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Geographic and seasonal variability in the isotopic niche of little auks

Running head: 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 five 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 $\delta^{15}\text{N}$ values amongst the colonies, suggesting different target species despite overall low $\delta^{15}\text{N}$ values in blood which indicates a diet primarily composed of copepods. A rise of $\delta^{15}\text{N}$ 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 feathers $\delta^{13}\text{C}$ values between colonies suggests a common moulting area off North-East 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, while birds from Spitsbergen maintained a higher trophic level. These findings highlight contrasted seasonal and regional diet in little auk populations, and reveal possible population overlaps during their 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, they 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 scientific 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 acids 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 two isotopic axes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$; Newsome et al. 2007) where the nitrogen isotopic ratio reflects trophic position/diet of the predator, while the carbon ratio reflects its spatial foraging distribution (Kelly 2000, Hobson et al. 1994). These isotopic axes therefore help 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 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 contrasted water masses (Gaston & Jones 1998, Stempniewicz 2001). With recent estimations of more than 80 million individuals (Gaston & Jones 1998, Kampp et al. 2000, Isaksen & Gavriilo 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 North-West Greenland account for 92-96% 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. Vertical migration of their main prey (*Calanus* spp.; Harding et al. 2008) during winter, which tend to descend to depths unreachable to little auks (>100m; 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 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 contrasted and fluctuating environments and resource availability.

Therefore, using isotopic signatures of different body tissues from birds breeding at different geographical sites, the present study had two objectives: (1) to assess trophic level variability in little auks throughout the annual cycle to investigate how birds respond to a change of their feeding environment, and (2) to 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 four colonies on Spitsbergen and one colony at East Greenland. A total of 291 breeding adults and 20 chicks of little auks were sampled, and 28 chick meals collected (Table 1, Fig. 1). Hereafter, these five 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 and Ellegren (1999).

Little auks have two distinct moults per year: 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, two batches of cover feathers were plucked on each breeding adult in summer: one from their body (back or belly, reflecting the autumn period), and one from the head (cheek, neck or throat, reflecting the winter period). These 2 batches are hereafter called 'body feathers' and 'head feathers'. All feathers were randomly plucked to avoid a 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 5-10 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 after Keast & Lawrence (1990), Kwasniewski et al. (2003), and Walkusz (*personal communication*). To estimate the composition by mass of the chick meals, we dried items of each taxon and calculated individual dry mass. We then reconstituted the proportion by dry mass of each taxon in the different chick meal samples.

Twenty additional birds legally shot at sea by Greenlandic hunters for commercial sale were bought. 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' randomly plucked from belly, back or throat, and birds were visually sexed from gonads. Blood and body feathers were stored as for 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 identifying them.

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 2x 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 powder. Lipids and carbonates were then removed from food samples by rinsing them successively in cyclohexane and 1N HCl. All isotopic analyses were performed by Mylnefield Research Services Stable Isotope Laboratory (SCRI, Dundee, Scotland). Analyses were performed on 1 mg subsamples of dried and homogenized materials loading into tin cups and combusting at 1000°C in an ANCA-GSL elemental analyzer (Sercon, Crewe, UK). Resultant CO₂ and N₂ gases were then analyzed for carbon-13 and nitrogen-15 isotope abundance in continuous-flow mode using a SerCon 20:20 isotope ratio mass spectrometer (SerCon, Crewe, UK). Measured data were scale-calibrated using two 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: $\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$, where X is ¹³C or ¹⁵N and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N. The R_{standard} values were based on the Vienna-PeeDee Belemnite (VPDB) for ¹³C and atmospheric N₂ (AIR) for ¹⁵N.

Data analysis. Using allometric equations between body mass and carbon half-life in avian blood (Carleton & del Rio 2005), stable isotopes half-lives in little auk blood was estimated to 12-15 days. Given this result, and following little auk moulting sequences (see above), blood

collected from breeding birds reflects 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, to 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 (Quillfeldt et al. 2008a, Podlesak & McWilliams 2006). We thus compared stable isotope ratios obtained from feathers and blood samples simultaneously collected on chicks, and calculated correction factors to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from these two tissues in adult birds. To avoid effects of growth on $\delta^{15}\text{N}$ blood values (Sears et al. 2009) and therefore to allow comparison of chicks and adults, chicks were sampled during the late chick-rearing period, just before fledging, when growth was 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 feathers 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 compare simultaneously $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between colonies, as well as analysis of variance (ANOVA) followed by *post-hoc* range tests (Tukey multiple comparison test for unequal sample sizes) to compare independently $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sexes, seasons and colonies. Presented values are means \pm SD, and statistical significance was assumed at $p < 0.05$.

RESULTS

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

Chick meals and adult $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ measured on chick meals was similar for both colonies (Mann-Whitney test, $U = 72.0$, $p = 0.28$, $n = 12$ and $n = 16$ for S4 and EG, respectively) (Table 1, Fig. 3). Moreover, chicks and adults from EG had similar $\delta^{15}\text{N}$ values measured in blood samples (t-test, $t = 1.56$, $df = 38$, $p = 0.13$) (Table 1).

Adult breeding birds at EG showed significant variation in their $\delta^{15}\text{N}$ isotopic ratio during the different seasons (ANOVA, $F_{2,55} = 43.99$, $p < 0.001$). *Post hoc* Tukey multiple comparison tests indicated an increase of this ratio between summer and autumn ($p < 0.001$), followed by a decrease between autumn and winter ($p < 0.001$). $\delta^{15}\text{N}$ isotopic values were similar between summer and winter ($p = 0.59$) (Fig. 3). Birds breeding in Spitsbergen also present a significant variation in $\delta^{15}\text{N}$ 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 similar mean value to that in autumn ($p = 0.100$). This winter ratio was significantly higher than in summer ($p < 0.001$) (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 an univariate analysis, by their $\delta^{13}\text{C}$ (ANOVA, $F_{4,88} = 282.20$, $p < 0.001$) and $\delta^{15}\text{N}$ values ($F_{4,88} = 51.15$, $p < 0.001$) measured for blood samples (Fig. 4A). *Post hoc* Tukey multiple comparison tests indicated that among Spitsbergen birds, the 2 southern colonies (S3 and S4) had higher $\delta^{15}\text{N}$ values than the 2 northern colonies (S1 and S2). Also S3 had higher $\delta^{13}\text{C}$ values than S2 and S4, whereas S4 had lower $\delta^{13}\text{C}$ values than S1. Moreover, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ ($F_{5,113} = 10.30$, $p < 0.001$) and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ values (all $p < 0.01$). Furthermore, only birds from S4 had significantly higher $\delta^{15}\text{N}$ values than those from S3, EG and WG ($p = 0.02$, $p = 0.003$ and $p = 0.03$, 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 an univariate analysis by their $\delta^{13}\text{C}$ ($F_{5,114} = 12.75$, $p < 0.001$) and their $\delta^{15}\text{N}$ values ($F_{5,114} = 30.14$, $p < 0.001$). However, multiple comparison tests indicated that $\delta^{13}\text{C}$ values measured on birds from S3 and WG were similar ($p = 1.00$) but differed from all other colonies (all $p < 0.01$), whereas $\delta^{15}\text{N}$ values of Greenland birds (EG and WG) were similar ($p = 1.00$) but differed from all Spitsbergen colonies (all $p < 0.001$) (Fig. 4C).

DISCUSSION

Detailed knowledge of seabirds 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 North-West 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.

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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). Indeed, while a difference between measured values might reflect contrasted 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 large geographical scale (Graham et al. 2010) enables such an integration, and therefore provide guidance for future isotopic research. Little auk distribution is limited to the North Atlantic and the Arctic (above ca. 50°N; Gaston and Jones 1998), where $\delta^{15}\text{N}$ values are homogeneous (Graham et al. 2010). This homogeneity is confirmed by similar $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ values at the base of the food web within the distribution range of little auks, and allows comparing nitrogen signatures assumed to reflect their relative trophic position on the basis of homogeneous $\delta^{15}\text{N}$

baseline levels. In great contrast, $\delta^{13}\text{C}$ values are spatially structured throughout this region, showing contrasted 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 $\delta^{13}\text{C}$ signatures due 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic signatures in birds from a given colony, thus confirming the results of Karnovsky and colleagues (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 are 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 two sexes, therefore leading to contrasted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic values in autumn. Contrary to this expectation, our results show that both sexes have an identical isotopic niche during this season. While this result indicates that males and females are likely to moult in the overall same geographic area, it cannot confirm at smaller spatial scale whether both sexes moult together or within a close area. Further specific studies, using methods complementary to stable isotopes, 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 two highly contrasted 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 two distinct summer isotopic habitats ($\delta^{13}\text{C}$ values) of the East Greenland and Spitsbergen birds (Fig. 1) reflect these two 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, Karnovsky et al. 2008, Harding et al. 2008). Here, only chick meals were collected, but the similar $\delta^{15}\text{N}$ 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 amongst colonies at large and small spatial scales (Fig. 2 and Fig. 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. in press). 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 two northern colonies are also segregated from the two southern colonies by their $\delta^{15}\text{N}$ values (Fig. 4A). However, the difference observed is only marginally significant, a fact that might be explained in two 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, allowing them to feed in areas over 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 (Harding et al. 2009a, Tamelander et al. 2006). 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 (Jakubas et al. unpublished data). Moreover, the prey *Apherusa glacialis* was present in chick meals collected at S1 in 2007 and 2008 (Kwasniewski et al. in press) while it has not found at S4 (this study, Kwasniewski et al. in press). Consequently, it is likely that adults from the two northern colonies feed on a higher proportion of *Apherusa glacialis* (and therefore at a lower trophic level) than those from the two 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 now required to define $\delta^{15}\text{N}$ baseline 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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 found in other seabird species elsewhere (Cherel et al. 2007, 2008). This strongly suggests that non-breeding little auks disperse across contrasted 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 $\delta^{15}\text{N}$ isotopic ratio). Indeed, their $\delta^{15}\text{N}$ increased by approximately 3‰ between both seasons. This change of more than one 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) caught by little auks while breeding (Fig. 2) are known to perform a vertical migration to depths of several hundred meters to undergo diapause, thereby becoming inaccessible to the birds, which can only dive to 40 meters (Harding et al. 2009a). These copepods are thought to migrate back to surface waters a few months later to match the phytoplankton spring 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 $\delta^{13}\text{C}$ 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 common/different moulting places. However, existing information from long-term ring recoveries (e.g. Stempniewicz 2001) and recent biotelemetry studies (Mosbech et al. unpublished 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 (Mosbech et al. unpublished 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 of bird trophic levels between autumn and winter is different for the East Greenland and Spitsbergen colonies. Birds breeding in East Greenland display a second dietary shift in winter since they feed at a lower trophic level than during autumn. Interestingly, their $\delta^{15}\text{N}$ winter 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, Mosbech et al. unpublished data). In this region, phytoplankton spring 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 adopt a different feeding strategy during winter. Their $\delta^{15}\text{N}$ values show that little auks maintain a high trophic level during the winter that is similar to that in the autumn.

During the winter moult, Greenland and Spitsbergen populations share similar isotopic habitat (reflected by similar $\delta^{13}\text{C}$ isotopic ratios). However, $\delta^{15}\text{N}$ values show that birds feed at different trophic levels (see 'Results'), suggesting contrasted targeted prey, and therefore

distinct moulting grounds, where prey availability is different. Interestingly, during all the non-breeding season, birds from S3 clearly adopted a different strategy and moult 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).

The isotopic niche of birds wintering off South-West Greenland

During the autumn, birds collected off South-West 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 occupy a different isotopic niche than birds from Spitsbergen and a different habitat (different $\delta^{13}\text{C}$ values) than EG birds, even if feeding at similar trophic levels (similar $\delta^{15}\text{N}$ values). Therefore, it seems that wintering birds caught off Nuuk (WG) represent a different population than those sampled during summer, though our study does not permit to determine 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 upon ring recoveries and biotelemetry. However, it is important to note that the analysis performed on winter bird blood samples reflects isotopic signatures from January, a period during which birds are still on their wintering grounds. In contrast, analyses performed on breeding bird head feather samples reflect isotopic signatures from the March moult, during which birds already start 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 about 1-2 months during which birds probably moved,

potentially affecting their $\delta^{13}\text{C}$ isotopic ratios. Therefore, these isotopic results are not totally comparable and have to be interpreted carefully, supporting the fact that further studies are necessary to confirm bird location during the different seasons.

Conclusions

Consideration of temporal and spatial variation in seabirds feeding ecology is essential to a better understanding of how they adapt to environmental stochasticity, and of how varying constraints affect their survival. Few 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 considered both variables simultaneously in a seabird species. Presenting two distinct moults per year, 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 to study spatio-temporal variation in feeding ecology by way of 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, and 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, which need 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 (present study, Karnovsky et al. 2008). 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 as a result 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 upon these new resources may determine the fate of their populations in a warming Arctic.

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Table 1. Stable isotopic signatures of samples collected from little auks. Stable isotope data presented are raw (uncorrected).

Status	Site	Colony	Symbol	Tissue	Time period	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)			
Breeding adults	East Greenland	Kap Hoegh (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				
	Longearbyen (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)	SWG	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 Hoegh	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			

Values are mean ± SD

Fig. 1. Map of the studied little auk breeding colonies which are labelled as follows in the text: S1 to S4 for Spitsbergen (from north to south), EG for the East Greenland and WG for West Greenland wintering birds. After AMAP (1998)

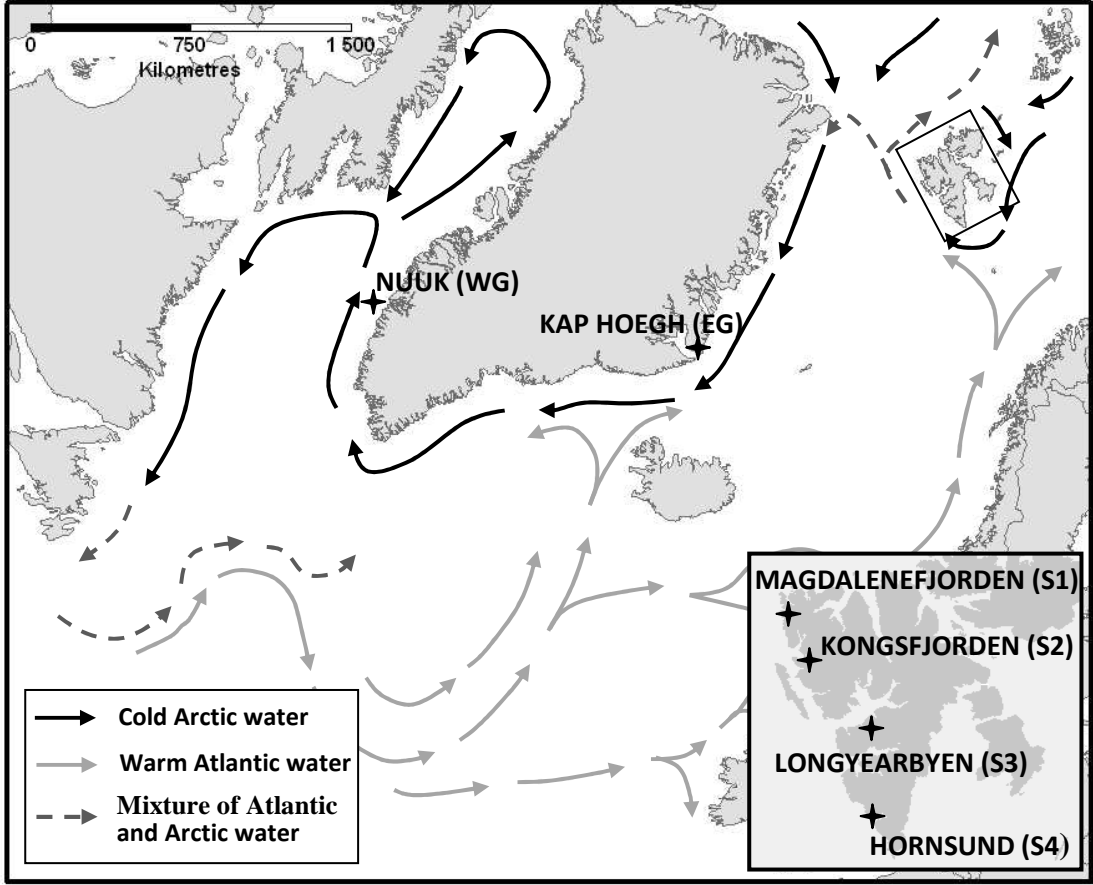


Fig. 2. Composition of little auk chick meals (expressed in % dry mass) collected from adults at Kap Höegh (East Greenland, EG; n=16) and Hornsund (Spitsbergen, S4; n=12).

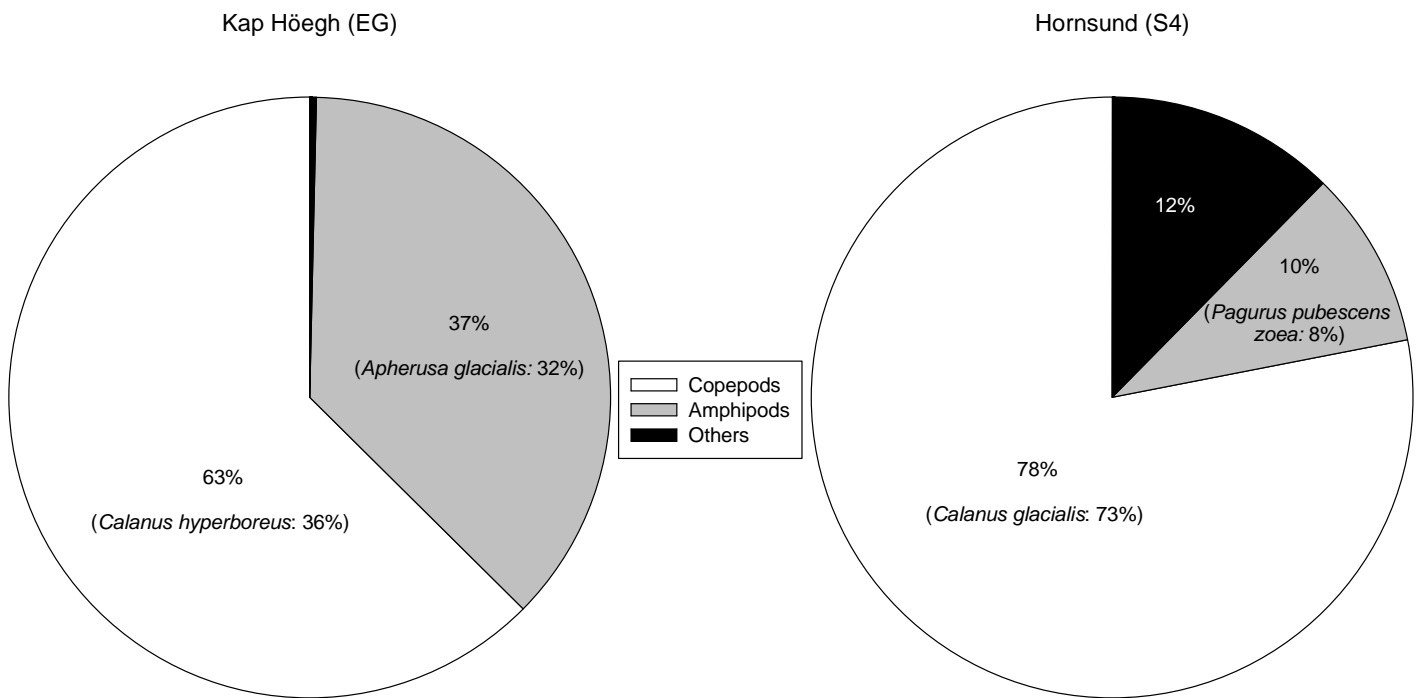


Fig. 3. Stable nitrogen isotope values of little auks samples from East Greenland and Spitsbergen during the different seasons, and of chick meals collected at two colonies (EG and S4). Values (uncorrected) are means \pm SD. At each site, values not sharing the same superscript letter are significantly different (see results).

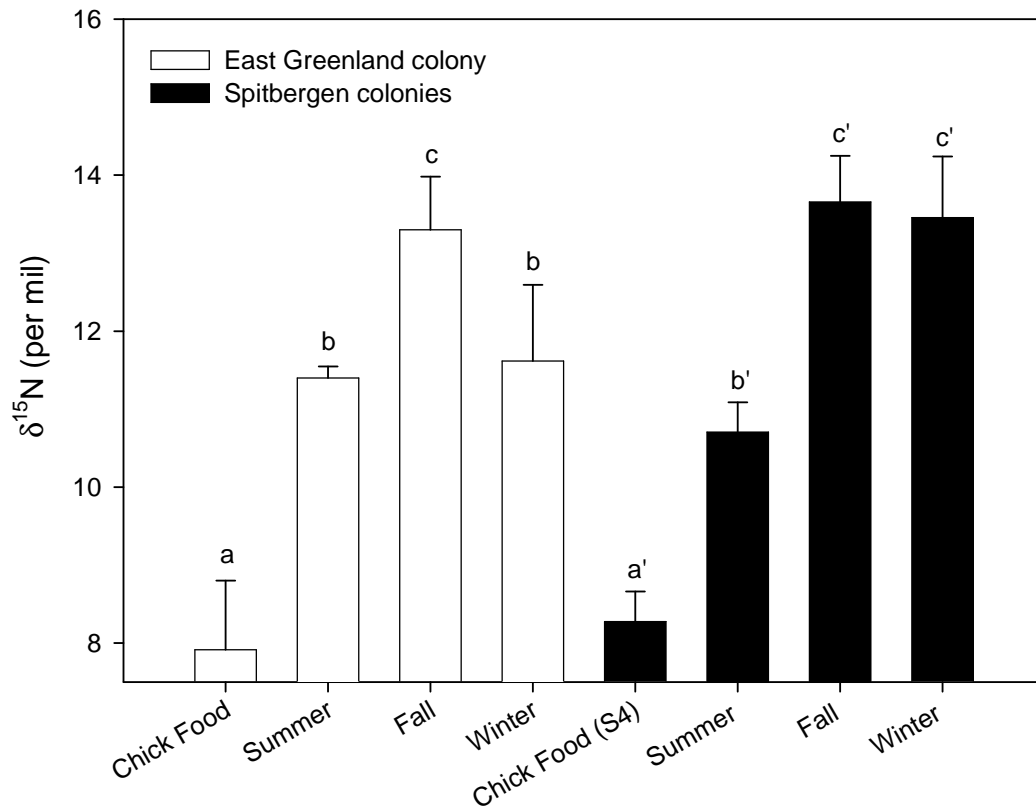


Fig. 4. Stable carbon and nitrogen isotope values of adult little auk samples from each colony and during the different seasons. Values are means \pm SD. Summer values (from blood) are uncorrected values while autumn and winter values (from feathers) are corrected values. Open symbols are values measured on birds from the East Greenland colony, black-filled symbols are values from the Spitsbergen colonies, and grey-filled symbols are values for the West-Greenland winter-shot birds.

