

Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models

Keith A. Hobson*

Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 0W0

ABSTRACT: The measurement of stable isotopes of nitrogen and carbon in tissues of marine consumers can provide trophic-level information that is a time-integrated approximation of assimilated diet. By measuring $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations in liver, muscle and bone collagen of 7 species of seabirds inhabiting the Barrow Strait - Lancaster Sound region, Northwest Territories, Canada, estimates of short-, intermediate-, and long-term trophic level (TL), respectively, were established. Trophic estimates were based on a simple model incorporating diet-tissue fractionation established through the captive rearing of piscivorous birds on known isotopic diets. $\delta^{13}\text{C}$ was not a useful indicator of trophic position in this marine food web but may indicate inshore or benthic vs offshore or pelagic feeding preferences in seabirds. $\delta^{15}\text{N}$ was a useful indicator and ranged from $12.7 \pm 0.3\text{‰}$ (TL 3.3) in liver of dovekeys *Alle alle* to $19.1 \pm 0.8\text{‰}$ in the bone collagen of glaucous gulls *Larus hyperboreus*. Consistent with their known diets, dovekeys and common eiders *Somateria mollissima* showed lowest trophic positions for all tissues; black-legged kittiwakes *Rissa tridactyla*, thick-billed murre *Uria lomvia*, northern fulmars *Fulmarus glacialis* and black guillemots *Cepphus grylle* showed intermediate trophic positions (TL 3.9 to 4.3) and glaucous gulls showed highest trophic position (TL 4.5 to 4.8). In general, seabirds increased their consumption of lower-trophic-level invertebrates during the breeding season over their lifetime averages but fed their chicks diets consisting of high proportions of fish. Isotopic estimates suggest greater dependence on lower-trophic-level prey by murrelets, fulmars, kittiwakes and guillemots than previously established through conventional dietary techniques.

INTRODUCTION

Seabirds are important components of marine ecosystems and several studies have attempted to define trophic relationships between seabirds and their marine environment, allowing species' roles in energy flow through marine food webs to be defined (Ainley & Sanger 1979, Weins 1984, Sanger 1987, Schneider et al. 1987). Unfortunately, despite their potential use in research on marine systems, seabird dietary investigations have been severely limited by our inability to determine species' diets through time, a limitation common to most studies of species or communities.

Since seabirds typically occupy remote and inaccessible habitats, especially during the non-breeding

season, conventional dietary studies have usually been limited to breeding season information based on stomach contents, regurgitations or on observations of foraging birds. A consequence of this approach is that chick diets are usually better known than adult diets, and soft-bodied invertebrates or other material that is not easily detected are often inaccurately represented in data sets (Harrison 1984, Duffy & Jackson 1986). Furthermore, until recently the interpretation of dietary overlap in these studies has been limited by a lack of statistical methods for testing the significance of differences among such values (Diamond 1983, but see Manly 1991). Studies concerned with determining trophic positions of seabirds avoid some of these limitations since they require only estimates of the *proportion* of prey taken from each trophic level (see Sanger 1987), and seabird trophic position is a continuous variable readily amenable to statistical analysis. In addi-

*Present address: Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada S7N 0X4

tion, in simple 2-prey systems where prey are segregated trophically, seabird trophic level may be related directly to estimates of the contributions of each prey type to seabird diets (see Sanger 1987).

Recent investigations of marine food webs have demonstrated that stable-carbon and nitrogen isotope ratios in consumer tissues are correlated with trophic level (reviewed by Schoeninger & DeNiro 1984, Wada et al. 1987, Fry 1988, Hobson & Welch 1992, Rau et al. 1992). Moreover, because turnover rates of stable isotopes vary according to tissue metabolic activity, the isotopic measurement of various tissues from the same population of seabirds can provide both long- and short-term dietary information (Tieszen et al. 1983, Hobson & Sealy 1991). The isotopic analysis of seabird tissues and prey may thus form the basis of a useful analytical tool in seabird trophic studies (Hobson 1990, 1991).

In this paper, I use stable-isotope analysis to establish trophic relationships among 7 species of seabirds inhabiting the Barrow Strait-Lancaster Sound region of the high Arctic. By measuring stable-nitrogen isotope abundances in liver, muscle and bone collagen, short-, intermediate- and long-term trophic relationships among species were determined. Stable-carbon isotope analysis of muscle tissue was used also to investigate possible species segregation according to sources of prey. Seabirds in this area were ideally suited to an isotopic investigation since the marine food web, although long, is relatively simple compared with temperate or tropical systems (Diamond 1983, Welch et al. 1992), and seabirds here were known to rely on prey from different trophic levels (e.g. Bradstreet & Cross 1982). Moreover, a pattern of step-wise enrichment in ^{15}N with trophic level throughout the food web from primary producers through polar bears *Ursus maritimus* was demonstrated previously (Hobson & Welch 1992). To my knowledge, this is the first isotopic study of a marine system that has used several tissue types in order to establish how trophic relationships might change through time.

METHODS

Seabirds and other marine organisms were collected from early July to late August 1988 to 1990, primarily in the Barrow Strait-Lancaster Sound region of the Northwest Territories, Canada (Fig. 1). The breeding stage of

black-legged kittiwakes *Rissa tridactyla*, taken from a single breeding colony on Browne Island, was identified according to the 3 periods: egg-laying, incubation, and chick-rearing. For other seabirds, I could not associate a particular bird with a known breeding attempt and so arbitrarily considered 3 collection periods defined according to: Period 1, 1 to 15 July; Period 2, 16 July to 10 August; Period 3, 11 to 31 August. A detailed description of methods of collecting marine organisms from phytoplankton through marine mammals is given in Hobson & Welch (1992). Seabirds were collected either at sea or on breeding colonies (summarized in Table 1). Chick ages were estimated using mass or morphometric comparisons with known-age birds. Below, I describe the seabird sample according to species.

Breeding adult kittiwakes were collected from nest sites at the Browne Island colony (ca 3000 pairs) in Resolute Passage. The sample of 9 chicks (ca 3 wk old) was obtained from those nests where adults were collected.

Three major colonies of northern fulmar *Fulmarus glacialis* exist in Lancaster Sound and Barrow Strait (Brown et al. 1975); about 60 000 nest at Prince Leopold Island, 10 000 at Cape Liddon and 70 000 at Hobhouse Inlet on the south coast of Devon Island. Adult birds collected in this study could have been from any of these colonies, but were likely from those on south Devon Island. Fulmars collected near the Cape Liddon colony during Period 3, 1988 and 1989, were from feeding flocks near the entrance to Gascoyne Inlet. Adults collected in Allen Bay in 1989 were also from a

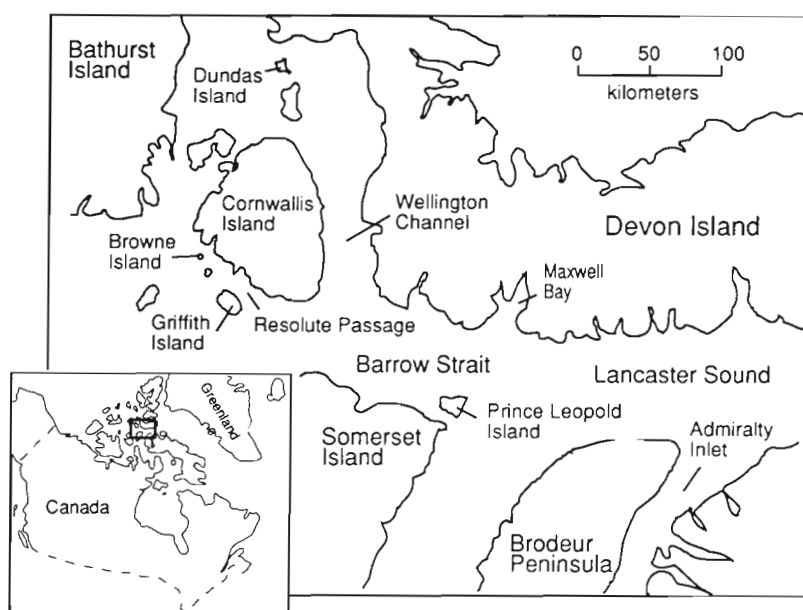


Fig. 1. Location of the Barrow Strait-Lancaster Sound region of the high Arctic

Table 1. Details of the samples of marine birds collected in the Barrow Strait - Lancaster Sound region, 1988 to 1990

Species ^a	Year	Period	Males	Females	Chicks	Source ^b
BLKI	1988	Incubation	6	4	—	BI
	1989	Egg laying	4	4	—	BI
	1989	Incubation	5	2	—	BI
	1989	Chick-rearing	3	3	9	BI
NOFU	1988	3	8	4	—	SDI
	1989	2	7	8	4	SDI
	1989	3	4	6	—	AB
	1990	3	—	—	4	PLI
GLGU	1988	3	6	4	—	BI
	1989	3	3	5	—	BI
	1988	3	2	2	—	DI
	1990	3	3	2	—	DI
	1990	3	3	2	6	PLI
TBMU	1988	2	11	4	—	BS
	1989	2	14	7	—	BS
	1990	3	—	—	6	PLI
BLGU	1988	2	8	6	—	GI
	1989	2	3	1	—	GI
	1989	3	4	8	—	SDI
DOVE	1988	1	5	3	—	RP
COEI	1989	1	5	3	—	BI

^a BLKI: black-legged kittiwake; NOFU: northern fulmar, GLGU: glaucous gull; TBMU: thick-billed murre; BLGU: black guillemot; DOVE: dovekie; COEI: common eider

^b AB: Allen Bay; BS: Barrow Strait; BI: Browne Island; DI: Dundas Island; GI: Griffith Island; RP: Resolute Passage; SDI: South Devon Island

single feeding flock. Four chicks (ca 2 wk old) were taken from the Cape Liddon colony in 1989 and 4 chicks (2 to 3 wk old) from the Prince Leopold Island colony in 1990. Glaucous gull *Larus hyperboreus* chicks obtained from Prince Leopold Island in 1990 were ca 4 wk old.

Most adult thick-billed murres *Uria lomvia* were taken on open water south of Devon or Cornwallis islands during Period 2. All breeding birds were assumed to be from the Prince Leopold Island colony (ca 86 000 pairs), the only murre colony in the vicinity. A sample of 6 chicks (ca 12 to 15 d old) were obtained from Prince Leopold Island during Period 3, 1990.

Black guillemots *Cephus grylle* were collected as they staged on the water off breeding sites south of Griffith Island and from foraging flocks south of Devon Island. Dovekies *Alle alle* were taken from a single feeding flock in Resolute Passage in Period 1. They do not breed in this area and occur only sporadically in western Lancaster Sound. Wings of common eiders *Somateria mollissima* obtained in late June 1989 were purchased from Inuit hunters and had been obtained near Browne Island.

Isotopic analysis. After collection, birds were weighed, external measurements taken, and then sexed after dissection. Pectoral muscle, liver and bone (humerus)

samples were obtained for isotopic analyses and stored frozen. Isotopic measurement of these 3 tissues was expected to yield dietary information based on different periods of assimilation. For example, Hobson & Clark (1992a) determined experimentally the turnover rates of stable isotopes derived from diet in the tissues of captive birds and found isotopic half-lives to be a few days for liver, about 2 wk for pectoral muscle, and at least half a year for bone collagen (see also Tieszen et al. 1983). Practically, the isotopic measurement of a tissue represents an integration of diet over 2 to 3 half-lives and so I considered liver to yield dietary information on the order of about a week, muscle tissue about 4 to 6 wk, and thus indicative of the breeding season, and bone at least 1 yr.

Muscle and liver samples were freeze-dried and powdered using an analytical mill. Bone collagen was extracted as a gelatin according to the methods of Chisholm et al. (1983) and then freeze-dried. Lipids were extracted from all tissues using a Soxhlet apparatus with chloroform solvent and then dried at 60°C for 24 h to remove any residual solvent. Samples for ¹⁵N/¹⁴N analysis were converted to

ammonia by Kjeldahl reaction and then to N₂ gas using LiBrOH (Porter & O'Dean 1977). Samples for ¹³C/¹²C analysis were loaded into Pyrex tubes with 1 g of wire-form CuO and silver foil, sealed under vacuum and combusted at 550°C for at least 6 h. This technique gave similar results to that using Vycor tubes and higher temperature combustion (Swerhone et al. 1991). Carbon dioxide and nitrogen gas were analyzed using a Micromass 602E mass spectrometer. Stable-isotope concentrations were expressed in δ notation as parts per thousand according to the following:

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

where $X = ^{15}\text{N}$ or ^{13}C , and R = the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. R_{standard} for ^{15}N and ^{13}C is that for atmospheric N₂ (air) and the PDB standard, respectively. Several hundred replications of a glycine and wheat grain standard indicated a combined measurement error of $\pm 0.3\%$ for nitrogen and $\pm 0.1\%$ for carbon.

Isotopic models. Hobson & Welch (1992) determined previously that, beyond the first 2 trophic levels, carbon was not a useful indicator of trophic position in this marine food web (see also Fry 1988). For this reason, seabird trophic positions were not estimated using $\delta^{13}\text{C}$ values. Nevertheless, the analysis of 2

stable isotopes in consumer tissues may allow greater segregation of species than the use of a single isotope (e.g. Peterson et al. 1985, Hobson 1991). For this reason, $\delta^{13}\text{C}$ values were measured in a subsample of seabird muscle tissue.

Isotopic concentrations of various biochemical components of foods fractionate or change when incorporated into consumer tissues according to the relationship:

$$D_t = D_d + \Delta_{dt} \quad (1)$$

where D_t = isotopic concentration in the tissue; D_d = isotopic concentration of the diet, and Δ_{dt} = isotopic fractionation factor between diet and tissue. In order to relate isotopic concentrations in a given tissue to those in a consumer's diet, it is necessary, then, to establish isotopic fractionation values for each tissue type (Tieszen et al. 1983).

Hobson & Welch (1992) previously derived a nitrogen trophic enrichment value of +3.8‰ for muscle tissue in the marine food web in this area. A model based on this fractionation value adequately described the trophic positions of organisms from phytoplankton (TL 1) to polar bears (TL 5.1) according to the following simple relationship:

$$\text{TL} = 1 + (D_m - 5.4)/3.8 \quad (2)$$

where D_m = $\delta^{15}\text{N}$ value of a consumer's muscle tissue; TL corresponds to the trophic position of that consumer; and 5.4 refers to the mean $\delta^{15}\text{N}$ in phytoplankton (in ‰) measured by Hobson & Welch (1992) for our study area.

Recent research using captive raised, piscivorous birds indicates that the nitrogen isotopic fractionation factor between bird diet and muscle tissue may be less than that derived for the rest of the Barrow Strait-Lancaster Sound marine food web (Mizutani et al. 1991, Hobson & Clark 1992b) and that this difference may be linked to the fact that birds produce uric acid rather than urea (but see Minagawa & Wada 1984). For this reason, and to allow for analyses using several bird tissue types, the above equations were modified by incorporating the term Δ_{dt} . Using the relationship $\text{TL}_{\text{bird}} = \text{TL}_{\text{prey}} + 1$ and combining Eqs. 1 & 2 yields:

$$\text{TL}_{\text{bird}} = 2 + (D_t - \Delta_{dt} - 5.4)/3.8 \quad (3)$$

where D_t = the bird's tissue $\delta^{15}\text{N}$ value. Using tissues of an adult cormorant held in captivity on a known isotopic diet, Mizutani et al. (1991) provided estimates of Δ_{dt} for liver, muscle and bone as +2.3, +2.4 and +3.9‰, respectively. Hobson & Clark (1992b) raised juvenile ring-billed gulls *Larus delawarensis* on a fish diet and established mean nitrogen liver, muscle and bone enrichment values as +2.7, +1.4, and +3.1‰, respectively. Thus, I used Mizutani et al.'s (1991) ^{15}N

enrichment estimates for trophic models involving adult seabirds and Hobson & Clark's (1992b) enrichment estimates for those of chicks.

For the simple situation involving only 2 dietary options that are segregated trophically, the relative contribution of each prey type to the diet of a consumer may be estimated according to the following relationship:

$$P_a = (D_t - D_b) / (D_b - D_a) \quad (4)$$

where P_a = proportion of the diet derived from source 'a', D_t = isotopic value of the consumer tissue measured; and D_a and D_b = the consumer tissue isotopic values corresponding to exclusive diets of type 'a' and 'b', respectively. This relationship was used to estimate relative contributions of Arctic cod *Boreogadus saida* and amphipods, or amphipods and copepods, to the diets of seabirds in the study area.

For each species-tissue combination, the effects of sex, location, year and period of collection on $\delta^{15}\text{N}$, and any interactions between these factors, were tested using analysis of variance (ANOVA). When significant differences ($p < 0.05$) were indicated using Type III sums of squares, Tukey's multiple comparison test was used to test for differences between pairs of values. For each species, tissue $\delta^{15}\text{N}$ values showing no significant difference according to categories of sex, location, period of collection, or year were grouped for analysis and then compared with other species-tissue categories using a 1-way ANOVA. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for muscle tissue were each compared simultaneously using a multivariate analysis of variance (MANOVA) with the Wilk's Lambda statistic. All analyses were performed using the Statistical Analysis System (SAS Institute 1985).

RESULTS

Patterns of ^{15}N abundance

For both dovekeys and eiders, sex had no influence on muscle or bone $\delta^{15}\text{N}$ values ($F < 4.3$, $p > 0.05$ for all comparisons). In addition, sex, location and year did not influence $\delta^{15}\text{N}$ values for tissues of black guillemots ($F < 3.1$, $p > 0.1$ for all comparisons).

Kittiwake liver $\delta^{15}\text{N}$ values were not influenced by sex ($F_{1,18} = 2.32$, $p > 0.14$) or period ($F_{2,17} = 3.34$, $p > 0.05$) but were influenced by year with adults showing more enriched values during incubation in 1989 (17.4 ± 0.4 ‰, $n = 7$) compared with the same period in 1988 (16.4 ± 0.9 ‰, $n = 10$, $F_{1,15} = 8.46$, $p < 0.01$). No effect of period ($F_{2,19} = 1.4$, $p > 0.28$) or year ($F_{1,29} = 0.03$, $p > 0.86$) was found for kittiwake muscle $\delta^{15}\text{N}$ values but, overall, males showed more

enriched muscle values ($15.7 \pm 0.7\text{‰}$, $n = 16$) than females ($14.9 \pm 0.6\text{‰}$, $n = 15$, $F_{1,19} = 9.2$, $p < 0.01$). No influence of sex ($F_{1,29} = 1.0$, $p > 0.32$), period ($F_{2,28} = 0.75$, $p > 0.49$) or year ($F_{1,29} = 3.4$, $p > 0.08$) was found for bone $\delta^{15}\text{N}$ values.

Liver $\delta^{15}\text{N}$ values for male fulmars were more enriched over those of females in late August 1989 ($17.7 \pm 1.0\text{‰}$, $n = 4$, vs $15.2 \pm 0.9\text{‰}$, $n = 6$; $F_{1,8} = 22.6$, $p < 0.001$) but, otherwise, period and year had no influence on liver isotope values ($F < 1.6$, $p > 0.2$ for both factors). Fulmar muscle and bone $\delta^{15}\text{N}$ values were not influenced by sex, year, or period of collection ($F < 1.6$, $p > 0.2$ for all comparisons).

For glaucous gulls, location had a significant effect on adult liver ($F_{2,19} = 8.62$, $p < 0.01$) and muscle ($F_{2,19} = 16.4$, $p < 0.001$) $\delta^{15}\text{N}$ values. Liver had lower enrichment values for gulls at Dundas Island ($16.9 \pm 0.6\text{‰}$, $n = 9$) than for those at both Browne ($18.3 \pm 1.0\text{‰}$, $n = 17$, Tukey's $p < 0.05$) and Prince Leopold islands ($18.2 \pm 1.0\text{‰}$, $n = 5$, $p < 0.05$). Similarly, muscle showed lower enrichment at Dundas Island ($16.0 \pm 0.5\text{‰}$, $n = 9$) compared to Browne ($17.1 \pm 0.7\text{‰}$, $n = 17$, $p < 0.05$) or Prince Leopold islands ($17.9 \pm 0.8\text{‰}$, $n = 5$, $p < 0.05$).

Liver $\delta^{15}\text{N}$ values for thick-billed murres were not influenced by sex or year ($F_{1,34} < 1.53$, $p > 0.22$ in both cases). Similarly, these factors had no influence on muscle $\delta^{15}\text{N}$ values ($F_{1,34} < 0.05$, $p > 0.5$ in both cases). Bone collagen $\delta^{15}\text{N}$ values were not influenced by year ($F_{1,34} = 0.45$, $p > 0.5$) but showed a weak relationship to sex (female: $16.9 \pm 0.7\text{‰}$, $n = 11$; male: $17.5 \pm 0.9\text{‰}$, $n = 25$; $F_{1,34} = 3.99$, $p = 0.054$).

The above-described effects of year, sex and location were taken into account when comparing all species by tissue type. Since most seabirds were collected in 1989, data for this year was used exclusively if tissue $\delta^{15}\text{N}$ values differed between years (i.e. kittiwake and fulmar liver tissue samples). Males and females were separated if they differed significantly (e.g. kittiwake muscle sample) and only glaucous gull data for Browne and Prince Leopold islands were used. Species $\delta^{15}\text{N}$ comparisons by tissue type are given in Fig. 2. For each tissue, seabirds differed significantly in their $\delta^{15}\text{N}$ distributions (Table 2). Consistently, dovekeys and common eiders showed the lowest, and glaucous gulls the greatest $\delta^{15}\text{N}$ values compared to other species for all tissues. Considerable overlap in $\delta^{15}\text{N}$ for all tissues was found for kittiwakes, fulmars, murres and guillemots (Fig. 2).

Patterns of ^{13}C abundance

$\delta^{13}\text{C}$ values for seabird muscle tissue were plotted against $\delta^{15}\text{N}$ values in order to determine if greater species segregation could be obtained (Fig. 3). Species

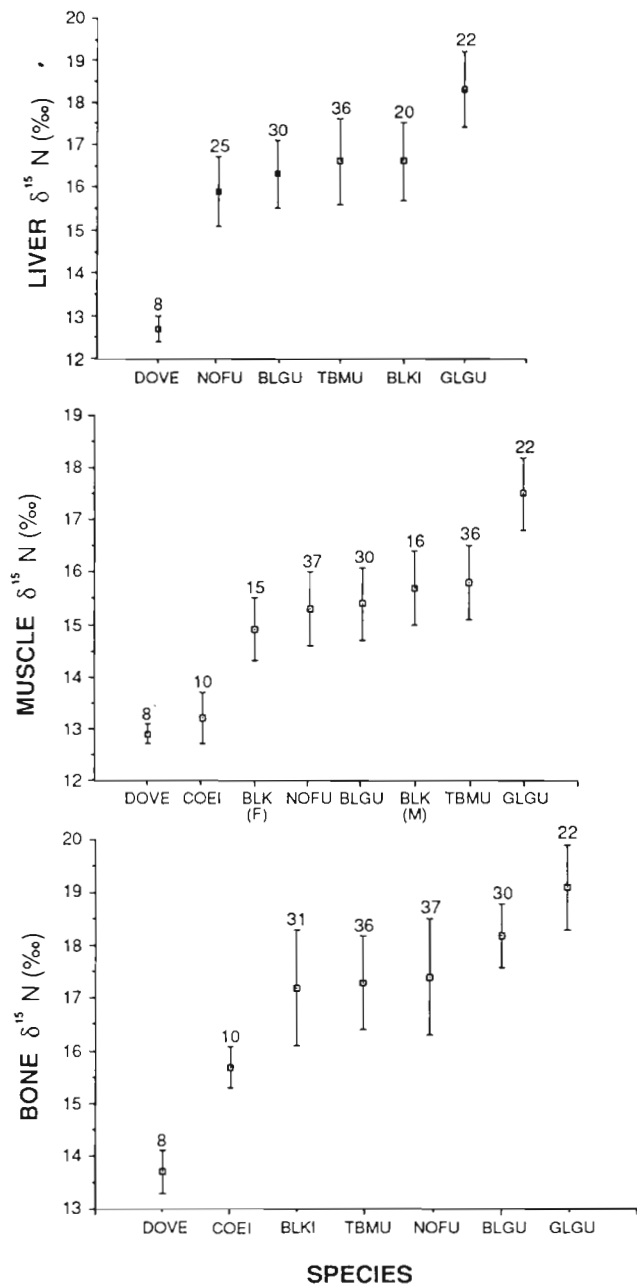


Fig. 2. Mean stable nitrogen isotope concentrations (\pm SD) in liver, muscle and bone collagen of seabirds inhabiting Barrow Strait and Lancaster Sound, 1988 to 1990. Species abbreviations as in Table 1. Sample sizes indicated above error bars

were segregated by this technique (MANOVA: Wilk's Lambda, $F_{12,154} = 24.34$, $p < 0.001$) in a pattern that would not be apparent using single isotope analyses. Seabirds segregated trophically according to their $\delta^{15}\text{N}$ values (see above) and appeared to segregate further according to their $\delta^{13}\text{C}$ values (ANOVA: $F_{6,78} = 10.23$, $p < 0.001$). Fulmars, murres, kittiwakes and dovekeys had lower $\delta^{13}\text{C}$ values than gulls, guillemots and eiders (Fig. 3).

Table 2. Stable nitrogen isotope abundances in seabird tissues in Barrow Strait-Lancaster Sound, 1988 to 1990 and results of 1-way ANOVA tests for differences between species for each tissue type. Within tissues, species with at least 1 common superscript letter are not significantly different (Tukey's multiple comparison, $p < 0.05$). Species abbreviations as in Table 1; *** $p < 0.001$. F: female; M: male

Species	Liver		Tissue $\delta^{15}\text{N}$ (‰)		Bone	
		n	Muscle	n		n
DOVE	12.7 ± 0.3^b	8	12.9 ± 0.2^d	8	13.7 ± 0.4^c	8
COEI	—	—	13.2 ± 0.5^d	10	15.7 ± 0.4^d	10
NOFU	15.9 ± 0.8^a	25	15.3 ± 0.7^{ab}	37	17.4 ± 1.1^{ab}	37
BLGU	16.3 ± 0.8^a	30	15.4 ± 0.7^{ac}	30	18.2 ± 0.6^{be}	30
BLKI	16.6 ± 0.9^a	20	F: 14.9 ± 0.6^a	15	17.2 ± 1.1^a	31
			M: 15.7 ± 0.7^{bc}	16		
TBMU	16.6 ± 1.0^a	36	15.8 ± 0.7^{bc}	36	17.3 ± 0.9^{ab}	36
GLGU	18.3 ± 0.9^c	22	17.5 ± 0.7^e	22	19.1 ± 0.8^e	22
ANOVA F:	35.97		58.88		36.43	
p:	***		***		***	

However, of these apparent groups, only fulmars in one group and guillemots in the other had $\delta^{13}\text{C}$ values that were significantly different from all other species not in their group (Tukey's $p < 0.05$ in all cases).

Trophic-level and dietary predictions

In order to compare dietary predictions for various tissues within species and age classes, it was necessary

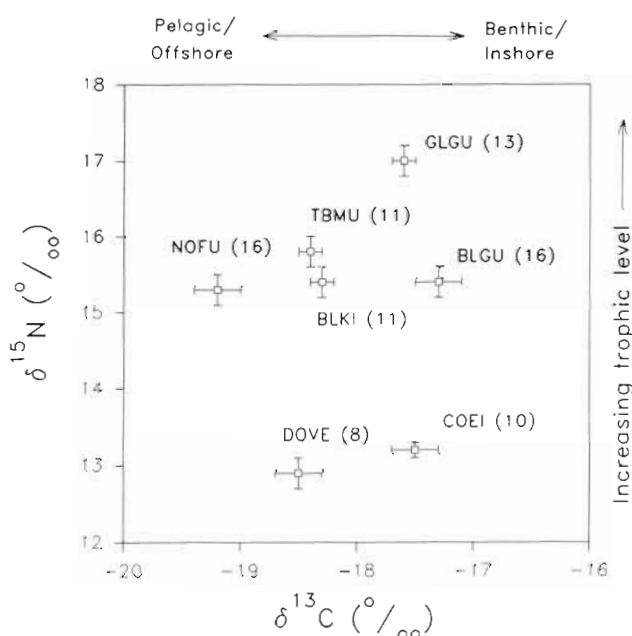


Fig. 3. Stable nitrogen and carbon isotope concentrations (mean \pm SE) of muscle tissue of seabirds inhabiting the Barrow Strait-Lancaster Sound area, 1988 to 1990. Species abbreviations as in Table 1. Sample sizes given in parentheses

to convert average $\delta^{15}\text{N}$ values to average trophic levels using Eq. 3. All species showed significant differences among tissue trophic predictions (Table 3) and, in general, trophic level corresponding to summer diets tended to be lower than those corresponding to short- (i.e. liver) or long-term (i.e. bone) diets.

Adult and chick trophic positions were compared for thick-billed murres, black-legged kittiwakes, glaucous gulls, and northern fulmars (Table 4). For kittiwakes, a parent-chick sample was analysed. For fulmars and glaucous gulls the adult sample corresponded to those individuals taken approximately during the chick-rearing period. Murre

chicks taken in 1990 could only be compared with adults taken during the chick-rearing period of 1988 and 1989. Murre and kittiwake chicks generally occupied higher trophic positions than their parents, a trend significant for calculations based on muscle and bone analyses. No significant difference in adult and chick trophic position was found for fulmars or gulls. No significant correlations were found between adult tissue $\delta^{15}\text{N}$ values for each species (Pearson correlation: $p > 0.2$, in all cases) indicating that the tendency for a species to feed at a given trophic level during one period was not correlated with its feeding behaviour at another period.

Several genera of amphipods commonly utilized by seabirds in the study area, including *Parathemisto libellula*, occupy approximately TL 2.7, and Arctic cod *Boreogadus saida* TL 3.6 (Table 5). Seabirds feeding exclusively on amphipods or Arctic cod are expected, then, to occupy TL 3.7 and TL 4.6, respectively. By assuming seabirds foraged only between these 2 trophic levels and that cod were the only fish consumed, relative contributions of amphipods and cod to the diets of murres, kittiwakes, fulmars and guillemots were calculated (Table 6).

DISCUSSION

The $\delta^{15}\text{N}$ model successfully segregated seabirds according to our general understanding of their feeding habits in the high Arctic. Trophic positions derived for dovekeys and eiders were consistent with their almost exclusive diets of invertebrate prey and those of glaucous gulls consistent with diets that include higher-trophic-level organisms. The intermediate values for murres, kittiwakes, guillemots and fulmars also agree generally with their mixed diets of fish and inverte-

Table 3. Derived trophic levels of seabirds in Barrow Strait-Lancaster Sound according to tissue type and the results of 1-way ANOVAs testing differences between tissues (horizontal) for each species. Within species, tissues sharing a common superscript letter are not significantly different (Tukey's multiple comparison criteria, $p < 0.05$). Species abbreviations as in Table 1; * $p < 0.05$, *** $p < 0.001$. F: female; M: male

Species	Tissue						ANOVA	
	Liver	n	Muscle	n	Bone	n	F	p
DOVE	3.3 ± 0.1^a	8	3.3 ± 0.1^a	8	3.2 ± 0.1^b	8	11.38	...
COEI	—	—	3.4 ± 0.1^a	10	3.7 ± 0.1^b	10	27.29	...
NOFU	4.2 ± 0.3^a	25	4.0 ± 0.2^b	37	4.2 ± 0.2^a	37	9.63	...
BLGU	4.3 ± 0.2^a	30	4.0 ± 0.2^b	30	4.3 ± 0.2^a	30	25.94	...
BLKI	4.3 ± 0.2^a	20	F: 3.9 ± 0.2^b	15	4.1 ± 0.3^c	31	18.98	...
			M: 4.1 ± 0.2^c	16			10.55	...
TBMU	4.3 ± 0.3^a	36	4.1 ± 0.2^b	36	4.1 ± 0.2^b	36	12.24	...
GLGU	4.8 ± 0.3^a	22	4.5 ± 0.2^b	22	4.6 ± 0.4^b	22	3.94	.

brates, particularly pelagic crustaceans. Additional insights provided by the stable-isotope approach are based on the power of this technique to produce unbiased estimates of the importance of lower-trophic-level prey that are often poorly preserved in stomachs and on the fact that time-integrated estimates of diet were obtained. Previous conventional seabird dietary studies in the study area (e.g. Bradstreet 1976) and elsewhere allow comparison of information obtained using the stable-isotope approach with that based on stomach analyses and these comparisons are considered below for each species.

Black-legged kittiwake

Bradstreet (1976) investigated the summer diet of kittiwakes in eastern Lancaster Sound during 1976 and concluded that, while amphipods and copepods were frequent in their diets, Arctic cod made up 93 to 98 % of

the dry weight estimate. In contrast, while the isotope model predicted mean short-term cod contributions as high as 70 % using liver analyses, it further suggested that, over the breeding season, amphipods may contribute about half the assimilated dietary protein of males and nearly 80 % that of females, and that the year-round amphipod contribution to the diet of both sexes was close to 50 %. To my knowledge, sex differences in kittiwake diets have not been suggested previously but have been shown in other larids (e.g. Pierotti 1981). Males showed higher trophic position relative to females over the breeding season, suggesting greater dependence of males on fish. Male culmen and tarsus measures were significantly larger than those of females [culmen ($\bar{x} \pm \text{SD}$): 33.9 ± 1.2 mm vs 32.2 ± 1.2 mm, $F_{1,27} = 15.51$, $p < 0.001$; tarsus: 33.4 ± 1.2 mm vs 32.4 ± 1.1 mm, $F_{1,26} = 4.94$, $p < 0.05$] and males tended to have greater mass than females (406.1 vs 374.3 g, $F_{1,26} = 3.6$, $p = 0.07$), but it is not known whether this is related to dietary differences between the sexes. It is also possible that isotopic differences between male and female kittiwakes may be related to differences in feeding locations preceding the breeding season.

Muscle and bone isotope values of kittiwake chicks suggest that they were fed primarily fish, likely Arctic cod. Gulls feed chicks by regurgitation of stomach contents, so it is possible that males fed chicks more than females since adult male kittiwakes fed more on cod than females. Such differences in parental provisioning have been noted in western gulls *Larus occidentalis* (Pierotti 1981).

Black guillemots

Black guillemots consume a broad variety of prey throughout their range (Bradstreet

Table 4. Comparison of the mean trophic levels (\pm SD) calculated for adult (A) and chick (C) thick-billed murre, black-legged kittiwakes and northern fulmars from the Barrow Strait-Lancaster Sound region, 1989 to 1990, and results of tests for differences between age classes for each tissue type. Adult samples are of parents (e.g. BLKI) or of birds taken during the chick-rearing period. Species abbreviations as in Table 1. NS: not significant; * $p < 0.05$; *** $p < 0.001$

Species	n	Age	Tissue					
			Liver	p	Muscle	p	Bone	p
TBMU	21	A	4.3 ± 0.3	NS	4.2 ± 0.2	...	4.2 ± 0.2	...
	6	C	4.5 ± 0.1		4.7 ± 0.2		4.9 ± 0.2	
BLKI	7	A	4.3 ± 0.2	NS	4.0 ± 0.1	...	4.1 ± 0.4	.
	9	C	4.3 ± 0.1		4.4 ± 0.1		4.5 ± 0.2	
NOFU	10	A	4.1 ± 0.4	NS	4.3 ± 0.1	NS	4.4 ± 0.2	NS
	8	C	4.0 ± 0.3		4.5 ± 0.3		4.4 ± 0.3	
GLGU	5	A	4.8 ± 0.3	NS	4.8 ± 0.2	NS	4.6 ± 0.4	NS
	6	C	4.6 ± 0.2		4.7 ± 0.1		4.8 ± 0.3	

Table 5. Mean stable nitrogen isotope concentrations (\pm SD) in typical seabird prey in the Barrow Strait-Lancaster Sound region 1988 to 1990, and their calculated trophic positions according to Hobson & Welch (1992)

Prey	n	Mean $\delta^{15}\text{N}$ (‰)	Trophic position
Invertebrates			
Bivalve molluscs			
<i>Mya truncata</i>	7	9.5 ± 0.7	2.1
<i>Serripes groenlandica</i>	7	8.9 ± 0.8	1.9
<i>Hiatella arctica</i>	10	9.8 ± 0.5	2.2
<i>Macoma calcarea</i>	4	10.8 ± 0.5	2.4
<i>Musculus discors</i>	4	7.9 ± 0.4	1.7
<i>Buccinum</i> sp.	5	12.6 ± 0.7	2.9
Copepods			
<i>Calanus hyperboreus</i>	6 ^a	9.2 ± 0.5	2.0
Mysids			
<i>Mysis oculata</i>	2 ^a	10.3 ± 0.3	2.3
Amphipods			
<i>Rozinante fragilis</i>	5 ^a	11.5 ± 0.3	2.6
<i>Gammarus wilkitzkii</i>	5	11.5 ± 0.3	2.6
<i>Parathemisto libellula</i>	6 ^a	11.7 ± 0.7	2.7
<i>Onisimus glacialis</i>	4 ^a	11.4 ± 0.5	–
Fish^b			
<i>Boreogadus saida</i> (48–247)	26	15.2 ± 0.7	3.6
<i>Gymnellus virides</i> (14–16)	4	16.2 ± 0.5	3.8
<i>Liparis</i> sp. (46–125)	4	15.0 ± 0.4	2.5
<i>Icelus bicornis</i> (39–81)	4	14.6 ± 1.5	3.4
<i>Myoxocephalus scorpiodes</i> (92)	1	15.2	3.6

^a Sample composed of several (>5) individuals
^b Range in fish fork length (mm) given in parentheses

Table 6. Estimated mean percent proportion of amphipods (\pm SD) in the diets of thick-billed murres, black-legged kittiwakes, black guillemots and northern fulmars based on 3 tissue types. Species abbreviations as in Table 1. Age: A = adult; C = chick. F: female; M: male

Species	Age	Amphipod contribution (mean %)					
		Liver	n	Muscle	n	Bone	n
TBMU	A	33 ± 6	36	56 ± 8	36	55 ± 8	36
	C	11 ± 10	6	<0	6	<0	6
BLKI	A	33 ± 6	20	F: 78 ± 9	15	56 ± 10	31
	C	33 ± 14	6	M: 56 ± 8	16		
BLGU	A	33 ± 5	30	67 ± 6	30	33 ± 5	30
NOFU	A	44 ± 9	25	67 ± 12	37	44 ± 7	37
	C	67 ± 27	8	11 ± 14	8	33 ± 15	8

& Brown 1985). In Lancaster Sound, Bradstreet (1976) found that while amphipods made up 93 % of the prey items in guillemot stomachs, Arctic cod made up 84 % of the prey biomass. Using stable-isotope analysis, I similarly found that short-term assimilated diet of guillemots during the early chick-rearing period was composed of approximately two-thirds fish. However, the isotope results show that amphipods contribute as much as 67 % of the assimilated dietary protein over the

summer. Much of this crustacean input may occur during the late spring to early summer when guillemots forage at the ice edge (Bradstreet 1980). Fish contribute the majority of guillemot prey all year round.

Thick-billed murre

Adult thick-billed murres consume both fish and crustaceans and are known generally to exploit invertebrates more than their closely related congener, the common murre *Uria aalge* (reviewed by Bradstreet & Brown 1985). In the Lancaster Sound region, Bradstreet (1976, 1980) determined that, in the spring, Arctic cod comprised typically 70 to 90 % of the diet dry weight of murres at both coastal and offshore ice edges. Summer diet was found to be more variable with crustaceans, primarily *Parathemisto* spp., being taken when cod were apparently less abundant (Bradstreet & Brown 1985). The isotope model predicts that the diet of adult murres in Lancaster Sound during the early to mid chick-rearing period consisted of about 70 % cod but that crustaceans contributed about half of the assimilated diet during the summer. Similarly, crustaceans are estimated to contribute about half the yearly dietary intake of murres.

The diet of murre chicks in the central high Arctic consists primarily of fish, with Arctic cod being dominant (Bradstreet & Brown 1985). At Prince Leopold Island, Gaston & Nettleship (1981) determined that cod and sculpins *Triglops* sp. made up 78 % and 18 % of the chick diet, respectively. The isotope model is in general agreement with these findings, suggesting only a small contribution of crustaceans to the short-term diet of murre chicks with fish making up the entire long-term diet. The inclusion of benthic fish such as *Gymnellus virides* (see Table 2) in chick diets,

with higher $\delta^{15}\text{N}$ values than Arctic cod, may account for the higher muscle and bone $\delta^{15}\text{N}$ values of chicks compared with those expected for exclusive diets of cod.

Northern fulmar

In his studies of fulmars in the Barents Sea, Belopol'skii (1961) claimed that this species only occasionally

eats fish. Fisher (1952) also claimed that it is unlikely that fish are a major part of the diet of fulmars, an opinion held also by Salomonson (1950) who reviewed the diet of fulmars in Greenland. At Prince Leopold Island, Nettleship (1976) found that amphipods and copepods were present in the diet of adult and nestling fulmars from May to September, and that Arctic cod first appeared in the diet at the time of hatching and was an important component of the diet until mid-September. In his dietary investigations of fulmars in eastern Lancaster Sound in 1976, Bradstreet (1976) determined also that fish comprised about 70% dry weight during the chick-rearing period but that amphipods increased in importance toward the end of that period.

The highly omnivorous diet of fulmars presents problems of interpretation of the isotope data beyond the establishment of average trophic level. Copepods, amphipods and cod represent prey types from 3 distinct trophic levels ranging from 2.0 to 3.6 (Hobson & Welch 1992) and thus complicate analyses of the relative contributions of prey from each of these categories. In addition, intact and well-preserved squid *Gonatus fabricii* beaks were found in the stomachs of several fulmars in Lancaster Sound (see also Bradstreet 1977) and these are known to persist in seabird stomachs for as long as 50 d (Furness et al. 1984). However, squid were not measured isotopically since none were ever caught in this area.

Based on a simple 2 trophic option model that assumes fulmars fed only on amphipods and Arctic cod, the isotope model suggests that amphipods made up about two-thirds of the overall summer diet. Short-term diet in both periods consisted of approximately equal contributions of cod and amphipods. Collagen isotope values indicate that the year-round average diet for fulmars consisted of approximately 45% amphipods. Further isotopic analyses of squid would be useful to determine if contributions of this prey to fulmar winter diets (see Lydersen et al. 1989, Erikstad 1990) could be determined isotopically.

Dovekie

Dovekies consistently showed the lowest tissue $\delta^{15}\text{N}$ values of all seabirds examined. This result is in agreement with previous studies that indicate primarily a diet of zooplankton including amphipods, mysids, copepods and euphausiids, with only small contributions of fish (Bradstreet & Brown 1985).

Making the assumption that dovekies feed primarily between the 2 trophic levels represented by copepods and amphipods, the isotope data indicated that copepods made up about 57% of the summer diet and about 70% year-round. This increase in amphipod use

during the summer is consistent with Bradstreet's (1982) findings that while copepods were consumed primarily during the northward migration through Baffin Bay in the spring, amphipods made up most of the adult diet in August. Trophic-level estimates based on collagen suggest that the winter diet of dovekies consists primarily of copepods rather than amphipods.

Common eider

Like dovekies, common eiders showed relatively low $\delta^{15}\text{N}$ values for muscle and bone tissues. This result is consistent with the generally low-trophic-level prey known for this species. Bivalve molluscs, especially *Mytilus edulis* and *Littorina* spp., as well as barnacles *Balanus* spp. and crustaceans dominate both summer and winter diets (Madsen 1954, Dementiev & Gladkov 1967, Palmer 1976). Without knowledge of the range of isotopic values of prey available in winter, it is difficult to understand the dietary consequences of the distinct rise in trophic level from summer to year-round diet as evidenced by the isotopic data. Eiders may take a greater proportion of amphipods relative to molluscs during the non-breeding season or may move to areas where the benthos is more enriched isotopically (see McConnaughey & McRoy 1979, Dunton et al. 1989).

Glaucous gull

Glaucous gulls are known to feed on the young and adults of other birds, a pattern recorded on both the breeding and wintering grounds (Lydersen et al. 1989, Barry & Barry 1990, Erikstad 1990). The elevated $\delta^{15}\text{N}$ values for the tissues of this species are consistent with the higher trophic position of gulls relative to the other seabirds in the study area.

Short-term trophic positions of gulls from Browne and Prince Leopold Islands in late August were the highest recorded and suggest a significant input of birds in the diets of adult gulls and their chicks. On Browne Island, gulls nested close to a large kittiwake colony, and on Prince Leopold Island are known to consume and feed murre chicks to their young (Gaston & Nettleship 1981). Interestingly, glaucous gulls from Dundas Island, where there were no other major seabird colonies nearby, showed lower $\delta^{15}\text{N}$ values for liver and muscle tissues than those gulls from Browne and Prince Leopold Islands. This suggests that gulls at Dundas Island consumed instead larger proportions of lower-trophic-level prey during the breeding season. Barry & Barry (1990) also reported inter-colony differences in diets of glaucous gulls breeding at inland and coastal sites along the Beaufort Sea, and related part of

this difference to differential access to other species of nesting birds. The similar collagen $\delta^{15}\text{N}$ values of gulls from all 3 colonies indicates that winter trophic position was similar regardless of breeding colony.

The isotope model

A major advantage of using stable-isotope analysis to study seabird diet is the potential for delineating trophic information during the non-breeding season when birds are largely inaccessible. The model developed here assumes that the relationship between trophic level and isotopic composition of food web components does not change between the breeding and wintering grounds, but extensive isotopic analyses outside the breeding grounds were not conducted (see Schell et al. 1989). Nonetheless, preliminary evidence suggests that the isotopic model developed for Lancaster Sound is likely applicable to areas of the northwest Atlantic where several of these seabirds winter (Hobson & Montevecchi 1991), and the isotope model provided a number of hypotheses regarding changes in species diets during the non-breeding season that may be tested using both conventional and isotopic dietary analyses.

Another factor that may affect seabird dietary estimates using stable-isotope models is seasonal variation within respective prey species. Other studies have shown that considerable isotopic variation within low-trophic-level biomass may occur at a single location (e.g. Goering et al. 1990, Rau et al. 1990). In this study, the seabird breeding season is relatively short and dietary information was based on models using isotope values for prey collected throughout the breeding seasons of 1988 to 1990 (Hobson & Welch 1992). While seasonal variation in isotope values for prey was not investigated rigorously, variance in prey isotope values, including that due to any seasonal effects, was incorporated into seabird dietary estimates. However, future studies using stable isotopes to examine seasonal patterns in seabird diet should take into account possible seasonal variation in the isotopic composition of prey.

Isotopic fractionation factors between diet and bird tissues are poorly understood, particularly for adult birds. The only estimates available are based on captively reared birds using known isotopic diets. However, even estimates based on these controlled studies have limitations since captive animals usually have restricted diets that may result in undetected physiological stresses, which may in turn influence isotopic fractionation (Hobson & Clark 1992b). Additional studies on marine birds are clearly required to determine factors influencing possible differences in isotopic fractionation factors between individuals (see

Minagawa & Wada 1984, Sutoh et al. 1987). At the moment, the tissue isotopic fractionation values used in this study are the best available for piscivorous birds, but further refinements to the model presented here may be warranted as our knowledge of the influence of nutrition and metabolism on the behavior of stable isotopes increases.

While no error could be assigned to the fractionation values used in this study for adult birds, Hobson & Clark (1992b) determined previously that the error (SD) associated with fractionation factors derived for captive juvenile gulls ($n = 14$) ranged from 0.1‰ for liver to 0.2‰ for muscle. If similarly small variances can be expected in wild birds, they represent an insignificant contribution to overall variance in the mean trophic-level and dietary estimates since they are within analytical error, and are small relative to the variance associated with species' $\delta^{15}\text{N}$ values.

Real dietary differences between individual birds and their prey contributed to the high variance associated with estimates of the relative contributions of cod and amphipods to species diets. Such individual variation has typically not been addressed in conventional dietary studies, since dietary estimates are often given as simple percent occurrence or percent biomass of all stomachs examined. This study reveals that dietary differences may be substantial within species (see also Kuletz 1983, Pierotti & Annett 1986) and this should be considered in future dietary studies of single species and communities.

Despite the limitations of the stable-isotopic approach, important new evidence on trophic relationships among seabirds in Lancaster Sound has been obtained. $\delta^{15}\text{N}$ provided dietary and trophic information, and $\delta^{13}\text{C}$ analysis may be useful in delineating benthic or inshore feeders vs pelagic or offshore feeders. Northern fulmars, a species having the most pelagic feeding habits, showed the lowest $\delta^{13}\text{C}$ values whereas guillemots, eiders and gulls, species that feed primarily inshore and often on benthic prey, showed the highest $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values of Arctic cod compared to those of benthic fish provide further support for this hypothesis (Hobson & Welch 1992). Other researchers have found similarly high $\delta^{13}\text{C}$ values associated with coastal or benthic vs pelagic food webs (McConnaughey & McRoy 1979, Rau et al. 1983, Dunton et al. 1989, K. A. Hobson & J. F. Piatt unpubl.).

Implications for seabird community studies

Of the 7 species of seabirds examined, 4 overlapped significantly in their trophic positions, a pattern that was generally consistent across all tissue types. However, while trophic overlap does not necessarily

imply real dietary overlap, the possibility for similar diets among these species certainly exists in this relatively simple food web (Bradstreet 1976, Bradstreet & Cross 1982). Dietary overlap among sympatric seabirds occurs in both temperate and tropical biomes and is highly influenced by prey availability and diversity (Pearson 1968, Diamond 1983). Both influences may apply especially to seabird communities in the high Arctic where food, in particular lower-trophic-level invertebrates, can be superabundant but are of relatively low diversity (Welch et al. 1992).

According to the isotope data, seabirds in the Lancaster Sound area consumed more lower-trophic-level prey than suggested by previous studies based on stomach content analysis during the breeding season. Moreover, these consumption estimates generally represented increases over those for year-round diets, suggesting that these seabirds increase their consumption of lower-trophic-level prey on breeding compared to wintering grounds, an effect most noticeable among guillemots. Like many marine systems, the Arctic marine environment is variable with sea-ice conditions (among other factors) greatly influencing seabird foraging opportunities and breeding success (e.g. Gaston & Nettleship 1981; see also Ainley & DeMaster 1990, Ainley et al. 1991). Invertebrates can be abundant in these systems, and distinct selective advantages accrue to species with the behavioural and morphological ability to exploit them. In this respect, the high Arctic biome shows some similarity to that of the Antarctic where the marine food web is short and seabirds depend primarily on krill (Croxall & Prince 1980, Rau et al. 1992, but see Ainley et al. 1991).

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