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DIET–FEATHER STABLE ISOTOPE ($\delta^{15}N$ AND $\delta^{13}C$) FRACTIONATION IN COMMON MURRES AND OTHER SEABIRDS

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Abstract. We measured the fractionation of stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes in the breast and primary feathers of 11 Common Murres (*Uria aalge*) maintained on a diet of capelin (*Mallotus villosus*). Diet–feather $\delta^{15}N$ fractionation from delipidated capelin muscle to murre feathers was 3.6‰ ± 0.2‰ in breast feathers and 3.7‰ ± 0.2‰ in primary feathers. Fractionation of $\delta^{13}C$ was 2.5‰ ± 0.2‰ in breast feathers and 1.9‰ ± 0.3‰ in primary feathers. Prey–feather fractionation (for delipidated, muscle-only prey samples) for nine other species of seabirds ranged from 3.0‰ to 4.6‰ for $\delta^{15}N$ and 0.1‰ to 2.5‰ for $\delta^{13}C$. Studies that did not remove lipids from prey samples showed higher $\delta^{15}N$ and $\delta^{13}C$ fractionation, and those that used whole prey items rather than muscle tissue alone showed higher $\delta^{15}N$ fractionation. We suggest that: (1) prey samples be delipidated to facilitate interpretation of $\delta^{13}C$ fractionation, (2) high interstudy and interspecific variation in $\delta^{13}C$ makes species-specific studies essential, and (3) use of muscle tissue rather than whole bodies of fish will minimize unexplained variation in $\delta^{15}N$ fractionation.

Key words: Common Murre, feather, fractionation, stable carbon isotope, stable nitrogen isotope, Uria aalge.

Fraccionamiento de Isótopos ($\delta^{15}N$ y $\delta^{13}C$) Entre la Dieta y las Plumas en *Uria aalge* y en Otras Aves Marinas

Resumen. Medimos el fraccionamiento de isótopos estables de nitrógeno ($\delta^{15}N$) y carbono ($\delta^{13}C$) en las plumas del pecho y las primarias de 11 individuos de la especie *Uria aalge* mantenidos con una dieta basada en el pez *Mallotus villosus*. El fraccionamiento de $\delta^{15}N$ entre la dieta y las plumas a partir de músculo de *M. villosus* sin lípidos fue del 3.6‰ ± 0.2‰ en las plumas del pecho y de 3.7‰ ± 0.2‰ en las primarias. El fraccionamiento de $\delta^{13}C$ fue del 2.5‰ ± 0.2‰ en las plumas del pecho y del 1.9‰ ± 0.3‰ en las primarias. El fraccionamiento observado entre las presas y las plumas (únicamente para muestras de músculo de presas sin lípidos) para otras nueve especies de aves marinas varió entre el 3.0‰ y el 4.6‰ para el $\delta^{15}N$ y entre el 0.1‰ y el 2.5‰ para el $\delta^{13}C$. Los estudios en los que no se removieron los lípidos de las muestras de presas mostraron niveles de fraccionamiento de $\delta^{15}N$ y $\delta^{13}C$ mayores, y los que usaron presas enteras en lugar de únicamente tejidos

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musculares mostraron niveles de fraccionamiento de $\delta^{15}N$ mayores. Sugerimos que a las presas se les remuevan los lípidos para facilitar la interpretación del fraccionamiento de $\delta^{13}C$, que la alta variación en el $\delta^{13}C$ entre estudios y entre especies hace que sea esencial realizar estudios específicos para cada especie y que el uso de tejidos musculares en lugar de cuerpos completos de peces minimizará la variación no explicada en el fraccionamiento de $\delta^{15}N$.

Stable isotope analysis is a powerful and increasingly popular tool for investigating food webs, trophic relationships, and energy flow through ecosystems (Kelly 2000, West et al. 2006). Stable isotope ratios in consumers generally reflect the ratios in dietary items and therefore function as food web tracers (Bearhop et al. 1999). However, many stable isotopes fractionate (change ratio between the heavier and lighter isotopes) when assimilated into consumer tissues, thus the tissues of consumers often contain a higher ratio of heavy to light carbon and nitrogen isotopes than the tissues of their prey. Isotopic fractionation can vary among species with different diets (Thompson et al. 1999), among individuals under nutritional stress (Hobson et al. 1993, Cherel et al. 2005a, 2005b, 2005c), and among different physiological pathways (Hobson and Clark 1992b, Vanderklift and Ponsard 2003). Furthermore, isotope values can differ among different tissues within an individual, due to varying rates of tissue turnover or lipid concentration (Tieszen et al. 1983, Vanderklift and Ponsard 2003). Since lipids are generally isotopically lighter in $\delta^{13}C$ than other body tissues and because organisms often vary in their lipid content, failing to remove lipids can confound fractionation estimates in food web studies (Montiero et al. 1991, Hobson et al. 1995, Cherel et al. 2000, Bearhop et al. 2002). Additional confusion may arise among studies due to inconsistent use of either whole prey items (Mizutani et al. 1992, Cherel et al. 2005b) or specific prey tissues such as muscle (Hobson et al. 1995, Cherel et al. 2005b) to calculate fractionation and diet. Accurate fractionation values are essential for stable isotope studies that use models to estimate the proportions of potential food items in the diet of consumers (Ben-David et al. 1997, Ben-David and Schell 2001, Phillips 2001, Phillips et al. 2005). If fractionation is uncertain, it will be difficult to resolve diet composition or trophic level, especially when isotopic values of potential prey items are not very different (Gannes et al. 1997, Rosing et al. 1998, West et al. 2006).

Stable isotope studies are often conducted on seabirds (Hobson et al. 1994, Becker et al. 2007) because they are usually more difficult to observe foraging than their terrestrial counterparts. Stable-isotope ratios in feathers are generally derived from food ingested during molt (but see Bearhop et al. 2002), can track seasonal and annual variation in diet, and remain preserved in museum collections, facilitating examination of long-term changes in diet (Becker and Beissinger 2006). Seabird studies have used fractionation values either from individuals on presumed diets in the wild (Thompson and Furness 1995), or from captive studies of a limited number of species kept on known diets (Hobson and Clark 1992a, 1992b, Mizutani et al. 1992).

While these studies individually provide insight into preferred sample preparation and tissue-type effects, there has been no review of seabird feather isotope studies to recommend best practices and provide an overview of fractionation to apply to unstudied species. We measured the isotopic fractionation of $\delta^{15}N$ and $\delta^{13}C$ in the feathers of captive Common Murres (*Uria aalge*) on a controlled capelin (*Mallotus villosus*) diet. We then compared these values to those from existing studies of diet–feather $\delta^{15}N$ and $\delta^{13}C$ fractionation in seabirds to provide an overview of seabird diet–feather fractionation patterns when using: 1) whole prey items versus muscle only, and 2) delipidated tissue versus tissue still containing lipids.

METHODS

Eleven after-hatching-year Common Murres were caught on 30 May 1999 from Middleton Island, Alaska, and maintained at the Alaska SeaLife Center in Seward, Alaska for a radio-transmitter attachment study. All birds were kept on a constant diet of capelin from August 1999 through December 2000. The capelin was collected from Newfoundland, Canada, in a single bulk shipment, so the isotopic signature of the prey should be relatively uniform. During the time they were on the capelin diet, the birds completed a wing and body feather molt (August–September 2000), so the isotopic signature in their feathers represented a pure Newfoundland-caught capelin diet. We collected several breast feathers and the tips (~3 cm) of the first and second primaries from each bird in December 2000 and stored them at $-5^{\circ}C$.

Prior to analyses, murre feathers were cleaned of any surface contamination or oils with a methanol: chloroform:water (50:25:20 by volume) rinse (Thompson and Furness 1995). Capelin lateral muscle tissue was freeze-dried, subjected to lipid extraction with the same type of methanol:chloroform solution for at least 24 hr, and then redried. Approximately 1.2 mg of dried feather (Thompson and Furness 1995) or capelin muscle was loaded into a tin capsule, combusted at $1000^{\circ}C$ into N_2 and CO_2 gas, and analyzed for $\delta^{15}N$ and $\delta^{13}C$ with a Europa 20/20 continuous-flow isotope-ratio mass spectrometer at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley. Peach leaves (45% C, 2.96% N; National Institute of Standards and Technology (NIST) #1577b) and bovine liver (45% C, 10.6% N; NIST #1547) were used as standards for C and N, respectively. Feathers are typically 45% C and 12%–15% N. Standards were analyzed between every eight feather or capelin samples, and a nonlinear least squares regression model was used to correct any instrumental drift during the analysis. Based on the error of the laboratory standard measurements, the analytical precision (SD) of the analysis was 0.24‰ for $\delta^{15}N$ and 0.06‰ for $\delta^{13}C$. Isotopic ratios are expressed in the delta (δ) notation as parts per thousand (‰) relative to the standards of atmospheric nitrogen (for

TABLE 1. Comparison of diet–feather isotope fractionation for different species of seabirds. Prey items were muscle only and delipidated unless noted. Where data are available, values are shown as mean ± SD.

Consumer	Feather type	*n*	Fractionation		Source
			δ^{15}N (‰)	δ^{13}C (‰)	
King Penguin (*Aptenodytes patagonicus*)	Back	9	2.7	0.1[ns]	Cherel et al. (2005)
	Back	9	3.5	0.3[ns]	Cherel et al. (2005)[‡]
Humboldt's Penguin (*Spheniscus humboldti*)	Body	16	4.8 ± 0.5	2.9 ± 0.2	Mizutani et al. (1992)[†‡]
Rockhopper Penguin (*Eudyptes chrysocome*)	Back	11	3.5	0.6	Cherel et al. (2005)
	Back	11	4.4	0.1[ns]	Cherel et al. (2005)[‡]
Broad-billed Prion (*Pachyptila vittata*)	Primary	6	4.3 ± 0.7	2.5 ± 0.3	Thompson and Furness (1995)
Great Cormorant (*Phalacrocorax carbo*)	Primary	17	3.7 ± 0.6	3.8 ± 0.5	Mizutani et al. (1992)[†‡]
	Remex	12	4.2	2.3	Bearhop et al. (1999)
Subantarctic Skua (*Stercorarius antarcticus lonnbergi*)	Primary	8	3.0 ± 0.9	0.4 ± 0.6	Thompson and Furness (1995)
Great Skua (*Stercorarius skua*)	Remex	24	4.6	2.1	Bearhop et al. (2002)
	Remex	24	4.4	5.3	Bearhop et al. (2002)[†]
Black-tailed Gull (*Larus crassirostris*)	Primary	22	5.3 ± 0.8	3.6 ± 0.5	Mizutani et al. (1992)[†‡]
Ring-billed Gull (*Larus delawarensis*)	Primary	14	3.0 ± 0.2	0.2 ± 1.3	Hobson and Clark (1992)
Arctic Tern (*Sterna paradisaea*)	Body	8	3.4 ± 0.2	2.1 ± 0.1	Thompson and Furness (1995)
Common Murre (*Uria aalge*)	Body	11	3.6 ± 0.2	2.5 ± 0.2	This study
	Primary	11	3.7 ± 0.2	1.9 ± 0.3	This study
	Body	8	3.3 ± 0.4	1.0 ± 0.1	Thompson and Furness (1995)
Mean (range), all species[§]			3.6 (3.0–4.6)[§]	1.4 (0.1–2.5)[§]	

[†] Lipids not removed from prey items prior to analyses.
[‡] Whole prey item analyzed.
[ns] Nonsignificant fractionation.
[§] Mean and range only includes samples based on delipidated prey muscle tissue ($n = 11$).

δ^{15}N) or Pee Dee Belemnite (for δ^{13}C) according to the equation:

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

where $X = {}^{13}$C or ^{15}N, and $R_{sample} = {}^{13}$C/^{12}C or ^{15}N/^{14}N.

Analysis of variance (ANOVA) and Bonferroni post-hoc tests were used to test for differences in δ^{15}N or δ^{13}C between capelin, breast feathers, and primary feathers. Means are reported ± SD unless otherwise indicated. Fractionation was calculated as the mean isotope ratio of the feather tissue minus the mean isotope ratio of the prey tissue. We also compiled δ^{15}N and δ^{13}C diet–feather fractionation values from other controlled studies of seabirds and used non-parametric one-way Kruskal-Wallis tests to compare effects of: (1) using whole prey items versus only muscle tissue, and (2) removing lipids from prey prior to analysis.

RESULTS

Capelin δ^{15}N averaged 13.4‰ ± 0.5‰ ($n = 15$), murre body feather δ^{15}N averaged 16.9‰ ± 0.2‰ ($n = 11$), and murre primary feather δ^{15}N averaged 17.1‰ ± 0.2‰ ($n = 11$). Capelin muscle δ^{15}N differed significantly from murre body and primary feather δ^{15}N ($F_{2,34} = 484.9$, $P < 0.001$; Bonferroni inequality, all $P < 0.001$), but δ^{15}N in murre body and primary feathers did not differ. Fractionation of δ^{15}N was 3.6‰ and 3.7‰ for murre body and primary feathers, respectively.

Capelin δ^{13}C averaged −19.9‰ ± 0.7‰ ($n = 15$), murre primary feather δ^{13}C averaged −18.0‰ ± 0.3‰ ($n = 11$), and murre body feather δ^{13}C averaged −17.3‰ ± 0.2‰ ($n = 11$). There were significant differences in δ^{13}C values between capelin and murre body and primary feathers, and also between murre body and primary feathers ($F_{2,34} = 102.5$, $P < 0.001$; Bonferroni inequality, all $P < 0.001$). Fractionation of δ^{13}C was 2.5‰ and 1.9‰ for murre body and primary feathers, respectively.

Diet–feather stable isotope fractionation values from controlled studies of 11 species of seabirds are summarized in Table 1. Fractionation based on delipidated fish muscle averaged 3.6‰ for δ^{15}N and 1.4‰ for δ^{13}C. Studies that used whole fish tended to report greater fractionation for δ^{15}N, while those that did not remove lipids had significantly higher fractionation for both δ^{15}N and δ^{13}C (Table 2).

TABLE 2. Differences in diet–feather isotope fractionation in seabirds when prey items are whole fish vs. muscle tissue only, and contain lipids vs. have been delipidated. Species used are in Table 1 and fractionation is reported as mean ± SE.

Diet	*n*	Mean fractionation	*U*	*P*
$\delta^{15}N$				
Whole fish	5	4.3 ± 0.3	12.5	< 0.06
Muscle only	12	3.6 ± 0.2		
Prey + lipid	4	4.6 ± 0.3	46.0	< 0.02
Prey − lipid	13	3.6 ± 0.2		
$\delta^{13}C$				
Whole fish	5	2.1 ± 0.8	24.5	> 0.56
Muscle only	12	1.8 ± 0.4		
Prey + lipid	4	3.9 ± 0.5	52.0	< 0.01
Prey − lipid	13	1.2 ± 0.3		

DISCUSSION

In this study, Common Murre feathers showed a clear $\delta^{15}N$ fractionation pattern for both breast and primary feathers that was similar to that measured in other seabird species. Fractionation of $\delta^{13}C$ varied slightly (0.6‰) between primaries and body feathers for muscle-based, delipidated prey–feather fractionation, but also fell within the general range observed in previous studies. It is unclear why this small but significant difference in $\delta^{13}C$ values occurred, as both primaries and body feathers molted during the same few weeks while the murres were fed a capelin diet and the birds were not subjected to any nutritional stress during molt.

The patterns of higher $\delta^{15}N$ and $\delta^{13}C$ fractionation in studies that did not remove lipids from prey samples and higher $\delta^{15}N$ fractionation in those that used whole prey items rather than muscle tissue alone suggest that: (1) prey samples should be delipidated to facilitate interpretation of $\delta^{13}C$ fractionation, (2) species-specific studies are essential to account for high interstudy and interspecific variation in $\delta^{13}C$, and (3) use of muscle tissue rather than whole bodies of fishes will minimize unexplained variation in $\delta^{15}N$ fractionation.

Vanderklift and Ponsard (2003) found that marine organisms tended to have lower $\delta^{15}N$ fractionation than terrestrial or freshwater organisms. However, they attributed this pattern to a high proportion of marine invertebrate and detritus feeders in their meta-analysis. Vanderklift and Ponsard's (2003) average of ~1.4‰ $\delta^{15}N$ fractionation in marine systems is likely too low a value for seabird trophic studies. Overall, the range of $\delta^{15}N$ diet–feather fractionation for delipidated muscle of 3.0‰–4.6‰ shown here suggests that values within this range are probably acceptable when determining dietary sources. Vanderklift and Ponsard (2003) also found that many $\delta^{15}N$ fractionation differences may be explained by differences in nitrogen excretory physiology (i.e., uric acid, urea, or ammonia). Since all seabirds excrete uric acid, this should not be an issue for seabird studies. Similarly, most seabird prey (e.g., copepods, krill, squid, and fish), excrete ammonia, so variation in fractionation due to differences in nitrogen excreta should be minimal.

Removal of lipids from prey items prior to analyses is another factor that may affect fractionation values, especially for $\delta^{13}C$ (Sotiropoulos et al. 2004, Søreide et al. 2006). Because controlled fractionation studies are generally designed to help field studies infer dietary inputs, the removal of lipids from prey tissues (and predator tissues as well) removes any bias from variation in lipid content by only considering fractionation from prey muscle tissue to predator tissue (Cherel et al. 2005b). For example, Bearhop et al. (2002) compared fractionation from both lipid-containing and lipid-free prey samples to feathers and found that while $\delta^{15}N$ was minimally affected (+0.2‰) with lipids extracted, $\delta^{13}C$ fractionation climbed from 2.1‰ to 5.3‰ in Great Skuas (*Stercorarius skua*). Furthermore, Sotiropoulos et al. (2004) found that removal of lipids from whole freshwater juvenile fish resulted in significant increases of 3.4‰ for $\delta^{13}C$ and 2.8‰ for $\delta^{15}N$ (and therefore in apparent fractionation). Finally, the most compelling reason to remove lipids from prey may be that mass balance equations suggest that lipids are only minimally used for production of feathers and blood (Bearhop et al. 2002).

Another important consideration in stable isotope studies of seabirds is whether to analyze whole prey fish or only muscle tissue. Some of the highest $\delta^{15}N$ feather fractionation values (3.7‰–5.3‰) in seabirds were found by Mizutani et al. (1992). One possible reason for these high fractionation values, especially in the Black-tailed Gull (*Larus crassirostris*) and Humboldt's Penguin (*Spheniscus humboldti*), is that Mizutani et al. (1992) homogenized entire prey samples of saurel (*Cololabis* spp.) and anchovies (*Engraulis* spp.) for isotope analysis. Most other studies used only muscle tissue from fish (Hobson and Welch 1992, Hobson et al. 1994, Sydeman et al. 1997). Thus, other prey tissues, including recently ingested food in the guts of prey, may have had lower $\delta^{15}N$ values, and certainly had differing turnover times (Sotiropoulos et al. 2004), which would have lowered the isotope ratio and artificially inflated fractionation. Sotiropoulos et al. (2004) also reported that lipid extraction done just on muscle tissue yielded only small (<1.0‰) changes in fractionation for both isotopes. They concluded that prey muscle tissue rather than whole organism analyses are better suited for using $\delta^{13}C$ and $\delta^{15}N$ in food web studies. Cherel et al. (2005b) tested differences in $\delta^{13}C$ and $\delta^{15}N$ fractionation from delipidated herring and capelin whole bodies versus muscle tissue to King Penguins (*Aptenodytes patagonicus*) and Rockhopper Penguins (*Eudyptes chrysocome*). They found that whole bodies had small but significantly lower $\delta^{15}N$ values (0.2‰–0.4‰) than fish muscle alone. Similarly, $\delta^{13}C$ was 0.8‰–0.9‰ lower in fish muscle alone. This further supports our suggestion that $\delta^{15}N$ diet–feather fractionation in seabirds generally ranges from 3.0‰–4.6‰ when only considering delipidated prey muscle tissue (or whole invertebrates) as a baseline.

Fractionation of $\delta^{13}C$ was more variable among studies than that of $\delta^{15}N$, regardless of whether or not lipids were removed from prey items before analyses. This may be further confounded by potential impacts of age class on $\delta^{13}C$ fractionation, which we did not test since juvenile birds were in varying stages of development in this review. Consequently, $\delta^{13}C$ appears to be more problematic as a reliable tracer in marine food web and trophic level studies. While removal of lipids from prey tissues may reduce this variation, the broad range of fractionation values for this isotope suggests that controlled, species-specific studies of fractionation are more important for $\delta^{13}C$ than $\delta^{15}N$.

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