



## FEATURE ARTICLES

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# ISOTOPIC INVESTIGATIONS OF SEABIRDS OF THE NORTH WATER POLYNIA: CONTRASTING TROPHIC RELATIONSHIPS BETWEEN THE EASTERN AND WESTERN SECTORS

KEITH A. HOBSON<sup>1,4</sup>, GRANT GILCHRIST<sup>2</sup> AND KNUD FALK<sup>3</sup>

<sup>1</sup>Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, SK S7N 0X4, Canada

<sup>2</sup>Canadian Wildlife Service, Yellowknife, NT X1A 1E2, Canada

<sup>3</sup>Ornis Consult, Vesterbrogade 140A, DK-1620 Copenhagen V, Denmark

**Abstract.** We used  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  analyses of blood, muscle, and liver tissues to evaluate similarity of diet among five seabird species: Black Guillemot (*Cepphus grylle*), Black-legged Kittiwake (*Rissa tridactyla*), Dovekie (*Alle alle*), Glaucous Gull (*Larus hyperboreus*), and Thick-billed Murre (*Uria lomvia*) nesting at Coburg Island on the west and Hakluyt Island on the east side of the North Water Polynya between Ellesmere Island, Canada, and northwest Greenland. We hypothesized that dietary differences should occur because the two neighboring sites are subject to different oceanographic conditions, one result of which is differential timing of spring open water. Relative trophic level, derived from tissue  $\delta^{15}\text{N}$  values, ranged from 3.6 for Dovekie from Hakluyt Island to 4.7 for late-breeding-season diets of Thick-billed Murre adults from Coburg Island. At Coburg Island, trophic level of hatching year (HY) kittiwakes, murres, and Glaucous Gulls was higher than that for adults. This pattern was not found at Hakluyt Island, where chicks of all species generally occupied lower trophic positions. These findings suggest that lower-trophic-level prey were more important to Hakluyt Island seabirds, possibly due to lower availability of arctic cod (*Boreogadus saida*).

**Key words:** arctic, carbon-13, diet, nitrogen-15, polynya, seabirds, trophic level.

### Investigaciones Isotópicas de Aves Marinas en el Canal Aguas del Norte: Contrastando las Relaciones Tróficas entre los Sectores Este y Oeste

**Resumen.** Usamos análisis de  $\delta^{15}\text{N}$  y  $\delta^{13}\text{C}$  en tejidos sanguíneos, musculares y hepáticos para evaluar la similitud en la dieta entre cinco especies de aves marinas (*Cepphus grylle*, *Rissa tridactyla*, *Alle alle*, *Larus hyperboreus* y *Uria lomvia*). Estas especies anidan en la Isla Coburg en el lado oeste y en la Isla Hakluyt en el lado este del Canal de las Aguas del Norte, que se presenta libre de hielos y está situado entre la Isla Ellesmere en Canadá y el noroeste de Groenlandia. Hipotetizamos que las diferencias en la dieta se deberían a que los dos sitios vecinos están sujetos a diferentes condiciones oceanográficas, resultando en un ajuste temporal diferencial en la apertura de las aguas en primavera. El nivel trófico relativo, derivado de los valores de  $\delta^{15}\text{N}$  en los tejidos, fluctuó entre 3.6 para *A. alle* de la Isla Hakluyt hasta 4.7 para la dieta del final de la época reproductiva de adultos de *U. lomvia* de la Isla Coburg. En la Isla Coburg, el nivel trófico de individuos de *R. tridactyla*, *U. lomvia* y *L. hyperboreus* que eclosionaron ese año fue mayor que el nivel de los adultos. No encontramos este patrón en la Isla Hakluyt, donde los pichones de todas las especies generalmente ocuparon posiciones tróficas inferiores. Estos resultados sugieren que las presas de niveles tróficos inferiores fueron más importantes para las aves marinas de la Isla Hakluyt, posiblemente debido a una menor disponibilidad de bacalao del Ártico (*Boreogadus saida*).

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<sup>4</sup> E-mail: keith.hobson@ec.gc.ca

## INTRODUCTION

In polar regions, the seasonal occurrence and extent of ice-free areas, or polynyas, and the subsequent availability of marine-derived nutrients are expected to importantly influence the distribution, relative abundance, and productivity of seabirds and other vertebrates (Stirling 1980, Stirling and Cleator 1981). In particular, the North Water Polynya (NOW) in northern Baffin Bay, one of the largest and most productive polynyas in the northern hemisphere, is a region of immense biological activity and a focal point in the transfer of energy from primary producers to higher trophic levels in the eastern Canadian Arctic (Stirling 1980, Hobson et al., in press).

Both sensible heat (i.e., upwelling or introduction of warmer water) and latent heat (i.e., wind-driven) mechanisms contribute to the opening and maintenance of the NOW, and these processes play different roles in different areas (Melling et al. 2001). Notably, the east side of the polynya, along the northwest coast of Greenland, opens earlier, primarily a result of warmer Atlantic waters moving north along the Greenland coast. The western side of the polynya opens later and appears to be driven by latent heat processes where wind clears the area of ice following the formation of an ice bridge in Nares Strait (Barber et al. 2001). The differential timing of open water on the east and west sides of the polynya may result in variation in the availability of prey to seabirds. We speculated that these oceanic conditions would be reflected in differences in the diets of seabirds nesting on opposite sides of the polynya (i.e., Coburg Island on the west, and Hakluyt Island on the east side of the polynya).

The study of seabird diet by conventional approaches in remote polar regions is often logistically difficult (Hobson and Welch 1992, Hobson et al. 1994). A technique that can augment conventional approaches to dietary or trophic-level analyses in marine systems involves the measurement of naturally occurring stable isotopes in food webs. This approach has been particularly useful in the study of seabird trophodynamics (Rau et al. 1992, Hobson 1993, Hobson et al. 1994, Cherel et al. 2000). In particular, stable isotope analyses have been used to investigate both contemporary and historic trophic positions of seabirds (Hobson and Montevecchi 1991) and have been applied to a broad array of

tissues including eggs (Hobson 1995, Hobson et al. 1997), feathers (Mizutani et al. 1990, Thompson and Furness 1995, Thompson et al. 1995), blood (Hobson and Clark 1993, Hodum and Hobson 2000), and muscle (Hobson et al. 1994). The primary principle underlying this approach is that the relative abundance of the heavier stable isotopes of carbon ( $^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ ) available to consumers in marine systems change according to a variety of biogeochemical processes (Michener and Schell 1994). For carbon, slight enrichment in  $^{13}\text{C}$  with trophic level may occur, but more importantly, this isotope appears to be generally more enriched in inshore or benthic food webs compared with offshore or more pelagic food webs (Hobson and Welch 1992, France 1995). For nitrogen,  $^{15}\text{N}$  often shows a stepwise enrichment with trophic level, and the measurement of this isotope has been used successfully in modeling trophic relationships among a variety of marine food webs (Minagawa and Wada 1984, Fry 1988, Hobson and Welch 1992, Rau et al. 1992).

Our study was part of a larger food web analysis of the North Water Polynya designed to provide an understanding of the role upper-trophic-level vertebrates play in the carbon flux through this system (Hobson et al., in press). We were particularly interested in how seabird diet and trophic level differs across the polynya in order to evaluate the applicability of generalized models of trophic relationships. We focused on food web samples throughout the polynya and on sampling seabird species breeding at Coburg and Hakluyt Islands. Here, we present the results of our isotopic analyses of birds from these two colonies. We suspected that differences in the dynamics of the polynya at these locations would translate into different foraging strategies, particularly the relative dependence on ice-associated fauna for food, but we formed no *a priori* predictions. In addition to examining trophic relationships among species and between colonies, we also wished to contrast trophic level within species, particularly between adults and chicks. Studies using stable isotopes are showing increasingly that chick diet cannot be equated with adult diet and that clear trophic segregation can occur between these age classes (Hobson 1993, Hodum and Hobson 2000).

## METHODS

### STUDY SITES AND FIELD METHODS

The study was carried out in 1997 and 1998 at two colonies about 220 km apart: Coburg Island

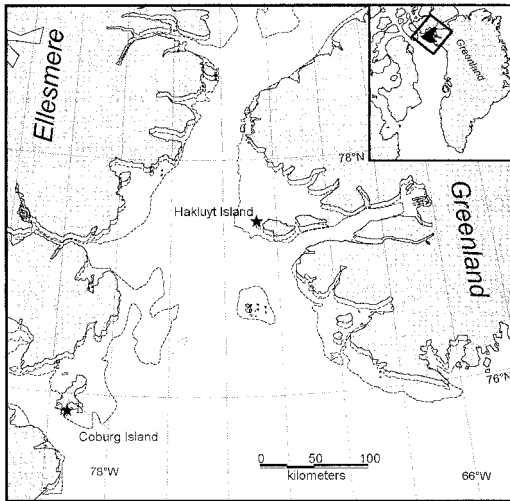


FIGURE 1. Location of the study sites on the east and west sides of the North Water Polynya. The black area in the inset depicts the polynya at full opening, extending almost from shore to shore. The dashed line indicates the 200-m bathymetric contour.

(75°48'N, 78°25'W) at the entrance to Jones Sound between Ellesmere and Devon Island in the southwestern side of the NOW, and Hakluyt Island (77°26'N, 72°42'W) in the Avanersuaq (Thule) district of northwest Greenland (Fig. 1). The seabird communities at these sites are described by Birkhead and Nettleship (1981) and Falk and Kampp (1997), respectively.

We used two methods for sampling seabirds at colonies. When possible, birds were captured, sampled for blood using brachial vein puncture, and then released. Blood samples (ca. 1–2 mL) were transferred immediately to vials containing 5 mL of 70% ethanol and stored (Hobson et al. 1997). Other individuals were shot and their pectoral muscle and liver tissue sampled and stored in vials with ca. 20 mL of 70% ethanol (see Table 1 for details of sample sizes for bird tissue-year combinations).

Reproductive stage of birds and tissues were generally similar for collections made at Hakluyt and Coburg Islands. We sampled murre chicks at 7–12 days of age and adults during July through early August, encompassing the pre-hatch and early post-hatch periods. Black-legged Kittiwake (*Rissa tridactyla*) chicks were sampled at 3 weeks of age in 1997 at Hakluyt but at about 2 weeks of age in 1998 at both sites. Glaucous Gull (*Larus hyperboreus*) chicks were sampled at approximately 3 weeks of age at both

sites. Black Guillemots (*Cepphus grylle*) were sampled only at Coburg Island, July 25–27, 1997 and 1998. Adult Dovekies were sampled only at Hakluyt Island, during July 1997 and 1998, during chick rearing. Small discrepancies between timing of sampling at both sites and between years were expected to be evened out by the integrative nature of the stable isotope technique, since all chick tissues represented diet over their lifetime and for at least a month for adult muscle or blood tissue (Hobson and Clark 1992).

Most prey items were collected at sea from the Canadian Coast Guard Vessel *Pierre Radisson* throughout the polynya in 1998 and were frozen prior to analysis. We analyzed only those prey samples collected during June and early July at fixed sampling stations in the vicinity (60 km) of both colonies. We also collected and analyzed sculpins (*Triglops pingelii*) brought to murre chicks at Hakluyt Island.

#### STABLE ISOTOPE ANALYSES

As soon as samples were returned from the field (approximately 1 month), ethanol was evaporated from blood and other tissue samples using a drying oven at 60°C for 24 hr and then a freeze dryer. Muscle tissue or whole organisms representing prey samples were cleaned in distilled water and then freeze dried. All dried tissues were powdered using a dental amalgam mill. Lipids were extracted from muscle tissue using a 1:2 methanol:chloroform rinse and then dried for 24 hr in a fume hood. Powdered samples were loaded into tin cups and combusted in a Robo-Prep elemental analyzer at 1800°C. The resultant gases were separated and analyzed in a Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) for stable-carbon and nitrogen isotope ratios on the same sample. CFIRMS automatically measures sequences of samples and reference material for isotopic composition. We used two laboratory standards (egg albumen) for every five unknowns in sequence. Stable-isotope ratios were expressed in  $\delta$ -notation as parts per thousand deviation from the international standards PDB (carbon) and AIR (nitrogen). Measurement precision for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values was estimated to be  $\pm 0.1\text{‰}$  and  $\pm 0.3\text{‰}$ , respectively.

Isotopic fractionation factors, or the relationship between the stable isotope ratio in diet and that in the tissue of a consumer, can depend on

TABLE 1. Stable-nitrogen and carbon isotope values of tissues of seabirds sampled at Coburg and Hakluyt Islands together with derived trophic level (TL) based on  $\delta^{15}\text{N}$  values (see Methods). AD = adult; HY = hatch year; Coburg Island is on the west side of the North Water Polynya; Hakluyt is on the east side.

Species	Age	Tissue	Year	n	$\delta^{15}\text{N}$ (‰)	Range (‰)	TL	$\delta^{13}\text{C}$ (‰)	Range (‰)
Coburg Island									
	Black Guillemot								
	AD	liver	97	10	$15.5 \pm 1.2$	12.6 to 16.6	4.4	$-19.1 \pm 0.4$	-20.0 to -18.6
	AD	muscle	97	10	$14.8 \pm 1.0$	13.6 to 17.1	4.2	$-18.5 \pm 0.4$	-19.2 to -17.9
Black-legged Kittiwake	AD	liver	98	20	$15.6 \pm 0.7$	14.6 to 16.9	4.4	$-18.4 \pm 0.4$	-19.0 to -17.8
	AD	muscle	98	26	$15.0 \pm 0.7$	14.0 to 16.1	4.2	$-18.7 \pm 0.4$	-19.5 to -18.1
	AD	liver	97	12	$13.7 \pm 0.8$	12.7 to 15.5	3.9	$-20.7 \pm 0.3$	-21.2 to -20.2
	AD	muscle	97	14	$13.2 \pm 0.7$	12.5 to 15.1	3.8	$-19.3 \pm 0.4$	-19.9 to -18.6
Thick-billed Murre	AD	blood	98	18	$14.6 \pm 0.8$	13.5 to 16.0	4.0	$-19.8 \pm 0.5$	-20.9 to -19.1
	AD	muscle	98	19	$14.1 \pm 0.7$	13.2 to 15.8	4.0	$-19.7 \pm 0.3$	-20.5 to -19.2
	HY	blood	98	25	$16.5 \pm 0.4$	15.4 to 17.1	4.5	$-19.5 \pm 0.2$	-19.9 to -19.0
	HY	muscle	98	26	$16.1 \pm 0.4$	14.9 to 16.7	4.5	$-18.9 \pm 0.3$	-19.6 to -18.4
Thick-billed Murre	AD	blood	97	18	$15.1 \pm 0.2$	14.6 to 15.5	4.1	$-19.6 \pm 0.3$	-20.2 to -19.2
	AD	muscle	97	3	$14.7 \pm 0.3$	14.5 to 15.0	4.2	$-19.9 \pm 0.2$	-20.1 to -19.7
	AD	liver	97	3	$15.3 \pm 0.2$	15.1 to 15.5	4.3	$-20.3 \pm 0.5$	-20.6 to -19.8
	AD	blood	98	68	$14.8 \pm 0.5$	13.6 to 16.3	4.0	$-18.9 \pm 0.3$	-19.8 to -18.1
Glaucous Gull	AD	muscle	98	26	$14.4 \pm 0.5$	13.3 to 15.7	4.1	$-19.1 \pm 0.3$	-19.7 to -18.7
	HY	blood	98	33	$15.9 \pm 0.4$	14.7 to 17.5	4.3	$-19.6 \pm 0.4$	-20.4 to -18.1
	HY	muscle	97	10	$15.6 \pm 0.2$	15.3 to 15.9	4.4	$-19.6 \pm 0.2$	-19.9 to -19.2
	HY	muscle	98	33	$15.9 \pm 0.4$	14.6 to 17.1	4.5	$-19.4 \pm 0.4$	-19.9 to -18.4
Glaucous Gull	HY	blood	97	3	$16.5 \pm 0.2$	16.3 to 16.6	4.5	$-19.1 \pm 0.2$	-19.3 to -18.9
	HY	blood	98	13	$17.0 \pm 0.7$	16.2 to 18.1	4.6	$-19.1 \pm 0.4$	-19.7 to -18.4
	AD	muscle	98	4	$14.5 \pm 0.2$	14.3 to 14.7	4.1	$-18.2 \pm 0.3$	-18.5 to -17.9
Hakluyt Island									
	Black-legged Kittiwake								
	AD	blood	98	12	$15.4 \pm 1.2$	13.4 to 17.1	4.2	$-20.2 \pm 0.6$	-21.1 to -19.5
	HY	blood	98	13	$15.3 \pm 0.8$	13.8 to 16.5	4.1	$-20.2 \pm 0.3$	-20.6 to -19.8
Dovekie	HY	blood	97	13	$15.1 \pm 0.6$	14.1 to 16.4	4.1	$-20.3 \pm 0.5$	-21.4 to -19.4
	AD	liver	96	27	$13.6 \pm 0.5$	12.0 to 14.1	3.9	$19.2 \pm 0.4$	-20.2 to -18.6
	AD	muscle	98	32	$12.5 \pm 0.5$	12.0 to 13.8	3.6	$19.3 \pm 0.4$	-20.1 to -18.5
	AD	blood	97	10	$13.2 \pm 0.1$	12.9 to 13.4	3.6	$-19.2 \pm 0.2$	-19.6 to -19.0
Thick-billed Murre	AD	blood	98	20	$15.3 \pm 0.8$	13.8 to 17.5	4.1	$-19.2 \pm 0.5$	-21.1 to -18.5
	HY	blood	98	14	$14.4 \pm 0.4$	13.0 to 15.6	3.9	$-19.5 \pm 0.3$	-19.9 to -18.9
	AD	muscle	97	9	$15.2 \pm 0.4$	14.4 to 15.5	4.3	$-19.3 \pm 0.1$	-19.3 to -19.0
	AD	liver	97	9	$16.8 \pm 0.4$	16.0 to 17.5	4.7	$-19.0 \pm 0.2$	-19.3 to -18.6
Glaucous Gull	HY	blood	97	12	$15.5 \pm 1.0$	13.2 to 17.4	4.2	$-18.6 \pm 0.3$	-18.9 to -18.0
	HY	blood	98	9	$15.8 \pm 0.5$	13.4 to 16.8	4.3	$-19.2 \pm 0.2$	-19.5 to -18.8

TABLE 2. Comparison of mean ( $\pm$  SD) isotopic value for food web components collected within 60 km of Coburg and Hakluyt Islands, showing similarity between local food webs. Sample size refers to number of sampling stations within range of each colony. Each sample represents a bulk sample consisting of several ( $>5$ ) individuals.

Species	Colony	<i>n</i>	$\delta^{15}\text{N}$ (‰)	Range (‰)	$\delta^{13}\text{C}$ (‰)	Range (‰)
<i>Calanus hyperboreus</i>	Hakluyt	5	$6.9 \pm 0.3$	6.3 to 7.3	$-23.2 \pm 0.5$	-23.6 to -22.3
	Coburg	12	$7.2 \pm 0.6$	6.5 to 8.3	$-23.1 \pm 0.7$	-24.5 to -22.4
<i>Metridia longa</i>	Hakluyt	3	$8.7 \pm 0.5$	8.5 to 9.3	$-23.3 \pm 0.3$	-23.7 to -22.9
	Coburg	7	$9.1 \pm 0.3$	8.8 to 9.2	$-23.2 \pm 0.2$	-24.0 to -22.9
<i>Themisto libellula</i>	Hakluyt	3	$9.5 \pm 1.1$	8.8 to 10.0	$-22.9 \pm 0.4$	-23.4 to -22.7
	Coburg	26	$9.7 \pm 1.2$	5.7 to 11.6	$-22.1 \pm 0.8$	-24.5 to -20.7
<i>Boreomysis arcticus</i>	Hakluyt	8	$10.2 \pm 0.4$	9.7 to 11.3	$-22.6 \pm 0.3$	-23.5 to -22.0
	Coburg	32	$10.3 \pm 0.4$	9.2 to 11.3	$-22.9 \pm 0.6$	-24.2 to -21.5
<i>Euchaeta glacialis</i>	Hakluyt	3	$11.6 \pm 0.6$	10.9 to 12.2	$-24.3 \pm 0.5$	-24.9 to -23.9
	Coburg	5	$11.7 \pm 0.4$	11.4 to 11.9	$-24.1 \pm 0.4$	-24.8 to -23.7
<i>Clione</i> sp.	Hakluyt	4	$9.3 \pm 1.0$	8.0 to 10.0	$-24.5 \pm 1.5$	-26.0 to -22.9
	Coburg	5	$9.5 \pm 0.5$	8.9 to 10.2	$-26.4 \pm 1.3$	-28.2 to -25.1
Chaetognaths	Hakluyt	5	$10.5 \pm 0.9$	10.1 to 11.6	$-22.8 \pm 0.7$	-23.7 to -21.9
	Coburg	16	$10.1 \pm 0.6$	8.9 to 10.9	$-23.4 \pm 0.5$	-24.5 to -22.5

the tissue of interest. For this reason, in order to evaluate trophic level of seabirds, we used a model based on  $\delta^{15}\text{N}$  values which incorporated tissue-dependent isotopic relationships (Hobson 1993). This allowed the comparison of seabirds for which we had isotopic values for different tissue types using the common currency of trophic level. We obtained sufficient samples of invertebrates from east and west sides of the polynya to allow us to evaluate the isotopic similarity of food webs involving seabirds at Hakluyt and Coburg Islands. We assigned the copepod *Calanus hyperboreus* a trophic level of 2.0 (Hobson and Welch 1992) and used a diet-tissue isotopic fractionation factor of 2.4‰ for seabird muscle, 2.3‰ for liver (Mizutani et al. 1990) and 3.1‰ for blood (Hobson and Clark 1993). Trophic level was derived according to the relationship developed in Hobson et al. (1994). This was based on the assumption that a bird feeding exclusively on *C. hyperboreus* would occupy TL 3.0 and have a tissue  $\delta^{15}\text{N}$  value of  $\delta^{15}\text{N}_c + \Delta_{dt}$ , where  $\delta^{15}\text{N}_c$  is the isotopic ratio corresponding to *C. hyperboreus*, and  $\Delta_{dt}$  the isotopic fractionation factor between seabird tissue and diet. Thus:

$$\text{TL}_{\text{bird}} = 3 + \frac{[\delta^{15}\text{N}_t - (\delta^{15}\text{N}_c + \Delta_{dt})]}{3.8} \quad (1)$$

where  $\delta^{15}\text{N}_t$  is the stable-nitrogen isotope ratio of bird tissue and 3.8 corresponds to the average trophic enrichment factor expected for arctic marine food webs (Hobson and Welch 1992).

Our extensive analysis of food web components in the NOW indicates that the best average value for *C. hyperboreus* is 7.9‰ ( $n = 80$ ) with little variation between Hakluyt and Coburg regions (Table 2; Hobson et al., in press). Our TL values for birds feeding exclusively on diets of *C. hyperboreus*, the amphipod *Themisto libellula* (mean polynya  $\delta^{15}\text{N} = 9.7 \pm 0.1$ ‰,  $n = 106$ ), and *Boreogadus saida* (arctic cod, mean ( $\delta^{15}\text{N} = 14.0 \pm 0.2$ ‰,  $n = 8$ ) are 3.0, 3.5 and 4.6, respectively. For statistical comparisons, we converted  $\delta^{15}\text{N}$  data to trophic level and used ANOVA with a level of significance of  $P < 0.05$ . Means are presented  $\pm$  SD.

## RESULTS

### TROPHIC LEVEL

Seabird trophic level varied among species and age class and also between colonies (Fig. 2). At Coburg Island, Black Guillemots showed no difference in patterns of trophic level between years ( $F_{1,66} = 0.3$ ,  $P = 0.61$ ; Table 1). Their diet did differ within a breeding season, where short-term diets inferred from liver data indicated higher trophic level than longer-term diets inferred from muscle data ( $F_{1,66} = 11.7$ ,  $P = 0.001$ ).

The overall trophic-level model for Black-legged Kittiwakes including year, age, colony, and tissue was significant ( $F_{8,152} = 20.4$ ,  $P < 0.001$ ) with all effects significant ( $P < 0.014$  for all cases) but tissue ( $F_{2,152} = 1.5$ ,  $P = 0.24$ ). No statistical difference in tissue suggests that there

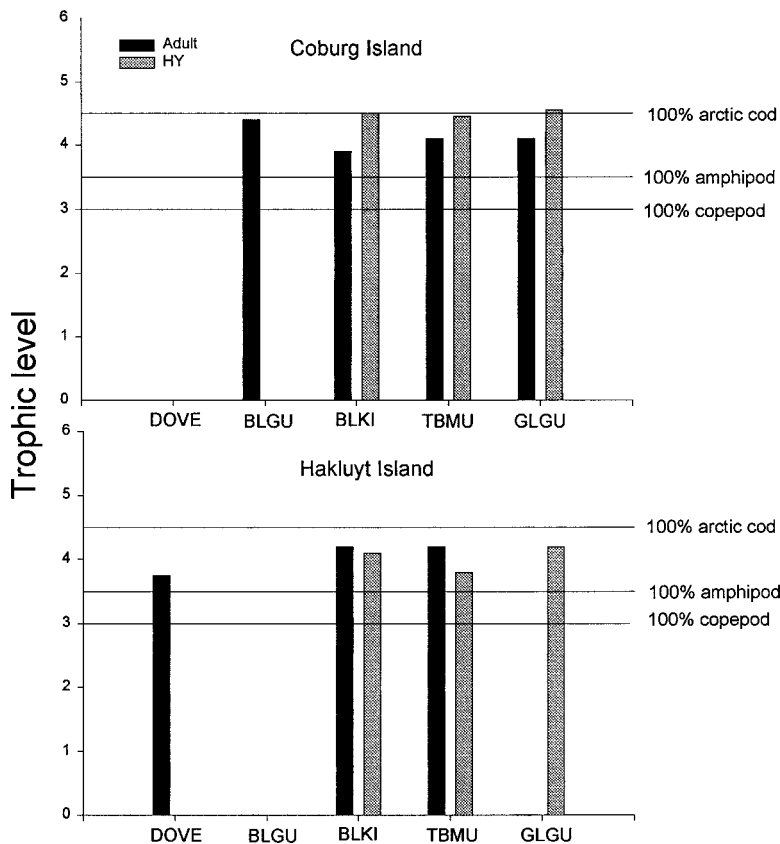


FIGURE 2. Trophic relationships among seabirds from Coburg (west of the polynya) and Hakluyt (east of the polynya) Islands. For reference, the horizontal lines indicate the positions a hypothetical seabird would occupy if its diet consisted of 100% of the indicated prey item. Data for blood and muscle were combined to give estimates of average breeding-season trophic position, and these estimates were averaged over the two years of the study. BLGU = Black Guillemot, BLKI = Black-legged Kittiwake, DOVE = Dovekie, GLGU = Glaucous Gull, TBMU = Thick-billed Murre.

was no trophic shift among kittiwakes within a breeding season. A significant interaction was found between colony and age ( $P = 0.02$ ), since at Coburg HY birds had significantly higher trophic level than adults ( $F_{1,114} = 64.1$ ,  $P < 0.001$ ). This pattern was not seen at Hakluyt ( $F_{1,38} = 0.1$ ,  $P = 0.82$ ). At Coburg, adult kittiwakes had significantly higher trophic level in 1998 compared with 1997 ( $F_{1,114} = 9.9$ ,  $P = 0.002$ ). No year effects were noted at Hakluyt ( $F_{1,38} = 0.3$ ,  $P = 0.59$ ).

Our trophic model for Thick-billed Murres was significant ( $F_{14,233} = 50.3$ ,  $P < 0.001$ ). All effects with the exception of colony ( $P = 0.14$ ) were significant at  $P < 0.005$ . The only significant interaction was between age and tissue ( $P = 0.04$ ). At Coburg, age had a significant effect

on murre trophic level ( $F_{1,176} = 95.3$ ,  $P < 0.001$ ) with higher relative trophic level for HY birds compared to adults. At Hakluyt, we found an opposite effect with HY birds occupying lower relative trophic level compared to adults ( $F_{1,57} = 20.7$ ,  $P < 0.001$ ). Tissue of Hakluyt birds also significantly influenced trophic level ( $F_{2,57} = 4.7$ ,  $P = 0.01$ ), an effect driven by the high adult trophic level inferred from liver data compared to other tissues. Sculpins ( $n = 9$ ) brought to murre chicks had a mean  $\delta^{15}\text{N}$  value of  $15.2 \pm 0.7\%$  and a mean  $\delta^{13}\text{C}$  value of  $-19.1 \pm 1.0\%$ . Our food web model placed sculpins at TL 4.9.

The overall model for Glaucous Gull was significant ( $F_{4,41} = 9.2$ ,  $P < 0.001$ ), and this was driven by colony differences ( $F_{1,41} = 14.9$ ,  $P < 0.001$ ). HY birds at Hakluyt occupied a lower



trophic position than HY birds at Coburg ( $F_{1,35} = 5.1$ ,  $P < 0.001$ ). In turn, HY birds at Coburg had higher trophic positions compared to adults at Coburg ( $F_{1,20} = 25.4$ ,  $P < 0.001$ ).

Dovekie adults from Hakluyt Island showed higher short-term trophic level based on liver compared to those based on muscle or blood tissues ( $F_{6,79} = 24.1$ ,  $P < 0.001$ ).

#### STABLE-CARBON ISOTOPE

In contrast to our seabird  $\delta^{15}\text{N}$  data,  $\delta^{13}\text{C}$  values showed less variation within and among species (Table 1). Our overall model that included species, year, colony, age, and tissue was significant ( $F_{39,589} = 27.3$ ,  $P < 0.001$ ) with significant effects of species ( $F_{4,589} = 106.7$ ,  $P < 0.001$ ) and year ( $F_{1,589} = 7.4$ ,  $P = 0.001$ ), and significant interactions between species and year ( $P < 0.001$ ), species and age ( $P < 0.001$ ), year and age ( $P = 0.02$ ), and species and tissue ( $P < 0.001$ ). Considering a model including only the effects of species and year, we determined that Black-legged Kittiwakes had lower  $\delta^{13}\text{C}$  values than all other species (mean  $\pm$  SD:  $-19.7 \pm 0.6\text{‰}$ ,  $n = 152$ ), Dovekie and Thick-billed Murre did not differ from each other but differed from all other species (both means  $-19.3 \pm 0.5\text{‰}$ ,  $n = 79$  and  $251$ , respectively) and Glaucous Gull and Black Guillemots had similar  $\delta^{13}\text{C}$  values (mean  $-18.9 \pm 0.4\text{‰}$ ,  $n = 41$ , and  $-18.6 \pm 0.5\text{‰}$ ,  $n = 66$ , respectively) that were higher than all other species. Year effects on  $\delta^{13}\text{C}$  values were slight with 1997 having lower values than 1998 on average by  $0.2\text{‰}$ .

#### DISCUSSION

Our study follows from previous isotopic attempts to understand trophic interactions of seabirds in high-latitude marine environments (Rau et al. 1992, Hobson 1993, Hobson et al. 1994, 1995, Hodum and Hobson 2000). Using stable isotope analyses of various tissues from five seabird species breeding at Coburg and Hakluyt Islands, we compared diet among these colonies and between age classes within species. This approach was possible because we confirmed that the isotopic signatures of both food webs were comparable (Table 2) and we used tissue-specific models to calculate trophic level, thus allowing several tissue types to be considered. Although such an approach depends on assumptions concerning isotopic fractionation factors between diet and various bird tissues, these were

based on captive-rearing studies and are simply the best estimates we have currently (Mizutani et al. 1990, Hobson and Clark 1992, Hobson and Welch 1992). Further studies may provide the opportunity to modify our present estimates. Below, we consider dietary insights provided for each species.

#### BLACK GUILLEMOT

Data on this species were available only for adults from Coburg Island. In both years, we found an identical pattern of liver tissue predicting higher trophic level than muscle tissue. Because liver represents a short-term dietary integration over about a week and muscle over a few months (Hobson and Clark 1993), we interpret this to indicate that guillemots feed to a greater degree on invertebrates earlier in the season and then switch to more fish during the breeding period. Invertebrates associated with ice pans or ice edges are expected to be more abundant or available to seabirds earlier in the season than during breeding (e.g., Bradstreet 1980). Hobson (1993) similarly determined that guillemots breeding in Lancaster Sound showed increasing relative trophic level from spring through the breeding season when benthic fish were common in diets. Benthic foraging was also suggested by the generally enriched  $\delta^{13}\text{C}$  values of guillemots compared to Dovekie, kittiwakes, and murre. Previous observations of 30 feedings to Black Guillemot chicks on Coburg Island in 1998 (separate birds) support our isotopic data (24 sculpins, 2 Greenland shrimp [*Pandalus borealis*], 2 gunnells [Pholidae], 1 capelin [*Mallotus villosus*], and 1 arctic cod; Robards et al. 2000).

#### BLACK-LEGGED KITTIWAKE

Adult kittiwakes breeding on Coburg Island occupied the lowest relative trophic level of all birds examined there. Their trophic level of 4.0 was consistent with a diet of secondary (carnivorous) zooplankton or a mixture of primary zooplankton (e.g., copepods) and tertiary fish (e.g., arctic cod). We noted that many stomachs contained mysids (*Mysis oculata*) and these were modeled as TL 2.7 for the NOW by Hobson et al. (in press). Thus, an exclusive diet of mysids would result in kittiwakes occupying TL 3.7.

Chicks occupied a higher relative trophic level than adults on Coburg Island, a result found previously for kittiwakes nesting on Browne Is-

land, Nunavut, Canada (Hobson 1993). The chick trophic level of 4.5 would be consistent with an exclusive diet of arctic cod (Hobson and Welch 1992, Hobson et al., in press). This suggests that adults selectively fed fish to their young, while consuming more invertebrates themselves. The pattern of differential provisioning of chicks was not apparent at the Hakluyt colony where adults and chicks both occupied a lower trophic position. Our data suggest that adult kittiwakes at Hakluyt and Coburg occupied a similar relative trophic level, but chicks at Hakluyt consumed more invertebrates than chicks at Coburg. The relatively low  $\delta^{13}\text{C}$  values of Hakluyt kittiwakes compared to other species there suggests kittiwakes generally fed on more offshore or pelagic prey, especially compared with guillemots at Coburg and Glaucous Gulls at both sites.

#### THICK-BILLED MURRE

On Coburg Island, adult murres occupied a relative trophic level of about 4.0 during both years, suggesting significant input of invertebrates in addition to planktivorous fish such as arctic cod. In contrast, chicks were fed higher trophic-level prey (mean prey TL 3.7), reflecting their observed diet which was dominated by arctic cod (Gilchrist et al., unpubl. data). This pattern was seen previously for this species nesting on Prince Leopold Island, Nunavut, where it was assumed that adults fed themselves more *Themisto libellula* amphipods and preferentially provisioned their chicks arctic cod (Hobson 1993).

Thick-billed Murres nesting on Hakluyt Island showed a different pattern to those on Coburg. While adult trophic level was about the same in 1997, suggesting a diet which included amphipods, it was significantly higher at Hakluyt in 1998, at least in the short term, as evidenced by analysis of liver tissue. In addition, in 1997, we found no evidence that chicks were fed higher trophic-level prey compared with adults. Preliminary analyses of chick-feeding observations confirmed that at Hakluyt Island sculpins and blennies (*Lumpenus* sp.) made up about one-third of the chick meals, while hardly any species other than arctic cod were noted at Coburg Island (Gilchrist et al., unpubl. data). Similarly, adult diet in a sample from 1997 consisted mainly of arctic cod but with about 12% (by number) of prey being sculpins (Falk, un-

publ. data). Based on isotope data, sculpins were higher in trophic level than arctic cod (4.9 vs. 3.6), and their inclusion in the diet would result in higher murre TL and more enriched  $\delta^{13}\text{C}$  values. This would explain higher TL of Hakluyt adult murres in 1997. However, our estimate of Hakluyt chick TL of 3.9 in 1998 suggests little sculpin in the diet.

#### GLAUCOUS GULL

Adult Glaucous Gulls breeding on Coburg Island had a similar trophic level to murres and kittiwakes. Again we found evidence for adults provisioning chicks higher trophic-level prey than adults consumed themselves, a phenomenon recorded also at Prince Leopold Island (Hobson 1993). Gulls breeding solitarily at seabird colonies are typically specialist feeders on the eggs and chicks of other seabirds such as murres and kittiwakes (Gilchrist and Gaston 1997, Gilchrist et al. 1998). However, that Glaucous Gull chicks had a similar trophic level to murre chicks suggests that gull chick diets were a combination of murre eggs, marine fish, and invertebrates with perhaps only occasional murre or kittiwake chicks. This pattern may change as gull chicks grow and more murre or kittiwake chicks become available. The generally enriched  $\delta^{13}\text{C}$  values for Glaucous Gull reflects either more inshore foraging (as with the Black Guillemot) or the consumption of higher trophic-level prey, or a combination of these factors.

At Hakluyt, we were able to obtain data only for Glaucous Gull chicks. Their trophic level of 4.2 was comparable to those of adult murres and kittiwakes at this colony, but we have no evidence that they were provisioned higher trophic-level prey compared to adults. We observed that Glaucous Gulls at Hakluyt Island, including the large chicks, fed extensively on adult Dovekies. Because gull TL was not a full step higher than that of Dovekies, gull chicks were fed lower TL prey as well.

#### DOVEKIE

Dovekies were available only from Hakluyt Island on the Greenland side. As expected, this largely planktivorous alcid occupied the lowest trophic position of all seabirds examined. The higher trophic level found for liver vs. muscle or blood suggests that, at the time of collection, birds had switched to a diet containing more sec-



ondary zooplankton, likely from *Calanus hyperboreus* (TL 2.0) to one containing more *C. glacialis* (TL 2.3) or *Themisto libellula* (TL 2.5; Hobson et al., in press). In fact, a relative increase in the proportion of *C. glacialis* compared to *C. hyperboreus* was recorded in the chick diet at Hakluyt Island as the season progressed (Pedersen and Falk 2001). The generally lower  $\delta^{13}\text{C}$  values compared to other species reflects the more consistent pelagic foraging behavior of this species.

#### IMPLICATIONS

Based on our isotopic investigations and personal observation of stomach samples, invertebrates such as mysids, copepods, and amphipods constituted a large percentage of the diets of adult seabirds using the North Water Polynya. This finding agrees with previous studies of other high-latitude seabird communities (Rau et al. 1992, Hobson and Welch 1992, Hobson 1993, Hobson et al. 1994). In relatively simple Arctic marine food webs, the exploitation of lower trophic-level prey is likely a more stable strategy than specialization on higher trophic-level prey that may fluctuate in abundance or be more unpredictable in time and space (Sanger 1987). With the exception of Dovekie and possibly Glaucous Gull, all of the seabirds we examined in the NOW show an ability to readily exploit invertebrates as well as fish. This lack of dietary specialization may provide greater stability in such stochastic environments. Nevertheless, murres, kittiwakes, and gulls at Coburg Island provisioned their chicks higher trophic-level prey than they fed themselves, suggesting that the role of arctic cod at that colony was a significant determinant of annual breeding success as it is at Prince Leopold Island, Nunavut (Gaston and Nettleship 1981, Hobson 1993). Other studies have similarly noted trophic segregation between adults and chicks (Hobson 1993, Hodum and Hobson 2000, Forero et al., in press), and this is undoubtedly related to the need for high-nutrition foods for growing chicks compared with adults. Both the nature of the prey species and their fat and caloric contents have been identified as factors influencing growth rates of two species of albatross (Prince and Ricketts 1981) and the chicks of Jackass (*Spheniscus demersus*) and Yellow-eyed Penguins (*Me-gadyptes antipodes*; Heath and Randall 1985, van Heezik and Davis 1990).

Recent investigations of arctic cod in the NOW suggest that this prey species may be more abundant on the west side of the polynya and may favor shallow banks to the northeast of Coburg Island, within foraging range of murres and other seabirds breeding there (Ringuette et al., unpubl. data). Thus, although phytoplankton and zooplankton blooms occur earlier on the east side of the NOW compared to the west side (Mei et al., unpubl. data), factors occurring later in the season, namely movement and availability of arctic cod, may ultimately influence foraging behavior or energetics of birds provisioning chicks. For example, among chicks of kittiwakes, murres, and gulls occurring on both sides of the polynya, those on the east side generally fed at lower trophic levels compared with those on the west. The early opening of the polynya on the east side may favor invertebrate populations that exploit earlier carbon fixation through phytoplankton growth compared to the west side. However, while an earlier pulse in invertebrate biomass on the east side favors the zooplanktivorous Dovekie, adult kittiwakes and murres may be at a disadvantage during the chick-rearing stage, when arctic cod is not available for chicks. In place of arctic cod on the east side of the polynya, sculpins may be used by adult murres and chicks in some years, but such prey likely require different foraging strategies. This is supported by findings that foraging effort was higher for chick-rearing Thick-billed Murres at Hakluyt Island than for Coburg birds in 1998 (Falk et al., in press). Finally, our findings indicate that in addition to accounting for differences between age groups within species, a generalized trophic model for seabirds using the North Water Polynya should ideally be refined to include trophic differences between east and west sectors.

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## LITERATURE CITED

- BARBER, D., R. MARSDEN, P. MINNETT, G. INGRAM, AND L. FORTIER. 2001. Physical processes within the North Water (NOW) Polynya. *Atmosphere-Ocean* 39:163–166.
- BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1981. Reproductive biology of Thick-billed Murres (*Uria lomvia*): an inter-colony comparison. *Auk* 98:258–269.
- BRADSTREET, M. S. W. 1980. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. *Canadian Journal of Zoology* 58:2120–2140.
- CHEREL, Y., K. A. HOBSON, AND H. WEIMERSKIRCH. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* 122:155–162.
- FALK, K., S. BENVENUTI, L. DALL'ANTONIA, G. GILCHRIST, AND K. KAMPP. In press. Foraging behaviour of Thick-billed Murres breeding in different sectors of the North Water Polynya: an inter-colony comparison. *Marine Ecology Progress Series*.
- FALK, K., AND K. KAMPP. 1997. A manual for monitoring Thick-billed Murre populations in Greenland. Technical Report No. 8, Greenland Institute of Natural Resources, Nuuk, Greenland.
- FORERO, M. G., K. A. HOBSON, G. R. BORTOLOTTI, J. A. DONAZAR, M. BERTELOTTI, AND G. BLANCO. In press. Food resource utilization by Magellanic Penguin evaluated through stable isotope analysis: segregation by sex and age and influence on offspring quality. *Marine Ecology Progress Series*.
- FRANCE, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series* 124:307–312.
- FRY, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* 33:1182–1190.
- GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island—a study of the breeding ecology of a colonial high arctic seabird. *Canadian Wildlife Service Monograph Series* No. 6, Ottawa, Ontario, Canada.
- GILCHRIST, H. G., AND A. J. GASTON. 1997. Effects of murre nest site characteristics and wind conditions on predation by Glaucous Gulls. *Canadian Journal of Zoology* 75:518–524.
- GILCHRIST, H. G., A. J. GASTON, AND J. N. M. SMITH. 1998. Wind and prey nest sites as foraging constraints on an avian predator, the Glaucous Gull. *Ecology* 79:2403–2414.
- HEATH, R. G. M., AND R. M. RANDALL. 1985. Growth of Jackass Penguin chicks (*Spheniscus demersus*) hand reared on different diets. *Journal of Zoology (London)* 205:91–105.
- HOBSON, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Marine Ecology Progress Series* 95:7–18.
- HOBSON, K. A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. *Condor* 97:752–762.
- HOBSON, K. A., W. G. AMBROSE JR., AND P. E. RENAUD. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Marine Ecology Progress Series* 128:1–10.
- HOBSON, K. A., AND R. G. CLARK. 1992. Assessing avian diets using stable isotopes. I: turnover of carbon-13. *Condor* 94:181–188.
- HOBSON, K. A., AND R. G. CLARK. 1993. Turnover of  $^{13}\text{C}$  in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. *Auk* 110:638–641.
- HOBSON, K. A., A. T. FISK, N. KARNOVSKY, M. HOLST, J.-M. GAGNON, AND M. FORTIER. In press. A stable isotope ( $^{13}\text{C}$ ,  $^{15}\text{N}$ ) model for the North Water Polynya foodweb: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep Sea Research*.
- HOBSON, K. A., H. L. GIBBS, AND M. L. GLOUTNEY. 1997. Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. *Canadian Journal of Zoology* 75:1720–1723.
- HOBSON, K. A., K. D. HUGHES, AND P. J. EWINS. 1997. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. *Auk* 114:467–478.
- HOBSON, K. A., AND W. A. MONTEVECCHI. 1991. Stable isotopic determinations of trophic relationships of Great Auk. *Oecologia* 87:528–531.
- HOBSON, K. A., J. F. PIATT, AND J. PITOCHELLI. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63:786–798.
- HOBSON, K. A., AND H. E. WELCH. 1992. Determination of trophic relationships within a high Arctic marine food web using stable-isotope analysis. *Marine Ecology Progress Series* 84:9–18.
- HODUM, P. J., AND K. A. HOBSON. 2000. Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analysis. *Marine Ecology Progress Series* 198:273–281.
- MELLING, H., Y. GRATTON, AND G. INGRAM. 2001. Oce-

- anic circulation within the North Water Polynya in Baffin Bay. *Atmosphere-Ocean* 39:301–325.
- MICHENER, R. H., AND D. M. SCHELL. 1994. Stable isotope ratios as tracers in marine and aquatic food webs, p. 138–157. *In* K. Lajtha and R. H. Michener [EDS.], *Stable isotopes in ecology and environmental science*. Blackwell Scientific Publications, Oxford, UK.
- MINAGAWA, M., AND E. WADA. 1984. Stepwise enrichment of  $\delta^{15}\text{N}$  along food chains: further evidence and the relation between  $\delta^{15}\text{N}$  and animal age. *Geochimica et Cosmochimica Acta* 48:1135–1140.
- MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Stable-carbon isotope ratios of feathers reveals feeding behavior of cormorants. *Auk* 107: 400–403.
- PEDERSEN, C. E., AND K. FALK. 2001. Chick diet of Dovekies *Alle alle* in northwest Greenland. *Polar Biology* 24:53–58.
- PRINCE, P. A., AND C. RICKETTS. 1981. Relationships between food supply and growth in albatrosses: an interspecies cross-fostering experiment. *Ornis Scandinavica* 12:207–210.
- RAU, G. H., D. G. AINLEY, J. L. BENGSTON, J. J. TORRES, AND T. L. HOPKINS. 1992.  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$  in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Marine Ecology Progress Series* 84:1–8.
- ROBARDS, M., H. G. GILCHRIST, AND K. ALLARD. 2000. Breeding Atlantic Puffins, *Fratercula arctica*, and other bird species of Coburg Island, Nunavut. *Canadian Field Naturalist* 114:72–77.
- SANGER, G. A. 1987. Trophic levels and trophic relationships of seabirds in the Gulf of Alaska, p. 229–257. *In* J. P. Croxall [ED.], *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, UK.
- STIRLING, I. 1980. The biological importance of polynyas in the Canadian Arctic. *Arctic* 33:303–315.
- STIRLING, I., AND H. CLEATOR. 1981. Polynyas in the Canadian Arctic. Canadian Wildlife Service Occasional Papers No. 45, Ottawa, Ontario, Canada.
- THOMPSON, D. R., AND R. W. FURNESS. 1995. Stable isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in Northern Fulmars. *Auk* 112:493–498.
- THOMPSON, D. R., R. W. FURNESS, AND S. A. LEWIS. 1995. Diets and long-term changes in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Northern Fulmars (*Fulmaris glacialis*) from two northeast Atlantic colonies. *Marine Ecology Progress Series* 125:3–11.
- VAN HEEZIK, Y., AND L. DAVIS. 1990. Effects of food variability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*. *Ibis* 132:354–365.