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Stable-isotope Ratios Of Carbon And Nitrogen In Feathers Indicate Seasonal Dietary Shifts In Northern Fulmars

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Ratios of the stable isotopes of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) have been used to elucidate structure and interaction within food webs. There is a stepwise enrichment of ^{15}N at each trophic level (Minagawa and Wada 1984, Schoeninger and DeNiro 1984, Hobson and Welch 1992, Hobson 1993). Carbon-isotope ratios give weak trophic information, but indicate relative contributions from differing sources (e.g. marine vs. terrestrial; biota from these two systems having distinct $\delta^{13}C$ signatures based on differences in $\delta^{13}C$ of carbon incorporated at photosynthesis) to the diet of particular species (Fry et al. 1983, Dunton and Schell 1987, Hobson 1987, 1990, Mizutani et al. 1990, Hobson and Sealy 1991). When combined, stable-isotope ratios of nitrogen and carbon can be used to discriminate between species on the basis of dietary input to a greater extent than that afforded by one ratio alone (Hobson 1991, 1993). However, most such studies to date have utilized internal tissues (especially collagen extracted from bone or muscle), an approach that requires the killing of individuals in investigations of contemporary systems (Hobson 1990, 1991, Rau et al. 1992, Hobson 1993, Hobson et al. 1994). In contrast, Hobson and Clark (1993) provided isotopic information based on the analysis of avian blood, while Schaffner and Swart (1991) analyzed stable-isotope ratios of oxygen and carbon from eggshells to assess the diet of laying female seabirds.

In studies of birds, feathers offer a further nondestructive alternative to the use of internal tissues, yet potentially should provide information relating to the diet and trophic position of an individual. However, few studies have made use of feathers in this way. A prerequisite for using feathers is an assessment of the fractionation of isotopes between the bird's diet and feathers. Such information is required to enable accurate interpretation of feather-isotope signatures when dietary preferences or trophic status are to be inferred, the implicit assumption being that isotopic signatures of diets can be related to those of consumers in a predictable manner. Feathers also offer several potential advantages. Historical samples are readily available in museum collections, and sampling feathers grown at particular times of year may permit investigations of seasonal changes in diet.

Several studies have investigated diet-feather fractionation factors for captive birds fed monotonous diets (Mizutani et al. 1990, 1991, Hobson and Clark 1992a, b, Mizutani et al. 1992). Although the determination of diet-feather fractionation factors under controlled conditions are clearly important, few wild, free-living species of birds conform to such narrow dietary sources. It would be useful, therefore, to make use of a bird species that is wild, free-living, and also stenophagous in a complementary approach to the elucidation of diet-feather fractionation factors, since matching the nutritional and metabolic conditions of wild birds to those in captive studies would be difficult; there have been no such studies to date.

Most bird species feed on a range of prey and, hence, a range of isotopic inputs. Since feathers are molted and regrown, and the isotopic signature of a feather is thought to reflect that of the diet at the time of feather growth (Hobson and Clark 1992a), the isotopic signature of a feather sample potentially will be influenced by the choice of feather(s) for analysis. In contrast, isotopic signatures of collagen extracted from bone, for example, show little if any variation between different bones from the same individual (DeNiro and Schoeniger 1983).

For comparisons of isotopic signatures between relatively large numbers of individuals of a range of species, for example, it would be useful to be able to analyze a feather sample that reflected the isotopic signature of the plumage as a whole and that can be considered an "index," effectively integrating any isotopic variation within and among feathers. Such an approach would be particularly appropriate since most isotopic measurements require samples in the order of only a few milligrams; all but the smallest body feathers greatly exceed this mass. Conversely, any marked isotopic variation among particular feathers regrown at different stages of the molt cycle may be indicative of temporal shifts in diet and trophic status of an individual or population. Again, there has been no investigation of the isotopic variation within and among feathers.

In this paper we present data on: diet-feather fractionation factors of stable isotopes of carbon and nitrogen for free-living stenophagous birds; intertissue

carbon and nitrogen isotopic variation; and variation in carbon and nitrogen isotopic signatures both within and among different feather types.

Methods.—Isotopic variation within and among feathers, and among tissues was investigated in five adult Northern Fulmars (*Fulmarus glacialis*). The birds were obtained during the breeding season under licence from St. Kilda (57°49'N 08°35'W) for a previous study of heavy-metal burdens, and stored deep frozen (ca. −20°C). Primary feathers 2, 6, and 10 (primary 1 is innermost) were removed from the birds' left wing. Subsamples were taken from the distal tip and from near the base of each primary feather for isotopic analysis. Samples from both the tip and base of primaries consisted of a section of rachis with barbs. In addition, five small body feathers were removed from both the breast and the back (between the wings) of each bird, each body feather representing a separate sample. All feather samples were cleaned of any surface contamination in an ultrasonic bath using a chloroform/acetone washing regime (Muirhead 1986) and dried in an oven at 50°C for at least 24 h prior to isotopic analysis.

Collagen was extracted from the birds' left humerus following Chisholm et al. (1983). A sample was removed from the pectoralis muscle and dried to constant mass in an oven at 50°C. Dried collagen and muscle samples were ground to powder using a commercial food grinder, and any lipids were removed using a Soxhlet apparatus with chloroform solvent for at least 6 h. Lipid-free collagen and muscle samples were redried to await isotopic analysis.

Prey samples and feather samples from predators used to elucidate diet-feather fractionation factors were obtained from a variety of sources. In all cases, however, predators were chosen that are known to be stenophagous. Regurgitated zooplankton food samples comprising a mixture of large numbers (>30 individuals) of the copepod *Calanus tonsus* and/or the euphausiid *Nyctiphanes australis* were collected from Broad-billed Prions (*Pachyptila vittata*) at South-east Island, Chatham Islands (44°22'S 176°11'W), and were dried to constant mass in an oven. Dried zooplankton samples were ground to powder, and inorganic carbonates were removed by treatment with excess 1N hydrochloric acid until bubbling stopped. The ground and treated samples were then rinsed in distilled water and dried to constant mass in an oven at 50°C. Small body feathers (about 6–10 per individual) were taken from Broad-billed Prion chicks, and also from chick and adult Subantarctic Skuas (*Catharacta lönnbergi*), which fed predominantly on Broad-billed Prions (Furness unpubl. data). Sandeels (*Ammodytes marinus*) were obtained from Common Murres (*Uria aalge*), Razorbills (*Alca torda*), Atlantic Puffins (*Fratercula arctica*), and Arctic Terns (*Sterna paradisaea*) returning to the colony at Foula, Shetland (60°08'N 2°05'W), and stored deep-frozen prior to further treatments. On thawing, total fish length was measured (to the nearest millimeter), and the sandeels were dried to constant mass. Body-feather samples were taken from Common Murre and Arctic Tern chicks, both of which, at Foula, are fed entirely sandeels during their development (Furness 1990, Furness and Barrett 1991). The dried sandeels were ground to powder, and they and the zooplankton samples were subjected to lipid extraction using a Soxhlet apparatus. These lipid-free prey samples were redried to await isotopic analysis. All body-feather samples were washed, dried, and then chopped into very small pieces to produce a homogenous feather sample to await isotopic analysis.

In all cases, a sample (zooplankton, sandeel, or homogenized body feather) of about 20 mg was combusted in an evacuated and sealed quartz tube containing excess copper (II) oxide (wire form) and silver wire. The furnace temperature was maintained at 850°C for 6 h, then allowed to cool to ambient laboratory temperature over a further 8 h. The resulting carbon dioxide and nitrogen were separated cryogenically. Carbon dioxide samples were analyzed using a VG SIRA10 triple collector mass spectrometer, while nitrogen samples were analyzed using a VG Micromass 602D double-collector mass spectrometer. Stable-isotope concentrations were expressed in conventional δ notation:

$$\delta X = 1{,}000\ ([R_{\text{sample}}/R_{\text{standard}}] - 1), \qquad (1)$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The values for R_{standard} for ^{13}C and ^{15}N are PDB and atmospheric nitrogen from AIR, respectively. Analytical errors, based on replicate analyses of IAEA-N1, IAEA-N2 and NBS-21 standards, were ±0.2‰ for both carbon and nitrogen. Intercalibration analyses of feather samples performed by the Institute of Terrestrial Ecology (Merlewood, Cumbria, England) gave very similar results. The mean values of seven homogenized body feather samples obtained from the two laboratories differed by only 0.04‰ (paired t-test; $t = 0.11$, 6 df, $P > 0.05$).

Results.—There was significant interfeather variation in $\delta^{15}N$ values among primary, breast, and back feathers (ANOVA; $F_{2,50} = 4.88$, $P < 0.05$); $\delta^{15}N$ values of primary feathers were elevated compared to those of breast feathers (Table 1). There was no significant difference in $\delta^{13}C$ values among the three feather groups (ANOVA; $F_{2,50} = 1.24$, $P > 0.05$; Table 1).

There was no significant difference between the $\delta^{15}N$ values of the tip and the base of primaries 2, 6, and 10 from five fulmars (tip, $\bar{x} = 15.4$ ±SD of 1.6‰, $n = 15$; base, $\bar{x} = 15.3 \pm 1.4$‰, $n = 15$; paired t-test, $t = 0.31$, 14 df, $P > 0.05$); similarly, the $\delta^{13}C$ values were no different between tip and base sections (tip, $\bar{x} = -16.4 \pm 1.3$‰, $n = 15$; base, $\bar{x} = -16.5 \pm 1.4$‰, $n = 15$; paired t-test, $t = 0.03$, 14 df, $P > 0.05$). However, average $\delta^{15}N$ values (i.e. [tip value + base value]/2, for each primary feather) were significantly different among primaries (Friedman two-way ANOVA; $X^2 =$

TABLE 1. $\delta^{15}N$ and $\delta^{13}C$ values[a] in a range of feathers and tissues from five Northern Fulmars.

Tissue	Bird 1	Bird 2	Bird 3	Bird 4	Bird 5	Mean
Nitrogen						
Primary feather	16.5 ± 1.7	16.9 ± 0.5	14.6 ± 0.2	14.3 ± 0.9	14.4 ± 0.4	15.3 ± 1.4
Breast feather	15.1 ± 1.0	13.4 ± 0.3	14.9 ± 0.5	14.7 ± 0.2	14.0 ± 0.6	14.4 ± 0.9
Back feather	14.7 ± 1.5	14.9 ± 0.7	14.9 ± 0.2	14.6 ± 1.1	14.8 ± 0.3	14.8 ± 0.9
Collagen	14.6	15.1	14.6	14.7	15.1	14.8 ± 0.2
Muscle	13.7	14.6	12.8	12.1	12.4	13.1 ± 0.9
Carbon						
Primary feather	−15.7 ± 0.6	−14.7 ± 0.4	−16.6 ± 0.9	−17.3 ± 0.4	−18.0 ± 0.5	−16.5 ± 1.3
Breast feather	−16.4 ± 0.6	−16.2 ± 0.6	−17.0 ± 0.1	−16.3 ± 0.4	−17.8 ± 0.3	−16.7 ± 0.8
Back feather	−16.5 ± 0.6	−15.2 ± 0.7	−16.9 ± 0.1	−17.0 ± 0.3	−17.6 ± 0.2	−16.6 ± 0.9
Collagen	−15.2	−15.1	−15.7	−15.0	−15.7	−15.3 ± 0.3
Muscle	−17.8	−17.8	−17.9	−18.7	−18.2	−18.1 ± 0.3

[a] For primary feathers, $\bar{x}$ ± 1 SD of primaries 2, 6 and 10; for breast and back feathers, $\bar{x}$ ± 1 SD of five individual feathers. For collagen and muscle, values from individual samples.

7.6, $P < 0.05$; Fig. 1), as were $\delta^{13}C$ values ($X^2 = 6.4$, $P < 0.05$; Fig. 1).

There was close agreement between the mean $\delta^{15}N$ value in bone collagen (14.8‰) and in body feathers of five fulmars (breast 14.4‰; back 14.8‰), but the mean $\delta^{15}N$ value of muscle samples was up to 2.2‰ depleted in ^{15}N in comparison with other tissues (Table 1). In contrast, the mean $\delta^{13}C$ value of bone collagen was 1.6‰ enriched compared to body-feather samples, while the mean $\delta^{13}C$ value of muscle was considerably depleted in ^{13}C compared to other tissues (e.g. 2.8‰ lower than bone collagen; Table 1).

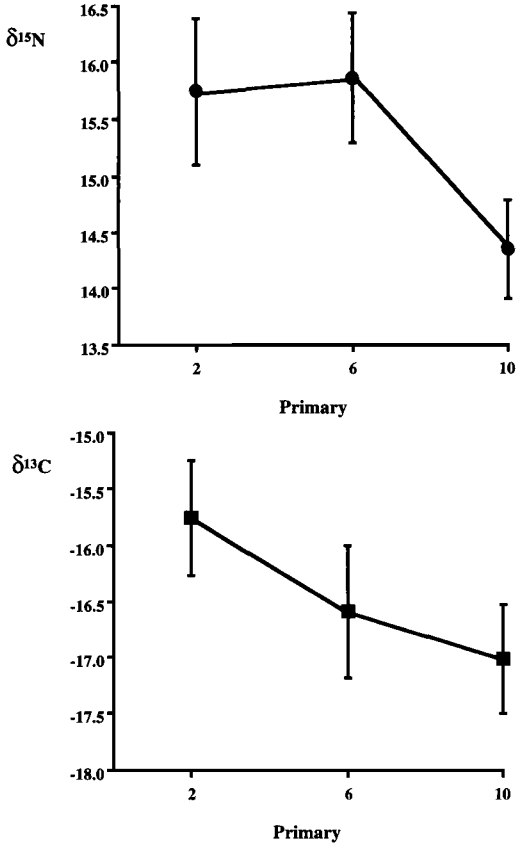

Fig. 1. Variation ($\bar{x}$ ± 1 SE) in $\delta^{15}N$ and $\delta^{13}C$ signatures of primary feathers of Northern Fulmars.

Mean $\delta^{15}N$ and $\delta^{13}C$ values of prey species and body-feather samples from seabird predators are presented in Tables 2 and 3. Body-feather samples from Common Murre chicks ($\delta^{15}N$, $\bar{x}$ = 11.6‰) and Arctic Tern chicks ($\delta^{15}N$, $\bar{x}$ = 11.7‰) were significantly enriched in ^{15}N relative to their sandeel prey by 3.3 and 3.4‰, respectively (one-way ANOVA, $F_{2,27} = 194.38$, $P < 0.001$; Table 2). There was no significant relationship between the $\delta^{15}N$ value and sandeel length ($r = -0.057$, $P > 0.05$;). Body-feather samples from Broad-billed Prion chicks exhibited a mean $\delta^{15}N$ value (10.8‰) that was 4.3‰ higher than that of their zooplankton diet (6.5‰). The mean $\delta^{15}N$ value of body feathers from Subantarctic Skuas (13.8‰) was 3.0‰ enriched compared to that of prion feathers (Table 3). These enrichments were highly significant (one-way ANOVA, $F_{2,17} = 76.24$, $P < 0.001$).

Diet-feather fractionation factors were lower for $\delta^{13}C$. Body-feather samples from Common Murre chicks ($\delta^{13}C$, $\bar{x} = -15.9$‰) and Arctic Tern chicks ($\delta^{13}C$, $\bar{x} = -14.8$‰) were significantly enriched by 1.0 and 2.1‰, respectively, compared to their sandeel prey ($\delta^{13}C$, $\bar{x} = -16.9$‰; one-way ANOVA, $F_{2,27} = 51.64$, $P < 0.001$; Table 2). There was no significant relationship between $\delta^{13}C$ value and the body length of sandeels ($r = 0.402$, $P > 0.05$). The mean $\delta^{13}C$ for body feathers of Broad-billed Prion chicks (−17.6‰) was significantly enriched by 2.5‰ compared to values for zooplankton prey ($\bar{x} = -20.1$‰; one-way ANOVA, $F_{2,17} = 54.35$, $P < 0.001$; Table 3). The mean $\delta^{13}C$ value of body feathers from Subantarctic Skuas (−17.2‰)

TABLE 2. $\delta^{15}N$ and $\delta^{13}C$ values ($\bar{x} \pm 1$ SD, with n in parentheses) for homogenized sandeels and homgenized body-feather samples from avian predators. Common Murre and Arctic Tern chicks are both fed sandeels during their development.[a]

	Nitrogen	$\bar{\Delta}_{DF}$	Carbon	$\bar{\Delta}_{DF}$
Sandeel	8.3 ± 0.6 (14)	—	−16.9 ± 0.6 (14)	—
Common Murre (chick)	11.6 ± 0.4 (8)	+3.3	−15.9 ± 0.1 (8)	+1.0
Arctic Tern (chick)	11.7 ± 0.2 (8)	+3.4	−14.8 ± 0.1 (8)	+2.1

[a] $\bar{\Delta}_{DF}$ is diet-feather fractionation factor.

was only slightly, and not significantly, enriched (0.5‰) compared to that for prion body feathers (Table 3).

Discussion.—The extent to which isotopic signatures vary both within and among feathers has clear implications for the use of feathers for isotope measurements. Since the amount of sample required to perform such measurements is small, typically on the order of a few milligrams, any variation in isotopic signature becomes particularly relevant. Furthermore, from a procedural perspective, it might be advantageous to be able to analyze a single sample from feathers that was indicative of the isotopic signature of the plumage as a whole, one that integrated variation over the whole plumage and effectively represented an index of the isotopic signature of the plumage.

It is clear from the results of our study that for some types of feather there is considerable interfeather variation in both $\delta^{13}C$ and $\delta^{15}N$ values of Northern Fulmars. The significant decline in $\delta^{13}C$ and $\delta^{15}N$ from primary 2 through to primary 10 (Fig. 1) would tend to render this feather type less appropriate for isotopic assessment where an isotopic value for the plumage as a whole is required. However, such variation is itself informative. It indicates a switch in diet over the period of primary-feather molt and regrowth to one consisting of prey of lower trophic status, since $\delta^{15}N$ and probably, though less unambiguously, $\delta^{13}C$ values are lower in biota of lower trophic position (Schoeninger and DeNiro 1984, Hobson and Welch 1992). Hobson and Clark (1992a) have shown that in American Crows (*Corvus brachyrhynchos*) the isotopic signature of feathers reflects that of the diet, even within an individual growing feather. The primary molt in fulmars begins towards the end of chick-rearing with the loss and replacement of the inner feathers; the molt then progresses, being completed well into the winter with the outermost feathers (Ginn and Melville 1983). Hence, the lower $\delta^{15}N$ and $\delta^{13}C$ values in primary 10 in particular (Fig. 1), towards the end of the primary molt sequence, reflect the winter diet of these fulmars. Although for the five fulmars and all primaries combined, intraprimary feather isotopic variation was not statistically significant, in some individual primary feathers, isotopic signatures differed markedly between the tip and the base. This trend supports the findings of Hobson and Clark (1992a), and indicates that feather isotopic signatures can track pronounced dietary shifts in free-living birds.

In contrast to the results for primary feathers, there was relatively little variation between the $\delta^{15}N$ and $\delta^{13}C$ values in samples of body feathers. Furthermore, the mean $\delta^{15}N$ values of both breast and back feathers were very similar to the mean $\delta^{15}N$ value for fulmar bone collagen (Table 1). At any given time, fulmars possess body feathers that are of varying ages; the body plumage is not replaced annually and contains individual feathers that may represent several years' growth (Ginn and Melville 1983). Therefore, by analyzing a homogenized sample from several body feathers, the isotopic information from a period of years is effectively integrated. Bone-collagen isotopic values are thought to represent close to the lifetime average of an individual's dietary intake (Stenhouse and Baxter 1979), while Hobson and Clark (1992a) estimated the isotopic half-life of collagen from growing Japanese Quail (*Coturnix japonica*) in diet-switching experiments to be in the order of hundreds of days. It may be that the dietary information integrated by several body feathers from Northern Fulmars is similar to that from bone collagen. Homogenized body feathers may provide an alternative to bone collagen in studies of long-term dietary preferences. Mizutani et al. (1991) presented isotopic data from different

TABLE 3. $\delta^{15}N$ and $\delta^{13}C$ values ($\bar{x} \pm 1$ SD, with n in parentheses) for homogenized zooplankton and homogenized body-feather samples from avian predators. Zooplankton are eaten by Broad-billed Prions, which in turn are eaten by Subantarctic Skuas.[a]

	Nitrogen	$\bar{\Delta}_{DF}$	Carbon	$\bar{\Delta}_{DF}$
Zooplankton (euphausiids/copepods)	6.5 ± 1.4 (6)	—	−20.1 ± 0.5 (6)	—
Broad-billed Prion (chick)	10.8 ± 0.7 (6)	+4.3	−17.6 ± 0.3 (6)	+2.5
Subantarctic Skua	13.8 ± 0.9 (8)	+3.0	−17.2 ± 0.6 (8)	+0.4

[a] $\bar{\Delta}_{DF}$ is diet-feather fractionation factor.

tissues of a Common Cormorant (*Phalacrocorax carbo*) fed a monotonous diet. However, comparison with their data is hampered by the fact that lipids, which are relatively "light" in ^{13}C compared to proteins (Tieszen et al. 1983), apparently were not removed from the internal tissues of the cormorant.

The diet-feather fractionation factors derived from mean $\delta^{15}N$ and $\delta^{13}C$ values of prey and predator body-feather samples presented in Table 2 are in broad agreement with those from studies of captive birds. For ^{13}C, diet-feather fractionation factors ranging from 2.5‰ to 4.4‰ have been reported for several species of adult birds (Mizutani et al. 1990, 1991, 1993, Hobson and Clark 1992a). Hobson and Clark (1992b) found that ^{13}C diet-feather fractionation factors in chicks varied from −0.4 to 2.1‰ in three species. Diet-feather fractionation factors for ^{15}N ranging from 3.6 to 5.6‰ have been determined in adults of several bird species (Mizutani et al. 1991, 1992), while in chicks of three species, factors of 1.1 to 3.0‰ have been reported (Hobson and Clark 1992b). The zooplankton-feather fractionation step presented in our paper for Broad-billed Prions provides the first data of such a shift between prey and predator at this point in a food chain (i.e. primary consumer to avian predator). The fractionation factors of 4.3 and 2.5‰ for ^{15}N and ^{13}C, respectively, are not dissimilar from other prey-predator combinations. Overall, ^{15}N fractionation factors tend to be greater than corresponding ^{13}C fractionation factors, a pattern reflected in studies of captive birds.

The data for Subantarctic Skuas (Table 3), although not directly comparable to other diet-feather fractionation factors, since isotopic signatures of skua feathers would be the result of feeding upon prion internal tissues and not prion feathers, are nonetheless interesting. Prions make up the majority of the skuas' diet, and are preyed upon at all times of the year. The $\delta^{15}N$ value of skua feathers ($\bar{x}$ = 13.8‰; Table 3) is elevated compared to that of their prion prey ($\bar{x}$ = 10.8‰; Table 3), indicative of and consistent with an upward trophic shift. The Subantarctic Skua mean $\delta^{13}C$ value ($\bar{x}$ = −17.2‰; Table 3) is, however, only slightly higher than that of the prions ($\bar{x}$ = −17.6‰; Table 3). Such a finding, whereby $\delta^{13}C$ values increase only slightly (or remain fairly constant) at higher trophic positions within a food chain, has been reported elsewhere (Hobson and Welch 1992).

The data we present support the use of feathers for isotopic work in elucidating dietary preferences and trophic status. Furthermore, the use of feathers has the advantage of being nondestructive compared to the use of bone collagen and muscle, and the analysis of selected feathers should allow seasonal variations in diet to be investigated. Feathers also permit an analysis of trends in isotopic signatures over long temporal periods. Feather samples from study skins held in museum collections provide great potential for analysis of historical trends in diet and trophic status (see Thompson et al. 1992, 1993).

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Literature Cited

Chisholm, B. S., D. E. Nelson, K. A. Hobson, H. P. Schwarcz, and M. Knyf. 1983. Carbon isotope measurement techniques for bone collagen: Notes for the archaeologist. J. Archaeol. Sci. 10:355–360.

Deniro, M. J., and M. J. Schoeniger. 1983. Stable carbon and nitrogen isotope ratios of bone collagen: Variations within individuals, between sexes and within populations raised on monotonous diets. J. Archaeol. Sci. 10:199–203.

Dunton, K. H., and D. M. Schell. 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: $\delta^{13}C$ evidence. Mar. Biol. 93:615–625.

Fry, B., R. S. Scanlan, and P. L. Parker. 1983. $^{13}C/^{12}C$ ratios in marine food webs of the Torres Strait, Queensland. J. Aust. Mar. Freshwater Res. 34: 707–715.

Furness, R. W. 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981–83. Ibis 132:205–217.

Furness, R. W., and R. T. Barrett. 1991. Seabirds and fish declines. Natl. Geogr. Res. Explor. 7:82–95.

Ginn, H. B., and D. S. Melville. 1983. Moult in birds. British Trust for Ornithology, Tring, Hertfordshire, England.

Hobson, K. A. 1987. Use of stable-carbon isotope analysis to estimate marine and terrestrial protein content in gull diets. Can. J. Zool. 65:1210–1213.

Hobson, K. A. 1990. Stable isotope analysis of Marbled Murrelets: Evidence for freshwater feeding and determination of trophic level. Condor 92: 897–903.

Hobson, K. A. 1991. Stable isotopic determinations

of the trophic relationships of seabirds: Preliminary investigations of alcids from coastal British Columbia. Pages 16–20 *in* Studies of high-latitude seabirds. 1. Behavioural, energetic and oceanographic aspects of seabird feeding ecology (W. A. Montevecchi, and A. J. Gaston, Eds.). Canadian Wildlife Service Occasional Paper 68.

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. 1992a. Assessing avian diets using stable isotopes, I: Turnover of ^{13}C in tissues. Condor 94:181–188.

HOBSON, K. A., AND R. G. CLARK. 1992b. Assessing avian diets using stable isotopes, II: Factors influencing diet-tissue fractionation. Condor 94: 189–197.

HOBSON, K. A., AND R. G. CLARK. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: Implications for nondestructive sampling in avian dietary studies. Auk 110:638–641.

HOBSON, K. A., J. F. PIATT, AND J. PITOCCHELLI. 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 Sawwhet 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 $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. 84:9–18.

MINAGAWA, M., AND E. WADA. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta 48:1135–1140.

MIZUTANI, H., M. FUKUDA, AND Y. KABAYA. 1992. ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. Ecology 73:1391–1395.

MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Carbon isotope ratio of feathers 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.

MUIRHEAD, S. J. 1986. The accumulation, storage and elimination of metals and organochlorines in the Great Skua *Catharacta skua* and metal accumulation in Atlantic Procellariiformes. Ph.D. thesis, Univ. Glasgow, Glasgow, Scotland.

RAU, G. H., D. G. AINLEY, J. L. BENGSTON, J. J. TORRES, AND T. L. HOPKINS. 1992. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals and fish: Implications for diet and trophic structure. Mar. Ecol. Prog. Ser. 84:1–8.

SCHAFFNER, F. C., AND P. K. SWART. 1991. Influence of diet and environmental water on the carbon and oxygen isotopic signatures of seabird eggshell carbonate. Bull. Mar. Sci. 48:23–38.

SCHOENINGER, M. J., AND M. J. DENIRO. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochim. Cosmochim. Acta 48:625–639.

STENHOUSE, M. J., AND M. S. BAXTER. 1979. The uptake of bomb ^{14}C in humans. Pages 324–341 *in* Radiocarbon dating (R. Berger and H. Suess, Eds.). Univ. California Press, Berkeley.

THOMPSON, D. R., P. H. BECKER, AND R. W. FURNESS. 1993. Long-term changes in mercury concentrations in Herring Gulls *Larus argentatus* and Common Terns *Sterna hirundo* from the German North Sea coast. J. Appl. Ecol. 30:316–320.

THOMPSON, D. R., R. W. FURNESS, AND P. M. WALSH. 1992. Historical changes in mercury concentrations in the marine ecosystem of the north and north-east Atlantic ocean as indicated by seabird feathers. J. Appl. Ecol. 29:79–84.

TIESZEN, L. L., T. W. BOUTTON, K. G. TESDAHL, AND N. A. SLADE. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia 57:32–37.

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