ALCID WINTER DIET IN THE NORTHWEST ATLANTIC DETERMINED BY STABLE ISOTOPE ANALYSIS

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SUMMARY

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We used stable isotope (δ^{13}C, δ^{15}N) analysis to investigate winter foraging ecology of three species of alcids off Newfoundland and Labrador, Canada, 1996–2004. Muscle samples from salvaged Thick-billed Murres *Uria lomvia* ($n = 89$), Common Murres *U. aalge* ($n = 45$) and Razorbills *Alca torda* ($n = 7$), were measured isotopically to determine trophic-level (TL) differences among species and temporal patterns in TL and source (inshore vs. offshore) of feeding over the winter. As indicated by δ^{15}N values, Thick-billed Murres fed at a higher trophic level than did Common Murres. Razorbill δ^{15}N values were highly variable and overlapped those of both murre species. We found no significant differences in δ^{13}C values among the three species, confirming a common spatial feeding pattern. Both murre species became depleted in ^{13}C during winter, suggesting that the birds' foraging location or the provenance of prey species shifted from nearshore to offshore. In Common Murres, hatching-year individuals fed at a higher trophic level and foraged farther offshore than after–hatching year birds. In Thick-billed Murres, we contrasted TL determined previously for the breeding colony at Prince Leopold Island, Nunavut, Canada, with those determined for winter over a period of four years and found considerable interannual variation in patterns of seasonal difference in TL. However, the proportion of lower TL (amphipod) to higher TL (fish) prey was generally greater in winter than in summer.

Key words: Alcidae, winter diet, stable isotope, carbon-13, nitrogen-15, *Uria lomvia, Uria aalge, Alca torda*

INTRODUCTION

It is increasingly clear that migratory birds are influenced by factors occurring at broad temporal and spatial scales, so that connections between breeding, wintering and stopover sites for specific populations are important research topics (Webster *et al.* 2002, Hobson 2005, Norris 2005). For example, events on wintering grounds, such as food shortages or climatic conditions, can affect the timing of breeding (Saino *et al.* 2004), reproductive success (Marra *et al.* 1998, Norris *et al.* 2004) and adult survival (Jones *et al.* 2002, Barbraud & Weimerskirch 2003).

For seabirds, linking events between breeding and wintering grounds is complicated, because although many species breed colonially, they disperse over large areas of open ocean during winter. For example, Thick-billed Murres *Uria lomvia* wintering off Eastern Canada breed colonially in high-Arctic colonies where their behaviour, diet and breeding parameters are reasonably well known (e.g. Gaston & Nettleship 1981). Gaston (2003) suggested that food available to murres during winter or spring migration may affect spring body condition and therefore colony attendance and breeding propensity. But because winter diet is so poorly understood, such connections remain speculative.

Previously, murre winter diet was reconstructed using stomach content analysis of birds collected during the Newfoundland "turr" hunt (Tuck 1960), Gaston *et al.* 1983, Elliot *et al.* 1990, Rowe *et al.* 2000). The hunt primarily takes Thick-billed Murres, but also includes small numbers of Common Murres *U. aalge* and Razorbills *Alca torda* (Gaston *et al.* 1983). These three alcids are similar in size, occupy similar foraging locations in winter (Gaston & Hipfner 2000, Ainley *et al.* 2002, Hipfner & Chapdelaine 2002) and, in other regions studied, tend to have similar diets when they occur together (Erikstad & Vader 1989, Ogi & Shiomi 1991). We used stable isotope analysis (SIA) of murre tissues obtained opportunistically from the hunt to infer trophic level (TL) and spatial distribution of winter feeding (inshore vs. offshore) in murres occurring off Newfoundland.

Studies of seabird diet, especially in non-breeding individuals, have been hampered by conventional approaches. Stomach content analysis tends to overestimate the importance of prey with hard body parts (e.g. squid beaks and fish otoliths) because of differential digestion rates (Duffy & Jackson 1986). Most stomach contents are digested in 24 hours (Uspenski 1958), but hard prey items may remain for several weeks (Bradstreet 1980). Thus stomach content analysis provides a "snapshot" of what was ingested in the previous 24 hours and a biased indication of diet over a longer time period. In addition, significant proportions of murres may have empty stomachs (up to 44% in Rowe *et al.* 2000; up to 15% in Elliot *et al.* 1990) and therefore provide no information on diet.

Measurement of the naturally occurring abundance of ^{15}N and ^{13}C in consumers' tissues has become an established means to investigate seabird diet (Hobson *et al.* 1994, Hodum & Hobson 2000, Cherel *et al.* 2002, Ainley *et al.* 2003, Forero *et al.* 2004). Consumer δ^{15}N values are used to estimate trophic level, because marine systems show systematic increases in δ^{15}N with trophic level (Hobson & Welch 1992, Hobson 1993, Michener & Schell

1994). Stable abundance in carbon isotope shows slight enrichment with trophic level, but it is more commonly used to approximate the relative importance of benthic versus pelagic sources of carbon (Hobson & Welch 1992, Hobson *et al.* 1994). Individuals that forage nearshore tend to be enriched in ^{13}C as compared with those that forage offshore (Hobson 1993). Stable isotope values are not affected by differential digestion rates of prey items and provide information on assimilated, not just ingested, diet. Unlike stomach content analysis, SIA does not provide information on prey frequency at the species level; however, it does allow estimation of trophic level or proportion of fish versus lower trophic level prey such as invertebrates (Hobson 1993, Hobson *et al.* 2004)

Differences in the turnover of elements between tissues means that SIA can indicate the average diet over periods of time ranging from several days (liver and blood plasma) to years (bone collagen) (Hobson & Clark 1992). Muscle tissue, readily available from hunted murres, has an intermediate elemental half life (about 12 days) and therefore reveals average diet over the previous month [i.e. 2–3 half lives (Hobson & Clark 1992)]. We used these features of SIA to quantify relative trophic levels and changes in diet or foraging locations, or both, of murres and razorbills in the non-breeding period off Newfoundland.

MATERIALS AND METHODS

Field methods

Wintering bird samples were collected from October to March, 1998–2004, from various areas off eastern Newfoundland (Newfound and Labrador), Canada (Fig. 1). Most winter samples were salvaged from birds legally shot by hunters during the annual hunt. The remainder (36 from Thick-billed Murres and 25 from Common Murres), taken from St. Mary's Bay in 2004, were collected under scientific permit by Canadian Wildlife Service personnel. Birds were sexed by examination of gonads following dissection and aged to hatching year (HY: first winter) or after hatching year (AHY: second or later winter) by differences in the wear of greater covert feathers (S. Wilhelm unpubl. data). A muscle sample was taken from the breast or wing of each bird and frozen for later use in stable isotope analysis. Whole stomachs (proventriculus and gizzard) from birds taken in 2004 were removed and examined for contents.

A total of 89 Thick-billed Murres, 45 Common Murres, and 7 Razorbills were collected from 1996 to 2004 (Table 1). Most Common and Thick-billed Murres were taken in February 2004. AHY Thick-billed Murres were taken in November (n = 1), January (n = 1), February (n = 27) and March (n = 7). HY Thick-billed Murres were taken in November (n = 12), February (n = 25) and March (n = 4). HY Common Murres were collected in November (n = 3), December (n = 3), February (n = 26) and March (n = 1). AHY Common Murres were collected in November (n = 6) and January (n = 2). Razorbills were taken in November from Twillingate, 2000–2003, except for one of unknown date and location.

In a related study, blood samples were collected from breeding Thick-billed Murres on Prince Leopold Island [PLI (74°02′N, 90°00′W)], Nunavut, from June to August in 2000, 2001 and 2003. Sample sizes were 13 (2000), 68 (2001) and 23 (2003). Birds in summer 2002 had anomalously low stable isotope values and reproductive success—findings to be fully reported elsewhere—and are therefore excluded from the present analysis. Band returns have shown that Thick-billed Murres breeding on PLI winter off Newfoundland and Greenland (Gaston 1980). We compare our samples from Newfoundland and PLI for insights on summer versus winter foraging habits of Thick-billed Murres.

Stable isotope analysis

Relative to other body constituents, lipids tend to be depleted of ^{13}C (Hobson & Clark 1992). To avoid complications in interpretation arising from a varying lipid content among individuals, we used a 2:1 chloroform:methanol soak and rinse (Hobson *et al.* 2002) to remove lipids from muscle samples. We used HCl (Hobson & Welch 1992) to remove carbonates from crustacean samples. Blood, muscle and prey samples were analysed at the Department of Soil Science, University of Saskatchewan, in a Europa 20:20 continuous flow isotope ratio mass spectrometer interfaced with a Robo-Prep elemental analyzer. Laboratory standards—Bowhead whale baleen (BWB) and egg albumen—were inserted between groups of five unknowns. Measurement error has been estimated to be ±0.1‰ for δ^{13}C and ±0.3‰ for δ^{15}N (Hobson & Clark 1992).

Stable isotope values are presented in delta (δ) notation in units of parts per thousand (‰)

$$\delta X = [(R_{sample} / R_{standard}) - 1] * 1000, \quad [1]$$

where R is the ratio of the heavy to the light isotope of element X. Standards for this equation were the stable isotope values of Pee Dee belemnite and atmospheric nitrogen for δ^{13}C and δ^{15}N respectively.

Dietary models and statistical analysis

In comparing stable isotope values of consumer tissues among locations to infer dietary or trophic differences, it is important to consider that food webs can differ in their baseline isotopic values (Michener & Schell 1994, Schell *et al.* 1998). To ensure that dietary models are comparable between areas, stable isotope values of potential prey items in each system must be compared. We adopted this approach by estimating TL based on prey available on the breeding and wintering grounds. Stable isotope values of prey in winter were taken from whole prey items in murre stomachs. Stable isotope values from PLI (Hobson *et al.* 2002) were used in reference to the breeding season.

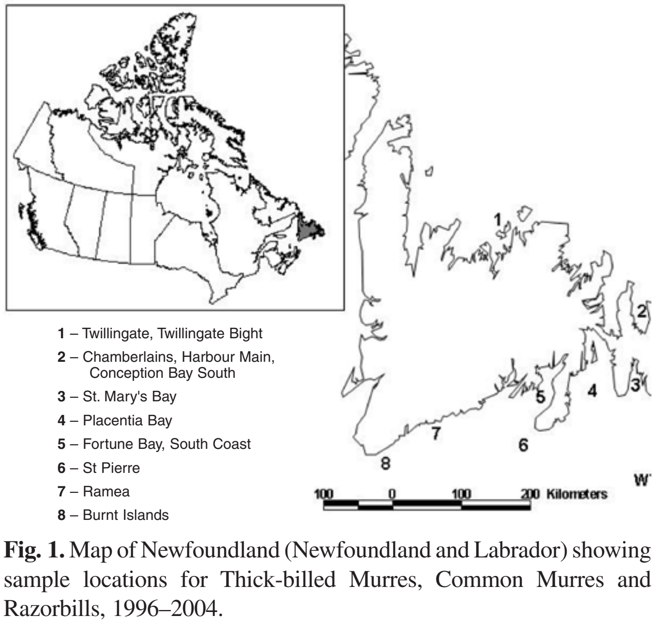

Fig. 1. Map of Newfoundland (Newfoundland and Labrador) showing sample locations for Thick-billed Murres, Common Murres and Razorbills, 1996–2004.

In a two-prey system, where prey items differ isotopically, prey proportions can be estimated as

$$P_A = (D_t - D_B) / (D_B - D_A), [2]$$

where P_A is the proportion of the diet of prey type A, D_t is the isotopic value of the consumer's tissue, and D_B and D_A are the resulting consumer tissue isotope values if only prey B and A are eaten (Hobson 1993). The expected stable isotopic value of tissue under a diet of 100% prey type A can be calculated as

$$D_A = D_P + \delta_t \; [3]$$

where D_A is the stable isotope value of the consumer's tissue, D_P is the stable isotope value of prey species A, and δ_t is the isotopic discrimination factor between diet and murre tissue—3.4‰ for muscle (Hobson *et al.* 1994) or 3.1‰ for blood (Hobson & Clark 1992). Combining equations 2 and 3, and incorporating the mean isotopic values that we measured for dietary fish and invertebrate samples and bird tissues, we estimated the relative importance of vertebrate prey (fish) and invertebrates (amphipods) within each season and location.

We used analysis of variance (ANOVA) to examine effects of species, age, sex and year on stable isotope signatures (Zar 1999). Not all birds were of known age or sex, thus sample sizes were lower than the total number of individuals for some analyses. Effects of age, sex and year were not examined in Razorbills. Interaction terms were examined where sample size permitted. When results from ANOVA were significant, we used Tukey post-hoc tests to determine where differences existed between groups. Pearson correlations were used to quantify changes in stable isotope values of murres during the course of the winter. Data were analyzed using SPSS, version 12.0. Means are reported ± 1 standard error.

TABLE 1
Date, location and coordinates of seabird samples collected off Newfoundland (Newfoundland and Labrador), Canada, for stable isotope analysis

Species[a]	Year	Samples	Location	Latitude, longitude
TBMU	1996	1	St. Mary's Bay	46°49′N, 53°45′W
	1998	1	Hibernia	
		1	St. Pierre	46°50′N, 56°20′W
	2000	2	Twillingate Bight	49°40′N, 54°46′W
	2001	1	Unknown	
		13	St. Mary's Bay	46°49′N, 53°45′W
	2002	1	Chamberlains	47°31′N, 52°57′W
		1	Placentia Bay	47°00′N, 54°30′W
		1	St. Pierre	46°50′N, 56°20′W
		2	South Coast	
		1	St. Mary's Bay	46°49′N, 53°45′W
		15	Twillingate	49°40′N, 54°46′W
	2004	13	Burnt Islands	47°36′N, 58°52′W
		1	Henry Goodrich Oil Rig	
		36	St. Mary's Bay	46°49′N, 53°45′W
COMU	2000	1	Harbour Main	47°25′N, 53°10′W
	2001	1	Ramea	47°31′N, 57°22′W
		1	St. Mary's Bay	46°49′N, 53°45′W
	2002	3	Conception Bay South	47°30′N, 53°00′W
		1	St. Mary's Bay	46°49′N, 53°45′W
		12	Twillingate	49°40′N, 54°46′W
	2004	25	St. Mary's Bay	46°49′N, 53°45′W
	Unknown	1	Fortune Bay	47°15′N, 55°30′W
RAZO	2000	2	Twillingate	49°40′N, 54°46′W
	2001	2	Twillingate	49°40′N, 54°46′W
	2002	1	Twillingate	49°40′N, 54°46′W
	2003	1	Twillingate	49°40′N, 54°46′W
	Unknown	1	Unknown	

[a] TBMU = Thick-billed Murre; COMU = Common Murre; RAZO = Razorbill.

RESULTS

Species differences

The three alcid species showed significant differences in muscle $\delta^{15}N$ values ($F_{1,132} = 4.9$, $p = 0.009$) but not in $\delta^{13}C$ values ($F_{2,137} = 2.1$, $p = 0.127$) during the wintering period (Table 2). Thick-billed Murres were enriched in ^{15}N as compared with Common Murres (Tukey post-hoc: $p = 0.008$). Razorbill $\delta^{15}N$ values were not different from those of either Thick-billed Murres ($p = 0.419$) or Common Murres ($p = 0.999$).

Temporal patterns

Thick-billed Murre $\delta^{13}C$ values were related to month ($F_{3,78} = 5.4$, $p = 0.002$) and also (but not significantly so) to year ($F_{3,78} = 2.6$, $p = 0.061$). No month-by-year interaction was evident ($F_{1,78} = 0.33$, $p = 0.568$). Neither year ($F_{3,78} = 1.9$, $p = 0.132$) nor month ($F_{3,78} = 1.2$, $p = 0.328$) affected values of $\delta^{15}N$ in this species, but the month-by-year interaction was relatively strong ($F_{1,78} = 3.7$, $p = 0.057$). In 2004, murre ^{13}C was depleted as compared with that in 2002 (Tukey post-hoc: $p < 0.001$), but we observed no differences in $\delta^{13}C$ values between the other years ($p > 0.062$). Thick-billed Murres generally became more depleted in ^{13}C from November to March ($r = -0.557$, $p < 0.001$).

Our sample of Common Murres was too small for a full factorial analysis of monthly and annual variation. With months pooled, $\delta^{13}C$ values showed significant variation year to year ($F_{2,40} = 7.2$, $p = 0.002$), but $\delta^{15}N$ values did not ($F_{2,40} = 3.0$, $p = 0.063$). As in Thick-billed Murres, $\delta^{13}C$ values in Common Murres were significantly depleted in 2004 as compared with 2002 ($p = 0.001$). Neither the 2001 to 2004 comparison ($p = 0.698$) nor the 2001 to 2002 comparison ($p = 0.692$) was significant. With years pooled, Common Murre $\delta^{15}N$ values did not vary significantly month to month ($F_{5,39} = 1.7$, $p = 0.148$), but $\delta^{13}C$ values did ($F_{5,39} = 7.7$, $p < 0.001$). Like Thick-billed Murres, Common Murres became more depleted in ^{13}C during the winter ($r = -0.655$, $p < 0.001$, n = 45).

Stable isotope values were similar in male and female Common Murres ($F_{1,9} = 1.6$, $p = 0.241$ for $\delta^{15}N$; $F_{1,9} = 0.02$, $p = 0.894$ for $\delta^{13}C$) and in male and female Thick-billed Murres ($F_{1,4} = 0.06$, $p = 0.812$ for $\delta^{15}N$; $F_{1,4} = 0.12$, $p = 0.747$ for $\delta^{13}C$). HY and AHY murres have different migration phenology between breeding and wintering grounds (Gaston & Hipfner 2000), and so we considered the effects of age and month. Thick-billed Murres showed no relation of $\delta^{15}N$ values to age ($F_{1,70} = 0.02$, $p = 0.877$) or month ($F_{3,70} = 1.0$, $p = 0.400$), but an age-by-month interaction was evident ($F_{2,70} = 3.7$, $p = 0.031$), as expected. Common Murres showed no effect of age on $\delta^{13}C$ values ($F_{1,70} = 1.4$, $p = 0.234$), but month was important ($F_{3,70} = 7.9$, $p < 0.001$). HY Common Murres were significantly enriched in ^{15}N ($F_{1,39} = 8.3$, $p = 0.006$) and depleted in ^{13}C ($F_{1,39} = 8.9$, $p = 0.005$) as compared with AHY individuals (Fig. 2). AHY Thick-billed and Common Murres differed significantly in $\delta^{15}N$ ($F_{1,42} = 16.1$, $p < 0.001$) but not in $\delta^{13}C$ ($F_{1,42} = 1.3$, $p = 0.269$). Little difference was evident between HY and AHY Thick-billed Murres in either $\delta^{15}N$ ($F_{1,72} = 0.89$, $p = 0.349$) or $\delta^{13}C$ ($F_{1,72} = 2.6$, $p = 0.110$).

Five Thick-billed Murres and four Common Murres collected in 2004 had identifiable prey items in their stomachs. Two types of prey tissue were identified, fish, which could not be identified to species, and amphipods. Fish (n = 4) had mean $\delta^{15}N$ values of 13.2 ± 0.3‰ and mean $\delta^{13}C$ values of –19.7 ± 0.1‰. All of the identified amphipods were *Parathemisto libellula* (J.M. Gagnon, Canadian Museum of Nature, Ottawa, ON, pers. comm.). Based on five samples, each consisting of 6–7 individuals, the amphipods had mean $\delta^{15}N$ values of 7.3 ± 0.7‰ and mean $\delta^{13}C$ values of –22.2 ± 0.2‰. The two prey types were different in both $\delta^{15}N$ ($F_{1,8} = 62.6$, $p < 0.001$) and $\delta^{13}C$ ($F_{1,8} = 128.0$, $p < 0.001$). Breeding season *P. libellula* from Lancaster Sound, Nunavut, had a mean $\delta^{15}N$ value of 9.7 ± 0.1‰ (Hobson *et al.* 2002), and Arctic Cod *Gadus morhua,* the main prey item of Thick-billed Murres on PLI (Gaston & Nettleship 1981), had a mean $\delta^{15}N$ value of 14.0 ± 0.2‰ (Hobson *et al.* 2002).

Thick-billed Murres breeding on PLI were enriched in ^{15}N ($F_{1,226} = 11.0$, $p = 0.001$) and ^{13}C ($F_{1,167} = 236.1$, $p < 0.001$) compared with winter samples. The proportion of fish versus *P. libellula* eaten by Thick-billed Murres was estimated for the winter and breeding seasons from 2000 to 2004. Winter samples were those taken from October to March. Using equation 3, we determined that winter $\delta^{15}N$ endpoints of Thick-billed Murre muscle were 10.7‰ (corresponding to a 100% amphipod diet) and 16.6‰ (corresponding to a 100% fish diet). Breeding season $\delta^{15}N$ endpoints for Thick-billed Murre blood were 12.8‰ (diet of 100% amphipods) and 17.1‰ (diet of 100% Arctic Cod). Dietary proportions calculated using equation 2 varied with season ($F_{1,184} = 316.7$, $p < 0.001$; Fig. 3). The mean percentage of amphipods was 22.8 ± 1.2% in summer and 30.1 ± 0.8% in winter.

DISCUSSION

Murre trophic level

In the 1950s, the diet of Thick-billed and Common Murres wintering off Newfoundland consisted entirely of Capelin *Mallotus villosus* and other fish (Tuck 1960). Later studies of Newfoundland murres found that Capelin, along with Arctic Cod and Squid *Gonatus fabricii,* were important in the early winter diet, but that a shift to lower trophic level prey (euphausiids and amphipods) occurred in January–March (Gaston *et al.* 1983, Elliot *et al.* 1990). Most recently, Rowe *et al.* (2000) found that Thick-billed Murres off Newfoundland had diets similar to those in the 1980s and 1970s (a mixture of fish and lower trophic level organisms), but those authors found no evidence of decreasing trophic level in late winter. Our SIA suggests that murres off Newfoundland feed substantially on invertebrate prey and that trophic level does not decrease in late winter, because murre $\delta^{15}N$ values remained constant through the season.

Murre foraging location

In contrast to $\delta^{15}N$ values, $\delta^{13}C$ values in both Common and Thick-billed Murres became depleted over winter, indicating a possible shift in foraging location from nearshore to offshore (Hobson 1993). Several scenarios are possible. Both murre species are known to follow the ice edge in pursuit of prey in winter (Elliot *et al.* 1990), and as ice advances through the winter, birds could

TABLE 2
Mean (± standard error) muscle values of $\delta^{15}N$ and $\delta^{13}C$ in Thick-billed Murres, Common Murres and Razorbills in Newfoundland (Newfoundland and Labrador), Canada, 1996–2004

Species	Samples	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Common Murre	45	14.6 ± 0.1	–19.9 ± 0.1
Thick-billed Murre	89	14.8 ± 0.1	–19.8 ± 0.1
Razorbill	6	14.6 ± 0.3	–19.6 ± 0.2

shift to offshore foraging grounds. Alternatively, ^{13}C depletion could result from migration of birds wintering in different areas. As winter progresses, and birds begin to migrate north to breeding grounds, birds wintering nearshore may give way to birds with lower ^{13}C values that have wintered further offshore. Moreover, $\delta^{13}C$ values of murre tissue may reflect the foraging locations of their prey as well as those of the birds themselves. During spring, Capelin migrate into coastal waters from pelagic areas (Winters 1970, Nakashima 1992). Therefore, declining $\delta^{13}C$ values may reflect changing foraging locations of the prey population instead of, or in addition to, murres switching from one foraging location to another. Stable isotope values can vary greatly over relatively small scales within the food web. For example, $\delta^{13}C$ values of euphausiids varied significantly over areas sampled in the Bering, Chukchi, and Beaufort seas (Schell *et al.* 1998), and even adjacent fjords in southeastern Newfoundland (Fortune Bay and Bay d'Espoir) differed in $\delta^{13}C$ values of common species (Dickson 1986). In both cases, the spatial variation was thought to arise from differences in water movement, temperature and rates of primary production.

Comparing Common and Thick-billed Murres

During the breeding season, Thick-billed Murres tend to feed on a wider variety of prey, including more benthic species, than do Common Murres (Bradstreet & Brown 1985). Few studies have examined Common and Thick-billed Murre diets in winter, in places where these species occur together. In northern Japan, Common and Thick-billed Murres both fed on Sand Lance *Ammodytes* spp. (Ogi & Shiomi 1991). In Norway, both fed on Capelin, although Common Murres tended to feed on smaller, more energy-rich Capelin when in mixed flocks (Erikstad & Vader 1989). Bradstreet & Brown (1985) reported that wintering Thick-billed Murres in the western Atlantic consumed more invertebrate prey than did Common Murres, a conclusion supported by anatomic comparisons (Spring 1971). From limited sampling, Elliot *et al.* (1990) concluded the two murres fed on similar diets in Newfoundland during winter.

Our analysis of stable isotopes shows that AHY Thick-billed Murres fed at a higher trophic level and ate fewer invertebrates than did AHY Common Murres. AHY Common Murres tended to be taken early in the season because they migrate earlier (Elliot 1991). However, because $\delta^{15}N$ values did not vary through the season, $\delta^{15}N$ values in Thick-billed and Common Murres imply real differences in trophic level, not an artefact of sampling time.

The difference in $\delta^{13}C$ and $\delta^{15}N$ values between HY and AHY Common Murres (not seen in Thick-billed Murres) was unexpected. In contrast to our results, Lorentsen & Anker-Nilssen (1999) found that immature Common Murres in Norway tended to feed less on gadids and therefore at a lower trophic level (Ruus *et al.* 2002) than adult birds did. On the breeding grounds in the Canadian Arctic, Thick-billed Murre chicks fed at a higher trophic level than did adults (Hobson 1993), and Arctic Cod remained important in the diet of chicks upon leaving the colony (Bradstreet 1979). Because muscle tissue represents average diet over the previous month (Hobson & Clark 1992), trophic level differences would be apparent from September to November given that males may continue to feed chicks at sea for 1–2 months (Harris & Birkhead 1985). We expected differences in $\delta^{15}N$ and $\delta^{13}C$ values between HY and AHY birds to decline as the season progressed, but such a decline was not evident.

We observed no sex differences in stable isotope values in either Common or Thick-billed Murres wintering off Newfoundland. This finding agrees with both conventional (Bradstreet 1979) and SIA (Hobson 1993) approaches applied to breeding Thick-billed Murres. Sex differences in diet during winter have not been previously described in the western Atlantic (Gaston *et al.* 1983, Elliot *et al.* 1990, Rowe *et al.* 2000), but female Common Murres fed at lower trophic level than did males in Norway (Lorentsen & Anker-Nilssen 1999). Sex differences in diet after colony departure are not unexpected because of different roles in parental care. Male murres accompany their chicks at sea for 1–2 months, continuing to provide them with food (Harris & Birkhead 1985). Females are not known to participate in at-sea chick care—a potential source of variation in energy requirements, feeding behaviour and diet.

Razorbill diet

The diet of Razorbills in winter in the Northwest Atlantic is known mainly from birds collected in the Bay of Fundy. Stomachs contained mainly krill and other pelagic crustaceans in addition to fish and polychaetes (Huettmann *et al.* 2005). The Bay of Fundy

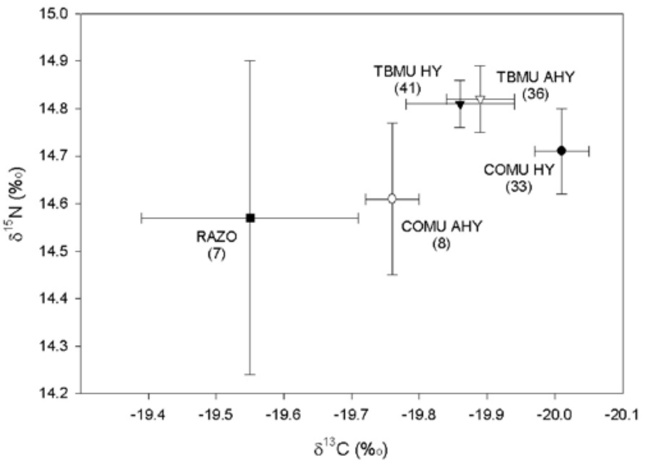

Fig. 2. Stable isotope values (mean ± standard error) of Razorbills (RAZO), hatching-year (HY) and after–hatching year (AHY) Thick-billed Murres (TBMU) and Common Murres (COMU) in Newfoundland (Newfoundland and Labrador), Canada, 1996–2004.

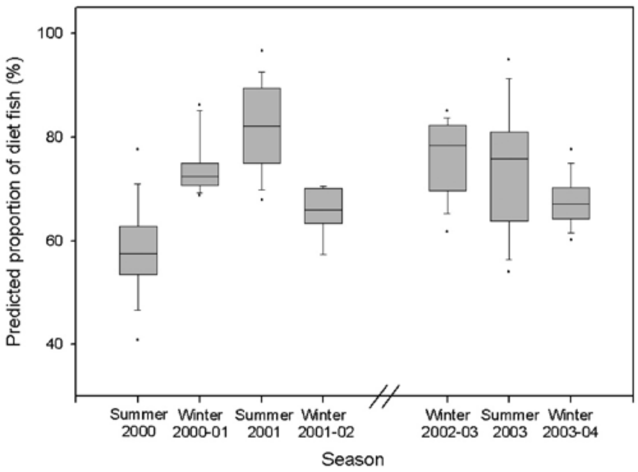

Fig. 3. Hypothesized proportion of Thick-billed Murre diet composed of fish (summer: Arctic Cod; winter: unknown fish spp.) from summer 2000 to winter 2003–04. Boxes represent 25th to 75th percentile around the median (solid line). Dots represent 5th and 95th percentiles.

is 4–5 degrees of latitude south of our study area, but the reported results of stomach analyses agree with Tuck (1960), who found that Razorbills off Newfoundland fed mainly on crustaceans. In contrast, our SIA suggests that wintering Razorbills fed at a trophic level similar to that for Common and Thick-billed Murres, and that consumption of fish may be higher than previously thought.

Diet modelling

The unidentified fish species found in the murres' stomachs had δ^{15}N values similar to those reported for fish in previous studies, but δ^{13}C values were lower (Table 3). Amphipods were similar in δ^{13}C values, but differed in δ^{15}N values as compared with previous work in Newfoundland and Labrador (Table 3).

In our two-endpoint, one-isotope (δ^{15}N) dietary model, we used fish and amphipods as two isotopically distinct prey types. This is not to suggest that birds did not feed on other prey types—for example, euphausiids and squid were found in Common and Thick-billed Murre diets (Gaston *et al.* 1983, Elliot *et al.* 1990) and polychaetes in the Razorbill diet (Huettmann *et al.* 2005)—however, in the late 1990s, amphipods (*Parathemisto* spp.) appear to have replaced euphausiids (*Thysanoessa* spp.) as the primary crustacean consumed by Thick-billed Murres off Newfoundland (Rowe *et al.* 2000). Our estimated proportion of invertebrates in the diet can be taken as conservative if euphausiids are a dietary component in the alcid species we examined. We do not expect squid to contribute significantly to diet given the absence of squid beaks in stomachs. Polychaetes were found in the Razorbill diet (Huettmann *et al.* 2005), but only in very low numbers (0.4% of stomachs) in the diet of Thick-billed Murres (Elliot *et al.* 1990). Like squid, polychaetes are relatively enriched in ^{13}C, and they had δ^{15}N values between those of fish and amphipods (Fry 1988). We consider the two-endpoint, one-isotope model useful in comparing the relative proportions of fish and amphipods among locations, but it should not be taken as a definitive description of alcid diets.

Variation between successive years in the winter diet of Thick-billed Murres has not been reported, but long-term changes have been described (Elliot *et al.* 1990, Rowe *et al.* 2000). Interannual variation in stable isotopes has been found in breeding Thick-billed Murres (A.T. Moody unpubl. data) and, in this study, in wintering murres. Common and Thick-billed Murres both differed in δ^{13}C values between 2004 and 2002, which suggests possible changes in foraging location. The lack of differences in δ^{15}N values across the

TABLE 3
Mean (± standard error) values of δ^{15}N and δ^{13}C for prey species sampled (except where noted) in Newfoundland (Newfoundland and Labrador), Canada [a]

Species	Location	Year or years	Samples	δ^{15}N (‰)	δ^{13}C (‰)	Reference
Amphipods						
Parathemisto gaudichaudii	Fortune Bay, NL	1984–85	4	10.2 ± 0.1	–22.3 ± 0.1	Dickson (1986)
	Bay d'Espoir, NL	1984–85	5	10.7 ± 0.1	–22.2 ± 0.2	Dickson (1986)
P. libellula	Nearshore	2004	5 [b]	7.3 ± 0.7	–22.2 ± 0.2	Present study
	Nearshore Lancaster Sound	1998	106 [b]	9.7 ± 0.1	–20.4 ± 0.1	Hobson *et al.* (2002)
Fish						
Capelin	Nearshore	2004	4	13.2 ± 0.3	–19.7 ± 0.1	Present study
Mallotus villosus	Fortune Bay, NL	1984–85	4	13.1 ± 0.2	–21.5 ± 0.4	Dickson (1986)
	Nearshore	1990	4	13.0 ± 0.3	—	Hobson & Montevecchi (1991)
	Nearshore	1986–90	11	12.2 ± 0.2	–21.4 ± 0.2	Ostrom *et al.* (1993)
Arctic Cod	Offshore	1995	10	13.7 ± 0.1	–18.8 ± 0.1	Lawson & Hobson (2000)
Boreogadus saida	Nearshore Lancaster Sound	1998	8	14.0 ± 0.2	–19.3 ± 0.1	Hobson *et al.* (2002)
Atlantic Cod			1	12.6	—	Fry (1988)
Gadus morhua	Nearshore	1990	2	15.1 ± 0.1	—	Hobson & Montevecchi (1991)
	Nearshore	1995	10	13.9 ± 0.2	–19.0 ± 0.1	Lawson & Hobson (2000)
Arctic Squid						
Gonatus fabricii	Offshore Labrador	1996	10	8.5 ± 0.6	–18.5 ± 0.1	Lawson & Hobson (2000)
Northern Sand Lance						
Ammodytes dubius	Offshore	1996	10	12.0 ± 0.1	–19.6 ± 0.1	Lawson & Hobson (2000)

[a] Adapted from Lawson & Hobson (2000).

[b] Refers to grouped samples, each consisting of a number of individuals.

years suggests that the proportions of vertebrates and invertebrates consumed in winter were fairly consistent. We caution, however, that temporal and spatial dynamics of stable isotope signatures of marine food webs off Newfoundland are poorly understood (e.g. Dickson 1986, Schell *et al.* 1998).

As expected, food webs associated with murres wintering in Newfoundland and breeding in the high Arctic differed isotopically. Using endpoints specific to site, season and tissue, we were able to control for this difference and conclude that a seasonal difference in trophic level in fact occurred. During the breeding season, the energy requirements of egg production, fasting during incubation shifts, and chick provisioning may be satisfied by targeting lipid-rich, high trophic level prey. Alternatively, differences between seasons may reflect food availability—fish being simply less available during winter (Rowe *et al.* 2000).

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