## A cross-shelf gradient in δ¹⁵N stable isotope values of krill and pollock indicates seabird foraging patterns in the Bering Sea

# A cross-shelf gradient in $\delta^{15}$N stable isotope values of krill and pollock indicates seabird foraging patterns in the Bering Sea

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## ARTICLE INFO

## ABSTRACT

Concurrent measurements of predator and prey $\delta^{15}$N isotope values demonstrated that a cross-shelf isotopic gradient can propagate through a marine food web from forage species to top-tier predators and indicate foraging areas at a scale of tens of kilometers. We measured $\delta^{13}$C and $\delta^{15}$N in muscle tissues of thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*), and in whole body tissues of walleye pollock (*Gadus chalcogrammus*) and krill (*Thysanoessa* spp), sampled across the continental shelf break in the Bering Sea in 2008 and in 2009. We found significant basin-shelf differences at fine scales ($< 100$ km) in $\delta^{15}$N among murres but not kittiwakes, and no such differences in $\delta^{13}$C in either seabird species at that scale. We then quantified the multi-trophic signal and spatial structure of a basin-shelf $\delta^{15}$Nitrogen gradient in the central and southern Bering Sea, and used it to contrast foraging patterns of thick-billed murres and kittiwakes on the open ocean. Seabird muscle $\delta^{15}$N values were compared to baselines created from measurements in krill and pollock tissues sampled concurrently throughout the study area. Krill, pollock, and murre tissues from northern, shallow, shelf habitat ($< 200$ m) were enriched 1–2‰ in $\delta^{15}$N relative to samples taken from deeper habitats ($> 200$ m) to the south and west. Krill $\delta^{15}$N 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 among sample values, and a congruence of geospatial patterns in $\delta^{15}$N among murre and prey tissues, suggest that murres forage repeatedly in specific areas. Murre isotope values showed distinct geospatial stratification, coincident with the spatial distribution of three colonies: St. Paul, St. George, and Bogoslof. This suggests some degree of foraging habitat partitioning among colonies.

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## 1. Introduction

Differences among stable isotope baselines of invertebrate prey species can exist between shallow near shore and deep offshore habitats in the marine environment, and can be referenced to infer patterns in the diet and movement of predators that routinely forage across pelagic/shelf boundaries (Schell et al., 1998; Forero et al., 2004; Miller et al., 2008; Barnes et al., 2009; Olson et al., 2010; Jaeger et al., 2013). In general, cross-shelf patterns have proven most useful for inferring movement across very large distances ($> 100$ 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; Quillfeldt et al., 2010; Jaeger et al., 2010, 2013). Fewer studies have used marine isoscapes and GIS techniques to elucidate 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 multitrophic influence of an apparent cross-shelf gradient in the Bering Sea. In this study, we measured isotopic values from two pelagic seabirds, thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*), and two prey taxa (age-0 walleye Pollock, *Gadus chalcogrammus* and krill, *Thysanoessa* spp) in the Southeastern Bering Sea. We quantified the multi-trophic influence and spatial structure of a cross-shelf $\delta^{15}$N isotopic gradient measured in krill and pollock, and used it to contrast the foraging patterns of the two seabird species. Measurements were developed from comparisons of $\delta^{15}$N isotope values in seabird muscle tissues to baseline krill and pollock values obtained from isoscape mapping techniques.

Stable isotopes are useful in ecology because physical and geochemical processes are known to affect their values 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).

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Isotopic values of new tissues reflect the diet and habitat use of an animal at the time of tissue synthesis. For example, among birds it has been shown that blood plasma and liver cellular turnover rates are quite rapid, representing tissue synthesis periods of a week or less, whereas red blood cell and muscle tissue turnover rates tend to range from four to seven weeks (Hobson and Clark, 1992; Bearhop et al., 2002; Cherel et al., 2005). Recent studies of both captive and wild seabirds have shown that isotopic values in blood, feather, and internal organ tissues can be used to infer long distance migratory movements (Quillfeldt et al., 2010), identify likely foraging habitat use (Phillips et al., 2009; Moreno et al., 2011; Roscales et al., 2011; Jaeger et al., 2013), and elucidate trophic relationships among birds and their prey (Hobson et al., 2002). 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 values (Hobson et al., 2007; Barnes et al., 2009; Bowen, 2010). Much isoscape work within the marine environment is based on coherent, cross-shelf patterns in $\delta^{13}C$ and $\delta^{15}N$ baseline values among shallow nearshore, and deep offshore systems (Goericke and Fry, 1994; Miller et al., 2008; Barnes et al., 2009; Kline, 2009; Quillfeldt et al., 2010). In broad scale studies of the Bering Sea, $\delta^{13}C$ and $\delta^{15}N$ values in euphausiids and copepods decreased from east (onshore, shallow, shelf system) to west (offshore, deep, pelagic system; Schell et al., 1998). Recently, Granger et al. (2011) measured a large cross-shelf gradient of $\pm 5\permil$ in $\delta^{15}N$ of suspended sediments, and Morales et al. (2014) measured a similar gradient in phytoplankton, with the greatest values measured to the north and east of the Pribilof Islands over shallow, shelf waters. Copepods in the Gulf of Alaska display a similar cross-shelf gradient, and in the Atlantic differences in $\delta^{15}N$ were measured between coastal and pelagic fishes in the diet of the European shag, *Phalacrocorax aristotelis* (Kline, 2009; Moreno et al., 2011). Such cross-shelf patterns result from differences in the source pools of nutrients, the extent of vertical mixing and seasonal ice cover, the length of the food chain, and the products of phytoplankton physiology that result in differential uptake of nutrients between shelf and pelagic systems (Schell et al., 1998; Smith et al., 2002; Kline, 2009; Granger et al., 2011; Morales et al., 2014). Based on previous studies that measured a south-to-north, basin-to-shelf enrichment in $\delta^{15}N$ of suspended sediments (Granger et al., 2011), phytoplankton (Morales et al., 2014), and in euphausiids (Schell et al., 1998), we hypothesized that if breeding seabirds foraged preferentially and repeatedly in specific regions within the vicinity of their breeding colonies, they could acquire an isotopic signal positively correlated with that of basal prey species present in the same region, and yield related patterns in predator and prey isotopic values that might indicate that cross shelf gradients in isotopic baselines can be detected at multiple trophic levels (Kelly, 2000; Post, 2002; Bowen, 2010; Kline 2010; Olson et al., 2010).

Morales et al. (2014) demonstrated large cross-shelf differences in phytoplankton $\delta^{15}N$ values across our study area, so we expected that isotopic relationships between seabirds and prey at a relatively fine spatial scale (10's–100's of kms) could be heavily influenced by variation in $\delta^{15}N$. Variability in $\delta^{15}N$ can be greater than in $\delta^{13}C$ among predators, and is based on the trophic level of prey species present in the diet. This is because $\delta^{15}N$ values of predator tissues tend toward a greater average enrichment of 3.2–3.4‰ with each increase in trophic level, whereas $\delta^{13}C$ values change little with increasing trophic level, and are often less variable (approximately 1‰ with each level; (Kelly, 2000; Post, 2002). We therefore expected that any isotopic relationships based on correlations between prey base and predators could be more easily detected at fine scales in $\delta^{15}N$ than in

$\delta^{13}C$. Characterizing the isotopic 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). Therefore, when building the prey $\delta^{15}N$ baseline isoscapes we chose to sample euphausiids (krill: *Thysanoessa* spp.) and age-0 walleye pollock (pollock: *G. chalcogrammus*) as proxies for the marine food web, because consumers at these levels integrate the more variable isotopic signal from phytoplankton and small zooplankton, 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 two prey types occur throughout the study region, they are among the dominant taxa of the eastern Bering Sea shelf in terms of biomass density (Aydin and Mueter, 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; Paredes et al., 2012; Harding et al., 2014).

Thick-billed murres and black-legged kittiwakes use contrasting foraging methods (pursuit-divers versus plunging surface-feeders, respectively) that are widely employed by seabirds throughout the world, thus making them relevant templates for study. In the central and southern Bering Sea, the breeding season for both species spans the period from May through 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 ($\sim$May–June), and the raising of young ($\sim$July–August), and therefore their foraging time and trip length are constrained by the need to return repeatedly to a nesting site at a central colony location (Paredes et al., 2012; Harding et al., 2014). Given such constraints, central place foraging seabirds are sensitive to local food availability (distribution, abundance, and density), and often demonstrate measurable patterns in foraging activity (specific diet or foraging site fidelity) that can appear as signals in isotopic measurements (Quillfeldt et al., 2005; Roscales et al., 2011; Jaeger et al., 2013). Isotopic signals in either (or both) species are influenced by diet specificity, however the pursuit-diving strategy of murres could necessitate a greater commitment to discrete foraging locations, so we suspected that their isotopic signal (if measureable) might be more noticeably enhanced by a local geospatial influence (Croll and McLaren, 1993; Gabrielsen et al., 1988; Byrd et al., 2008; Harding et al., 2014). It was therefore expected that any isotopic coupling between prey base and predator could be stronger among murres than among 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.

## 2. Methods

### 2.1. Study area

We conducted fine scale (20–100 km), simultaneous sampling of seabirds and their prey in waters within 185 km 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 encompass all habitat within 185 km to the north of Bogoslof Island (53.93°N, 168.03°W; Fig. 1). The two Pribilof islands host large seabird breeding colonies that are functionally isolated ($>350$ km to the nearest neighboring colonies) during the summer breeding season, and Bogoslof Island supports rapidly growing colonies of kittiwakes and murres (Kitaysky et al., 2000; Stephenson and Irons, 2003; Jahnke et al., 2008). Since Bogoslof and the Pribilof Island colonies
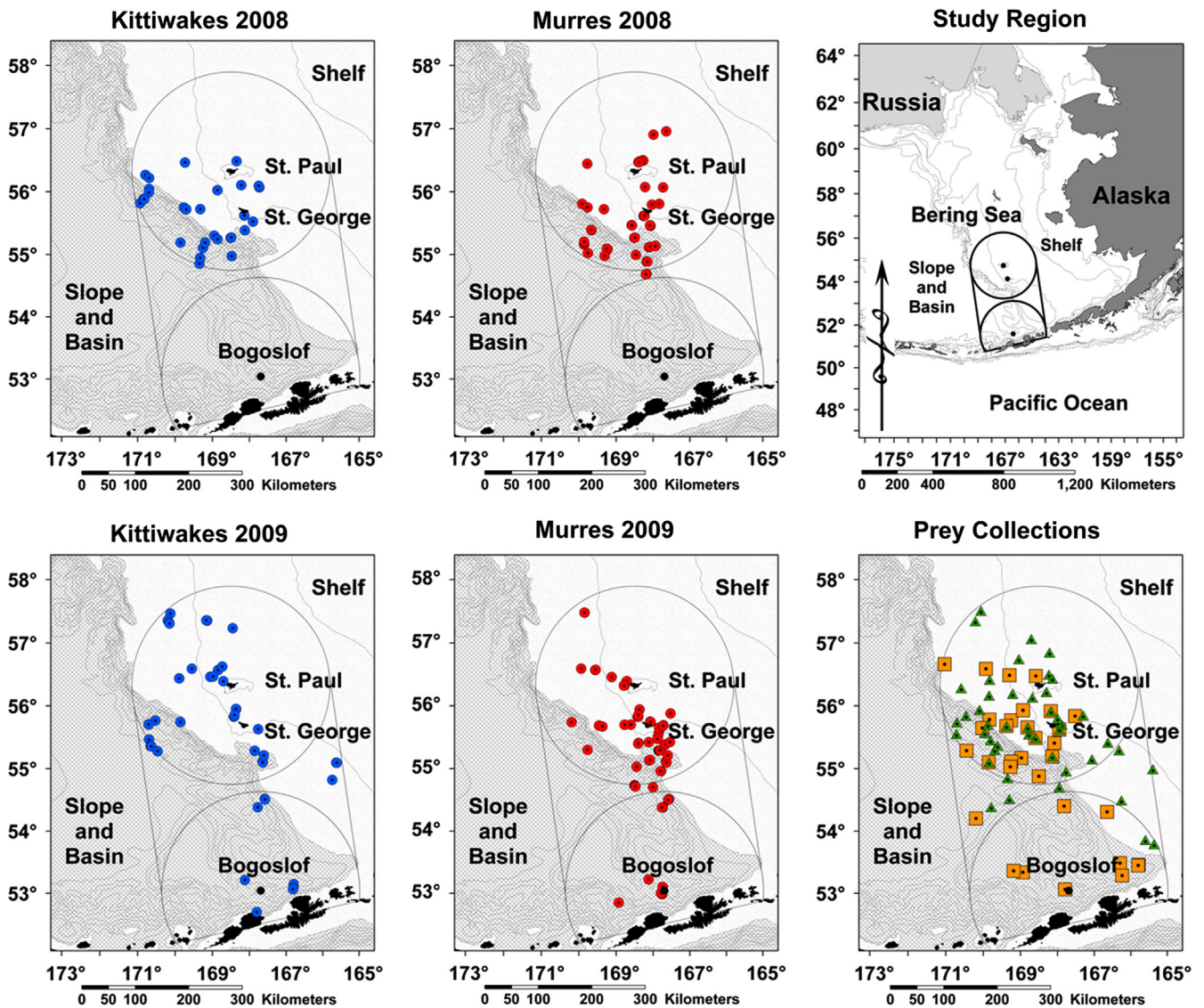
Fig. 1. Seabird, euphausiid and pollock collection locations.

are all relatively isolated, the sampling area was amenable to fine scale studies of foraging dynamics because birds collected near these islands were likely to have originated from those colonies and were using the local area specifically for foraging and breeding (Kitaysky et al., 2000; Stephenson and Irons, 2003; Byrd et al., 2008; Jahnke et al., 2008; Paredes et al., 2012; Harding et al., 2014). The portion of the North American continental shelf break encompassed by the study area is abrupt, and as such represents a discrete transition between oceanic basin and continental shelf habitats (Hunt et al., 2008). Broad scale, cross-shelf patterns in isotope baselines have been measured elsewhere, yet this environment offered an opportunity to study such phenomena on a more accessible scale than in many other ocean systems (Hunt et al., 2008; Miller et al., 2008; Jaeger et al., 2013).

## 2.2. Sample collections

### 2.2.1. Prey collections

Prey sampling was conducted at pre-determined, stratified, random 10 km transect survey (90%) locations, as well as adaptive 10 km transects (10%) that targeted prey patches discovered through acoustic measurements during the course of the study. In each location, prey specimens 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 ($-30\ ^{\circ}$C) for transport to laboratories onshore. Age-0 pollock were sampled in all cases, as well as the dominant krill species from each tow. However, prey patch compositions and locations varied throughout each year, and between years, and many net tows yielded neither krill nor pollock. Spatial coverage of intra-year krill and pollock sampling was too sparse to generate robust within-year isoscape maps. Therefore, we evaluated whether it was viable to pool samples from both years in order to achieve the greatest spatial coverage to create broadly predictive prey baselines. We were interested in looking at $\delta^{13}$C and $\delta^{15}$N individually to assess the potential of each as an independent tool in creating either $\delta^{13}$C or $\delta^{15}$N isoscapes that might be used to elucidate differences in habitat use among taxa. Data analyses indicated that $\delta^{15}$N values could be combined appropriately to create baseline $\delta^{15}$N models for prey taxa, but that $\delta^{13}$C values were not amenable. Therefore, isotope values from repeat net tow sampling at a given location were averaged to generate a single $\delta^{15}$N value for each prey type at each location. The resulting $\delta^{15}$N datasets consisted of 33 sample locations for krill and 46 locations for pollock (Fig. 1). These sampling locations were used for discrete basin–shelf $\delta^{15}$N

comparisons, and in the generation of isotopic baselines for comparisons of patterns in baselines and predator tissue values.

### 2.2.2. Seabird collection

Adult thick-billed murres and black-legged kittiwakes were collected with a shotgun as they engaged in foraging activity on the open ocean (Fig. 1). All collected birds were in breeding condition, as verified by evidence of a brood patch. We also assessed subcutaneous fat deposits and pectoral muscle condition to ascertain that all were healthy and showed no signs of nutritional stress (Baduini et al., 2006). All collection locations were associated with randomly distributed net tow sampling and strip transects being undertaken by the research vessel, and therefore a thorough stratification of sampling was achieved to include all potential habitat types, in each week of data collection, for the duration of collection activities in both years. Birds were collected at all times of day between the hours of 0300–2340 h, AKDT. We preferentially targeted foraging birds that were within 25 m range of the ship and on the water surface, rather than in flight, because foraging and on-water birds could be linked directly to simultaneous prey base measurements and could be more clearly associated with the specified collection location. Some limitations to the sampling method were obvious, as the research vessel motoring at sea traveled at speeds of only 5–9 knots, while birds foraging in surrounding waters routinely traveled at multiples of that pace. Kittiwakes, in particular, are accomplished fliers, and both species are theoretically capable of traversing the entire study area, so it was not possible to know how long a particular bird had spent at a given location when it was targeted for collection (Paredes et al., 2012). Despite these limitations, spatial patterns resulting from at-sea collections were very likely indicative of foraging activity. Specifically, whereas each bird was collected at one random point during one single foraging trip, muscle isotope values reflected that bird's foraging activity integrated over a period of weeks. Therefore, if foraging birds collected randomly throughout the study area during a 30 day period were found to be regionally similar in isotopic composition, and to correlate with prey measurements taken in close proximity, then such coherent geospatial patterns were unlikely to have resulted from chance alone. We collected no more than 3 birds from any given location (within 500 m radius of initial take). The birds were retrieved from the water using a long-handled dip net, and then frozen ($-30\,^\circ$C) immediately onboard the ship for preservation (Barrett et al., 2007; Bugoni et al., 2008). Upon return, samples of left pectoral muscle were removed for stable isotope analyses. We collected 47 murres and 39 kittiwakes in 2008, and 78 murres and 66 kittiwakes in 2009. We initially combined samples from both years by species and divided them into two groups, "basin" ($>200$ m depth), and "shelf" ($<200$ m depth), for testing based on bathymetry associated with the collection site. Subsequently, samples were grouped by species in each year to make 2008 and 2009 comparisons to isotopic baselines.

### 2.3. Stable isotope analyses

Before testing, all samples were dried at $40\,^\circ$C for 48 h, then ground into a fine powder and lipid-extracted using a methanol-chloroform mixture (Bligh and Dyer, 1959; Sotiropoulos et al., 2004; Kojadinovic et al., 2008). Seabird tissues were analyzed at the University of Alaska, Fairbanks. Fish and euphausiid tissues were analyzed at Northern Arizona University. Isotope values for $\delta^{13}$C and $\delta^{15}$N were measured with 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. Internationally-accepted isotope elemental calibration standards were used to determine accuracy (acetanilide, cyclohexanone, cystine, methionine, nicotinamide, and sulfanilamide). Secondary isotopic reference materials included NIST bovine liver, and NIST mussel, as well as NIST pine needles, and NIST tomato leaves. Calibration runs were conducted frequently to check for run drift and linearity. Blanks were analyzed every twenty samples and Secondary isotopic reference materials were analyzed every ten samples. Precision of secondary isotope reference material ($n=82$) was $<0.25$‰ for both carbon and nitrogen. Twice a year the secondary isotopic reference materials from these labs are compared to NIST standards for quality assurance. The $\delta^{13}$C and $\delta^{15}$N values are expressed relative to Vienna-Pee Dee Belemnite limestone V-PDB for carbon, and to air for nitrogen. Stable isotopes are reported here in $\delta$ notation as the deviation from standards, in parts per thousand (‰), according to the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1]$ 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).

### 2.4. Data analyses

#### 2.4.1. Measuring isotopic differences between continental shelf and deep basin habitats

Our goal in basin-shelf comparisons was to identify whether there were detectable differences in either $\delta^{13}$C or $\delta^{15}$N that might indicate the existence of a cross-shelf pattern in isotopes. Analyses of 2008 and 2009 krill and pollock $\delta^{15}$N isotopic values revealed no deviations from normality (Kolmogorov–Smirnov test), no differences in variance (Levene's test), and no statistical differences among means (Student's $t$-test, with Bonferroni corrections) between years within a given prey type, so $\delta^{15}$N data from both years were pooled for each prey taxon to create two homogeneous prey baseline $\delta^{15}$N datasets: one for krill and one for pollock. These were then used to compare basin and shelf habitats and to create $\delta^{15}$N isoscapes. Inter-year analyses (Student's $t$-test, with Bonferroni corrections) of prey $\delta^{13}$C isotope values indicated dissimilar mean values between years in both prey taxa, as well as significant differences (Levene's test) in variance among pollock samples between years. Therefore, prey $\delta^{13}$C values from 2008 and 2009 were not pooled, and we did not create a homogeneous $\delta^{13}$C baseline for comparison to seabird muscle values. Seabirds of a given species did not differ overall in $\delta^{13}$C or $\delta^{15}$N between years, so basin-shelf differences in $\delta^{13}$C and $\delta^{15}$N values in seabird muscle tissue were compared between habitat types using Student's $t$-tests (with Bonferroni corrections), because our interests lay specifically in assessing each isotope measure individually for its potential as a diagnostic tool in assessing habitat use. However, there were no overall basin-shelf differences in $\delta^{13}$C values of seabird tissues ($p > 0.5$ in both species), so further analysis focused on determining patterns of $\delta^{15}$N isotope distribution across habitats and trophic levels. We performed these statistics using the R 2.14.0 statistical computing package (R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing http://www.r-project.org).

#### 2.4.2. Spatial structure among isotope values of samples collected at sea

Given the likely muscle tissue turnover time ($\sim$48 days) in seabirds in the context of our 30 day sampling periods, we considered that significant isotope correlations between birds and prey would be indicative of 30–60 days of corresponding spatiotemporal similarities in the diet or foraging locations of the birds (Hobson and Clark, 1992). All datasets were standardized to $Z$-scores to account for the large differences in scale between

isotope values and distance measurements, and then we determined spatial structure (autocorrelation) by assessing the Moran's $I$ statistic using the statistical program R 2.14.0 (Moran, 1950; Legendre and Legendre, 1998, R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing http://www.r-project.org).

### 2.4.3. Isoscape mapping and patterns in trophic relationships among taxa

Mapping and visualization were accomplished using ArcGIS v.9.3 (ESRI Corporation, Redlands, CA). Seabird, euphausiid, and pollock sampling locations did not always directly coincide, so it was necessary to map patterns for each taxon independently and then compare them to one another. To examine basic patterns in isotopic values across the study region, we used Inverse Distance$^2$ Weighted interpolations to generate a simple contour map of each isotopic dataset ($\delta^{15}$N for tissues: krill, pollock, and seabird muscle (Fortin and Dale, 2005). Any resultant cross-shelf pattern that became evident for isotopic values of both 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 predictive isoscape surfaces by repeatedly fitting a first order polynomial through prey sampling points ($\delta^{15}$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 for krill and one for pollock, which were then used as 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, and predicted krill tissue), and enabled the comparison of measured $\delta^{15}$N values in seabird tissues to prey base $\delta^{15}$N values that were derived from the contemporaneously-sampled prey items. Pearson's correlation statistics identified a strong relationship ($r \geq 0.95$; $p < 0.001$) between krill and pollock $\delta^{15}$N baselines. Given this correlation, we focused our evaluation of the fundamental cross shelf gradient patterns using just the linear regression of krill prey baseline values on seabird $\delta^{15}$N muscle values, with the assumption that working with pollock would yield similar results. Dependent variables were seabird values, with krill baseline $\delta^{15}$N values as predictors (statistical program R 2.14.0).

## 3. Results

We measured significant differences in $\delta^{15}$N values for three of our four taxa between deep and shallow habitats during the years 2008 and 2009. Euphausiid, pollock, and murre tissues sampled in shallow, continental shelf habitat had greater $\delta^{15}$N values relative to tissues from samples taken over deeper basin habitats (Table 1). In contrast, we detected no differences in $\delta^{15}$N between habitat types for kittiwakes. There were no detectable differences in $\delta^{13}$C values of either murre or kittiwake muscle tissues sampled in 2008 and 2009, and sampling coverage was too sparse to enable robust intra-year comparisons of $\delta^{13}$C in prey species.

Spatial structure (autocorrelation) was detected among $\delta^{15}$N values of krill ($p=0.017$) and pollock ($p=0.0001$; Fig. 2), as well as murres ($p < 0.0001$ in both years; Fig. 3). Therefore, at scales of $< 100$ km, the $\delta^{15}$N values of animals collected in close proximity tended to be much more similar to one another than to $\delta^{15}$N values in animals collected at greater distances. There was no spatial structure ($p > 0.20$) in $\delta^{15}$N values of kittiwake muscle tissues in either year. Inverse Distance$^2$

**Table 1**
Differences in mean $\delta^{15}$N values of seabirds and prey collected in basin ( $> 200$ m depth) versus shelf ( $< 200$ m depth) habitats in the southeastern Bering Sea Alaska, 2008 and 2009.

| Taxon | Basin mean $\delta^{15}$N value $\pm$ SE | Shelf mean $\delta^{15}$N value $\pm$ SE | Test statistic | p-Value |
|---|---|---|---|---|
| Euphausiids | 9.4 $\pm$ 0.1 | 10.4 $\pm$ 0.1 | $T_{31}=6.79$ | **< 0.0001** |
| Pollock | 9.2 $\pm$ 0.2 | 11.2 $\pm$ 0.2 | $T_{44}=6.59$ | **< 0.0001** |
| Kittiwakes | 12.9 $\pm$ 0.1 | 13.1 $\pm$ 0.1 | $T_{103}=1.18$ | 0.1300 |
| Murres | 11.9 $\pm$ 0.1 | 12.4 $\pm$ 0.1 | $T_{123}=4.38$ | **< 0.0001** |

Samples were collected in the southeastern Bering Sea, Alaska, between July 15th–August 15th in two years: 2008 (within a 185 km radius of St. Paul Island), and 2009 (185 km radius of St. Paul Island and extending southward to within 185 km radius of Bogoslof Island). Dataset represents combined sampling effort from 2008 and 2009 after verification of statistical homogeneity (Kolmogorov–Smirnov and Levene's testing) between years. Bold indicates significance at $p < 0.0125$ after Bonferroni corrections were applied for multiple testing.

Weighted mapping of $\delta^{15}$N values in thick-billed murres and their prey yielded similar patterns at scales of $< 100$ km, suggesting fundamental differences between shallow, continental shelf habitat and deeper basin habitats. More specifically, the average $\delta^{15}$N values of the tissues of murres, krill, and pollock increased with increasing latitude (north of St. Paul Island), and decreasing depth (continental shelf; Figs. 2 and 3). Kittiwake isotope values exhibited no such spatial coherence with prey values in 2008, but demonstrated scattered clustering of like values in 2009, providing some suggestion of a basin-shelf dichotomy at least in that year (Fig. 3). 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 $\delta^{15}$N values. Krill and pollock sampled over northern, shallower shelf habitat yielded values that were 1–2‰ greater than samples taken over deeper basin habitats to the south, at distances of only 20–100 km (Fig. 2), and predicted values of krill and pollock at seabird collection locations were highly correlated with one another in both years ($r \geq 0.95$, $p \leq 0.0001$), indicating a utility in choosing krill specifically to represent the prey base in subsequent testing (Table 2). Kittiwake muscle $\delta^{15}$N values did not track krill and pollock $\delta^{15}$N in 2008, however, in 2009 there were some average enrichment patterns across the study area, and weakly significant relationships between 2009 kittiwake muscle values and those of krill baselines, although the prey base values had virtually no predictive influence ($r^2 < 0.06$; Fig. 4, Table 2). In contrast, murre muscle $\delta^{15}$N values tracked krill and pollock $\delta^{15}$N more closely in both years, demonstrating more consistency among average $^{15}$N enrichment trends throughout the study area (Fig. 4, Table 2). Krill baseline values predicted 35–42% of the $\delta^{15}$N variability in murre muscle tissues (Table 2). These results reflected the concordance of spatial structure in $\delta^{15}$N values of krill, pollock, and murre muscle tissue in both years; the Inverse Distance$^2$ Weighted maps and the regression plots demonstrated an increasing, basin-shelf trend in $\delta^{15}$N values of murre tissues and their prey, with the greatest enrichment occurring N-NW of St. Paul Island over shallow shelf waters (Fig. 3). Relationships between kittiwakes and the prey base measures were less coherent.

## 4. Discussion

Isotope values in murre and kittiwake pectoral muscle tissue represent a diet integrated over approximately 40–50 days, and our sampling periods were each $\sim 30$ days during the breeding seasons of 2008 and 2009 (Hobson and Clark, 1992; Bearhop et al., 2002; Cherel et al., 2005). Therefore, the degree of spatial structure (significance of Moran's $I$ statistic), coupled with the
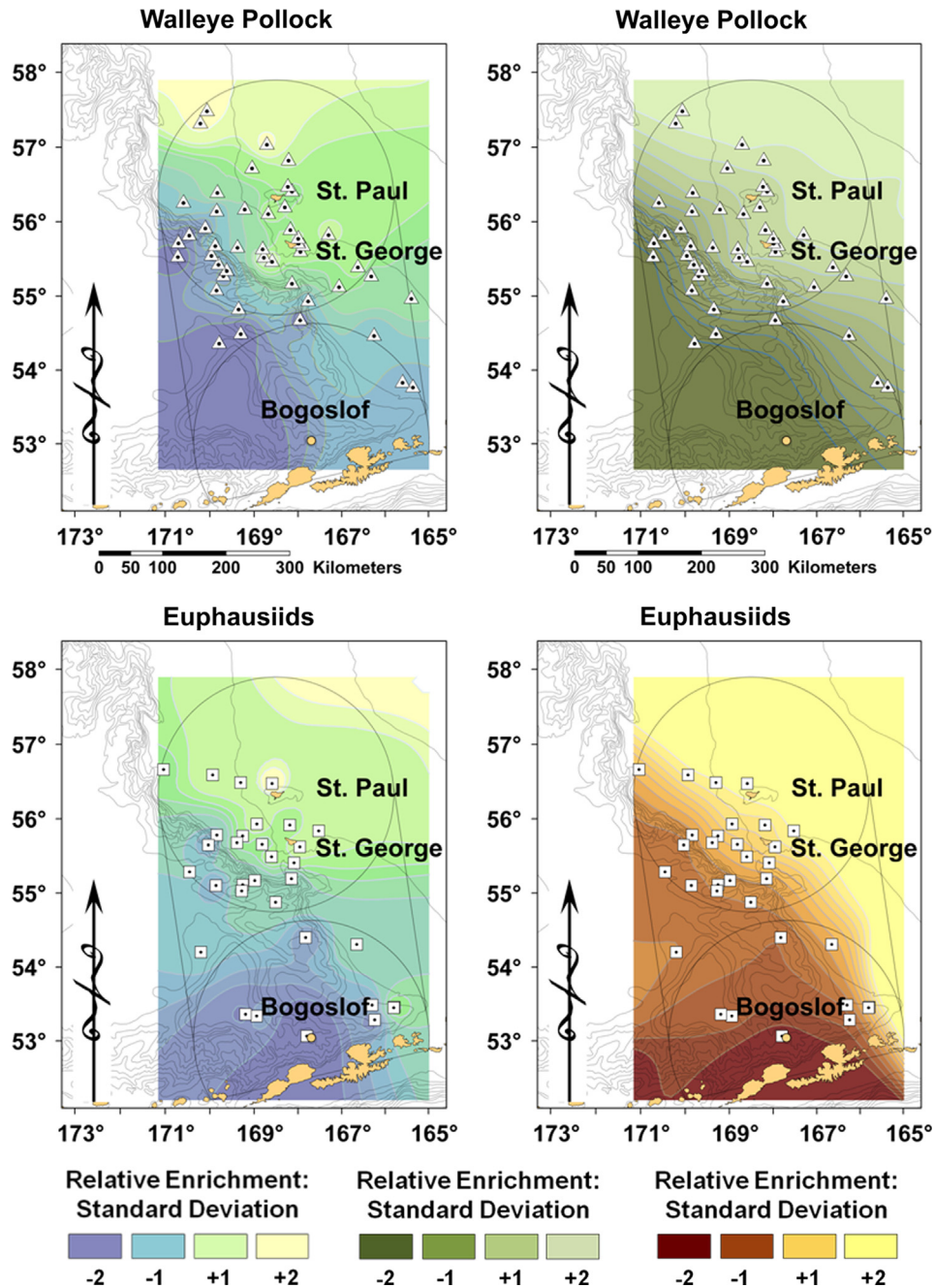
**Fig. 2.** Spatial autocorrelation patterns and predictive isoscape modeling of $\delta^{15}N$ values of seabird prey tissues.

strength of prey–predator linkage (magnitude and significance of regression $r^2$), could represent the degree to which birds foraged repeatedly in a given area during a given breeding season. Nitrogen values in murre muscle tissues yielded highly significant spatial structure in both years, and regression results indicated that prey baselines and murre tissue $\delta^{15}N$ values were spatially coupled throughout the entire sampling region in both years. This implied regional specificity, as well as intra-seasonal and inter-annual consistency, in murre choice of foraging areas during their breeding period. Patterns among kittiwake tissues were much less coherent. Differences in isotope patterns between the two bird species could reflect, in part, the physiological and morphological adaptations that accommodate the contrasting foraging strategies of pursuit-divers (murres) and plunging surface-feeders (kittiwakes).

Pursuit-diving murres have greater caloric needs (field metabolic rates) than surface-feeding kittiwakes (Gabrielsen et al.,

1988; 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 greater resistance to movement), 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. Our results are consistent with the hypothesis that greater flight costs for murres should require them to be more selective or consistent in their foraging effort in specific areas, returning repeatedly to locations where prey species were previously encountered with greater frequency or in greater abundance or density (Paredes et al., 2012; Harding et al., 2014). In doing so they should acquire a more distinct isotopic signal related to isotope values of prey items eaten in the locations in which they foraged. Other studies in the Bering Sea have indicated that sub-surface foragers such as murres may require prey patches of
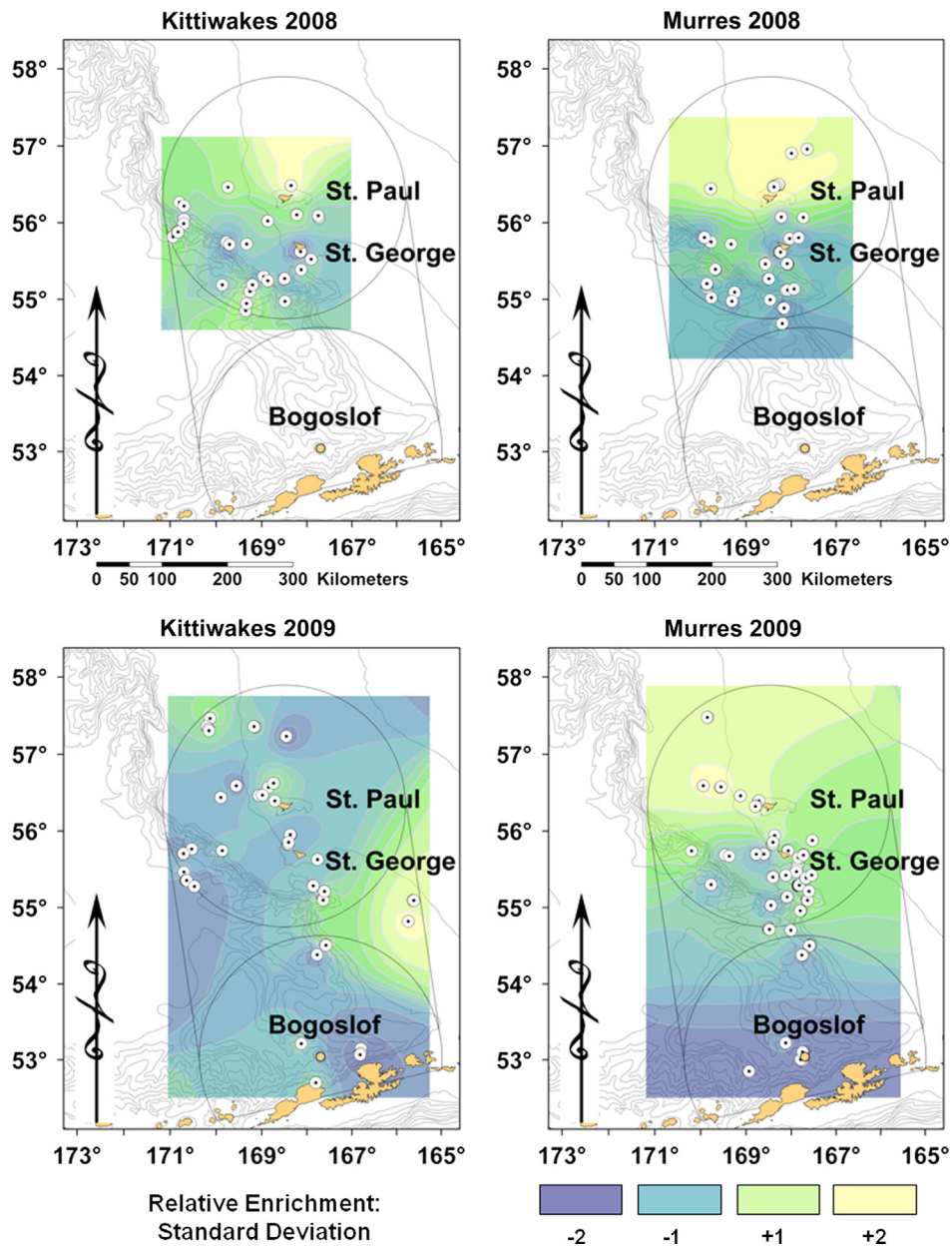
**Fig. 3.** Patterns in spatial autocorrelation of $\delta^{15}N$ values in seabird muscle tissues.

**Table 2**

Regression of $\delta^{15}N$ values in seabird liver and muscle tissues with those of predicted euphausiids (krill: *Thysanoessa* spp.) baseline tissues.

| Seabird species | Year | Seabird tissue | $\beta$ | $t$ | $R^2$ | $F$ | $p$ |
|---|---|---|---|---|---|---|---|
| Black-legged kittiwake | 2008 | Muscle | 0.06 | $t_{37}=0.27$ | 0.00 | $F_{1,37}=0.07$ | 0.7910 |
| Black-legged kittiwake | 2009 | Muscle | 0.29 | $t_{64}=2.09$ | 0.06 | $F_{1,64}=4.36$ | 0.0410 |
| Thick-billed murre | 2008 | Muscle | 0.55 | $t_{45}=5.71$ | 0.42 | $F_{1,45}=32.63$ | **0.0001** |
| Thick-billed murre | 2009 | Muscle | 0.64 | $t_{76}=6.34$ | 0.35 | $F_{1,76}=40.22$ | **0.0001** |

Samples were collected in an area within a 185 km radius of St. Paul Island and extending southward to within 185 km radius of Bogoslof Island in the Bering Sea, July 15th–August 15th, 2008 and 2009. Krill values were chosen to represent the prey base, and were also strongly correlated (Pearson's $r \geq 0.95$; $p < 0.0001$) to pollock values. Krill values were obtained for each seabird sampling location from isoscape maps generated through Local Polynomial Interpolation (ArcGIS 9.3) of $\delta^{15}N$ values measured in actual prey items sampled concurrently from randomly placed net tows throughout the study area. Bold indicates significance at $p < 0.0125$ after Bonferroni corrections were applied for multiple testing. The regression coefficients and significance levels indicate stronger coupling between murre and prey base values throughout the area.

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 regression results in the $\delta^{15}N$ values of kittiwakes were much weaker, which

suggests that individual kittiwakes perhaps foraged more widely across the study region, and more frequently consumed prey from both shelf and basin habitats. Indeed, a recent broad scale study comparing persistent hotspots for the murres and kittiwakes in the Bering Sea came to similar conclusions, and a concurrent study
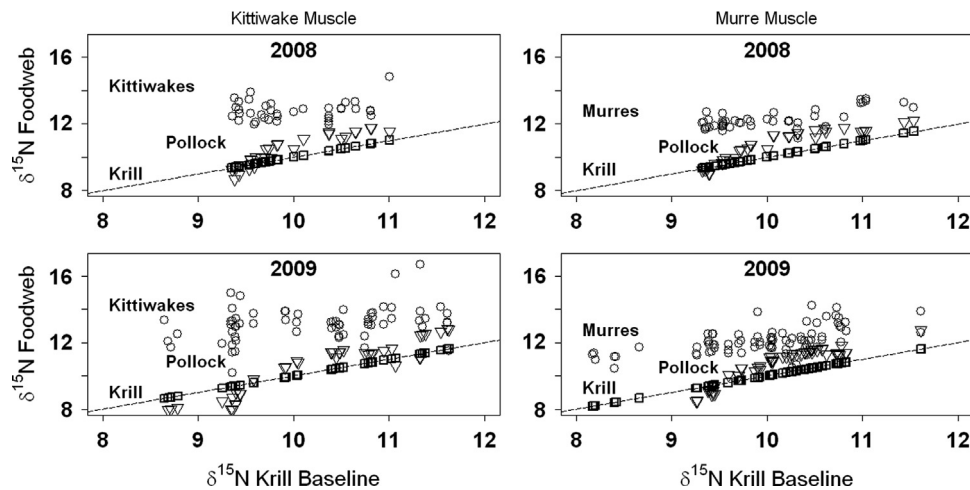
**Fig. 4.** Comparisons of $\delta^{15}N$ values in seabird muscle tissue and two measures of their prey base.

using tagged individual birds also found that kittiwakes foraged more widely across the eastern Bering Sea shelf (Paredes et al., 2012; Sigler et al., 2012).

There are other possible explanations for the lack of coherent isotope patterns among kittiwakes. Kittiwakes in the Gulf of Alaska and Bering Sea differ somewhat from thick-billed murres in their diet, and often consume larger proportions of myctophid fishes, the isotopic values of which might differ substantially from that of pollock (Sinclair et al., 2008; Renner et al., 2012). Mycto-phids are mesopelagic fishes and vertical migrators that inhabit deep water during the day, and may typically be under-represented in survey trawls due to trawl avoidance behavior (Catul et al., 2011; Kaartvedt et al., 2012). Myctophids were infrequently collected during our sampling trawls, and the poten-tial spatiotemporal mismatches between kittiwake foraging pat-terns, myctophid abundance and trawling effort made it difficult to assess the relationship of $\delta^{15}N$ in myctophid and kittiwake tissues. However, although our sampling yielded insufficient numbers of myctophids for isotope analyses, pollock nonetheless have been shown to constitute a consistent and important component of kittiwake diet in most years, and are commonly used as diagnostic tools in multi-year diet studies of predators in the Bering Sea (Sinclair et al., 2008; Renner et al., 2012). It is also likely there are differences in species composition among euphausiid commu-nities between shelf and basin environments, although species-specific differences in isotopic values have not been thoroughly examined to date. Therefore, a greater breadth in foraging loca-tions across the shelf break, coupled with differences in diet, could result in a more variable or diluted isotopic signal in kittiwake tissues, and weaker coupling to krill or pollock specifically.

The geospatial stratification of murre isotope values coincided in latitude with the three focal colonies (St. Paul, St. George, and Bogoslof). This suggests that the foraging habitat partitioning of individual tagged birds, measured by Harding et al. (2014) during the same time period, was likely representative of a much broader pattern. It could be expected that isotopes might identify a distinct foraging pattern for murres near Bogoslof, given its isolation from the Pribilof colonies. However, patterns in isotope values of murres collected within the Pribilof region also indicated the likelihood of con-specific habitat partitioning by colony, despite the close proximity ( < 75 km) of St. Paul to St. George. This suggests that these pursuit-diving seabirds might somehow be more closely linked to local patterns in resource availability than the wide-ranging, surface-feeding kittiwakes. Intra-specific habitat parti-tioning in the open ocean has been infrequently described in seabirds, however foraging site fidelity was inferred through

analyses of stomach contents and stable isotope values in short-tailed shearwaters (*Puffinus tenuirostris*). The shearwaters were collected while foraging in several locations throughout Bristol Bay and the Eastern Bering Sea, and stable isotope values of organs indicated that groups of shearwaters were likely feeding for multiple weeks at a time in discrete locations, even though they were theoretically capable of foraging freely across a wide seascape while not breeding on a colony (Baduini et al., 2006). Elsewhere, Gremillet et al. (2004) demonstrated that foraging areas of cape gannets (*Morus capensis*) from two neighboring colonies overlapped very little, even though the two study colonies were well within (65–85%) the theoretical foraging range of one another, and Wiley et al. (2012) inferred habitat partitioning between two colonies of Hawaiian petrels (*Pterodroma sandwichensis*) in the Hawaiian Islands. Thus, it appears that habitat partitioning among con-specific marine birds may become an influential force affecting the delineation of a seasonal isotopic niche, the nature of which could be influenced by variations in habitat use as well as by differences in diet, although the relative importance of these two elements can be difficult to discern (Baduini et al., 2006; Newsome et al., 2007; Wiley et al., 2012).

Traditionally, $\delta^{13}C$ has been used as a diagnostic marker to infer latitudinal patterns in habitat use and distinguish between shal-low, continental shelf and deep water, pelagic foraging areas, but in this study we found that $\delta^{15}N$ was also very useful in delineat-ing predator habitat use, and at a fine scale (Hobson et al., 1994; Sydeman et al., 1997). For example, murres sampled over deep ( > 1000 m) Pribilof Canyon habitat were relatively depleted in $^{15}N$ compared to murres sampled just 25–75 km away over continen-tal shelf habitat ( < 200 m depth) near St. Paul. On broader spatial scales, Forero et al. (2004) suggested isotope values of seabirds breeding along the Chubut coast of Argentine Patagonia reflected an enriched-depleted $\delta^{15}N$ cross-shelf gradient, Phillips et al. (2009) determined that stable nitrogen isotopes were useful markers for distinguishing wintering and pre-breeding habitat use by high latitude Atlantic procellariids, and Wiley et al. (2012) inferred habitat use of shearwaters in the central Pacific based on broad scale patterns in baseline $\delta^{15}N$ levels. We did not detect basin–shelf differences in $\delta^{13}C$ for either seabird species at the scale of our study, but Schell et al. (1998) detected a clear broad scale, cross-shelf pattern in $\delta^{13}C$ among copepods and krill. It is possible that a greater sampling effort, across a larger geographic area, would detect a similar cross-shelf pattern in $\delta^{13}C$ of our study species.

Isotope gradients in the Bering Sea appear to be persistent in time. The differences in basin/shelf $\delta^{15}N$ we measured for krill, pollock, and murres were similar in magnitude and spatial pattern to those measured by Schell et al. (1998) in copepods and

euphausiids in 1985–1995, and during our study we found no inter-annual differences in $\delta^{15}$N isotope values within a given prey taxon. This corroborates assertions by some researchers that the measurement of isotope values in 1° and 2° 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 we found in murres and their prey have been measured elsewhere in other northern hemisphere systems that are characterized by seasonally well-mixed, shallow waters abutting abrupt shelf break and deep pelagic habitat (Bode and Alvarez-Ossorio, 2004; Miller et al., 2008; Olson et al., 2010). Recent food web modeling and meta analyses conducted for southern hemisphere marine communities have suggested that baseline signals could be transmitted upwards through the marine food web, manifesting in similar trends in $\delta^{13}$C and $\delta^{15}$N values of crustaceans and seabirds (Quillfeldt et al., 2005). Our results offer an empirical confirmation at fine scales through the simultaneous sampling of seabirds and their prey.

It is important to strive for an accurate understanding of baseline isotope values when applying stable isotope analyses in food web studies. Our results demonstrate that variations in baseline signals among habitats can propagate upward through food webs and affect multiple trophic levels. If regional variation is not accounted for, it can present potentially significant sources of error in estimates of predator diet composition and trophic level (Wiley et al., 2012; Solomon et al., 2008; Flaherty and Ben-David, 2010). In seabirds this phenomenon was also 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 $\delta^{15}$N values of baseline mussel tissues between two study systems. Likewise, in the Bering Sea we found significant SW/NE, basin/shelf differences of approximately 2.0‰ in $\delta^{15}$N values of age-0 pollock tissues, and approximately 1.0‰ in krill tissues, which represent sizeable sources of variation in trophic estimates, when considering that the average difference in $\delta^{15}$N between an avian consumer and its prey in marine food webs is approximately 3.2‰ (Kelly, 2000).

Previous Bering Sea stable isotope research has successfully identified the long-distance migration routes and broad foraging habitats of fur seals (Kurle and Worthy, 2002), bowhead whales (Lee et al., 2005), and king eiders (Oppel and Powell, 2008). The habitat assignments of those studies were most successful at ecoregional scales (1000's km), whereas habitat studies based on isotopic signals at finer scales ($< 100$ km) elsewhere have met with somewhat more mixed results (Szymanski et al., 2007). Our use of isoscapes to infer habitat use at fine scale was most informative when applied to murres, a species whose geospatial foraging patterns were more likely than kittiwakes to be constrained by physiological as well as ecological demands (for example, adaptations for pursuit diving, and obligate central place foraging during breeding). We were less successful at detecting an isotopic gradient in kittiwakes, a more wide-ranging predator species, and this lack of fine scale isotopic patterns may be more common in species with less spatially-constrained foraging behaviors. Nonetheless our study, which clearly demarcated a cross-shelf $\delta^{15}$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.

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