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Geographic and seasonal variability in the isotopic niche of little auks

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ABSTRACT: The non-breeding season of seabirds is extremely challenging to study because it is often spent offshore under harsh environmental conditions. We used stable isotope analysis to investigate little auk *Alle alle* feeding ecology throughout the annual cycle. The geographic distribution of little auks in the Arctic covers a wide range of oceanographic conditions. We sampled birds from 5 different colonies located in the most important breeding areas (Greenland and Spitsbergen) to examine how individuals breeding in contrasting marine environments differ in their trophic niche throughout the year. We found differences in summer $\delta^{15}N$ values among the colonies, suggesting different target species despite low overall $\delta^{15}N$ values in blood, which indicates a diet that is primarily composed of copepods. A rise in $\delta^{15}N$ values between summer and autumn indicated that adults changed their trophic status to feed at a higher trophic level. During autumn, a large overlap in feather $\delta^{13}C$ values between colonies suggests a common moulting area off Northeast Greenland. During winter, the isotopic signatures show that the trophic status of Greenland and Spitsbergen birds differed, with birds from Greenland feeding at low trophic levels (probably mostly on copepods), and birds from Spitsbergen maintaining a higher trophic level. These findings highlight contrasting seasonal and regional diet in little auk populations, and reveal possible population overlaps during the autumn moult. We found substantial trophic variability in little auks, which may indicate unsuspected capabilities to adapt to current, drastic environmental change in the North Atlantic.

KEY WORDS: Alcid · Annual cycle · Copepod · Diet · North Atlantic · Pelagic ecosystem · Seabird · Stable isotopes

INTRODUCTION

In polar and temperate regions, the non-breeding season has a profound impact on seabird ecology. During this period, birds have to cope with harsh and highly variable environmental conditions, which can directly affect their body condition, energy balance and survival (Grosbois & Thompson 2005, Rolland et al. 2009) and ultimately shape their population dynamics (Barbraud & Weimerskirch 2003, Daunt et al. 2006). However, the underlying mechanisms and the different factors involved often remain a 'black box', and further studies are therefore needed to explore seabird ecology throughout the non-breeding period. Between breeding seasons, seabirds are typically far offshore and are consequently inaccessible for conventional sci-

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entific studies (Gaston 2004). In recent years, technical developments have started to alleviate this problem. For example, miniaturized electronic tracking tags allow investigations of winter movements and migration routes (e.g. Bost et al. 2009, Egevang et al. 2010), fatty acid analyses can provide information on specific dietary components (e.g. Williams et al. 2008), and modelling has improved our knowledge of seabird winter energetics (e.g. Fort et al. 2009). These studies are nonetheless often restricted temporally or spatially, thereby ignoring potential environmental variability, which may affect strategies across individuals and populations (Grémillet & Boulinier 2009). Stable isotope analysis is a powerful technique in the study of animal feeding ecology under variable conditions (West et al. 2006). This approach indeed permits the identification of animal isotopic niches (i.e. the δ-space used by an organism and defined by the 2 isotopic axes $\delta^{15}N$ and $\delta^{13}C$; Newsome et al. 2007), where the nitrogen isotopic ratio reflects trophic position/diet of the predator, while the carbon isotopic ratio reflects its spatial foraging distribution (Hobson et al. 1994, Kelly 2000). These isotopic axes therefore help in defining the ecological niche of the animal (Newsome et al. 2007, Cherel 2008). In seabirds, stable isotope analysis has been used to track both migration and diet (e.g. Hobson 1999, Cherel et al. 2007). Indeed, since different body tissues incorporate the isotopic signatures of resources at different rates, the analysis of different tissues allows tracking of changes in feeding ecology over different time periods and at different time scales, including the non-breeding period (Hobson 1993, Cherel et al. 2008).

The little auk *Alle alle* is a small diving seabird that feeds almost exclusively on zooplankton in Arctic and North Atlantic waters, with a breeding distribution covering a wide range of ocean current regimes and contrasting water masses (Gaston & Jones 1998, Stempniewicz 2001). With recent estimates of >80 million individuals (Gaston & Jones 1998, Isaksen & Gavrilo 2000, Kampp et al. 2000, Egevang et al. 2003), this species is the most abundant seabird of the North Atlantic and one of the most abundant seabirds in the world (Stempniewicz 2001). It therefore plays a crucial role within Arctic ecosystems, notably in terms of energy and organic matter transfer. For example, breeding little auks foraging in the North Water Polynya off Northwest Greenland account for 92 to 96% of the carbon flux to seabirds, and consume up to 24% of the copepod standing stock in this region (Karnovsky & Hunt 2002). During the non-breeding season, knowledge of their spatial distribution and diet are more elusive. Winter vertical migration of their main prey *Calanus* spp. (Harding et al. 2008), which tend to descend to depths unreachable by little auks (>100 m; Falk-Petersen et al. 2009), suggests a strong seasonal shift in little auk diet. Only one study (Karnovsky et al. 2008) has investigated the non-breeding diet of little auks, and this study concludes that these birds show dietary shifts during the different seasons, especially during autumn. However, this study was limited to one particular site, the North Water Polynya, where random birds were sampled during different seasons. This procedure does not allow the comparative analysis of little auk diet across the annual cycle for birds of known origin. Such investigations are nonetheless essential to assess dietary flexibility in little auk populations across a large portion of the North Atlantic, and their capacity to respond/adapt to contrasting and fluctuating environments and resource availability.

Therefore, using isotopic signatures of different body tissues from birds breeding at different geographical sites, the present study aimed to (1) assess trophic level variability in little auks throughout the annual cycle to investigate how birds respond to a change in their feeding environment, and (2) compare the isotopic niches across little auk populations at different spatial scales in order to determine how environmental conditions experienced by each population may affect little auk feeding ecology during the different seasons.

MATERIALS AND METHODS

Sample collection. This study was conducted during the 2007 breeding season at 4 colonies on Spitsbergen and 1 colony on East Greenland. A total of 291 breeding adults and 20 chicks of little auks were sampled, and 28 chick meals collected (see Table 1 & Fig. 1). Hereafter, these 5 colonies are referred to as EG for the East Greenland colony, and as S1 to S4 following a north–south gradient for the Spitsbergen colonies (Fig. 1).

Blood samples (~0.2 ml) were collected from the brachial vein. Seventy percent ethanol was then added to the whole blood, which was kept frozen at –20°C until isotopic analysis. To check if results were not sex-biased, an additional small amount of blood was taken at EG, S2 and S4 for subsequent molecular sexing as detailed in Fridolfsson & Ellegren (1999).

Little auks have 2 distinct moults yr^{-1}: one complete moult in autumn (September–October) that involves the replacement of the complete body plumage, and a partial moult in winter (March) when only feathers from the neck and head are replaced (Gaston & Jones 1998, Stempniewicz 2001). Therefore, 2 batches of cover feathers were plucked on each breeding adult in summer: 1 from the body (back or belly, reflecting the autumn period), and 1 from the head (cheek, neck or throat, reflecting the winter period). These 2 batches

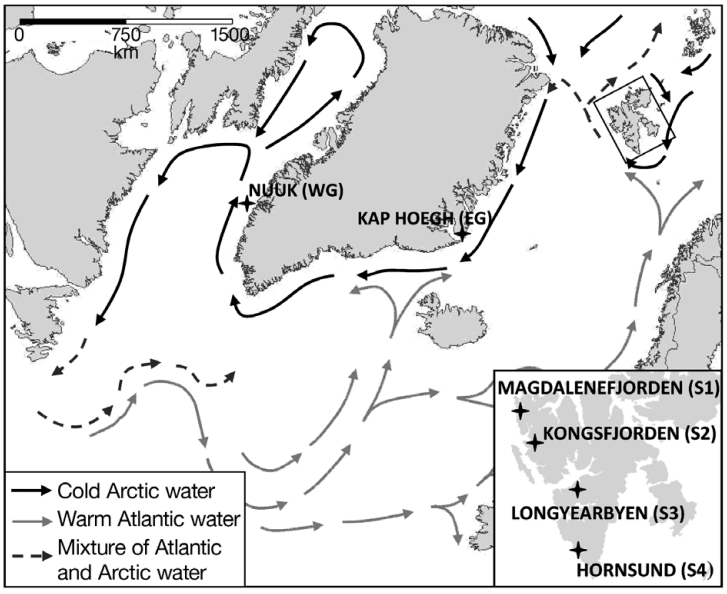

Fig. 1. Breeding colonies of the studied little auk *Alle alle* which are labelled as follows in the text: S1 to S4 for Spitsbergen (from north to south, inset), EG for East Greenland and WG for West Greenland wintering birds (after AMAP 1998). Geographical coordinates given in Table 1

are hereafter called 'body feathers' and 'head feathers'. All feathers were randomly plucked to avoid bias due to an eventual patchy moult pattern. For chicks, only newly grown cover feathers were plucked during the late chick-rearing period, when down had totally disappeared. All collected feathers were kept at ambient temperature in sealed plastic bags until analysis.

Chick meals were collected from adult birds, which carry food to the nest in a sublingual (gular) pouch (Stempniewicz 2001). Adult birds were caught in the colony using mist nets or noose carpets. Each food load was gently scooped out of the gular pouch and immediately preserved in 70% ethanol. Caught adults were released unharmed after 5 to 10 min of handling. In the laboratory, a random sample of each chick meal was taken for dietary analyses. Each diet sample was divided into broad prey classes (copepods, amphipods and others). Prey items were then numbered and identified based on Keast & Lawrence (1990), Kwasniewski et al. (2003), and W. Walkusz (pers. comm.). To estimate the composition of the chick meals by mass, we dried items of each taxon and calculated individual dry mass. We then reconstituted the proportion of each taxon by dry mass in the different chick meal samples.

Twenty additional birds that were legally shot at sea by Greenlandic hunters for commercial sale were bought. The birds were shot off Nuuk (64° 10' N, 51° 45' W; West Greenland, hereafter symbolized as WG) in winter (January 2007) and immediately kept frozen until dissected in the laboratory. Blood samples were collected from the cardiac clot, 'body feathers' were randomly plucked from the belly, back or throat, and birds were visually sexed from gonads. Blood and body feathers were stored as in breeding birds. No head feathers were sampled from these birds because both body and head feathers in winter plumage originate from the same moult (autumn moult). Stomach contents were also removed, but the advanced digestion stage of the prey precluded identification.

Sample preparation and isotopic analysis. Prior to isotopic analysis, blood samples were dried for 48 h at 60°C and homogenized. Feathers were rinsed in a 2:1 chloroform: methanol solution, rinsed 2× in a methanol solution, dried for 48 h at 60°C and homogenized with scissors. Food samples were dried for 48 h at 60°C and ground to a powder. Lipids and carbonates were then removed from food samples by rinsing them successively in cyclohexane and 1 N HCl. All isotopic analyses were performed by the Mylnefield Research Services Stable Isotope Laboratory (SCRI, Dundee, Scotland). Analyses were performed on 1 mg subsamples of dried and homogenized materials loaded into tin cups and combusted at 1000°C in an elemental analyzer (ANCA-GSL, Sercon). Resultant CO_2 and N_2 gases were then analyzed for ^{13}C and ^{15}N isotope abundance in continuous-flow mode using an isotope ratio mass spectrometer (SerCon 20:20, SerCon). Measured data were scale-calibrated using 2 international reference materials (IAEA-600 and IAEA-CH6) as well as one in-house standard (leucine). Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta X = [(R_{sample}/R_{standard})-1] \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The $R_{standard}$ values were based on Vienna-PeeDee Belemnite (VPDB) for ^{13}C and atmospheric N_2 (air) for ^{15}N.

Data analysis. Using allometric equations between body mass and carbon half-life in avian blood (Carleton & del Rio 2005), stable isotope half-lives in little auk blood were estimated to be 12 to 15 d. Given this result, and following little auk moulting sequences (see above), blood collected from breeding birds was taken to reflect the summer isotopic signature (from early to late July, following sampling dates at each colony), body feathers the autumn signature (September–October), and head feathers the winter signature (March) (Bearhop et al. 2002). Blood collected on hunted birds also reflects the winter isotopic niche (early January) of little auks.

In order to compare blood and feather isotopic signatures and, consequently, investigate the bird isotopic

niche at different periods of their annual cycle, we needed to take into account the tissue-dependent metabolic routing and enrichment factors for little auks (Podlesak & McWilliams 2006, Quillfeldt et al. 2008a). We thus compared stable isotope ratios obtained from feathers and blood samples that were simultaneously collected on chicks, and calculated correction factors to compare $\delta^{13}C$ and $\delta^{15}N$ values from these 2 tissues in adult birds. To avoid effects of growth on blood $\delta^{15}N$ values (Sears et al. 2009) and therefore allow comparison of chicks and adults, chicks were sampled during the late chick-rearing period, just before fledging, when growth is reduced (see Harding et al. 2009b). We found differences between chick feathers and blood of –0.25‰ for nitrogen and 0.65‰ for carbon, and used these values as correction factors. Therefore, we corrected adult body and head feather isotopic data by subtracting the correction factors before comparing them with blood and zooplankton (uncorrected) isotopic results.

Statistics were computed using Statistica 6.0. We used multivariate analysis of variance (MANOVA) with Wilk's lambda statistics to simultaneously compare $\delta^{15}N$ and $\delta^{13}C$ values between colonies, as well as analysis of variance (ANOVA) followed by post-hoc range tests (Tukey's multiple comparison test for unequal sample sizes) to independently compare $\delta^{15}N$ and $\delta^{13}C$ values between sexes, seasons and colonies. Presented values are means ± SD, and statistical significance was assumed at $p < 0.05$.

RESULTS

For all colonies on which birds were sexed and for all tissues, no differences in $\delta^{15}N$ and $\delta^{13}C$ values between adult males and females were observed (ANOVA, $\delta^{15}N$: $F_{5,162} = 1.27$, $p = 0.28$; $\delta^{13}C$: $F_{5,162} = 0.52$, $p = 0.76$). Therefore, results for the 2 sexes were pooled in the following analyses.

Chick meals and adult $\delta^{15}N$ values

Chick meals collected at EG and S4 were mostly (63 and 78%) composed of copepods (almost exclusively *Calanus hyperboreus* and *C. glacialis*, respectively; Fig. 2). However, chick meals from EG also included the ice-associated amphipod *Apherusa glacialis* (32%). The values of $\delta^{15}N$ measured on chick meals was similar for both colonies (Mann-Whitney test, $U = 72.0$, $p = 0.28$, $n = 12$ and 16 for S4 and EG, respectively) (Table 1, Fig. 3). Moreover, chicks and adults from EG had similar blood $\delta^{15}N$ values (*t*-test: $t = 1.56$, $df = 38$, $p = 0.13$) (Table 1).

Adult breeding birds at EG showed significant variation in $\delta^{15}N$ isotopic ratio during the different seasons (ANOVA, $F_{2,55} = 43.99$, $p < 0.001$). Post hoc Tukey's multiple comparison tests indicated an increase in this ratio between summer and autumn ($p < 0.001$), followed by a decrease between autumn and winter ($p < 0.001$). $\delta^{15}N$ isotopic values were similar between summer and winter ($p = 0.59$) (Fig. 3). Birds breeding in Spitsbergen also present a significant variation in $\delta^{15}N$ values between seasons ($F_{2,230} = 541.97$, $p < 0.001$). Like the Greenland birds, this ratio increased between summer and autumn ($p < 0.001$). However, it remained high in winter with a mean value similar to that found in autumn ($p = 0.100$). This winter ratio was significantly higher than the summer ratio ($p < 0.001$) (Fig. 3).

Seasonal and colony variations

During summer, the different colonies were segregated by their overall isotopic signatures (MANOVA, Wilk's lambda, $F_{8,174} = 95.50$, $p < 0.001$) and in a univariate analysis, by their blood $\delta^{13}C$ (ANOVA, $F_{4,88} = 282.20$, $p < 0.001$) and $\delta^{15}N$ values ($F_{4,88} = 51.15$, $p < 0.001$) (Fig. 4A). Post hoc Tukey's multiple comparison tests indicated that among Spitsbergen birds, the 2 southern colonies (S3 and S4) had higher $\delta^{15}N$ values than the 2 northern colonies (S1 and S2). Moreover, S3 had higher $\delta^{13}C$ values than S2 and S4, whereas S4 had lower $\delta^{13}C$ values than S1. Moreover, $\delta^{13}C$ and $\delta^{15}N$ values measured in EG were respectively lower and higher than in all Spitsbergen colonies (all $p < 0.001$).

During autumn, birds from the different colonies were also segregated by their overall isotopic signatures ($F_{10,224} = 7.31$, $p < 0.001$), as well as by their $\delta^{13}C$

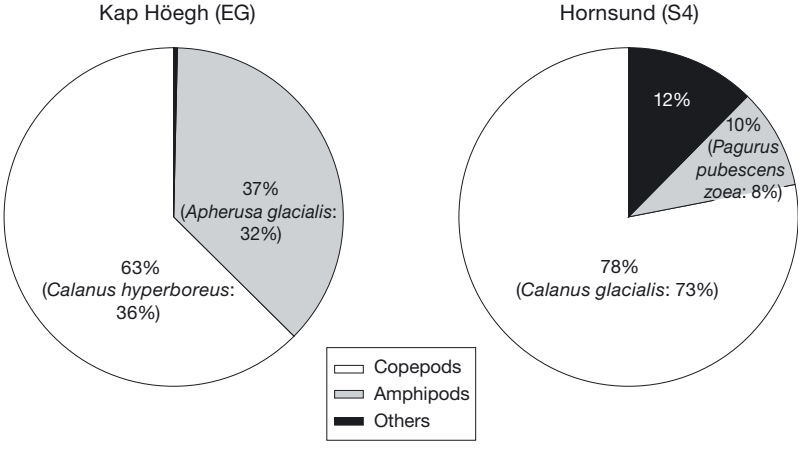

Fig. 2. *Alle alle*. Composition of chick meals (expressed in % dry mass) collected from adults at Kap Höegh (East Greenland, EG; n = 16) and Hornsund (Spitsbergen, S4; n = 12)

Table 1. *Alle alle*. Stable isotopic signatures (means ± SD) of tissue samples collected. Stable isotope data are raw (uncorrected)

Status	Site	Colony	Symbol	Tissue	Time period	n	δ^{13}C (‰)	δ^{15}N (‰)
Breeding adults	East Greenland	Kap Höegh (70° 43′ N, 21° 38′ W)	EG	Whole blood	Summer	20	−21.7 ± 0.1	11.4 ± 0.1
				Body feathers	Autumn	19	−20.5 ± 0.7	13.1 ± 0.7
				Head feathers	Winter	19	−19.6 ± 0.8	11.4 ± 1.0
	Spitsbergen	–	–	Mean whole blood	Summer	73	−20.1 ± 0.2	10.7 ± 0.4
				Mean body feathers	Autumn	80	−20.3 ± 0.6	13.4 ± 0.6
				Mean head feathers	Winter	80	−19.4 ± 0.5	13.2 ± 0.8
		Magdalenefjorden (79° 35′ N, 11° 05′ E)	S1	Whole blood	Summer	14	−20.1 ± 0.1	10.5 ± 0.2
				Body feathers	Autumn	20	−20.6 ± 0.6	13.5 ± 0.6
				Head feathers	Winter	20	−19.4 ± 0.5	12.9 ± 0.9
		Kongsfjorden (79° 01′ N, 12° 25′ E)	S2	Whole blood	Summer	20	−20.2 ± 0.2	10.4 ± 0.2
				Body feathers	Autumn	20	−20.3 ± 0.5	13.2 ± 0.7
				Head feathers	Winter	20	−19.8 ± 0.4	13.3 ± 0.8
		Longyearbyen (78° 13′ N, 15° 19′ E)	S3	Whole blood	Summer	20	−20.0 ± 0.3	11.0 ± 0.4
				Body feathers	Autumn	20	−19.6 ± 0.5	13.2 ± 0.5
				Head feathers	Winter	20	−18.9 ± 0.4	13.3 ± 0.6
		Hornsund (77° 00′ N, 15° 22′ E)	S4	Whole blood	Summer	19	−20.3 ± 0.2	11.1 ± 0.3
				Body feathers	Autumn	20	−20.6 ± 0.4	13.8 ± 0.3
				Head feathers	Winter	20	−19.5 ± 0.4	13.4 ± 0.8
Wintering adults	Nuuk	(64° 00′ N, 55° 00′ W)	WG	Whole blood	Winter	21	−19.5 ± 0.4	11.7 ± 0.4
				Body feathers	Autumn	20	−20.3 ± 0.4	13.2 ± 0.5
Chicks	East Greenland	Kap Höegh	EG	Whole blood	Summer	20	−22.3 ± 0.1	11.8 ± 1.2
				Body feathers	Summer	19	−21.6 ± 0.4	11.6 ± 0.3
				Chick food	–	16	−22.3 ± 0.5	8.4 ± 0.5
	Spitsbergen	Hornsund	S4	Chick food	–	12	−21.8 ± 0.3	8.3 ± 0.4

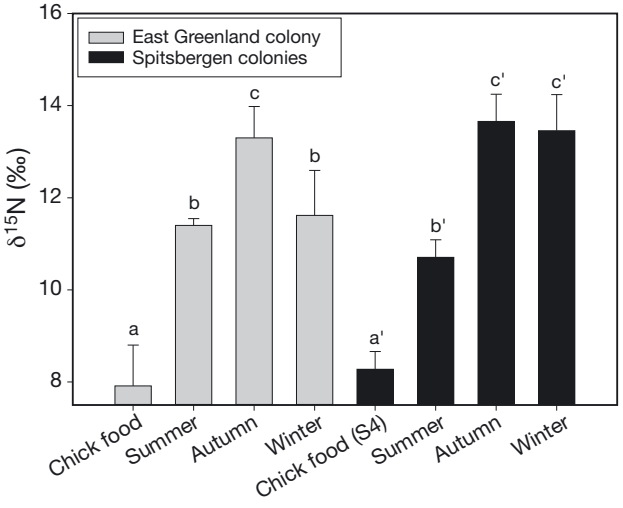

Fig. 3. *Alle alle*. Stable nitrogen isotope values (uncorrected; means ± SD) of samples from East Greenland and Spitsbergen during the different seasons and of chick meals collected at 2 colonies (EG and S4). At each site, values with different superscript letters are significantly different (see 'Results')

($F_{5,113}$ = 10.30, p < 0.001) and δ^{15}N values ($F_{5,113}$ = 4.00, p = 0.002). However, multiple comparison tests indicated that only birds from S3 differed from birds from the other sites, because of higher δ^{13}C values (all p < 0.01). Furthermore, only birds from S4 had significantly higher δ^{15}N values than those from S3, EG and WG (p = 0.02, 0.003 and 0.03, respectively) (Fig. 4B).

During winter, birds from all colonies were again segregated by their overall isotopic signatures ($F_{10,226}$ = 20.10, p < 0.001) and in a univariate analysis, by their δ^{13}C ($F_{5,114}$ = 12.75, p < 0.001) and δ^{15}N values ($F_{5,114}$ = 30.14, p < 0.001). However, multiple comparison tests indicated that δ^{13}C values measured on birds from S3 and WG were similar (p = 1.00) but differed from those in all other colonies (all p < 0.01), whereas δ^{15}N values of Greenland birds (EG and WG) were similar (p = 1.00) but differed from those in all Spitsbergen colonies (all p < 0.001) (Fig. 4C).

DISCUSSION

Detailed knowledge of seabird feeding ecology through the non-breeding season is essential to understand the determinants of winter mortality, and how individuals respond to environmental constraints and variability, notably in terms of prey availability. Karnovsky et al. (2008) studied little auk diet and found large seasonal changes throughout the year. However, their study was restricted to one site (the North Water Polynya off Northwest Greenland) and did not take into account intra-individual and spatial variations. Additional investigations were therefore needed to define the trophic niche of this essential seabird component of Arctic marine food webs across the North Atlantic.

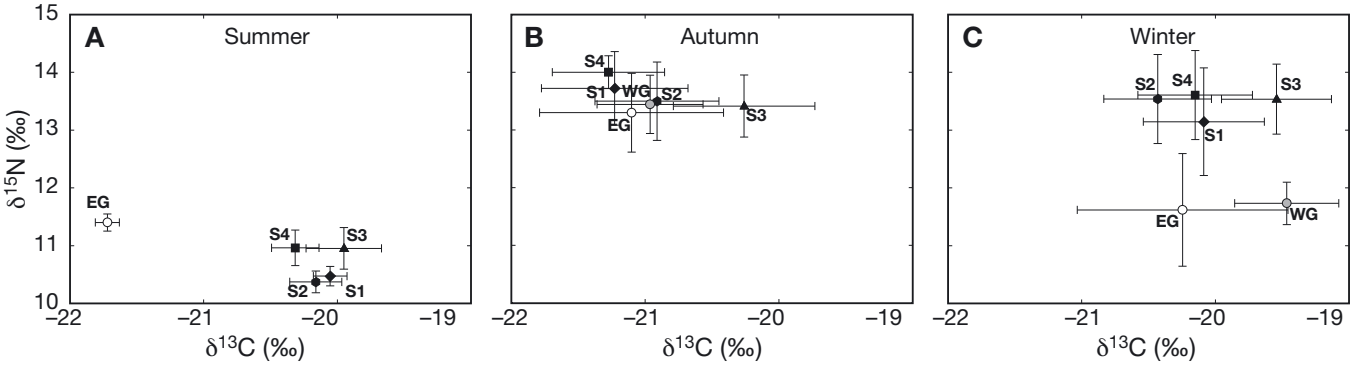

Fig. 4. *Alle alle*. Stable carbon and nitrogen isotope values (means ± SD) of adult samples from each colony during the different seasons. Summer values (from blood) are uncorrected, while autumn and winter values (from feathers) are corrected. Open symbols: values measured on birds from the East Greenland colony; black-filled symbols: values from the Spitsbergen colonies; grey-filled symbols: values for the West Greenland winter-shot birds. See Table 1 for details of colonies

The use of stable isotope analysis is particularly relevant in this context, but results and interpretations in terms of distribution and trophic status have to be formulated carefully, notably by integrating information from baseline isoscapes (geographical distribution of isotope values, here $\delta^{15}N$ and $\delta^{13}C$). Indeed, while a difference between measured values might reflect contrasting habitats occupied or prey consumed, it might also result from a variation (in space and/or time) in isotopic values at the base of the food web. A recent overview of isoscapes at a large geographical scale (Graham et al. 2010) enables such an integration, and therefore provides guidance for future isotopic research. Little auk distribution is limited to the North Atlantic and the Arctic (above ca. 50° N; Gaston & Jones 1998), where $\delta^{15}N$ values are homogeneous (Graham et al. 2010). This homogeneity is confirmed by similar $\delta^{15}N$ signatures measured on zooplankton (chick meals) from East Greenland and Spitsbergen (Fig. 3), and on adult diet at Hornsund (S4) in a previous year (Harding et al. 2008). This therefore suggests minor spatio-temporal changes in $\delta^{15}N$ values at the base of the food web within the distribution range of little auks, and allows comparison of nitrogen signatures that are assumed to reflect relative trophic position based on homogeneous $\delta^{15}N$ baseline levels. In great contrast, $\delta^{13}C$ values are spatially structured throughout this region, showing contrasting isotopic habitats. Nevertheless, this geographical gradient is not continuous, and some isotopic habitats represent vast areas where very distant regions (e.g. on both sides of Greenland) share similar baseline values (Graham et al. 2010). Interpretation of $\delta^{13}C$ signatures to indicate the movements and distribution of marine predators such as little auks must therefore integrate such essential isoscape information.

Our study shows strong inter-seasonal variation in $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures in birds from a given colony, thus confirming the results of Karnovsky et al. (2008). Moreover, we observed that little auks from the different study colonies (East Greenland and Spitsbergen) occupy variable isotopic niches throughout the different seasons of their annual cycle, with some important variations between bird populations at different spatial scales.

Interestingly, isotopic niches measured were similar for males and females during all seasons. A previous investigation also found no sexual differences in the isotopic niche of little auks during the summer breeding season (Harding et al. 2008). The present investigation further extends these findings to the autumn and winter. Like guillemots *Uria* spp., little auks switch from bi-parental to uni-paternal care prior to chick fledging (Harding et al. 2004). Females usually leave the colony earlier, while males accompany chicks during fledging and the first period at sea (Stempniewicz 2001). Given these behavioural differences, we expected autumn moulting grounds and migration routes to be different for the 2 sexes, therefore leading to contrasting $\delta^{15}N$ and $\delta^{13}C$ isotopic values in autumn. Contrary to this expectation, our results show that both sexes have identical isotopic niches during this season. While this result indicates that males and females are likely to moult in the same overall geographic area, it cannot confirm at smaller spatial scale whether both sexes moult together or in close proximity. Further specific studies using methods that are complementary to stable isotope analyses will have to be performed to investigate sex-specific strategies and potential segregation more accurately.

Spatial variability in the isotopic niche of little auks

The coasts of Spitsbergen and Greenland, on both sides of the Greenland Sea, are characterized by water masses from 2 highly contrasting sources (Buch 2000;

Fig. 1). The West coast of Spitsbergen is dominated by the northward flowing Norwegian Atlantic current, which is an extension of the relatively warm North Atlantic current. In contrast, the East Greenland coast is characterized by cooler, less saline water of the East Greenland current flowing southward from the central Arctic basin (Buch 2000). The 2 distinct summer isotopic habitats ($\delta^{13}C$ values) of the East Greenland and Spitsbergen birds (Fig. 1) reflect these 2 different oceanographic environments, and confirm recent isoscape meta-analyses (Graham et al. 2010).

The summer diet of little auks has been described in detail in previous studies (e.g. Karnovsky et al. 2003, Jakubas et al. 2007, Harding et al. 2008, Karnovsky et al. 2008). Here, only chick meals were collected, but the similar $\delta^{15}N$ isotopic values measured both in chick and adult blood samples strongly suggest that adult and chick little auks feed on similar prey. Therefore, results obtained in this study (isotopes and prey identification) confirm that all birds from the different colonies and populations mostly feed at low trophic levels and on *Calanus* copepods in summer. However, several differences are apparent among colonies at large and small spatial scales (Figs. 2 & 4A). For example, prey identification shows that the main copepod species consumed by East Greenland (EG; *C. hyperboreus*) and Spitsbergen (S4; *C. glacialis*) birds differ — a result that mirrors prey availability at both sites (Karnovsky et al. 2003, Falk-Petersen et al. 2009) and confirms previous investigations (Harding et al. 2008, 2009a, Kwasniewski et al. 2010). Moreover, the presence of sea-ice near the East Greenland colony allowed breeding birds to feed on the ice-associated amphipod *Apherusa glacialis* (Fig. 2).

In Spitsbergen, the 2 northern colonies were also segregated from the 2 southern colonies by their $\delta^{15}N$ values (Fig. 4A). However, the difference observed was only marginally significant — a fact that might be explained in 2 different ways. Firstly, and most likely, northern birds may feed at a slightly lower trophic level than southern birds, thereby reflecting different targeted prey. It is established that during summer, adult little auks perform long foraging trips that allow them to feed in areas >200 km from their breeding sites (Welcker et al. 2009). Birds from S1 and S2 are therefore able to reach distant feeding grounds in the Arctic Ocean, where multi-year ice prevails as well as associated amphipods *Apherusa glacialis* (Søreide et al. 2008), which is the prey with the lowest nitrogen isotopic signature consumed by little auks (Tamelander et al. 2006, Harding et al. 2009a). First investigations of little auk feeding grounds using GPS tracking confirmed that some breeding adults from Magdalenefjorden (S1) reach the sea ice edge at 130 km from their colony (D. Jakubas et al. unpubl. data). Moreover, the prey *A. glacialis* was present in chick meals collected at S1 in 2007 and 2008 (Kwasniewski et al. 2010), while it was not found at S4 (present study, Kwasniewski et al. 2010). Consequently, it is likely that adults from the 2 northern colonies feed on a higher proportion of *A. glacialis* (and therefore at a lower trophic level) than those from the 2 southern colonies which cannot reach northern, cooler waters. On the other hand, we cannot exclude a slight and regional baseline isotopic variation between North and South Spitsbergen, which may also explain the small difference between both groups, with birds from all Spitsbergen colonies feeding at similar trophic levels. To clarify this point, further, smaller-scale investigations are required to define baseline $\delta^{15}N$ values across the marine habitats of little auks from Spitsbergen.

Overall, the foraging distance of breeding little auks is constrained by the need to frequently feed the chick at the colony (Welcker et al. 2009). This constraint drives the behaviour of the birds, with all individuals from a given colony feeding in a similar habitat, and on the same range of prey available in their immediate environment. This phenomenon is reflected by a low variance in $\delta^{15}N$ and $\delta^{13}C$ isotopic values during summer (Fig. 4A). Conversely, during the non-breeding season, birds are free to occupy any area of their winter range, and to feed on any prey item. This is confirmed by our study, which clearly shows that the isotopic niche occupied by little auks from the same colony is wider during the non-breeding season, as has been found in other seabird species elsewhere (Cherel et al. 2007, 2008). This strongly suggests that non-breeding little auks disperse across contrasting water masses of the North Atlantic, where they feed on a wider range of prey.

Temporal variability in the isotopic niche of little auks

Between summer and autumn, little auks from all studied colonies showed a drastic change in their trophic status (reflected by the $\delta^{15}N$ isotopic ratio). Indeed, their $\delta^{15}N$ increased by ~3‰ between both seasons. This change of >1 trophic level (Hobson & Welch 1992) strongly suggests a dietary shift between summer and autumn. This change is consistent with that observed in little auks from the North Water Polynya (Karnovsky et al. 2008), and with our current knowledge of copepod ecology (Falk-Petersen et al. 2009). Indeed, soon after summer, copepods (including *Calanus* spp. species), which are caught by little auks during breeding (Fig. 2), are known to perform vertical migration to depths of several hundred meters to undergo diapause, thereby becoming inaccessible to the birds, which can only dive to 40 m (Harding et al.

2009a). These copepods are thought to migrate back to surface waters a few months later to match the spring phytoplankton bloom (Falk-Petersen et al. 2009, Henson et al. 2009). During autumn, little auks are thus expected to feed on alternate prey. For instance, larger, energy-richer amphipods feeding at higher trophic levels might be consumed by little auks in early autumn (Stempniewicz 2001).

During autumn, birds from all colonies displayed similar $\delta^{13}C$ values (except birds from S3; Fig. 4B). As mentioned above, and relying on this similarity only, it is difficult to interpret these results in terms of whether moulting places are common or different. However, existing information from long-term ring recoveries (e.g. Stempniewicz 2001) and recent biotelemetry studies (A. Mosbech et al. unpubl. data) suggested that (1) Spitsbergen birds move quickly after the breeding season to ice-filled areas of the West Greenland Sea, and start to moult there (Stempniewicz 2001), while (2) East Greenland birds move northerly after summer to moult in the Greenland Sea (A. Mosbech et al. unpubl. data). Combined results therefore indicate that during autumn, birds from East Greenland and Spitsbergen moult in a similar isotopic habitat/water mass, most likely in the Greenland Sea.

The pattern of changes in bird trophic levels between autumn and winter was different for the East Greenland and Spitsbergen colonies. Birds breeding in East Greenland displayed a second dietary shift in winter since they fed at a lower trophic level at this time than during autumn. Interestingly, their winter $\delta^{15}N$ values, similar to those of summer, are in agreement with birds preying upon copepods during this period (Sato et al. 2002, Karnovsky et al. 2008). Little auks from East Greenland mainly winter off Newfoundland (Stempniewicz 2001, A. Mosbech et al. unpubl. data). In this region, the spring phytoplankton bloom starts earlier than in the rest of the North Atlantic (i.e. from February; Henson et al. 2009) and it is likely that copepods, which migrate back to surface waters following this bloom, are available to diving little auks during their winter moult (Fort et al. 2010). In contrast, birds from all Spitsbergen colonies adopted a different feeding strategy during winter. Their $\delta^{15}N$ values showed that little auks maintained a high trophic level during winter, similar to that in autumn.

During the winter moult, Greenland and Spitsbergen populations shared a similar isotopic habitat (reflected by similar $\delta^{13}C$ isotopic ratios). However, $\delta^{15}N$ values showed that birds fed at different trophic levels (see 'Results'), suggesting contrasting targeted prey, and therefore distinct moulting grounds, where prey availability differed. Interestingly, during all the non-breeding seasons, birds from S3 clearly adopted a different strategy and moulted in different water masses than birds from all other colonies (Fig. 4). Mechanisms underlying this difference remain unknown and merit further investigation, notably by combining geolocation and isotope analysis (e.g. Bost et al. 2009).

Isotopic niche of birds wintering off Southwest Greenland

During autumn, birds collected off Southwest Greenland (WG) had identical isotopic niches as those from other colonies (with the exception of S3). This suggests that birds were moulting in a similar isotopic habitat, feeding at the same trophic level and most likely on the same prey. However, during winter, they occupied a different isotopic niche from that of birds from Spitsbergen and a different habitat (different $\delta^{13}C$ values) from that of birds from EG, even if they were feeding at similar trophic levels (similar $\delta^{15}N$ values). Therefore, it seems that wintering birds caught off Nuuk (WG) represent a different population from those sampled during summer, although our study did not permit determination of their origin. Interestingly, this result also indicates that birds from both East Greenland and Spitsbergen do not winter off Southwest Greenland, but rather in different isotopic/feeding habitats, thereby confirming previous investigations based on ring recoveries and biotelemetry. However, it should be noted that the analysis performed on winter bird blood samples reflects isotopic signatures from January, a period during which birds are still in their wintering grounds. In contrast, analyses performed on breeding bird head feather samples reflect isotopic signatures from the March moult, when birds have already started their spring migration (Stempniewicz 2001). Consequently, and even if both tissues represent the winter trophic status and isotopic niche, they are separated by a period of ~1 to 2 mo during which time birds probably moved, potentially affecting their $\delta^{13}C$ isotopic ratios. Therefore, these isotopic results are not totally comparable and have to be interpreted carefully, supporting the need for further studies to confirm bird locations during the different seasons.

CONCLUSIONS

Consideration of temporal and spatial variation in seabird feeding ecology is essential to a better understanding of how they adapt to environmental stochasticity, and how varying constraints affect their survival. Some studies have investigated seabird diet across seasons using stable isotopes on different tissues (e.g. Cherel et al. 2008, Quillfeldt et al. 2008b), while others have compared different populations during a specific

period (e.g. Cherel et al. 2006). However, hardly any study has considered both variables simultaneously in a seabird species. Presenting 2 distinct moults yr^{-1}, both occurring during a short time window, and with a geographic distribution covering a wide range of current regimes and water characteristics (Stempniewicz 2001), little auks are excellent candidates for the study of spatio-temporal variation in feeding ecology through stable isotopic analyses. Using these particularities, our study is therefore one of the first to track trophic niche variation in a seabird across the annual cycle while comparing strategies adopted by birds from distant colonies (but see Bearhop et al. 2000).

We showed that during their non-breeding season, individual little auks display an important seasonal change in trophic status. We also highlighted significant variations between colonies and populations at both small and large spatial scales. Our study also provides one of the first descriptions of the winter feeding ecology of little auks (e.g. Fort et al. 2010) and gives important insights into their moulting and wintering grounds, to be confirmed with complementary methods such as geolocation (see Bost et al. 2009).

Little auks from the North Atlantic are able to modulate their feeding ecology depending on the temporal availability of their prey and also to exploit a wide range of prey, ranging from calanoid copepods to fish larvae (Karnovsky et al. 2008, present study). Such information is essential to understand how this species responds to a constraining and fluctuating environment. Interestingly, we also hypothesize that such a spatio-temporal dietary flexibility might enable little auks to feed on zooplankton species which currently do not occur in the North Atlantic, but which may extend their northern distribution because of global warming (Beaugrand & Reid 2003) and may therefore invade North Atlantic waters and little auk foraging areas. The capacity of little auks to survive on these new resources may determine the fate of their populations in a warming Arctic.

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