

TROPHIC RELATIONSHIPS AMONG SIX SPECIES OF ICELANDIC SEABIRDS AS DETERMINED THROUGH STABLE ISOTOPE ANALYSIS¹

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Abstract. Stable-nitrogen and carbon isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were determined in liver tissue samples from six species of Icelandic seabirds. Stomach contents were primarily capelin (*Mallotus villosus*) in north Iceland, and primarily sandlance (*Ammodytes* sp.) in south Iceland. Stable isotope signatures also were measured in a range of typical prey species, including capelin and sandlance. Combined isotopic signatures in seabirds exhibited significant inter-species and inter-site variation. Similarly, combined isotope signatures differed significantly between prey species. The trophic relationships of the six seabird species differed between the two sites. Northern Fulmars (*Fulmarus glacialis*) exhibited a relatively depleted mean $\delta^{13}\text{C}$ value in the north, but the reverse was true in the south. We used a dual-isotope multiple-source mixing model to estimate contributions of different prey species to the diet of seabirds based on their isotope signatures. Whereas the general patterns of proportions of different prey in seabirds' diets in the north and south produced by the model supported conventionally-collected dietary data, the importance of some relatively rare prey species tended to be overestimated.

Key words: dietary analysis, mixing model, Icelandic seabird, stable isotopes, trophic relationships.

Analysis of trophic relationships within a seabird community through conventional dietary assessment can be potentially difficult and daunting (Sanger 1987). Furthermore, conventional dietary assessment tech-

niques, including analyses of stomach contents or of indigestible prey remains in regurgitated or fecal pellets, can introduce bias. Prey composition determined by these methodologies will depend in part on the digestibility of particular prey types, hard-bodied and relatively indigestible prey often being over-estimated compared to soft-bodied and easily digestible prey (Duffy and Jackson 1986). However, studies of seabird diet, and hence trophic structure, can yield valuable information about fishery resources and oceanographic fluctuations (Montevecchi 1993).

Complimentary to conventional dietary assessment techniques, stable isotope analysis has been applied to a number of investigations of seabird diet and trophic relationships. This approach is based on the fact that the ratios of the stable isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$, conventionally expressed as $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) in consumer proteins reflect those in their prey in a predictable manner (DeNiro and Epstein 1978, 1981, Peterson and Fry 1987).

In the case of nitrogen, $\delta^{15}\text{N}$ signature exhibits a stepwise enrichment at each successive level within a food chain (Hobson et al. 1994, Sydeman et al. 1997), such that predators occupying relatively high trophic positions have correspondingly elevated $\delta^{15}\text{N}$ values. For carbon, $\delta^{13}\text{C}$ values may also show a tendency to increase with trophic level, but to a lesser degree than to that of $\delta^{15}\text{N}$ (Fry and Sherr 1984, Hobson and Welch 1992). However, the $\delta^{13}\text{C}$ value can provide information about the source of carbon entering a food chain, for example distinguishing between marine and freshwater systems (Mizutani et al. 1990, Hobson and Sealy 1991, Smith et al. 1996), or discriminating between inshore/benthic feeding and pelagic feeding in seabirds (Hobson 1993, Hobson et al. 1994, Sydeman et al. 1997).

Multiple stable isotope analyses which have been applied to investigations of entire seabird communities

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have yielded important and novel insights into intra- and inter-species trophic relationships, and have defined trophic interactions on both spatial and temporal scales (Hobson et al. 1994, Thompson et al. 1995). Dual-isotope multiple-source mixing models have been developed to quantify the proportions of various prey in the diet of American martens (*Martes americana*) (Ben-David et al. 1997) and Glaucous Gulls (*Larus hyperboreus*) (Schmutz and Hobson 1998), further enhancing the role of stable isotope analysis in studies of diet and community trophic structure.

Here we present nitrogen and carbon stable-isotope data for seabird species from north and south Iceland. Previous work, based on conventional methodologies, demonstrated that the summer diets of these seabirds differed markedly between these two regions and reflected differences in local prey availability. Sandlance (*Ammodytes* sp.) predominated in the diet of most seabird species in the south, whereas capelin (*Mallotus villosus*) was the predominant prey of most seabird species in the north (Lilliendahl and Solmundsson 1997). Specifically, we test whether stable isotope analysis confirms the dietary patterns found using conventional techniques (Lilliendahl and Solmundsson 1997), and we compare seabird diet measured conventionally with the output of dual-isotope multiple-source mixing models.

METHODS

SAMPLE COLLECTION AND PREPARATION

Seabirds analyzed in this study were collected from north and south Iceland during the breeding season as part of a large investigation into Icelandic seabird diets as described by Lilliendahl and Solmundsson (1997). Species analyzed were Common Murre (*Uria aalge*), Thick-billed Murre (*U. lomvia*), Razorbill (*Alca torda*), Atlantic Puffin (*Fratercula arctica*), Black-legged Kittiwake (*Rissa tridactyla*), and Northern Fulmar (*Fulmarus glacialis*). From the large sample of birds described in Lilliendahl and Solmundsson (1997), 20 individuals (10 from the north and 10 from the south) were selected at random and transported frozen to Glasgow for further treatment. The only exception to this was for Northern Fulmar, for which there were nine individuals from the south. After thawing, liver tissue was excised, dried to constant mass in an oven at 50°C, then ground to an extremely fine powder using an impactor mill operating at liquid nitrogen temperature. Prior to stable isotope analysis, lipids were removed from dried and ground liver samples in a Soxhlet apparatus using refluxing chloroform as solvent. Lipid-free liver samples were re-dried as described above.

On the basis of previous conventional dietary studies of this group of seabirds, which revealed that in general seabirds in north Iceland fed predominantly on capelin and that seabirds in the south fed predominantly on sandlance (Lilliendahl and Solmundsson 1997), a representative selection of prey species were obtained from research vessels and commercial fishing operations. Whole fish species sampled were sandlance, from south Iceland, and capelin and redfish (*Sebastes marinus*) from the north. Additionally, intestines were removed from cod (*Gadus morhua*) col-

lected from a range of sites, and subsequently prepared for stable isotope analysis as fish offal. Two species of crustacean were sampled, northern shrimp (*Pandalus borealis*) and the euphausiid *Meganyctiphanes norvegica* mainly from north Iceland. Each whole individual fish, or cod intestine, was treated as an individual sample, whereas for the two crustacean species, some samples consisted of pooled individuals. For northern shrimp, four samples consisted of relatively large single individuals (3.3–7.8 g fresh mass), one sample contained two individuals of approximately 1.7 g fresh mass each, and a further three samples were each made up of four individuals of approximately 1.1 g fresh mass each. For *Meganyctiphanes*, each of three samples contained 10 individuals of approximately 0.3 g fresh mass each.

All prey samples were dried to constant mass as described above for seabird liver samples. Carbonates were removed from crustacean samples with excess 1N hydrochloric acid until bubbling ceased, and then re-dried. Dried prey samples were ground to a fine powder as described above, lipids removed using a Soxhlet apparatus with refluxing chloroform, and re-dried.

STABLE ISOTOPE ANALYSIS

All isotopic measurements were determined by continuous-flow isotope-ratio mass spectrometry (CF-IRMS) using a Finnigan Tracer Matt mass spectrometer. Isotope ratios are expressed conventionally as δ values in parts per thousand (‰), relative to Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric nitrogen ($\delta^{15}\text{N}$). All groups of analyses included reference materials (internal laboratory carbon standard [graphite] and International Atomic Energy Authority IAEA-N-2 nitrogen standard) for routine quality control and drift correction. All samples were determined in triplicate, with the outlying datum being discarded and the mean value calculated from the remaining two data points (Godley et al. 1998). Analytical precision was $\pm 0.2\text{‰}$ for carbon and $\pm 0.4\text{‰}$ for nitrogen.

DUAL-ISOTOPE MULTIPLE-SOURCE MIXING MODELS

We incorporated the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of each of the three main prey species (sandlance, capelin, and euphausiid; Lilliendahl and Solmundsson 1997) for the majority of seabirds into a dual-isotope three-source mixing model based on that outlined in Kline et al. (1993) and developed by Ben-David et al. (1997), in order to estimate the contribution of each prey to the diet of each individual seabird. Northern Fulmars were excluded from this model because conventional dietary information indicated that fish offal and other prey were relatively important in this species' diet (Lilliendahl and Solmundsson 1997).

The model requires that prey have statistically different isotope signatures and that each individual seabird consumes all possible prey types. Hence, relatively rare or unimportant prey types will be overestimated by the model, whereas relatively common or important prey types will be underestimated. For this reason, the output from the model represents an index of prey types consumed by the seabirds, rather than actual proportions of particular prey consumed. In order to calculate corrected prey isotope values, we applied diet

TABLE 1. Stable-nitrogen and carbon isotope signatures of liver tissue from Icelandic seabirds sampled in the north and south of the island, and results of ANOVA tests for significant differences between species' means following an overall MANOVA. Superscripts having at least one letter in common indicate no significant difference, Scheffé range tests, $P > 0.05$. Each sample consists of 10 individuals, except for Northern Fulmar from the south (9 individuals). Values are means \pm SE.

Species	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)	
	North	South	North	South
Common Murre	14.0 \pm 0.1 ^a	12.3 \pm 0.2 ^a	-19.5 \pm 0.2 ^{a,b,c}	-19.3 \pm 0.2 ^a
Thick-billed Murre	12.6 \pm 0.2 ^{b,c}	13.6 \pm 0.2 ^b	-20.0 \pm 0.2 ^{a,c}	-19.1 \pm 0.2 ^a
Razorbill	12.1 \pm 0.2 ^b	12.7 \pm 0.2 ^{a,b}	-19.1 \pm 0.2 ^b	-17.9 \pm 0.1 ^b
Atlantic Puffin	13.0 \pm 0.1 ^c	12.2 \pm 0.2 ^a	-19.2 \pm 0.1 ^{a,b}	-18.8 \pm 0.1 ^{a,b}
Black-legged Kittiwake	14.2 \pm 0.1 ^a	13.2 \pm 0.3 ^{a,b}	-20.1 \pm 0.1 ^c	-18.9 \pm 0.3 ^a
Northern Fulmar	14.0 \pm 0.2 ^a	13.5 \pm 0.1 ^b	-20.0 \pm 0.2 ^c	-18.6 \pm 0.2 ^{a,b}
1-way ANOVA	$F_{5,53} = 28.4$	$F_{5,53} = 7.3$	$F_{5,53} = 6.9$	$F_{5,53} = 6.1$
<i>P</i> -value	<0.001	<0.001	<0.001	<0.001

fractionation factors of +2.3‰ for nitrogen and +1.3‰ for carbon for sand lance and capelin, following results in Mizutani et al. (1991), and +2.8‰ for nitrogen and +1.9‰ for carbon for euphausiid, following results in Sydeman et al. (1997). Output from the model was averaged for each species and region (north and south) to produce overall mean percentage contributions of each prey type.

Additionally, we constructed a dual-isotope six-source mixing model to investigate dietary inputs in Northern Fulmars only. Here, all prey species were included in the model. All other aspects of the model were as described above.

STATISTICAL ANALYSES

Variation in stable isotope signatures between seabird species and locations and between prey species was tested using MANOVA, ANOVA, with Scheffé range tests, and Kruskal-Wallis tests. Differences in the pro-

portions of major prey species in the diets of seabirds between the north and south, produced by the three-source mixing model, were tested using ANOVA.

RESULTS

Stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) for all seabirds are presented in Table 1. Overall, there were significant effects of both species (MANOVA: Wilks' lambda, $F_{10,210} = 11.3$, $P < 0.001$) and location (Wilks' lambda, $F_{2,105} = 44.4$, $P < 0.001$) on the combined stable isotope signatures of Icelandic seabirds (Fig. 1). Generally, $\delta^{15}\text{N}$ values tended to be relatively enriched in seabirds from the north (maximum mean $\delta^{15}\text{N}$ value, 14.2‰ in Black-legged Kittiwakes) compared to seabirds in the south (maximum mean $\delta^{15}\text{N}$ value, 13.6‰ in Thick-billed Murres; Table 1). $\delta^{13}\text{C}$ values tended to be relatively enriched in seabirds from the south (maximum mean $\delta^{13}\text{C}$ value, -17.9‰ in Razorbills)

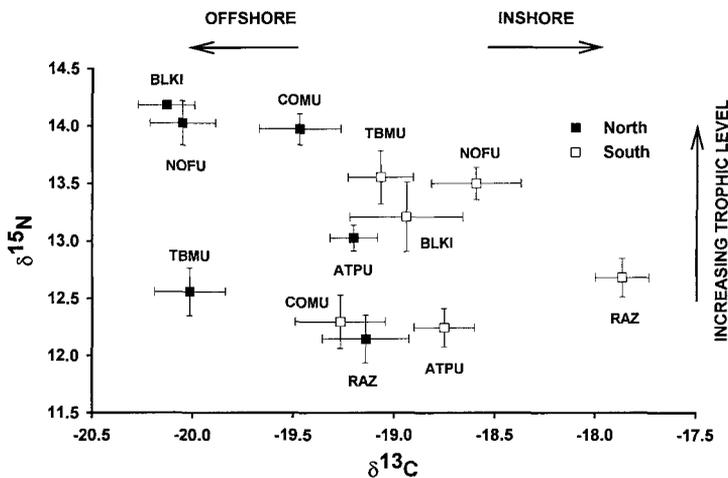


FIGURE 1. Trophic structure of the Icelandic seabird assemblage. Points are means (‰) \pm SE. Species abbreviations: COMU, Common Murre; TBMU, Thick-billed Murre; RAZ, Razorbill; ATPU, Atlantic Puffin; BLKI, Black-legged Kittiwake; NOFU, Northern Fulmar.

TABLE 2. Stable-nitrogen and carbon isotope signatures of selected prey species of Icelandic seabirds. Values are means \pm SE.

Species	<i>n</i>	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Sandlance	22	9.4 \pm 0.3	-18.8 \pm 0.2
Capelin	16	10.8 \pm 0.1	-21.3 \pm 0.3
Redfish	8	10.4 \pm 0.1	-19.9 \pm 0.1
Cod (intestines)	5	12.8 \pm 0.5	-18.4 \pm 0.9
Northern shrimp	8 ^a	11.0 \pm 0.1	-19.4 \pm 0.1
Euphausiid	3 ^b	7.6 \pm 0.2	-20.9 \pm 0.1

^a Each sample made up of between one and four individuals pooled.

^b Each sample made up of 10 individuals pooled (see Methods section).

compared to the north (maximum mean $\delta^{13}\text{C}$ value, -19.1‰ in Razorbills; Table 1).

There was no consistent pattern in isotope signatures in seabird species between the two locations, with the exception of Razorbills which exhibited the most enriched mean $\delta^{13}\text{C}$ values from both the north and the south (see above, Table 1, and Fig. 1). For example, Thick-billed Murres exhibited a relatively depleted mean $\delta^{15}\text{N}$ signature from the north (12.6‰), but a relatively enriched mean $\delta^{15}\text{N}$ value from the south (13.6‰; Table 1 and Fig. 1).

Stable isotope values for prey species are presented in Table 2. Overall, there was a significant effect of species on the combined stable isotope signature of prey (MANOVA: Wilks' lambda, $F_{10,110} = 19.6$, $P < 0.001$). Considered separately, $\delta^{15}\text{N}$ signatures varied significantly between prey species (Kruskal-Wallis one-way ANOVA: $\chi^2_5 = 33.1$, $P < 0.001$), as did $\delta^{13}\text{C}$ signatures ($\chi^2_5 = 37.8$, $P < 0.001$). Capelin had a more enriched mean $\delta^{15}\text{N}$ signature (10.8‰) than did sandlance (9.4‰; Table 2). Conversely, capelin exhibited a more depleted mean $\delta^{13}\text{C}$ signature (-21.3‰) than that in sandlance (-18.8‰; Table 2).

The mean percentage contributions of each of the three main prey species to the diet of seabirds from both locations, as produced by a dual-isotope three-source mixing model, are presented in Table 3. For all seabird species, the model indicated that capelin was significantly more important in the diet of seabirds from the north compared to seabirds from the south ($F_{1,90} = 38.1$, $P < 0.001$). The reverse was true for

sandlance ($F_{1,90} = 38.8$, $P < 0.001$). The model produced relatively low contributions of euphausiids (15–26%; Table 3) to the diet of all seabirds, with no clear pattern between the two locations ($F_{1,90} = 0.8$).

The output from the model incorporating all six prey species and Northern Fulmars as the only seabird revealed that capelin was the most important prey species in the north (39%), whereas northern shrimp was relatively important in the south (38%). Redfish was slightly more important in the south (22%) compared to the north (16%), whereas sandlance (10% at both north and south), euphausiids (5% at north, 8% at south), and cod intestines (9% at north, 11% at south) were of relatively minor importance at both locations.

DISCUSSION

TROPHIC STRUCTURE OF THE SEABIRD ASSEMBLAGE

Combined stable isotope signatures of Icelandic seabirds presented here (Table 1 and Fig. 1) exhibited significant inter-species and inter-site variation. The trophic structures of the seabird assemblages at north Iceland and south Iceland, as revealed by stable isotope analysis, were different, and may indicate dietary segregation not detected by conventional dietary assessment. For example, given the marked dietary differences between the two regions, in the north, Common Murres, Black-legged Kittiwakes, and Northern Fulmars occupied relatively high trophic positions, as indicated by relatively enriched mean $\delta^{15}\text{N}$ values, whereas in the south, Thick-billed Murre replaced Common Murre in this high trophic-level group. Additionally, relatively depleted $\delta^{13}\text{C}$ values indicate pelagic foraging in seabirds, and relatively enriched $\delta^{13}\text{C}$ values indicate inshore or benthic feeding (Hobson 1993, Hobson et al. 1994, Sydeman et al. 1997). Here again we found inter-site differences in the relative position on this pelagic-inshore scale as defined using $\delta^{13}\text{C}$ signature. For example, in the north, Black-legged Kittiwakes, Northern Fulmars, and Thick-billed Murres exhibited relatively depleted $\delta^{13}\text{C}$ signatures and can be considered pelagic foragers (Table 1 and Fig. 1). A recent study of Thick-billed Murres from the northwest of Iceland confirmed that this species forages relatively large distances (up to 168 km) from the breeding colony (Benvenuti et al. 1998). However,

TABLE 3. Mean percentages (\pm SE) of each prey in the diet of Icelandic seabirds as produced using a dual-isotope, three-source mixing model. Deviations from 100% are due to rounding.

Species	Area	Sandlance	Capelin	Euphausiid
Common Murre	North	21 \pm 2.7	64 \pm 4.0	15 \pm 1.4
	South	29 \pm 1.9	46 \pm 3.0	26 \pm 2.8
Thick-billed Murre	North	19 \pm 1.3	62 \pm 3.9	20 \pm 2.8
	South	26 \pm 2.4	57 \pm 3.1	17 \pm 1.2
Razorbill	North	33 \pm 3.1	40 \pm 3.3	26 \pm 2.9
	South	56 \pm 4.0	27 \pm 3.0	17 \pm 1.2
Atlantic Puffin	North	24 \pm 2.9	61 \pm 4.0	15 \pm 1.2
	South	41 \pm 4.9	38 \pm 4.7	21 \pm 1.8
Black-legged Kittiwake	North	20 \pm 0.5	63 \pm 0.7	17 \pm 0.3
	South	38 \pm 6.6	45 \pm 6.2	17 \pm 1.1

in the south, Common Murre replaced Northern Fulmar in this pelagic group. Perhaps the only similarity in trophic structure between the two sites was found in Razorbills, which exhibited the most enriched $\delta^{13}\text{C}$ signatures and relatively depleted $\delta^{15}\text{N}$ signatures at both locations.

Lilliendahl and Solmundsson (1997) found that sandlance predominated in the summer diet of Icelandic seabirds in the south and capelin predominated in the diet of seabirds in the north. The only notable exception to this general pattern was Northern Fulmar which, in addition to capelin (north) and sandlance (south), also consumed considerable amounts of fishery discards, including fish offal, redfish, and northern shrimp.

Because stable isotope signatures of liver tissue represent dietary information from a relatively short time-scale, one or two weeks at most (Hobson and Clark 1992), the isotope data presented here for Icelandic seabirds can be considered representative of breeding season (summer) diet. However, it is possible that some components of seabirds' summer diets assessed conventionally may have been under-represented, particularly those which varied temporally. Conventional and isotopic dietary information may, therefore, have spanned slightly different spatio-temporal scales. Nevertheless, whereas conventional (Lilliendahl and Solmundsson 1997) and isotopic assessments of Icelandic seabird diet and trophic structure may have revealed that pronounced dietary differences exist on a relatively large spatial scale (inter-site), stable isotope analysis has apparently refined the trophic relationships of these seabirds on a spatial scale (within-site; Fig. 1). Further research is required to understand fully these relatively subtle trophic relationships.

DUAL-ISOTOPE MULTIPLE-SOURCE MIXING MODEL

As pointed out by Ben-David et al. (1997), the output from a model of this type represents an index of a predator's diet, rather than actual proportions of specific prey consumed. This is mainly because the model computes proportions of all prey types included in the model in the diet of consumers, even if certain prey are extremely rare or absent in the diet of a particular consumer. With this in mind, the output from the dual-isotope three-source mixing model presented here (Table 3) generally supports the trends in conventional dietary information (Lilliendahl and Solmundsson 1997). Based on the model output, capelin were always more important in the diet of seabirds from the north compared to the south (Table 3), as would be expected based on conventional dietary information (Lilliendahl and Solmundsson 1997). The mean proportion of capelin in the diet of seabirds from the north produced by the model reached a maximum of only 64% in Common Murres (Table 3). In contrast, Lilliendahl and Solmundsson (1997) found over 90% capelin in the diet of this species. Similarly, the model found the proportion of sandlance to be consistently and significantly higher in the south compared to the north (Table 3), but in several cases the difference between south and north was relatively small and the model found that the maximum mean proportion of sandlance was only 56% in Razorbills (Table 3). Lil-

liendahl and Solmundsson (1997) found that the diet of Razorbills and Atlantic Puffins was comprised almost entirely (> 95%) of sandlance in south Iceland. These discrepancies between model output and conventional data highlight the fact that mixing models of this type produce an index of dietary importance. However, stable isotope signatures combined with a modeling approach are supportive of the general dietary patterns in seabirds from north and south Iceland.

The model found that euphausiids made up 15–26% of seabirds' diets (Table 3) and that for some species-location combinations (for example, Atlantic Puffins from the north) was in very close agreement with conventional dietary data (Lilliendahl and Solmundsson 1997). For many cases, however, the model output for euphausiids was likely to be an over-estimate.

Although the three-source dual-isotope model was able to identify general dietary trends, compared with stomach contents analysis, it under-represented the importance of sandlance and capelin, and tended to over-estimate the importance of euphausiids for many seabirds. Similarly, the output from the six-source model used for Northern Fulmars (see Results) would appear to under-estimate certain prey (for example, sandlance and fish offal). Model outputs presented here tend to confirm the prerequisite for very distinct isotope signatures of prey, possibly through the incorporation of additional isotope signatures, perhaps $\delta^{34}\text{S}$ (Ben-David et al. 1997, Schmutz and Hobson 1998), and further highlight under- and over-estimation of relatively common and relatively rare prey, respectively. However, the three-source mixing model used here was able to confirm major dietary differences in seabirds from two locations in Iceland, lending further support to this isotopic approach.

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LITERATURE CITED

- BEN-DAVID, M., R. W. FLYNN, AND D. M. SCHELL. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111:280–291.
- BENVENUTI, S., F. BONADONNA, L. DAL'ANTONIA, AND G. A. GUDMUNDSSON. 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115:57–66.
- DENIRO, M. J., AND S. EPSTEIN. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42:495–506.
- DENIRO, M. J., AND S. EPSTEIN. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* 45:341–351.
- DUFFY, D. C., AND S. JACKSON. 1986. Diet studies of

- seabirds: a review of methods. *Colonial Waterbirds* 9:1–17.
- FRY, B., AND E. B. SHERR. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems, p. 196–229. *In* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy [EDS.], *Stable isotopes in ecological research*. Springer-Verlag, New York.
- GODLEY, B. J., D. R. THOMPSON, S. WALDRON, AND R. W. FURNESS. 1998. The trophic status of marine turtles as determined by stable isotope analysis. *Mar. Ecol. Prog. Ser.* 166:277–284.
- HOBSON, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar. Ecol. Prog. Ser.* 95:7–18.
- HOBSON, K. A., AND R. G. CLARK. 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor* 94:181–188.
- HOBSON, K. A., J. F. PIATT, AND J. PITOCHELLI. 1994. Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* 63:786–798.
- HOBSON, K. A., AND S. G. SEALY. 1991. Marine protein contributions to the diet of Northern Saw-whet Owls on the Queen Charlotte Islands: a stable isotope approach. *Auk* 108:437–440.
- HOBSON, K. A., AND H. E. WELCH. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* 84:9–18.
- KLINE, T. C., J. J. GOERING, O. A. MATHISEN, P. H. POE, P. L. PARKER, AND R. S. SCANLAN. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in the Kvickak River watershed, Bristol Bay, southwestern Alaska. *Can. J. Fish. Aquat. Sci.* 50:2350–2365.
- LILLIENDAHL, K., AND J. SOLMUNDSSON. 1997. An estimate of summer food consumption of six seabird species in Iceland. *ICES J. Mar. Sci.* 54:624–630.
- MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Carbon isotope ratio reveals feeding behavior of cormorants. *Auk* 107:400–403.
- MIZUTANI, H., Y. KABAYA, AND E. WADA. 1991. Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. *Isotopenpraxis* 27:166–168.
- MONTEVECCHI, W. A. 1993. Birds as indicators of change in marine prey stocks, p. 217–266. *In* R. W. Furness and J. J. D. Greenwood [EDS.], *Birds as monitors of environmental change*. Chapman and Hall, London.
- PETERSON, B. J., AND B. FRY. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18:293–320.
- 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 Univ. Press, Cambridge.
- SCHMUTZ, J. A., AND K. A. HOBSON. 1998. Geographic, temporal and age-specific variation in diets of Glaucous Gulls in western Alaska. *Condor* 100:119–130.
- SMITH, R. J., K. A. HOBSON, H. N. KOOPMAN, AND D. M. LAVIGNE. 1996. Distinguishing between populations of fresh- and salt-water Harbour Seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. *Can. J. Fish. Aquat. Sci.* 53:272–279.
- SYDEMAN, W. J., K. A. HOBSON, P. PYLE, AND E. B. MCLAREN. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. *Condor* 99:327–336.
- 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 *Fulmarus glacialis* from two northeast Atlantic colonies. *Mar. Ecol. Prog. Ser.* 125:3–11.