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STABLE ISOTOPE ANALYSIS OF MARBLED MURRELETS: EVIDENCE FOR FRESHWATER FEEDING AND DETERMINATION OF TROPHIC LEVEL[1]

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Abstract. Stable carbon and nitrogen isotopic analyses were performed on tissues of 21 Marbled Murrelets (*Brachyramphus marmoratus*) collected in Barkley Sound ($n = 18$) and on Johnston Lake, British Columbia ($n = 3$). Three adult males had significantly lower muscle tissue $\delta^{13}C$ values ($\bar{x} \pm$ SD: $-23 \pm 2.7‰$, $n = 3$) than did all other murrelets ($-16.5 \pm 0.6‰$, $n = 18$). Based on a model predicting muscle $\delta^{13}C$ values for murrelets feeding on freshwater and marine prey these three individuals had short-term freshwater-derived protein inputs to their diets ranging from 50 to 100%. The mean $\delta^{13}C$ value for Marbled Murrelet bone collagen ($-16.8 \pm 0.3‰$, $n = 4$) was not significantly different from that found for Ancient Murrelets (*Synthliboramphus antiquus*) from Reef Island, Queen Charlotte Islands. This suggests that while some Marbled Murrelets may feed exclusively on freshwater prey for a short but important period of several weeks, freshwater protein is not a significant long-term dietary component in their diets. Marbled Murrelets had a mean muscle $\delta^{15}N$ value of $15.3 \pm 0.7‰$ ($n = 21$). Because $\delta^{15}N$ values for freshwater and marine prey species overlapped significantly, stable-nitrogen isotope analysis did not distinguish between Marbled Murrelets feeding on freshwater or marine prey. The stable-nitrogen isotope values of muscle tissue from Marbled Murrelets were compared with those of nine other species of alcids from British Columbia and the high Arctic. The comparison indicates that stable-nitrogen isotope analysis is potentially useful for establishing trophic relationships in seabird communities.

Key words: *Marbled Murrelet;* Brachyramphus marmoratus; *alcid; lake feeding; stable-isotope analysis; carbon; nitrogen; trophic level.*

INTRODUCTION

Throughout its range, the Marbled Murrelet (*Brachyramphus marmoratus*) feeds primarily on marine fish and invertebrates (Sealy 1975, Carter 1984, Sanger 1987) in inshore coastal waters (Cody 1973). Stomach analyses and feeding observations indicate that Marbled Murrelets also feed in freshwater lakes along the west coast of North America (Carter and Sealy 1986). The anecdotal nature of observations of Marbled Murrelets at lakes and the possibility that lakes may be used nocturnally make it difficult to determine the regularity of use of lakes and their importance as feeding sites (Carter and Sealy 1986). Here, I evaluate the possibility of using stable isotopic analyses of the tissues of Marbled Murrelets in order to determine their dependence on freshwater lakes and to provide an estimate of the trophic position of this species relative to other alcids.

Recently, it has been shown that isotopic distributions in animals are closely related to isotopic compositions in their diets (DeNiro and Epstein 1978, 1981; Peterson and Fry 1987; Tieszen and Boutton 1989). For a given trophic level, dietary protein derived from terrestrial sources may differ isotopically from that derived from marine sources. Using these two facts, various researchers have used stable isotopic measurements of consumer and prey tissues in order to predict relative contributions of terrestrial and marine protein in modern and ancient diets of animals including man (Chisholm et al. 1982, Schoeninger and DeNiro 1984, Hobson and Collier 1984, Hobson 1986, Mizutani et al. 1990). For carbon and nitrogen, heavy isotopic enrichment may occur between trophic levels (Miyake and Wada 1967, Rau et al. 1983, Fry 1988) and it is therefore possible to assign trophic status to consumers based on isotopic measurement of their tissues (e.g., Dickson 1986, Fry 1988).

The emergence of stable isotope techniques for dietary studies provides a new tool for avian ecologists. Such analysis is ideally suited to in-

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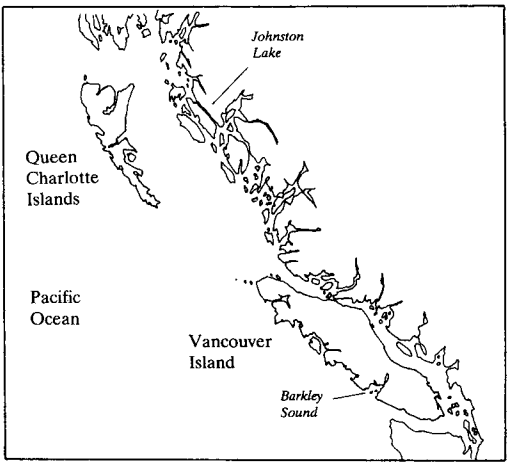

FIGURE 1. Coastal British Columbia showing locations of Marbled Murrelet collection sites.

vestigating the dependence of Marbled Murrelets on freshwater lakes, because stable carbon isotope concentrations of freshwater fish differ significantly from those of marine fish (Chisholm et al. 1982). In this paper I present the results of stable carbon and nitrogen isotope analysis of Marbled Murrelet muscle and bone tissues. I used stable-carbon isotope analysis to detect freshwater protein in Marbled Murrelet diets and stable-nitrogen isotope analysis to predict trophic position relative to other alcids (see also Hobson, in press). Alcids are particularly suited to an isotopic investigation of trophic level since species in this family are known to differ in their relative dependence on fish and invertebrate prey (Bédard 1969).

ISOTOPIC DIETARY MODELS

Carbon and nitrogen exist in nature in two stable forms. The lighter forms, ^{12}C and ^{14}N, are more common than the heavier isotopes ^{13}C and ^{15}N and it is convenient to refer to the concentrations of the heavier isotopes as a ratio in δ notation as parts per thousand (‰) as follows:

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

Where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. These values are measured using a mass spectrometer to precisions typically of the order of 0.1 to 0.3‰.

The stable isotopic composition of a consumer tissue is related to that of its diet according to:

$$\delta_{tissue} = \delta_{diet} + \Delta_{dt}$$

where Δ_{dt} represents the isotopic fractionation factor between dietary and consumer tissue. For carbon, estimates of fractionation differences between dietary protein and consumer muscle tissue (i.e., Δ_{dm}) are +1‰ (Tieszen et al. 1983) and between dietary protein and consumer bone collagen (Δ_{dc}) are +5‰ (van der Merwe and Vogel 1978). For nitrogen Δ_{dm} appears to be close to 3–4‰ (Dickson 1986, Fry 1988) and Δ_{dc} between 2.4 and 4‰ (DeNiro and Epstein 1981, Schwarcz et al. 1985). Using estimated or measured values of δ_{diet} and Δ_{dt} for each isotope, it is thus possible to predict $\delta_{collagen}$ or δ_{muscle} values expected in consumers feeding on various food types.

SAMPLE AND METHODS

Marbled Murrelets collected both at sea and on a coastal freshwater lake were used in this study. The at-sea sample consisted of 10 adult and one hatching-year male and eight adult female murrelets originally collected by H. R. Carter and S. G. Sealy in Barkley Sound, British Columbia, July–December 1979 (Carter 1984). The lake sample consisted of two adult males and one adult female collected on Johnston Lake, British Columbia, 19 June 1985 (Fig. 1). Tissues of all specimens had been kept frozen prior to analysis. Museum specimens of most individuals are housed at the University of Manitoba Vertebrate Museum and at the Royal British Columbia Provincial Museum.

Isotopic measurements of Marbled Murrelets were compared with those of other alcids from British Columbia (described in Hobson, in press) and the high Arctic. The Arctic sample included 11 Black Guillemots (*Cepphus grylle*), 10 Thick-billed Murres (*Uria lomvia*), and two Dovekies (*Alle alle*) collected in Barrow Strait, Northwest Territories, August 1988.

Bird and fish muscle tissue was freeze-dried, powdered, and lipids extracted using a soxhlet apparatus with chloroform solvent. Collagen was removed from bones as a gelatin according to a technique developed by Longin (1971) and modified by Chisholm et al. (1983). Samples for $\delta^{13}C$ analysis were loaded into Vycor tubes with powdered CuO and silver wire and combusted at 850°C for 4 hr. Nitrogen samples were converted to ammonia by Kjeldahl reaction and then to N_2 gas using LiBrOH (Porter and O'Dean 1977). Carbon and nitrogen gas was analyzed using a Micromass 602E mass spectrometer. Based on several hundred replications, standard devia-

tions for carbon (graphite) and nitrogen (glycine) internal standards were 0.1‰ and 0.3‰, respectively.

RESULTS

STABLE CARBON ISOTOPE ANALYSIS

Most Marbled Murrelets showed muscle $\delta^{13}C$ values between −15.5 and −17.5‰ (Fig. 2, $\bar{x} \pm$ SD: -16.5 ± 0.6‰, $n = 18$). Within this group, male and female murrelets did not differ in their $\delta^{13}C$ values for muscle tissue ($t = 0.22$, $P > 0.5$). Three individuals, an adult male from Barkley Sound and two adult males from Johnston Lake (-23.8 ± 2.7‰, range = −21.1 to −27.4‰), differed significantly from this group ($t = 11.07$, $P < 0.001$). The single hatching-year individual collected in October 1980 had a $\delta^{13}C$ value of −16.7‰, not significantly different from the majority of murrelets measured.

In order to obtain an estimate of expected $\delta^{13}C$ endpoint values for murrelets feeding exclusively on marine fish and freshwater fish, respectively, I obtained isotopic values for typical prey species in each of these biomes (Table 1). Based on these data, mean $\delta^{13}C$ values for marine and freshwater species were estimated as −17.8 and −27.9‰, respectively. Applying a Δ_{dm} value of +1‰ to the mean $\delta^{13}C$ prey values provides predicted muscle $\delta^{13}C$ values of −16.8‰ for murrelets feeding exclusively on a marine fish diet, and −26.9‰ for murrelets feeding exclusively on a diet of freshwater fish. Using these endpoints, estimates of relative freshwater protein contributions for individuals with intermediate $\delta^{13}C$ values can be calculated using linear interpolation. This indicates that the murrelet with the most negative muscle $\delta^{13}C$ value (−27.4‰) had a short-term diet consisting exclusively of freshwater fish whereas those with values of −21.1 and −22.9‰ had diets consisting of approximately 50% freshwater fish.

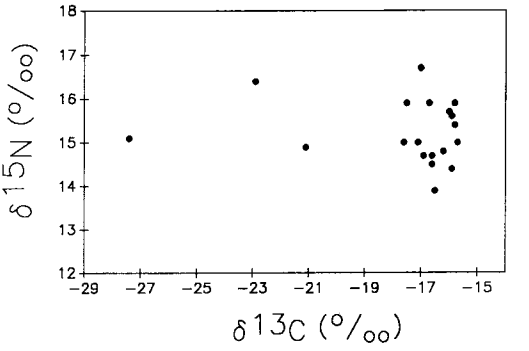

FIGURE 2. Distribution of Marbled Murrelet stable-carbon and nitrogen isotope values for pectoral muscle tissue.

In order to determine if there was evidence for long-term dietary dependence on freshwater fish I measured the bone collagen $\delta^{13}C$ values for the same individuals showing short-term freshwater protein input to their diets and for the single individual from Johnston Lake that did not show such an effect. The mean bone collagen value of -16.8 ± 0.3‰ ($n = 4$) for these individuals did not differ significantly from that found for adult Ancient Murrelets (-16.8 ± 0.4‰, $n = 5$) from Reef Island, Queen Charlotte Islands.

STABLE NITROGEN ISOTOPE ANALYSIS

Compared with $\delta^{13}C$ values, Marbled Murrelets showed a narrower distribution of muscle tissue $\delta^{15}N$ values (Fig. 2). The three individuals with $\delta^{13}C$ values of −21.1, −22.9, and −27.4‰ showed $\delta^{15}N$ values of 14.9, 16.4, and 15.1‰, respectively. The mean $\delta^{15}N$ value for these individuals (15.3 ± 0.4‰, $n = 3$) did not differ significantly from the mean value for all other

TABLE 1. Stable isotope values for muscle tissue of freshwater and marine fish from British Columbia and the Northwest Territories.

Species (n)	Location[a]	$\delta^{13}C$ (‰)[b]	$\delta^{15}N$ (‰)[c]	Source
Freshwater fish:				
Salvelinus malma (3)	B.C.	-28.8 ± 2.2	—	Chisholm (1986)
S. namaycush (6)	N.W.T.	-27.5 ± 1.8	13.9 ± 0.5	Hesslein et al. (1989)
Marine fish:				
Cupea pallasii (3)	coastal B.C.	-17.5 ± 1.0	—	Chisholm (1986)
Ammodytes sp. (5)	coastal B.C.	-17.9 ± 0.8	14.3 ± 0.3	This study

[a] Freshwater fish taken from Central Interior of British Columbia and from Travaillant Lake, N.W.T. Marine fish taken from Georgia Strait, B.C.
[b] $\delta^{13}C$ values expressed relative to the Peedee Belemnite (PDB) standard.
[c] $\delta^{15}N$ values expressed relative to AIR.

murrelets (15.3 ± 0.7‰, $n = 18$). Stable-nitrogen isotope values for freshwater and marine fish species of similar trophic position did not differ significantly (Table 1; $t = 1.6$, $P > 0.1$). Fingerling sockeye salmon (*Oncorhynchus nerka*) from a British Columbia coastal lake showed a mean muscle $\delta^{15}N$ value of 10.4 ± 0.5 ($n = 5$).

DISCUSSION

ISOTOPIC EVIDENCE FOR FEEDING IN LAKES

The period over which stable isotope values of an animal's tissues reflect its diet will depend, in part, on how quickly tissue proteins are replaced. Tissue proteins are in a state of dynamic equilibrium (Schoenheimer 1946, Bender 1975, Tieszen et al. 1983) but turnover rates for various tissue types are poorly known. In general, metabolically active tissues have faster turnover rates than less metabolically active tissues. In their laboratory study of gerbils (*Meriones unguiculatus*), Tieszen et al. (1983) found that carbon in muscle tissue had a half-life of 27.6 days. Equivalent turnover rates for alcid pectoral muscle tissue are unknown and, because of the high energetic demands of underwater swimming, may be considerably less than this. For the purposes of this study, it is appropriate to consider stable isotopic values for alcid muscle tissue as reflecting the origin of the birds' diets at least within the previous few weeks. Turnover rates for bone collagen are much slower, and dietary information based on this tissue type may represent a lifetime average for the individual (Stenhouse and Baxter 1979). By analyzing both of these tissue types in Marbled Murrelets, both short- and long-term dietary information has been obtained.

It is important to note that the $\delta^{13}C$ endpoint values calculated for Marbled Murrelets feeding in terrestrial-freshwater and marine biomes are only approximations. Nevertheless, average $\delta^{13}C$ values used here for potential dietary species agree closely with other published values (e.g., Chisholm et al. 1982) and the model I have used provides a useful *relative* measure of freshwater and marine-derived protein in the diets of individuals (see also Hobson 1986, Mizutani et al. 1990). It is also encouraging to note that the marine endpoint muscle $\delta^{13}C$ value of −16.8‰ agrees closely with the mean value found for Marbled Murrelets assumed to be feeding exclusively on marine prey (i.e., −16.5 ± 0.6‰, $n = 18$). The most negative muscle tissue $\delta^{13}C$ value I measured for other British Columbia alcids was for a Cassin's Auklet (*Ptychoramphus aleuticus*) (−19.8‰), a largely planktivorous species (Hobson, in press). It is reasonable to assume, then, that any Marbled Murrelet showing a muscle $\delta^{13}C$ value more negative than about −19.0‰ has a significant freshwater protein contribution to its diet.

ECOLOGICAL IMPLICATIONS

The results of this study indicate that some Marbled Murrelets may feed on freshwater lakes for several weeks during the breeding season. All three Marbled Murrelets showing significant freshwater derived protein in their diets were taken in June. While this may be an artifact of the small sample of birds made available for isotopic analysis, Carter and Sealy (1986) similarly noted that several records of murrelets using coastal lakes occurred during the breeding season. Stomach analyses of collected Marbled Murrelets on lakes have shown predominantly salmonid prey (Carter and Sealy 1986), and such prey species may be more accessible in summer (Robinson and Barraclough 1975). Moreover, murrelet feeding in lakes during the nonbreeding season is restricted to waters that do not regularly freeze over.

Marbled Murrelets are the only alcids known to forage in coastal lakes. In general, this species has a shorter nestling period (28 days) and faster chick growth rates than do other alcids (Simons 1980, Hirsch et al. 1981). Foraging in lakes may facilitate more frequent chick feedings, particularly for birds nesting far inland (Carter and Sealy 1986; Carter and Sealy, in press). Carter (1984) found that, in Barkley Sound, prey fed to nestlings was less available than that consumed by adults. Clearly, the decision to forage in freshwater lakes will be influenced by the relative abundances of suitable prey in marine waters and lakes and on energetic considerations of flying to and from these foraging areas.

To date we are unable to ascertain the relative importance of freshwater feeding in different murrelet populations. Stable-carbon isotope analysis is ideally suited to investigating the importance of coastal lakes to the foraging ecology of various populations of Marbled Murrelets. During the breeding season, murrelets may feed solitarily and nocturnally, often in remote areas

(Carter and Sealy, in press). It is therefore difficult to ascertain the extent of freshwater feeding by conventional dietary methods. The isotope technique provides time integrated dietary information. Tissues from murrelets found dead or collected for other studies should be salvaged for this type of analysis.

TROPHIC LEVEL DETERMINATIONS

In their survey of stable carbon- and nitrogen-isotope ratios in the bone collagen of a variety of animals, Schoeninger and DeNiro (1984) concluded that stable nitrogen isotope ratios in bone collagen may be used to delineate dietary freshwater and marine protein contributions. Nitrogen isotope ratios in the muscles of fish species in coastal lakes may overlap considerably, however, with those of marine fish (Table 1). Lower trophic-level fish such as fingerling salmonids also overlap in $\delta^{15}N$ with marine invertebrates (Dickson 1986, Fry 1988). Rather than being a useful indicator of feeding in coastal lakes, nitrogen-isotope analysis may be better suited to delineating the trophic level of Marbled Murrelets and other seabirds within marine ecosystems (Fig. 3). However, in general, the use of both carbon and nitrogen isotope analysis may provide greater segregation amongst individuals or species than the use of either isotope singly (Dickson 1986; Frey 1988; Hobson, in press).

Detailed isotopic surveys of prey organisms off the British Columbia coast and the high Arctic have not been conducted and it is not yet known how species' $\delta^{15}N$ values may vary within and between these marine systems. It may thus be inappropriate to compare trophic positions of alcids from each of these areas based on $\delta^{15}N$ values alone (Fry 1988). However, the preliminary results presented here are encouraging and suggest that stable-nitrogen isotope analysis may be a useful trophic indicator in seabird studies. Those species feeding primarily on lower trophic-level prey are expected to be least isotopically enriched compared to higher trophic-level feeders. Based on conventional dietary studies, the results of my nitrogen isotopic survey of alcids support this trend. Dovekies are considered to be largely planktivorous (Bradstreet and Brown 1985) and showed the lowest $\delta^{15}N$ values. Amongst alcids from British Columbia, Cassin's Auklets showed the least isotopic enrichment and this is also consistent with this species' largely nektonic diet (Payne 1965, Manuwal 1974). The

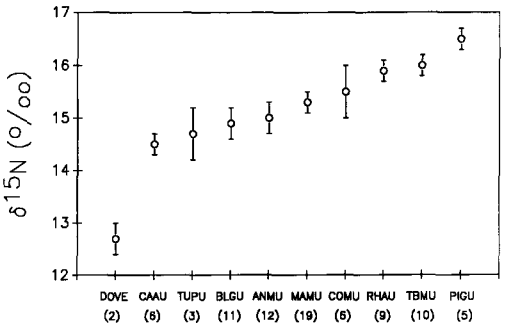

FIGURE 3. Stable-nitrogen isotope values for pectoral muscle tissue of Cassin's Auklets (CAAU), Tufted Puffins *Fratercula cirrhata* (TUPU), Ancient Murrelets (ANMU), Marbled Murrelets (MAMU), Rhinoceros Auklets *Cerorhinca monocerata* (RHAU), Common Murres *Uria aalge* (COMU), and Pigeon Guillemots *Cepphus columba* (PIGU) from coastal British Columbia, and Dovekies (DOVE), Black Guillemots (BLGU), and Thick-billed Murres (TBMU) from Barrow Strait, Northwest Territories. Sample sizes given in parentheses.

mean $\delta^{15}N$ value for Pigeon Guillemots was 3.8‰ higher than that for Dovekies suggesting about a one trophic-level difference between these species (Schoeninger and DeNiro 1984, Dickson 1986, Fry 1988).

Species occupying isotopically intermediate positions between Dovekies and Pigeon Guillemots probably had diets consisting of both fish and invertebrate prey. This appears to be consistent with the intermediate trophic position predicted for Marbled Murrelets. In Barkley Sound, Marbled Murrelets fed primarily on juvenile herrings (*Clupea harengus*) and sandlances (*Ammodytes hexapterus,* Carter 1984). However, other studies indicate that invertebrates, particularly euphausiids (e.g., *Thysanoessa spinifera*) may be seasonally important (Sealy 1975, Sanger 1987).

Several authors have investigated relationships between seabirds and their prey using an analysis of prey trophic levels (Knox 1970, Sanger 1972, Ainley and Sanger 1979, Sanger and Jones 1984). Based on earlier work by Mearns et al. (1981), Sanger (1987) recently advanced the concept of numerical average trophic levels for seabirds that feed at more than one level. Sanger's work provided an approach that allowed trophic relationships to be compared on a firmer quantitative footing, but his study suf-

fered from limitations inherent in most conventional dietary investigations.

Dietary information based on conventional techniques is usually short-term in scope and may be biased against soft-bodied invertebrates or other material that is not easily detected (reviewed by Duffy and Jackson 1986). These limitations appear unavoidable in cases where detailed knowledge of prey choice is required. Studies concerned with trophic level dependence, however, require estimates of the *proportion* of prey taken from each trophic level. Stable isotope values can reflect the relative importance of prey types from different trophic levels integrated over time. Thus, in marine systems where predictable trophic level enrichment can be demonstrated, stable nitrogen isotope values should be used as indicators of seabird trophic level, analogous to Sanger's numerical average trophic level.

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