

Extending an indicator: year-round information on seabird trophic ecology from multiple-tissue stable-isotope analyses

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ABSTRACT: Stable isotope analysis of tissues of seabirds and their prey has proven to be an extremely useful tool in seabird dietary studies in general and in the potential use of seabirds as ecological indicators in particular. The measurement of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values is important since they provide information on source of feeding and trophic position, respectively. However, the stable isotope approach provides information on spatial and trophic ecology of seabirds during a window of temporal integration that depends on the elemental turnover rate in the tissue being measured. Most researchers have relied on only 1 or 2 tissue types to study seabird diets and foraging ecology. Here, the potential for modeling trophic position and habitat use by seabirds over the annual cycle is demonstrated by using multiple tissues from the same individual. Isotopic measurements of bone collagen provide information integrated over the lifetime of the individual and those of feathers during the post-breeding molt period. Analysis of liver provides information integrated over the previous week and that of muscle integrated over a few months. We developed multi-tissue trophic models for thick-billed murre *Uria lomvia*, dovekie *Alle alle*, black guillemot *Cepphus grylle*, glaucous gull *Larus hyperboreus*, northern fulmar *Fulmarus glacialis*, black-legged kittiwake *Rissa tridactyla*, and ivory gull *Pagophila eburnea* using the Northwater Polynya in Northern Baffin Bay, 1998 to 1999. The careful application of stable isotope methods to a spectrum of tissue types represents a powerful means of extending our ability to investigate diet and potentially to use seabirds as ecological indicators.

KEY WORDS: Stable isotopes · Carbon-13 · Nitrogen-15 · Seabirds · Temporal integration

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INTRODUCTION

The study of seabird feeding ecology in temperate and polar regions can reveal a great deal of information about the relative abundance and dynamics of marine prey, from herbivorous invertebrates to piscivorous fish and squid (Cairns 1987, Furness & Camphuysen 1997, Barrett 2002, Piatt et al. 2007a). As such, a great deal of interest has emerged over the last few decades in using seabirds as indicators of the

health of marine ecosystems (Diamond & Devlin 2003, Burger & Gochfeld 2004, Frederiksen et al. 2007, Montevecchi 2007, Piatt et al. 2007a, Durant et al. 2009), as well as the prevalence and biomagnification of contaminants (Jarman et al. 1996, Fisk et al. 2001, Braune et al. 2002). However, despite compelling reasons to investigate seabird diets, researchers face extraordinary challenges in obtaining even simple baseline data, especially outside the breeding season when birds are much less accessible.

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Stable isotope methods have been developed to study seabird trophic interactions (Hobson 1987, Hobson & Welch 1992a, Hobson et al. 1994), and their application to consumers in the marine environment is now widely established. The essential advantage of the technique is that dietary or trophic information can be inferred based on the single isotopic measurement of an individual's tissue. When combined with conventional dietary techniques such as direct observation and stomach sampling and, more recently, with the measurement of fatty acids, the isotope technique can be a powerful and effective tool (Gilmour et al. 1995, Smith et al. 1996, Hooker et al. 2001, Dahl et al. 2003, Barrett et al. 2007, Karnovsky et al. 2012). Importantly, because different tissues reflect dietary integrations over different time periods, the sampling of several tissue types from the same individual can provide a time series analysis of dietary change. Hobson (1993) demonstrated this approach by modeling seabird trophic level based on bone collagen, muscle, and liver samples from 5 species of seabirds breeding in the Canadian high Arctic and so established long-term (i.e. years), intermediate (months), and short-term (days) dietary information, respectively. Many researchers have combined the analysis of non-destructive samples (e.g. feathers, red blood cells, blood plasma, claws), which only reflect short-term (days to weeks) foraging patterns (Hobson & Clark 1992a,b). Few researchers have combined the analysis of several tissue types with varying integration periods from individual seabirds in order to reconstruct foraging patterns over at least an annual cycle.

In this paper, the power of isotopic analysis of multiple tissue types to infer seasonal dynamics of trophic level and source of feeding (i.e. use of productive inshore versus less productive offshore food webs and geographically diverse marine systems) is emphasized by providing the example of a multiple-tissue stable isotope analysis of 7 diverse species of seabirds using the Northwater Polynya between northern Canada and Greenland. The Northwater is the largest and most productive Arctic polynya, or seasonally ice-free body of water (Hobson et al. 2002). Each year, millions of seabirds migrate to the polynya to feed in its waters and to breed along its shores. Isotopic measurements of bone collagen provide information integrated over the previous months to years (Hobson & Clark 1992a) and those of feathers during the post-breeding molt period. Analysis of liver tissue provides information integrated over the previous week and that of muscle for a few months depending on body mass (Hobson & Clark 1992a).

Dovekies *Alle alle* breed in large numbers along the western coast of Greenland adjacent to the Northwater. These small subsurface feeders dive up to 35 m (Falk et al. 2000) and molt all of their primary flight feathers (hereafter 'primaries') after breeding (Stempniewicz 2001). Black guillemots *Cephus grylle* are intermediate-sized diving alcids that feed on ice-associated invertebrates early in the breeding season and on benthic fish during breeding (Bradstreet & Brown 1985, Byers et al. 2010), and replace their primaries following breeding (Ewins 1988). Thick-billed murres *Uria lomvia* are large subsurface divers that regularly reach depths over 70 m (Falk et al. 2002), and like dovekies, they replace all primaries at once following breeding in November/December (Huettmann & Diamond 2000). Black-legged kittiwakes *Rissa tridactyla* and northern fulmars *Fulmarus glacialis* are surface feeders that also make shallow dives (Burt 1974, Hobson & Welch 1992b, Garthe & Furness 2001). Fulmars replace primaries in July/August following breeding (Huettmann & Diamond 2000, Allard et al. 2008), and kittiwakes molt their outer primaries after the breeding season in August/September (Meissner 2002). Ivory gulls *Pagophila eburnea* are listed as endangered in Canada, are declining (Gilchrist & Mallory 2005), and are of interest due to their broad diet of fish and invertebrates and seasonal habit of scavenging marine mammal carcasses (Renaud & McLaren 1982). Ivory gulls' outer primaries are replaced in August/September (Howell 2001). Glaucous gulls *Larus hyperboreus* are high trophic-level feeders during the breeding season, when they may consume eggs and young of other seabirds (Gilchrist et al. 1998). They replace their outermost primaries after breeding (Ingolfsson 1970). These 7 species represent the vast majority of seabirds utilizing the food web in the Northwater Polynya and encompass a broad diversity of feeding guilds.

The objectives of this study were to (1) demonstrate the utility of a multiple-tissue isotope approach to seabird dietary studies by constructing time-integrated models of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in tissues of seabirds foraging in the Northwater Polynya, and (2) investigate annual community foraging dynamics in the Arctic. This was part of a larger study designed to investigate the importance of the polynya to seabirds and marine mammals and to investigate the role of seabirds in the flux and trophodynamics of nutrients and contaminants and their potential as ecological indicators (Hobson et al. 2002, Karnovsky & Hunt 2002).

MATERIALS AND METHODS

Field collections

As part of a larger study (Hobson et al. 2002), seabirds were collected (under a permit from the Canadian Wildlife Service) at sea throughout the Northwater Polynya by shooting. Birds were sexed by dissection after tissue sampling. Bird collections were made from a zodiac deployed from the CCGS 'Pierre Radisson' in May to July 1998 and August to September 1999. Due to the timing of research cruises, more than a full year passed between summer and fall collections.

Stable isotope analysis

Immediately after collection, small subsamples (~1 g) of muscle and liver and 3 to 5 g of bone (humerus) and the outer 8th or 9th primary feather were collected from birds and frozen. Methods followed those described by Hobson et al. (2002). In the laboratory, muscle and liver tissue samples were thawed, washed in distilled water, freeze dried, powdered, and treated with a 2:1 chloroform:methanol solution to remove lipids (Bligh & Dyer 1959, Kojadinovic et al. 2008b). Samples were then dried under a fume hood. Feathers were cleaned of surface oils using a 2:1 chloroform:methanol solution (Kojadinovic et al. 2008b) and dried under a fume hood, and then a small piece of the distal portion of the vane was used for isotope analysis. Bone samples with marrow removed were similarly cleaned in the solvent solution and dried. This material was then ground to a fine powder, and collagen was extracted according to procedures described by Hobson & Montevecchi (1991).

Stable carbon and nitrogen isotope assays were performed on 1 mg subsamples of homogenized materials by loading into tin cups and combusting at 1200°C in a Robo-Prep elemental analyzer. Resultant CO₂ and N₂ gases were then analyzed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer, with every 5 unknowns separated by 2 laboratory standards. Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = \{(R_{\text{sample}}/R_{\text{standard}}) - 1\} \quad (1)$$

where X is ¹³C or ¹⁵N and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N. Isotopic reference materials were

Vienna Pee Dee Belemnite for ¹³C and atmospheric N₂ for ¹⁵N measurements. Replicate measurements of biologically relevant internal laboratory standards (albumen and whale baleen) indicated measurement errors of ±0.1‰ and ±0.3‰ for ¹³C and ¹⁵N measurements, respectively.

Trophic models and correcting for isotopic discrimination

Consumer ¹⁵N depends not only on trophic position, but also on tissue- and species-specific discrimination factors (Caut et al. 2009). To compare trophic level (TL) based on isotopic measurement of different tissues, we used the following tissue-specific equation as described by Hobson et al. (1994):

$$TL_x = 3 + (\delta^{15}N_{tx} - \Delta d_{tx} - \delta^{15}N_C)/3.8 \quad (2)$$

where $\delta^{15}N_{tx}$ is the stable nitrogen isotope ratio of bird tissue x and $\delta^{15}N_C$ is the average value for *Calanus hyperboreus*, a dominant herbivorous copepod in the Northwater with an assumed TL of 2.0. We used an average value of +7.9‰ for the ¹⁵N value for *C. hyperboreus* collected at the same time as our samples (Hobson et al. 2002). We used the following diet-tissue discrimination factors for d_{tx} based on Mizutani et al. (1991, 1992): muscle (+2.4‰), liver (+2.3‰), feather (+4.4‰), and bone collagen (+3.9‰). We assumed the average trophic enrichment factor for Arctic food webs to be +3.8‰ (Hobson & Welch 1992a).

Since isotopic discrimination values between diet and various tissues in animals vary by tissue type, in order to compare seabird ¹³C values for different tissues, we first applied discrimination values to seabird tissue ¹³C values in order to derive expected prey ¹³C values. Again, based on Mizutani et al. (1991, 1992), we subtracted the following discrimination values from tissue values: muscle (+2.1‰), liver (+1.3‰), feather (+3.3‰), and bone collagen (+2.5‰). Data from seabird muscle were presented by Hobson et al. (2002), and data from ivory gull tissues by Karnovsky et al. (2009).

Statistical analysis

We analyzed TL and ¹³C by period (tissue) and sex using a multivariate analysis of variance (MANOVA) for each species in SPSS 19 (IBM). When MANOVA results were significant as determined by Wilks' λ , we used univariate ANOVAs with Ryan's Q post hoc

test to examine differences among periods (Ryan 1959, 1960, Day & Quinn 1989). Ryan's *Q* gives *p* values (p_Q) of group similarity, where identical members of a group have $p = 1.0$, so we report $1 - p_Q$. Because prey-tissue discrimination factors are species-specific (Caut et al. 2009), and are not known for any of the seabirds examined here (Bond & Jones 2009), we did not test for differences in prey $\delta^{13}C$ or TL among species.

RESULTS

All species differed in TL and/or prey $\delta^{13}C$ by period (Wilks' λ , all $p < 0.001$); black guillemots, northern fulmars, and glaucous gulls differed by sex; the sex \times period interaction was significant only in black guillemots (Table 1, Figs. 1 & 2). Stable isotope values ($\delta^{15}N$, $\delta^{13}C$) for the 7 seabird species are presented in Appendix 1.

Dovekie

For the dovekie, there were no effects of sex on either prey $\delta^{13}C$ or TL (Wilks' $\lambda = 0.988$, $p = 0.29$), and the sex \times period interaction was not significant (Wilks' $\lambda = 0.996$, $p = 0.99$). TL differed by period ($F_{3,212} = 91.21$, $p < 0.001$), was highest in winter (Ryan's *Q*, $p < 0.001$), lowest in summer ($p < 0.001$), and intermediate during breeding and annually ($p = 0.84$). Prey $\delta^{13}C$ differed by period ($F_{3,212} = 8.51$, $p < 0.001$), was highest in annual measurements ($p < 0.001$), but did not differ among summer, breeding, and winter ($p = 0.94$).

Black guillemot

For the black guillemot, sex (Wilks' $\lambda = 0.812$, $p = 0.005$), period (Wilks' $\lambda = 0.304$, $p < 0.001$), and the sex \times period interaction (Wilks' $\lambda = 0.655$, $p = 0.001$) were significant overall. TL differed by period ($F_{1,51} = 14.685$, $p < 0.001$), but not by sex ($F_{1,51} = 0.968$, $p = 0.33$), and the sex \times period interaction was not significant ($F_{3,51} = 0.071$, $p = 0.11$). TL was highest during breeding ($p < 0.001$), and lower during the summer, winter, and annually ($p = 0.94$). Prey $\delta^{13}C$ was different between sexes ($F_{1,51} = 6.541$, $p = 0.014$) and among periods ($F_{1,51} = 8.880$, $p < 0.001$), and the sex \times period interaction was significant ($F_{3,51} = 5.129$, $p = 0.004$), so we examined differences within each sex using ANOVA. There was no significant difference in

Table 1. Derived trophic level and prey $\delta^{13}C$ for 7 seabirds breeding in the North Water Polynya in 1998 and 1999 based on tissue $\delta^{13}C$ and $\delta^{15}N$ measurements. Integration times (tissues) are: annual (bone collagen), winter (feather), chick-rearing (liver), and summer (muscle). Data are presented as mean \pm SD (n), in parts per thousand (‰). Periods within each sex that share the same superscript are not significantly different based on Ryan's *Q* post hoc tests. M: male, F: female

Species	Sex	Trophic level			Prey $\delta^{13}C$		
		Annual	Winter	Summer	Annual	Winter	Summer
Black guillemot	M	4.28 \pm 0.24 ^a (4)	4.38 \pm 0.21 ^a (5)	4.25 \pm 0.19 ^a (14)	-21.4 \pm 1.7 ^b (5)	-21.0 \pm 0.5 ^b (5)	-21.9 \pm 0.4 ^a (5)
	F	4.48 \pm 0.14 ^{bc} (5)	4.26 \pm 0.20 ^{ab} (5)	4.13 \pm 0.21 ^a (15)	-21.1 \pm 0.3 ^a (5)	-22.2 \pm 1.4 ^a (5)	-22.2 \pm 0.3 ^a (5)
Thick-billed murre	M	4.15 \pm 0.22 ^b (5)	3.91 \pm 0.09 ^a (5)	3.93 \pm 0.17 ^{ab} (21)	-21.1 \pm 1.0 ^b (5)	-20.7 \pm 0.6 ^b (5)	-21.7 \pm 0.5 ^a (5)
	F	4.09 \pm 0.12 ^b (5)	3.86 \pm 0.09 ^a (5)	4.03 \pm 0.15 ^{ab} (41)	-20.8 \pm 0.4 ^b (5)	-21.0 \pm 0.8 ^b (5)	-22.2 \pm 0.3 ^a (5)
Dovekie	M	3.46 \pm 0.35 ^b (5)	3.83 \pm 0.11 ^c (5)	3.28 \pm 0.13 ^a (64)	-21.4 \pm 0.8 ^b (5)	-22.5 \pm 0.8 ^a (5)	-22.1 \pm 0.4 ^a (39)
	F	3.42 \pm 0.20 ^b (5)	3.76 \pm 0.11 ^c (5)	3.25 \pm 0.16 ^a (56)	-21.7 \pm 0.6 ^b (5)	-22.7 \pm 1.2 ^a (5)	-22.2 \pm 0.1 ^a (36)
Black-legged kittiwake	M	4.24 \pm 0.29 ^c (6)	3.53 \pm 0.20 ^a (6)	3.94 \pm 0.22 ^b (15)	-20.5 \pm 0.3 ^c (6)	-22.9 \pm 2.4 ^a (6)	-22.1 \pm 0.2 ^{ab} (6)
	F	4.24 \pm 0.29 ^c (5)	3.34 \pm 0.11 ^a (5)	3.86 \pm 0.17 ^b (10)	-21.6 \pm 1.0 ^c (5)	-22.4 \pm 0.8 ^a (5)	-22.1 \pm 0.4 ^{ab} (5)
Northern fulmar	M	4.30 \pm 0.27 ^c (4)	3.57 \pm 0.17 ^a (4)	4.06 \pm 0.12 ^b (10)	-20.6 \pm 0.8 ^c (4)	-21.8 \pm 0.5 ^b (4)	-22.2 \pm 0.3 ^a (4)
	F	4.41 \pm 0.17 ^c (5)	3.77 \pm 0.22 ^a (5)	3.93 \pm 0.14 ^b (9)	-19.7 \pm 0.9 ^c (5)	-21.3 \pm 0.6 ^b (5)	-22.1 \pm 0.3 ^a (5)
Glaucous gull	M	4.83 \pm 0.25 ^b (5)	4.63 \pm 0.22 ^a (4)	4.79 ^{ab} (1)	-18.9 \pm 0.4 ^b (4)	-20.5 \pm 0.2 ^a (4)	-20.9 \pm 0.5 ^a (4)
	F	4.75 \pm 0.18 ^b (5)	3.30 \pm 0.41 ^a (5)	4.62 \pm 0.21 ^{ab} (4)	-19.4 \pm 0.7 ^b (5)	-20.9 \pm 0.9 ^a (5)	-21.7 \pm 0.4 ^a (5)
Ivory gull	M	-	3.67 ^{ab} (1)	4.46 ^{bc} (1)	-	-20.7 ^{ab} (1)	-21.8 ^a (1)
	F	4.82 \pm 0.10 ^c (3)	4.29 \pm 0.88 ^{ab} (2)	4.09 \pm 0.15 ^a (3)	-20.1 \pm 0.8 ^b (3)	-21.0 \pm 0.3 ^{ab} (2)	-21.8 \pm 0.1 ^a (3)

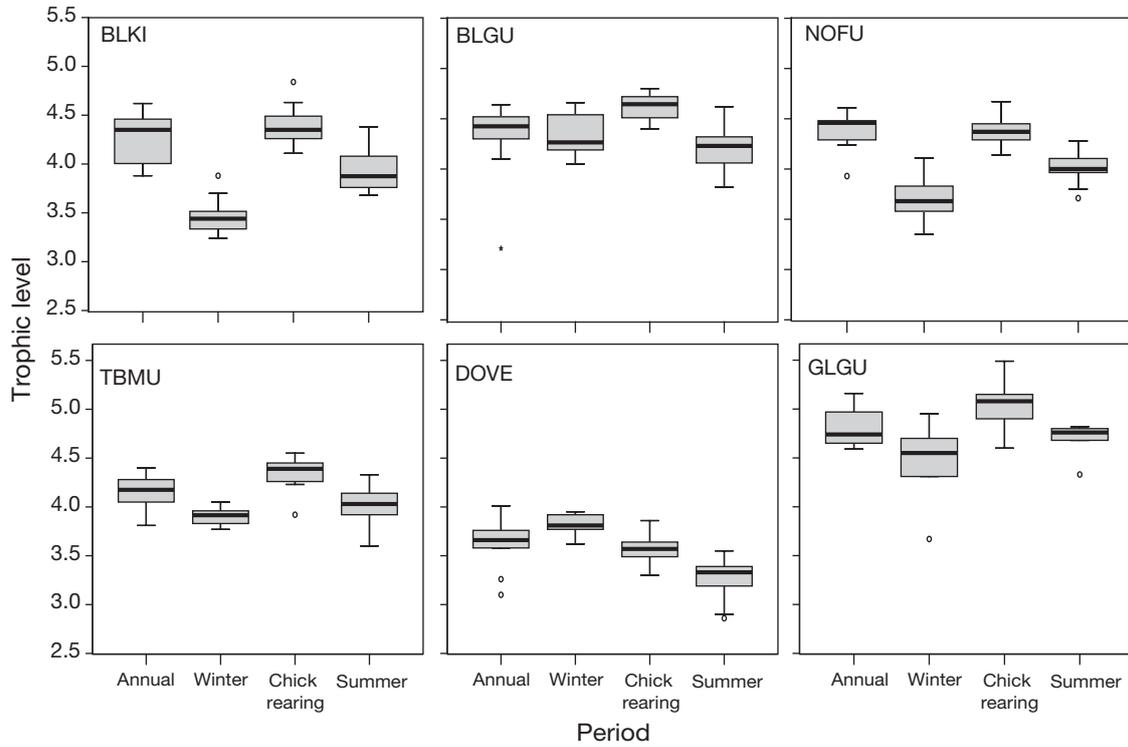


Fig. 1. Changes in derived trophic level by period for seabirds using the Northwater Polynya in 1998 and 1999. Annual data are based on bone collagen, winter data on primary feathers, chick-rearing data on liver, and summer data on muscle tissue. Black-legged kittiwake (BLKI), black guillemot (BLGU), northern fulmar (NOFU), thick-billed murre (TBMU), dovekie (DOVE), and glaucous gull (GLGU). Box plots: solid black line indicates the mean, boxes 25 and 75%, whiskers 10 and 90%, and dots are outliers

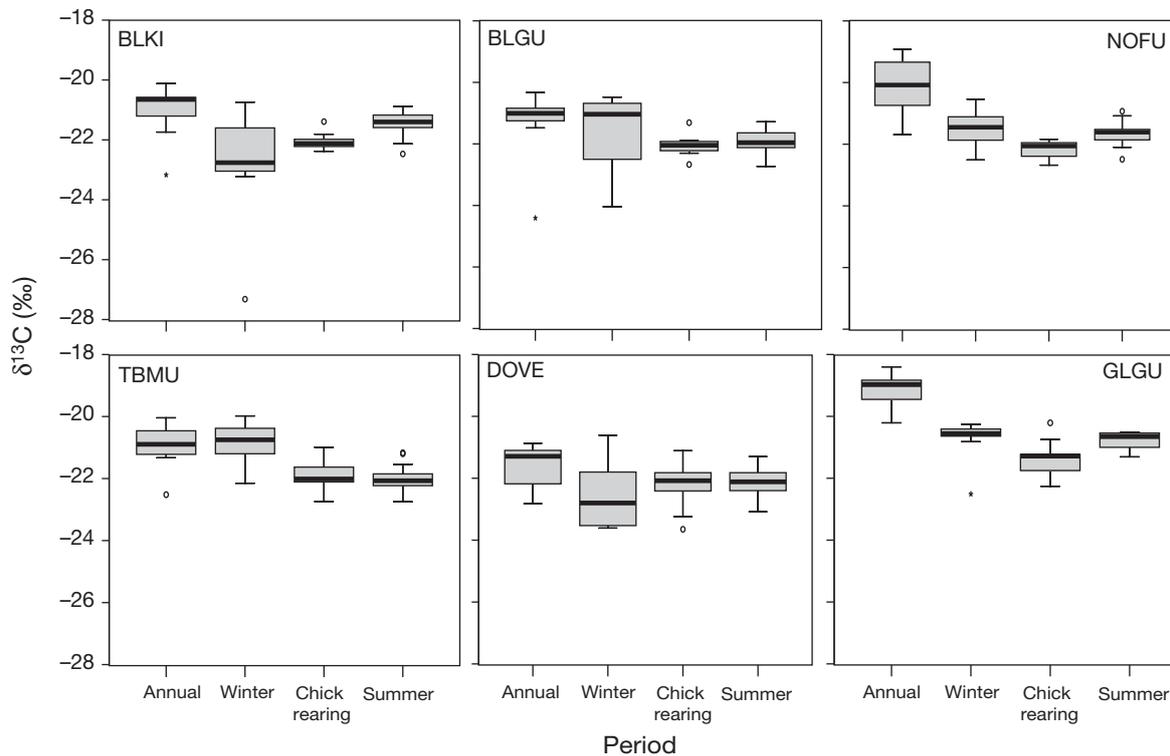


Fig. 2. Changes in derived seabird prey $\delta^{13}C$ values by period for seabirds using the Northwater Polynya in 1998 and 1999. Annual data are based on bone collagen, winter data on primary feathers, chick-rearing data on liver, and summer data on muscle tissue. Species codes and other details as in Fig. 1

prey $\delta^{13}\text{C}$ among periods in females ($p = 0.91$), but males' prey $\delta^{13}\text{C}$ was lowest in the summer and during breeding ($p = 0.18$), and highest during winter and annually ($p = 0.39$). Males' TL was highest during breeding ($p < 0.001$) and did not differ among other periods ($p = 0.49$). In females, the lowest TL was observed during summer and winter ($p = 0.52$), with the highest overall and during breeding ($p = 0.18$). Winter and annual TL were also statistically similar ($p = 0.83$).

Thick-billed murre

For the thick-billed murre, sex (Wilks' $\lambda = 0.977$, $p = 0.38$), and the sex \times period interaction (Wilks' $\lambda = 0.889$, $p = 0.13$) were not significant, but there were overall differences among periods (Wilks' $\lambda = 0.26$, $p < 0.001$). TL differed among periods ($F_{3,84} = 17.60$, $p < 0.001$), with the highest TL during breeding ($p < 0.001$), and the lowest during winter and summer ($p = 0.81$); annual TL did not differ from summer TL ($p = 0.87$). Prey $\delta^{13}\text{C}$ also differed among period ($F_{3,84} = 33.80$, $p < 0.001$) with summer and breeding $\delta^{13}\text{C}$ forming 1 homogenous subset ($p = 0.20$), and annual and winter forming another higher subset ($p = 0.15$).

Northern fulmar

For the northern fulmar, there were overall differences by sex (Wilks' $\lambda = 0.84$, $p = 0.041$) and period (Wilks' $\lambda = 0.10$, $p < 0.001$), but the sex \times period interaction was not significant (Wilks' $\lambda = 0.79$, $p = 0.17$). There was no difference between sexes in TL ($F_{1,38} = 0.13$, $p = 0.72$), but prey $\delta^{13}\text{C}$ was significantly lower in females than males in all seasons ($F_{1,38} = 7.16$, $p = 0.011$). TL was highest in breeding and annually ($p < 0.02$), lowest in winter ($p < 0.001$), and intermediate in summer ($p < 0.001$). Prey $\delta^{13}\text{C}$ was highest annually ($p < 0.001$), lowest during breeding and summer ($p = 0.90$), and intermediate during winter and summer ($p = 0.27$).

Black-legged kittiwake

For the black-legged kittiwake, there was no effect of sex (Wilks' $\lambda = 0.97$, $p = 0.48$), and the sex \times period interaction was not significant (Wilks' $\lambda = 0.87$, $p = 0.31$); period did have an overall effect (Wilks' $\lambda = 0.22$, $p < 0.001$). TL differed among periods ($F_{3,51} = 40.12$, $p < 0.001$), with the lowest TL during winter ($p < 0.001$) and the highest during breeding/annual

($p = 0.62$). Summer TL was intermediate, but significantly different from other periods ($p < 0.001$). Prey $\delta^{13}\text{C}$ also differed among periods ($F_{3,51} = 8.10$, $p < 0.001$), with the lowest $\delta^{13}\text{C}$ during winter and breeding ($p = 0.80$), and the highest during summer and annually ($p = 0.58$); summer and breeding $\delta^{13}\text{C}$ were also similar ($p = 0.83$).

Ivory gull

For the ivory gull, period (Wilks' $\lambda = 0.05$, $p = 0.001$), but neither sex (Wilks' $\lambda = 0.64$, $p = 0.20$) nor the sex \times period interaction (Wilks' $\lambda = 0.63$, $p = 0.72$), influenced foraging overall. TL differed among period ($F_{3,8} = 6.27$, $p = 0.017$): the lowest TL was during summer and winter ($p = 0.07$), the highest during breeding and annually ($p = 0.06$), while winter and breeding TL were not significantly different ($p = 0.94$). Prey $\delta^{13}\text{C}$ also differed by period ($F_{3,8} = 11.85$, $p = 0.003$), with the lowest prey $\delta^{13}\text{C}$ during breeding, summer, and winter ($p = 0.92$), and the highest during winter and annually ($p = 0.93$).

Glaucous gull

Sex (Wilks' $\lambda = 0.77$, $p = 0.047$) and period (Wilks' $\lambda = 0.12$, $p < 0.001$), but not their interaction (Wilks' $\lambda = 0.91$, $p = 0.88$), were significant overall for the glaucous gull. TL ($F_{1,24} = 5.47$, $p = 0.028$) and prey $\delta^{13}\text{C}$ ($F_{1,24} = 4.61$, $p = 0.042$) were significantly higher in males. TL differed by period ($F_{3,24} = 7.77$, $p = 0.001$), with the highest TL during breeding, and annually ($p = 0.93$), and the lowest TL during winter ($p = 0.62$) and intermediate in summer. Prey $\delta^{13}\text{C}$ also differed among periods ($F_{3,24} = 21.47$, $p < 0.001$), with high $\delta^{13}\text{C}$ over the year ($p < 0.001$) and lower $\delta^{13}\text{C}$ during all other periods ($p = 0.90$).

DISCUSSION

This study has demonstrated that the isotopic composition of seabird tissues that reflect diet and trophic position are dynamic, and so determination of these factors for 1 period of the annual cycle cannot necessarily be extrapolated to other periods. However, by examining multiple tissues isotopically, it is possible to infer diet and trophic position approximating the major phases of the annual cycle of individuals. Winter diet in particular consisted of lower TL prey for black-legged kittiwake, northern fulmar, glaucous

gull, thick-billed murre, and male black guillemots compared with other periods. For murre, this trend was recently confirmed through the isotopic measurement of muscle tissue of wintering birds off Newfoundland (Moody & Hobson 2007) where euphausiids contributed substantially to diet. For surface-feeding seabirds like kittiwakes and fulmars, it is possible that invertebrate prey were more available during the molting period at sea. Black guillemots, which are year-round residents of Arctic waters, showed the most consistent TL throughout the year, and this species likely makes use of ice-associated invertebrates primarily during spring and benthic fish at other times. As expected, dovekeys showed the lowest TL of all species examined, but there was evidence that trophic position was lowest during the summer. Stomach content analyses of dovekeys using the Northwater Polynya confirm that herbivorous copepods dominate the diet early in the year. More carnivorous copepods, the amphipod *Themisto libellula*, small Arctic cod *Boreogadus saida*, and other invertebrates tend to dominate in late summer and autumn (Karnovsky et al. 2008), but lower-trophic prey likely comprise the majority of dovekeys' winter diet (Fort et al. 2010). Glaucous gulls showed the highest TL of all species, and this was fairly constant with the possible exception of the winter molt period.

In contrast to TL estimates, derived prey $\delta^{13}\text{C}$ values did not vary greatly among species or within species annually. Although glaucous gulls had among the highest values among tissues, the range of $\delta^{13}\text{C}$ values within tissues was typically in the order of 1 to 2‰. Stable carbon isotope ratios can be influenced by a variety of processes in marine systems (Michener & Schell 1994), but it is generally assumed that food webs involving carbon derived from benthos are more enriched in ^{13}C than pelagic food webs. Indeed, in the nearby Lancaster Sound food web, Hobson & Welch (1992a) determined that muscle of black guillemots had among the highest $\delta^{13}\text{C}$ value, whereas muscle $\delta^{13}\text{C}$ values from dovekeys and fulmars were among the lowest. That we did not find a similar pattern among the seabirds of the Northwater Polynya, where all 3 species' prey had low $\delta^{13}\text{C}$, suggests that seabird diets there were dominated primarily by a pelagic food web. Furthermore, estimated prey $\delta^{13}\text{C}$ among species during the summer and breeding seasons, when birds are present in the Northwater, varied little (Table 1). Nonetheless, in general, $\delta^{13}\text{C}$ measurements of seabird tissues are encouraged since patterns of this isotope can vary spatially (Schell et al. 1998, Rau et al. 2001) and can provide useful information on source or latitude of

feeding in some areas (Hobson et al. 1994, Cherel et al. 2006, Jaeger et al. 2010).

We found no difference between sexes in TL, and $\delta^{13}\text{C}$ differed between sexes in only 3 cases (black guillemot, northern fulmar, and glaucous gull). Male fulmars' $\delta^{13}\text{C}$ was lower relative to that of females, and this pattern was reversed in glaucous gulls. In black guillemots, males had lower $\delta^{13}\text{C}$ prey relative to females, except during the summer when this trend was reversed. In some species, differences in foraging between sexes can have demographic and behavioral consequences (Awkerman et al. 2007). Given the pelagic-dominated Northwater system, the relatively small difference in absolute terms (generally <2‰), and the fact that males and females were not from the same pair, sex differences in the prey $\delta^{13}\text{C}$ during the breeding season in these species require further attention. Outside the breeding season, sex and individual differences in $\delta^{13}\text{C}$ could point to spatial or trophic segregation.

Large amounts of variation around isotopic population means could be the result of specialization at the group or individual level, whereas low variance within species would also indicate specialization. Even within sexes, the variation around TL and prey $\delta^{13}\text{C}$ values suggests some degree of individual differences (e.g. female black guillemots, or male black-legged kittiwakes in winter) in migration strategies (Quillfeldt et al. 2010).

The analysis of tissues with varying rates of turnover (and therefore differing in the length of time over which foraging is integrated) can provide insight into species' ecology that would otherwise be expensive, laborious, or even impossible to determine. In the Northwater Polynya, all of the seabirds we examined showed a higher trophic position during chick-rearing (liver) than during the breeding season as a whole. This could be the result of prey switching, within-season increases in prey $\delta^{15}\text{N}$, or both. Other seabirds have also shown this increase in $\delta^{15}\text{N}$ during chick rearing (e.g. Davies et al. 2009). At the same time, there were no significant differences in prey $\delta^{13}\text{C}$ between the chick-rearing and integrated summer diet (Table 1).

There is a long history of using seabird communities to study inter-specific foraging patterns and resource partitioning using stable isotopes (e.g. Hobson et al. 1994, Forero et al. 2004, Kojadinovic et al. 2008a), and some studies have used multiple tissues with rapid turnover (blood, feathers) to assess inter-seasonal differences (e.g. Davies et al. 2009, Fort et al. 2010, Young et al. 2010). The advantage of our multiple-tissue approach is that the integration pe-

riod for which foraging is assessed is extended by using tissues with slow metabolic turnover like muscle and bone collagen. Collagen is a tissue that has seldom been used in avian isotopic studies (Hobson 1990, Hobson et al. 1994, Steele 2005), but it can provide information on individuals' lifetime average diet (Schoeninger & DeNiro 1984). Because inter-annual variation is dampened by the integrative and slow nature of bone collagen protein turnover, analysis of collagen for isotope values can be a powerful tool for examining long-term ecosystem changes using seabirds as indicators.

Previously, seabird dietary analyses were necessarily based on the frequency of occurrence of prey items in stomachs, deliveries to chicks, pellets, or other dietary remains (Duffy & Jackson 1986, Barrett et al. 2007). While these data provide valuable taxonomic information on diets, they are limited from an analytical perspective. An advantage to deriving seabird TL based on seabird $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values is that these are continuous variables that each summarize different aspects of foraging in a single number, and thus are amenable to more extensive mathematical analysis (Karnovsky et al. 2012).

One area of particular interest is using stable isotope data to examine the bioaccumulation and acquisition of contaminants in food webs. For example, biomagnification of contaminants can be quantified as the slope of the relationship between contaminant concentration (typically on a logarithmic scale) and tissue $\delta^{15}\text{N}$ value or derived TL (Jarman et al. 1996, Braune et al. 2001, Fisk et al. 2001). Changes in contaminant levels over time can also be adjusted to account for dietary shifts using stable isotope values (Braune 2007). Previous studies have typically used a single consumer tissue type for quantifying such contaminant–TL level relationships, but, as demonstrated here, several tissue types could provide information for various time periods during the annual cycle. Such analyses could identify the location where contaminants are accumulated, even if the sites are beyond the immediate place of collection (Ofukany et al. 2012). In a more indirect way, derivation of periods or locations where TL is highest using tissue-dependent isotopic modeling allows the identification of those components of the annual cycle where species are most vulnerable to contaminant accumulation. We caution, however, that the integration periods of contaminants and stable isotopes must be comparable for a meaningful analysis (Bond 2010).

In many situations, actual collections of seabirds are necessary to obtain the appropriate tissues for multi-tissue isotopic sampling. This is typically the

case with at-sea work. However, at colony sites, adults and chicks can usually be captured, providing the opportunity for non-destructive sampling. Whole blood has a similar turnover rate to avian muscle (Hobson & Clark 1992a), as do plasma and liver (Hobson & Clark 1993). Due to similar elemental turnover rates, blood separated into plasma and cellular fractions provides equivalent isotopic information as liver and muscle, respectively (Hobson & Clark 1993). The isotopic analysis of claws may also provide information on TL and source of feeding over a period of several months of growth (Bearhop et al. 2003). Indeed, the only tissue that appears to be impossible to replace non-destructively is bone collagen, which provides a convenient means of assaying lifetime (or at least annual) average integrations of diet and stable isotope values. Some seabirds have a protracted period of sequential feather growth, and by sampling and isotopically measuring the vanes of several feathers from an individual, it may be possible to extend the period of inference to several months or years (Pyle 2009, Ofukany et al. 2012).

The isotope approach is well suited to deriving estimates of trophic position and source of feeding for those tissues associated with food webs that have been well described. This was the case for seabird muscle and liver tissues sampled in the Northwater Polynya since those tissues were synthesized there and we had an extensive isotopic survey of the polynya food web. However, inferences based on those tissues grown outside of the polynya, possibly including feathers and components of the bone collagen, may be less reliable if the marine food web differed substantively from that of the polynya. This is currently a challenge for many applications of the isotope technique because patterns and dynamics of marine isoscapes are not well known (Karnovsky et al. 2012). Similarly, some marine food webs can change isotopically across seasons or years, and such factors can affect the reliability of trophic estimates. Nonetheless, there is some evidence for long-term stability in the isotopic nature of marine food webs involving seabirds in the vicinity of the polynya (Moody et al. 2012), and the integrative nature of isotopic averaging is expected to dampen isotopic variation that may occur at lower TLs (Hobson 2011).

There has been considerable discussion about when seabirds can be used as reliable ecological indicators (e.g. Piatt et al. 2007a,b, Durant et al. 2009). A general prerequisite for any indicator is that we know what it is indicating. Since diet links seabirds with their marine environment, the accurate determination of seabird diet or trophic position is an essential

component of the indicator approach. This study has shown that by using several tissue types from the same individuals, stable isotope assays can be a more informative approach to defining seabird TL and general source of feeding. Future studies are now required to better refine and test the time-integrated models by establishing additional estimates of the diet-tissue discrimination factors upon which the models are based. In addition, studies that help define isotopic patterns in marine food webs (i.e. marine isoscapes) and the distribution of seabirds during the non-breeding season will ultimately benefit isotopic studies of seabirds as ecological indicators since it will allow greater inference on movements and the interpretation of corresponding tissue isotopic records (Minami & Ogi 1997, Barnes et al. 2009, Graham et al. 2010, Jaeger et al. 2010, Block et al. 2011).

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Appendix 1. Stable isotope values ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) for 7 seabird species breeding in the North Water Polynya in 1998 and 1999. Integration times (tissues) are: annual (bone collagen), winter (feather), chick-rearing (liver), and summer (muscle). Data are presented as mean \pm SD (n), in parts per thousand (‰). M: male, F: female

Species	Sex	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		Annual	Winter	Chick-rearing	Summer	Annual	Winter	Chick-rearing	Summer
Black guillemot	M	+16.1 \pm 2.1 (4)	+17.6 \pm 0.8 (5)	+16.7 \pm 0.3 (5)	+15.0 \pm 0.7 (14)	-18.9 \pm 1.7 (5)	-17.6 \pm 0.5 (5)	-20.6 \pm 0.4 (5)	-19.9 \pm 0.4 (14)
	F	+17.4 \pm 0.5 (5)	+17.1 \pm 0.8 (5)	+16.1 \pm 0.5 (5)	+14.6 \pm 0.8 (15)	-18.6 \pm 0.3 (5)	-18.9 \pm 1.4 (5)	-20.9 \pm 0.3 (5)	-19.7 \pm 0.5 (15)
Thick-billed murre	M	+16.2 \pm 0.8 (5)	+15.7 \pm 0.3 (5)	+14.8 \pm 0.8 (5)	+13.8 \pm 0.6 (21)	-18.6 \pm 1.0 (5)	-17.4 \pm 0.6 (5)	-20.3 \pm 0.5 (5)	-19.9 \pm 0.3 (21)
	F	+16.0 \pm 0.5 (5)	+15.5 \pm 0.4 (5)	+15.6 \pm 0.3 (5)	+14.2 \pm 0.6 (41)	-18.3 \pm 0.4 (5)	-17.7 \pm 0.8 (5)	-20.9 \pm 0.3 (5)	-19.9 \pm 0.4 (41)
Dovekie	M	+14.1 \pm 1.3 (5)	+15.4 \pm 0.4 (5)	+12.3 \pm 0.4 (39)	+11.4 \pm 0.5 (64)	-18.9 \pm 0.8 (5)	-19.2 \pm 0.8 (5)	-20.8 \pm 0.4 (39)	-20.0 \pm 0.4 (64)
	F	+14.0 \pm 0.8 (5)	+15.2 \pm 0.4 (5)	+12.2 \pm 0.4 (36)	+11.2 \pm 0.6 (56)	-19.2 \pm 0.6 (5)	-19.4 \pm 1.2 (5)	-20.9 \pm 0.5 (36)	-20.1 \pm 0.4 (56)
Black-legged kittiwake	M	+16.5 \pm 1.1 (6)	+14.3 \pm 0.8 (6)	+15.4 \pm 1.0 (6)	+13.9 \pm 0.8 (15)	-18.0 \pm 0.3 (6)	-19.6 \pm 2.4 (6)	-20.8 \pm 0.2 (6)	-19.4 \pm 0.3 (15)
	F	+16.5 \pm 1.1 (5)	+13.6 \pm 0.4 (5)	+15.3 \pm 0.7 (5)	+13.6 \pm 0.6 (10)	-19.1 \pm 1.0 (5)	-19.1 \pm 0.8 (5)	-20.7 \pm 0.4 (5)	-19.3 \pm 0.5 (10)
Northern fulmar	M	+16.8 \pm 1.0 (4)	+14.5 \pm 0.7 (4)	+15.5 \pm 0.4 (4)	+14.3 \pm 0.5 (10)	-18.1 \pm 0.8 (4)	-18.5 \pm 0.5 (4)	-20.9 \pm 0.3 (4)	-19.7 \pm 0.2 (10)
	F	+17.2 \pm 0.7 (5)	+15.2 \pm 0.9 (5)	+15.2 \pm 0.8 (5)	+13.8 \pm 0.5 (9)	-17.2 \pm 0.9 (5)	-18.0 \pm 0.6 (5)	-20.8 \pm 0.6 (5)	-19.4 \pm 0.5 (9)
Glaucous gull	M	+18.8 \pm 1.0 (5)	+18.5 \pm 0.8 (4)	+18.7 \pm 0.8 (4)	+17.1 (1)	-16.4 \pm 0.4 (4)	-17.2 \pm 0.2 (4)	-19.6 \pm 0.5 (4)	-18.4 (1)
	F	+18.5 \pm 0.7 (5)	+17.2 \pm 1.6 (5)	+17.3 \pm 0.7 (5)	+16.4 \pm 0.8 (4)	-16.9 \pm 0.7 (5)	-17.6 \pm 0.9 (5)	-20.4 \pm 0.4 (5)	-18.8 \pm 0.4 (4)
Ivory gull	M	-	+14.8 (1)	+15.7 (1)	+13.5 \pm 0.0 (2)	-	-17.4 (1)	-20.5 (1)	-19.5 \pm 0.0 (2)
	F	+18.7 \pm 0.4 (3)	+17.2 \pm 3.3 (2)	+17.3 \pm 0.5 (3)	+14.4 \pm 0.6 (3)	-17.6 \pm 0.8 (3)	-17.7 \pm 0.3 (2)	-20.5 \pm 0.1 (3)	-19.2 \pm 0.3 (3)