistence of spatial structure throughout a 30 day sampling period, as inferred by isotope values in murre tissues, indicated that murres were likely partitioning the available habitat and foraging repeatedly in distinctly separate areas. The geospatial stratification among thick-billed murre isotope values coincided in latitude with the three focal colonies (St. Paul, St. George, and Bogoslof), which indicated some amount of foraging habitat partitioning among birds from the colonies, despite the close proximity of St. Paul to St. George (< 75 km). Intra-specific habitat partitioning has been infrequently described in seabirds, however in Prince William Sound, Alaska, Ainley et al. (1993) noted that there was little overlap among the foraging areas used by neighboring black-legged kittiwake colonies, and that the largest colonies of black-legged kittiwakes were located as far apart from one another as geography allowed. In the Bering Sea, intra-specific foraging site fidelity was inferred through analyses of stomach contents and stable isotope values in short-tailed shearwater (*Puffinus tenuirostris*) tissues (Baduini et al. 2006). In this case the birds were collected while foraging in several locations throughout Bristol Bay and the eastern Bering Sea, and stable isotope signatures of organs indicated that groups of shearwaters were likely feeding for multiple weeks at a time in discrete locations, although they were theoretically free to forage widely while not breeding on a colony. Elsewhere, off the coast of South Africa, Gremillet et al. (2004) demonstrated that foraging areas of cape gannets (*Morus capensis*) from two neighboring colonies overlapped little, although the two study colonies were well within

(65-85%) the theoretical foraging range of one another. In addition, in the central Pacific, Wiley et al. (2012) recently inferred habitat partitioning between two colonies of Hawaiian petrels (*Pterodroma sandwichensis*) in the Hawaiian Islands. When considering the results of the current study in the context of those previously mentioned, it appears that habitat partitioning among conspecific marine birds can become an influential force affecting the delineation of a seasonal isotopic niche, the nature of which can be influenced as much by variations in the spatial patterns in habitat use as it is by differences in diet (Baduini et al. 2006, Newsome et al. 2007, Wiley et al. 2012).

The isoscape mapping in this study adds more detail to patterns described by Schell et al. (1998), and affirms the existence of a cross-shelf $\delta^{15}\text{N}$ gradient similar in nature to that measured by Granger et al. (2011) in the same region, and by Kline (2009,2010) in the Gulf of Alaska. The measurements at three trophic levels demonstrate that baseline signals of this gradient can be propagated through the food web to top-tier predators (thick-billed murre), and can inform the delineation of foraging areas of marine predators at a local scale of tens of kilometers. Previous stable isotope research in the Bering Sea has successfully identified the long-distance migration routes and broad foraging habitats of fur seals (Kurle et al. 2002), bowhead whales (Lee et al. 2005), and King Eiders (Oppel and Powell 2008). These previous habitat assignments were most successful at ecoregional scales (1000's km), whereas habitat studies based on isotopic signals elsewhere at finer scales (<100 km) have met with somewhat more mixed results (Szymanski et al. 2007). This study, which clearly revealed a cross-shelf $\delta^{15}\text{N}$ gradient in a prey base shared by most top-tier predators in the region, may enable future researchers

to increase the resolution at which it is possible to differentiate habitat use of multiple predators in the system. In addition, these results emphasize the importance of considering baseline signatures when using stable isotope analyses in food web studies. Clearly, variations in baseline signals among habitats can propagate upwards in food webs through multiple trophic levels and, if not accounted for, can present potentially significant sources of error in estimates of predator diet composition and trophic level (Solomon et al. 2008, Flaherty and Ben-David 2010, Wiley et al. 2012). In seabirds this phenomenon was demonstrated by Moreno et al. (2011) in a contrast of two food webs including European shags on the coast of northwest Spain, where they found differences of 2.0‰ in $\delta^{15}\text{N}$ values of baseline mussel tissues between two study systems. In the Bering Sea samples presented here there were significant shelf / basin differences of approximately 2.0‰ in $\delta^{15}\text{N}$ values of pollock tissues, and approximately 1.0‰ in krill tissues. Such differences represent sizeable sources of variation in trophic estimates, when considering that average differences in $\delta^{15}\text{N}$ between an avian consumer and its prey in marine food webs were approximately 3.2‰ (Kelly 2000).

The isotope gradient in the Bering Sea appears to be persistent in time. There were differences measured in $\delta^{15}\text{N}$ in krill sampled off and on the North American continental shelf that seem quantitatively similar to those of Schell (1998). Like Schell, this study found no inter-annual differences in isotope values within a given prey taxon. This corroborates assertions by some researchers that the measurement of isotope values in primary and secondary consumers effectively integrates any seasonal variation present in the isotopic values of phytoplankton, smoothing variability to create a reliable baseline

proxy (Post 2002, Barnes et al. 2009). Cross-shelf gradients similar to what were found in murre and their prey have been measured elsewhere in other northern hemisphere systems characterized by seasonally well-mixed, shallow waters abutting abrupt shelf break and deep pelagic habitat (Bode and Alvarez-Ossorio 2004, Miller et al. 2010, Olson et al. 2010). Recent food web modeling and meta analyses conducted for southern hemisphere marine communities have indicated that baseline signals are transmitted upwards through the marine food chain, manifesting in similar trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of crustaceans and seabirds (Quillfeldt et al. 2005, Jaeger et al. 2010b). Traditionally, $\delta^{13}\text{C}$ has been used as a diagnostic marker to infer latitudinal patterns in habitat use and to distinguish between shallow, continental shelf and deep water, pelagic foraging areas (Hobson et al. 1994, Sydeman et al. 1997), but in this study $\delta^{15}\text{N}$ was also useful in delineating animal habitat use at a fine scale. Similarly, Forero et al. (2004) suggested $\delta^{15}\text{N}$ signatures of seabirds breeding along the Chubut coast of Argentine Patagonia exhibited a similar enriched-depleted $\delta^{15}\text{N}$ cross-shelf gradient. Phillips et al. (2009) also determined that stable nitrogen isotopes were useful markers for distinguishing wintering and pre-breeding habitat use by a suite of procellariid birds in high latitude southern Atlantic waters. In addition, Wiley et al. (2012) inferred habitat use of shearwaters in the central Pacific based on broad scale patterns in baseline $\delta^{15}\text{N}$ levels.

Making use of a cross-shelf gradient in stable nitrogen isotopes, this study inferred that foraging habitat partitioning was stronger among thick-billed murre than it was among black-legged kittiwakes in two consecutive summer seasons (2008, 2009),

both of which were cooler than the average for the past 30 years (Overland et al. 2012). As top-tier predators and central place foragers, seabirds breeding on islands in the southeastern Bering Sea are sensitive to variations in local ocean conditions, which in turn are strongly influenced by the extent of winter ice cover and the timing and the patterns of its melt (Kitaysky et al. 2000, Hunt et al. 2002, Byrd et al. 2008). Although recent (4 years) ocean conditions have been cool in the study region, current modeling predicts steady warming, and a decreasing trend in the southern extent of the seasonal ice cover (Bond and Adams 2002, Overland and Stabeno 2004, Grebmeier et al. 2006, Wang et al. 2012, Hazen et al. 2012), a phenomenon reflecting a general warming that has been measured in high latitude oceans worldwide (McGowen et al. 1998, Barnett et al. 2005). Therefore, the patterns in habitat use measured here will necessarily change in response to fluctuations in ocean conditions that influence food web structure and the availability of prey (Mueter and Litzow 2008). The Pribilof Islands, however, represent unique breeding habitat for colonial pinnipeds and seabirds because they are positioned near the average southern extent of seasonal ice cover in the Bering Sea, and are perched in a productive transition zone between deep-basin and shallow-shelf habitats. In addition, the islands are the only land mass for a radius of > 300 km in any direction, and as such represent the only available breeding habitat for seabirds and pinnipeds in the region. Given their constraints as central place foragers, seabirds can be sensitive to variations in climate that drive local fluctuations in the distribution, abundance, and density of local food supplies (Anderson and Piatt 1999, Kitaysky et al. 2000, Pichegru et al. 2010, Wolf et al. 2010). Therefore, murre and kittiwake populations breeding on the relatively

remote Pribilofs could be disproportionately affected by fluctuations in climate conditions that fundamentally change prey patch dynamics in the central and southern Bering Sea (Hunt et al. 2002, Grebmeier et al. 2006, Mueter and Litzow 2008, Wang et al. 2012).

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THESIS CONCLUSIONS

Central place foraging constraints had a greater influence on niche widths of pursuit-divers (murres) than on surface-feeders (kittiwakes). This would make sense if niche width in this system is heavily influenced by variation in foraging habitat use; kittiwakes, with lesser flight costs, likely ranged more widely in the study area (Hatch et al. 2000, Sigler et al. 2012). In support of this hypothesis it can be noted that murre stomach contents indicated a more trophically diverse diet than was evident in kittiwakes, and diet diversity has been invoked as a potential driver of isotopic niche widths (Bearhop et al. 2004), yet overall niche widths between the two species differed little. Such a paradox indicated the importance of a geospatial influence in contributing to variability in isotope values of predator tissues.

Murres ate a greater proportion of invertebrates than did kittiwakes, most notably euphausiids and amphipods. It is likely that large proportions of easily digested invertebrates, such as these, are regularly missed during on-colony seabird diet sampling efforts because adults intercepted at the colony have already digested these taxa while foraging at sea (Barrett 2007). Gut contents of both species were spatially autocorrelated, and prey species composition in seabird diet varied with habitat type, indicating patchiness in prey availability, specificity in seabird foraging effort, or both.

Geospatial patterns in isotope values were highly significant in murres, but less so in kittiwakes. Muscle and liver isotope values were correlated in both species, implying consistency in their diet throughout the breeding season. Taken together, the

geospatial patterns in stomach contents and isotope values, in the context of highly correlated muscle and liver values, strongly indicated that murres were foraging repeatedly in distinct arenas (for example, N-NW of St. Paul, and S-SW of St. George) during their breeding period. The inverse distance² weighted mapping of enrichment values (PCA axis_1 scores) provided an isoscape map that clearly demonstrated stratification among values in murres at sea corresponding in latitude with the three focal seabird colonies. This pattern indicated the birds may have been partitioning their foraging habitat by colony. The lack of such strong patterns in kittiwakes implied that these birds foraged more widely and evenly across the study area.

The quantification of the extent of the foraging areas in this study was necessarily based on bird collection sites at sea, the specific locations of which were clustered to some degree. While this might be expected to bias spatial statistics, it should also be recognized that birds must themselves cluster if they are indeed foraging on patchy prey in the open ocean, and birds can of course only be collected from areas where they are encountered. In this case the study design included 60+ randomly-located net tows, and ensured broad spatial coverage that included areas where few birds were seen. It also must be noted that a research vessel, when fishing, surveying, and even transiting at average speeds, is in effect a nearly stationary platform in the midst of the dynamism that defines seabird foraging. Kittiwakes and murres both routinely fly several times faster than typical 5-8 kts per hour typical of ship travel. Kittiwakes, in particular, tend to forage widely and spend most of their time on the wing. This mismatch in mobility does make it difficult to sample foraging seabirds, and it could be that the relatively slow

speeds of the ship were less effective at capturing patterns in kittiwake foraging dynamics.

A geospatial analysis of $\delta^{15}\text{N}$ values in prey items identified a cross-continental shelf gradient in baseline isotopic enrichment that was clearly propagated to seabird tissues. This is the first time such a gradient has been clearly quantified at multiple trophic levels on a fine spatial scale in the Bering Sea. These results may enable future researchers to increase the resolution at which it is possible to differentiate the habitat use of predators in the system. This is of special relevance as foraging ranges and migration routes change through time in response to fluctuations in the marine environment (Furness et al. 1997, Mueter and Litzow 2008, Pichegru et al. 2010, Quillfeldt et al. 2010, Hunt et al. 2011). Indeed, the gradient described herein could itself become more dynamic with changing patterns in the spatiotemporal extent of the winter ice cover because the phenomenon is likely based on physical and geochemical processes related to the vertical mixing of bottom sediments in relatively shallow waters of the continental shelf (Granger et al. 2011).

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