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Winter diet of the little auk (*Alle alle*) in the Northwest Atlantic

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Abstract The little auk (*Alle alle*) is one of the most numerous seabirds in the world, but their winter prey selection has never been thoroughly studied. In the present study, we analyzed the proventricular contents of 205 little auks caught in coastal areas off southwest Greenland during December–February and off Newfoundland in March. Large Calanoid copepods are known to be the main prey during summer. We found krill to become the crucial winter prey in both areas, followed by *Themisto* spp. and young capelin (*Mallotus villosus*). No difference was found between the diet of juvenile and adult birds. Copepods constituted around 1 % of the diet and close to all copepods were in birds caught near Cape Farwell in December. These findings provide new and important insight into the forage ecology of the little auk, and they support other studies showing that large Calanoid copepods in the Arctic decent for winter hibernation at depths that are below the diving range of the little auks. More studies to determine offshore diet and annual variation are, however, needed in order to get a more complete picture.

Keywords Feeding ecology · Winter diet · Krill · *Themisto* spp · Greenland · Newfoundland

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Introduction

The little auk (*Alle alle*) is one of the most numerous seabirds in the world counting more than 100 million individuals (Egevang et al. 2003). They are small birds weighing around 160 g, and they forage in cold waters, so their energy demand is exceptionally high. Each bird has an estimated intake of 289 g wet food day^{-1} during winter (Fort et al. 2009), resulting in a total winter consumption of more than 28.900 ton wet food day^{-1}. The waters off southwest Greenland and Newfoundland host a large fraction of the wintering birds, and their ecological importance in these areas is therefore significant (Barrett et al. 2006).

Most little auk populations breed in the high Arctic, and studies have shown that Calanoid copepods are the main prey in these areas during summer (Mehlum and Gabrielsen 1993; Harding et al. 2009; Kwasniewski et al. 2010). Studies from breeding areas in Svalbard where the birds are close to both polar and subpolar water masses show that the Arctic and very energy-rich *Calanus glacialis* is preferred but supplemented with *Calanus finmarchicus*, which contain less energy but is very numerous in subpolar and boreal waters (Karnovsky et al. 2003; Kwasniewski et al. 2010; Jakubas et al. 2011, 2012; Kwasniewski et al. 2012). Most of the little auks winter in sub-Arctic or Boreal waters (Fort et al. 2013), but there are no published studies about their winter prey selection. A study using a combination of stable isotopes and behavioral analyses suggested that little auks also relay on copepods during winter and that swarms of copepods therefore come up to surface layers (less than 50 m) even during short daylight periods in winter (Fort et al. 2010a). This conclusion challenges several studies, which all show that North Atlantic copepods large enough to be taken by little auks (e.g., *Calanus hyperboreus, C.*

Fig. 1 The esophagus, the proventricular and the gizzard. The proventricular is cut open revealing a meal consisting of krill (*Meganyctiphanes norvegica*)

glacialis, C. finmarchicus) descend to hibernate at depths beyond the diving range of little auks during winter (Lee et al. 2006; Falk-Petersen et al. 2009; Arendt et al. 2013). Smaller copepod species (too small and dispersed to serve as food for the little auk) dominate the plankton community when this happens (Madsen et al. 2001; Arendt et al. 2013), and the little auks must therefore consume other prey during winter.

This study analyzes the proventricular content (Fig. 1) of 205 little auks caught in coastal areas off southwest Greenland during December–February and off Newfoundland during March. The aim of the study was to provide the first thorough and direct evidence of little auk prey selection during winter. This knowledge is important in relation to the biology of the little auk and in relation to ecosystem models for the North Atlantic. Furthermore, it can support or oppose the hypothesis that the large North Atlantic copepods regularly come up close to surface during winter.

Materials and methods

The material consisted of proventricular contents from 205 little auks. The birds were caught near Cape Farewell ($n = 90$) and near Nuuk ($n = 94$) in southwest Greenland during December 2010–February 2011 (the same sampling location for the birds used in the stable isotope study by Fort et al. (2010a) and in Placentia Bay, Newfoundland ($n = 21$) during March 2011 (Fig. 2). The birds from Greenland were caught by Greenlandic hunters who legally catch more than 20.000 of these birds annually (Anonymous 2012). The birds from Newfoundland were sampled by Environmental Canada, Canada Wildlife Service, Scientific Take Permit ST2753. The birds were frozen and stored at −18 °C until analysis.

Each bird was defrosted and hereafter weighed (to the nearest gram). The gizzard, the proventriculus and most of the esophagus were taken out (Fig. 1). The prey in the gizzard were grinded by its strong muscle and often difficult to distinguish beyond order. The proventricular content was largely unaffected by digestion and only subject to prey handling in a short period prior to capture, leaving this prey identifiable to at least genus and often species. Smaller prey-like copepods would most likely be quickly digested, and to reduce bias in the prey description, only the proventricular content was analyzed. The contents of the proventriculi were weighed (wet weight) (to ±0.1 g). More than 99.5 % of the total wet weight could be assigned to one of the following taxa: Krill, *Themisto* spp., fish, copepods and shrimps, and these data are presented as weight fractions (sums up to 100 %) and as frequency of occurrence (sums up to 100+ %). The proventricular content was often tightly packed, and water had to be added to separate the organisms from each other in a petri dish. When doing that, the partly digested (sometimes hollow) exoskeletons of crustaceans get filled with water, which change their weight. Therefore, in the cases of two or more prey categories, the measured weight (before water was added) was assigned to the categories (e.g., 20 % Themisto and 80 % krill) based on an estimation made from visual observation. When possible, prey items were assigned to species and their length was measured. Data for copepods were grouped in mm intervals, and krill and *Themisto* spp. were grouped in 0.5-cm intervals. For fish, fork length was measured. Krill and *Themisto* were measured from tip of the rostrum to the end of the telson, and the prosome length was measured for copepods.

The degree of digestion was noted as one of four categories: (1) fresh, (2) relatively fresh (fish would still have some meat on the bones), (3) strong decay but fragments still recognizable to species and (4) late stage of digestion that makes species determination difficult. The last two categories were mainly found when the proventriculus was close to empty and probably consisted of food returned from the gizzard. In this partly digested material fragments of krill, *Themisto* spp. and copepods could be distinguished from each other, but legs and other parts from krill and *Themisto* spp. were not easy to separate, and in such cases, they were grouped together as partly dissolved krill and Themisto.

The age of the birds was determined according to morphological criteria, by measuring intra-orbital skeletal ridge width, bird size and wing length (Bradstreet 1982; Pyle 2009; Anonymous 2013). Birds were grouped as (1) "juveniles" when the intra-orbital skeletal ridge was poorly ossified and smaller than 6.8 mm and (2) "adults" when the intra-orbital skeletal ridge was well ossified and wider than 8.0 mm. Birds with intra-orbital skeletal ridge width between 6.8 and 8.0 mm were aged as juveniles, adults or subadults according to its ossification and wing length (juveniles being smaller than adults; Bradstreet 1982). Birds were sexed by a visional inspection of gonads.

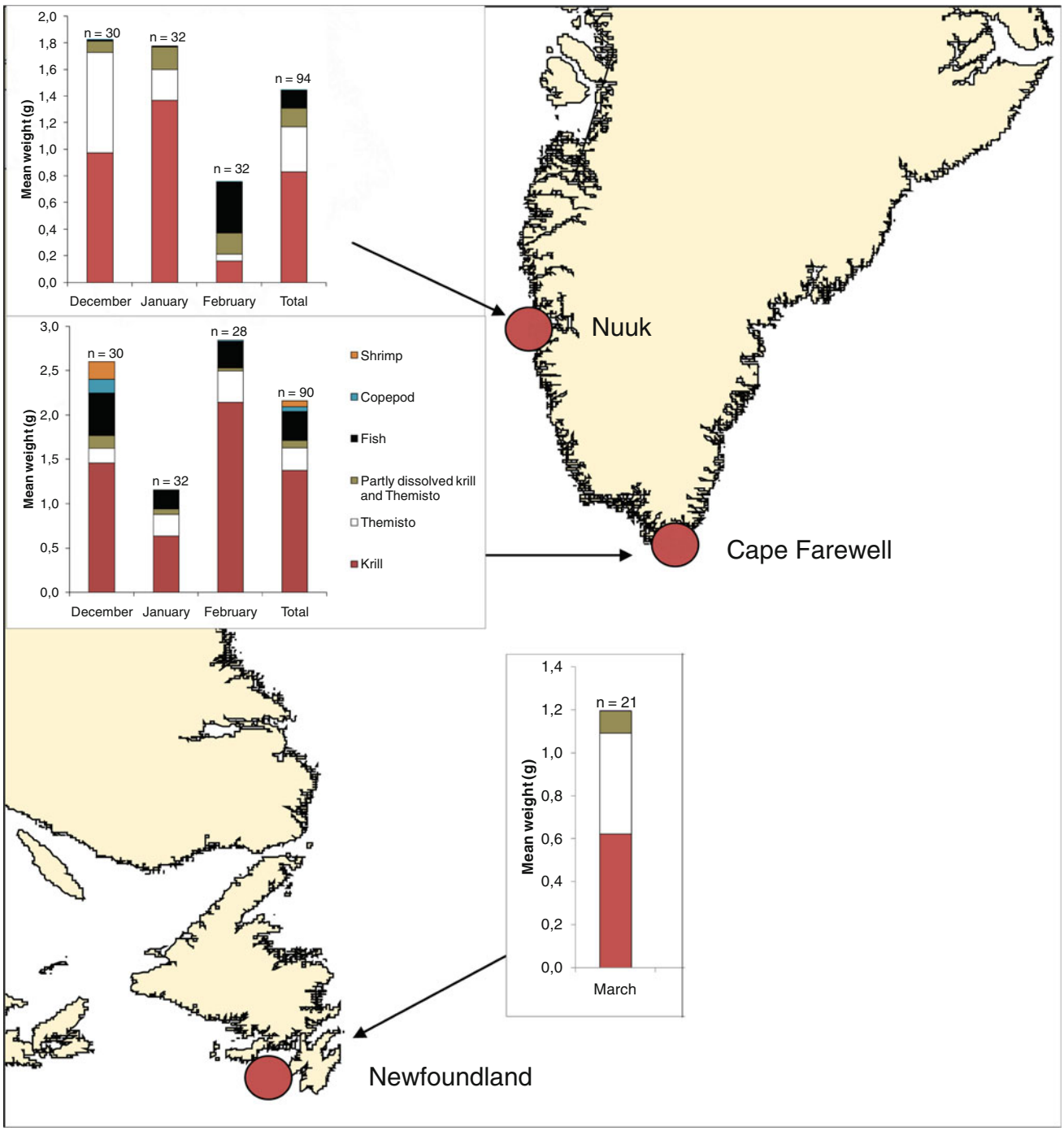

Fig. 2 Map with the average proventricular content by month at the three sampling locations

Results

The proventricular content from all birds summed up to 376 g of which 60 % was krill, 18 % *Themisto* spp., and 7 % was partly dissolved krill and *Themisto* spp., likely in the same ratio as non-dissolved specimens (roughly 3.5:1). The mean weight of each prey category (the total weight of the prey category divided by the number of birds examined) by month and area is shown in Fig. 2. Krill was the main prey in all areas and all seasons except off Nuuk in February when young capelin were found in 56 % of the birds with proventricular content and constituting 50 % of the prey by weight. Hyperidae amphipods of the genus *Themisto* were found in highest abundance and in most stomachs (for species see Table 1), but krill were more important by weight in all three areas. Off Nuuk, large

Table 1 The length distribution of krill, *Themisto* and copepods by area and species

Themisto and krill	<1 (cm)	1–1,5 (cm)	1,5–2 (cm)	2–2,5 (cm)	2,5–3 (cm)	3–3,5 (cm)	3,5–4 (cm)	4–4,5 (cm)	Stomachs (n)
Nuuk									
Themisto abyssorum	6								1
Themisto gaudichaudi (compressa)	101	381	23	15					41
Meganyctiphanes norvegica	31	0	38	60	47	30	28	59	23
Thysanoessa raschii	291	25	51	23					15
Cape Farewell									
Themisto abyssorum	106	19	1						20
Themisto gaudichaudi (compressa)	4	2							4
Themisto libellula	7	14	5	2					10
Thysanoessa raschii	1	21	206	84					7
Thysanoessa inermis		52	70	14					7
Meganyctiphanes norvegica			12	25	35	0	4		10
Nyctiphanes couchii		56							1
Krill spp.	269	288	107	22					14
Newfoundland									
Themisto gaudichaudi (compressa)	37	72							4
Themisto abyssorum	13	7							3
Themisto libellula	28								1
Themisto Spp	85								1
Thysanoessa raschii		122	82						9
Calanus	1–2 (mm)	2–3 (mm)	3–4 (mm)	4–5 (mm)	5–6 (mm)	6–7 (mm)	2–3 (mm)	2–3 (mm)	2–3 (mm)
Nuuk									
Calanus hyperboreus		1	1	3	5	14			
Cape Farewell									
Calanus Spp.		434	60			1			
Newfoundland									
Calanus hyperboreus						1			
Calanus Spp.				3					

Table 2 First column shows for each prey category: its weight fraction (WF) of the total content in all proventriculi and its frequency of occurrence (FO) in the proventriculi with prey content ($n = 174$)

Species All samples with food	Digestion stage 1 Fresh $n = 15$	Digestion stage 2 Slightly digested $n = 39$	Digestion stage 3 Strong decay $n = 50$	Digestion stage 4 Decomposed $n = 54$
Krill	MW: 3.6 g	MW: 3.2 g	MW: 1.8 g	MW: 0.9 g
WF: 60 %	Range 1.9–6.2 g	Range 0.1–9.1 g	Range 0.1–6.4 g	Range 0.2–1.6 g
FO: 49 %	FO = 60 % ($n = 9$)	FO = 67 % ($n = 26$)	FO = 56 % ($n = 28$)	FO = 7 % ($n = 4$)
Themisto	MW: 1.2 g	MW: 0.8 g	MW: 0.8 g	MW: 0.2 g
WF: 18 %	Range 0.1–2.8 g	Range 0.1–3.9 g	Range 0.1–4.4 g	Range 0.1–0.4 g
FO: 48 %	FO = 53 % ($n = 8$)	FO = 69 % ($n = 27$)	FO = 52 % ($n = 26$)	FO = 6 % ($n = 3$)
Partly dissolved Krill/Themisto	FO = 44 % FO = 50 %			MW: 0.2 g
WF: 7 %	($n = 77$ of all 174 samples)			Range 0.1–0.4 g
FO: 44 %				($n = 27$)
Fish		MW: 1.0 g	MW: 1.6 g	MW: 0.6 g
WF: 12 %		Range 0.1–3.9 g	Range 0.1–4.3 g	Range 0.1–3.0 g
FO: 31 %		FO = 13 % ($n = 5$)	FO = 30 %($n = 15$)	FO = 37 % ($n = 20$)
Copepods	MW < 0.1 g	MW < 0.1 g	MW: 0.8 g	MW: 0.1 g
WF: 1 %	FO = 7 % ($n = 1$)	FO = 8 % ($n = 3$)	Range < 0.01–3.6 g	Range 0.1 g
FO: 9 %			FO = 12 % ($n = 6$)	FO = 4 % ($n = 2$)
Shrimps		MW: 4.0 g	MW: 2,0 g	
WF: 2 %		Range 4.0	Range 2.0 g	
FO: 1 %		FO = 3 % ($n = 1$)	FO = 2 % ($n = 1$)	

The following four columns show the same for different stages of digestion, which are defined in the "Materials and methods" section (the digestion stages of 16 birds were not included either because they were not noted or because they were put in between two categories). Small quantities of partly dissolved krill/Themisto could be found among many samples of less-digested prey, and the FO of this prey category is therefore listed for all samples and as FO for digestion stage 4 only

Meganyctiphanes norvegica constituted the bulk of the krill (by weight) in December and January, but they became rare in February, when the average weight of the proventricular content dropped and capelin became the main prey. *Thysanoessa raschii* was the only krill species found near Newfoundland, and this species was also common on both sampling locations in southwest Greenland. Near Nuuk it was found in one out of six birds, but most specimens were small (<1 cm), and by weight, they were less important than *Meganyctiphanes norvegica.* The *T. raschii* were on average larger near Cape Farewell than in the other two areas, and their contribution in terms of weight in that area was about the same as *M. norvegica.*

Most fish meals were at a late stage of digestion. All recognizable fish parts, including otholits (17 out of 46 samples), were from capelin, but the species of 29 fish remains could not be identified with certainty. All specimens were small juvenile fish 35–50 mm long, except one adult capelin of more than 100 mm.

Copepods were found in the proventricular content of birds from all three areas but only in 14 of the 205 samples (7 %), constituting around 1 % of the total proventricular content by weight. Two birds caught near Cape Farewell on December 20, 2010, had 89 and 404 partly dissolved copepods, respectively, and they accounted for 98 % of the total estimated weight of copepods. Copepods constituted 6 % of the proventricular content near Cape Farewell in December, but were almost completely absent outside this period/area, and only constituted a few individual specimens when present. Six of these samples were fresh and were all identified as *C. hyperboreus* ranging from 2.5 to 6 mm in length.

Two birds from Cape Farewell had their proventriculus filled with small (1–1.5 cm) shrimps and that made up 2 % of the total proventricular content by weight. In addition to the categories mentioned, a few gammaridea, pteropods and small squids were found, but they all together constituted less than 1 % of the total proventricular content by weight.

Table 2 shows the mean weight (MW) and the frequency of occurrence (FO) of the prey in four categories of digestion. Krill and *Themisto* were found in most birds, and their FO was quite constant in the different categories of digestion. In stage 4, they were often listed as partly digested krill and *Themisto,* either because they were found together or hard to distinguish. Copepods were found as

Table 3 Two hundred birds were aged according to the procedure described in the "Materials and methods" section

Cape Farwell	Sex?	M	F	Total	Mean mass (g) (range)	Mean wingspan (mm) (range)
Age?	4	5	4	13	170.1 (143.4–207.6)	121.1 (116–125)
Juvenile	12	19	22	53	165.7 (122.7–213.0)	116.9 (108–128)
Subadult	0	1	0	1	161.2	124.0
Adult	4	9	6	19	173.1 (156.6–198.0)	124.4 (116–131)
Total	20	34	32	86		
Nuuk						
Age?	6	9	2	17	164.0 (149.2–181.8)	120.8 (117–125)
Juvenile	15	12	25	52	159.5 (135.5–190.0)	121.1 (112–129)
Subadult	0	0	0	0		
Adult	1	11	13	25	165.1 (143.7–181.8)	125.0 (116–130)
Total	22	32	40	94		
Newfoundland						
Age?	0	0	0	0		
Juvenile	3	7	19	19	154.2 (131.0–176.0)	114.1 (105–121)
Subadult	0	0	0	0		
Adult	1	0	1	1	138.0	113.0
Total	4	7	20	20		

In some cases, damage from the capture made measurements less precise or impossible. Those cases are categorized as age?/sex?

both fresh and slightly digested prey, but only as single or few (2–11) specimens (all *C. hyperboreus*). No fresh newly ingested fish were found, and unlike for the crustaceans, the FO for fish increased with the stage of digestion. The two sampling localities in southwest Greenland had a mixed population of juvenile and adult birds, whereas all but one specimen from Newfoundland were juveniles (Table 3). The relative frequency of occurrence of the prey categories shown in Fig. 2 was very similar for juvenile and adult birds in the two southwest Greenland areas (chi-square test, $p > 0.50$ in both areas), and no significant differences in morphometric measurements could be found between these two localities. The mean wingspan of the juvenile birds from Newfoundland (114.1 cm), however, was significantly smaller than that of juvenile birds from Greenland (120.3 cm) (unpaired t test $t = 6.337$, df $= 122$, $p = 0.0001$), and the birds were lighter (mean of 152 g vs. mean of 166 g, unpaired t test, $t = 3.46$, df $= 122$, $p = 0.0007$). The one adult bird from Newfoundland also had a shorter wingspan than any of the 44 adult birds from southwest Greenland.

Discussion

This study shows that the little auk wintering in southwest Greenland is heavier and has a longer wingspan than the birds wintering off Newfoundland, indicating that they originate from different summer populations. This confirms recent results that showed using tracking technology that little auks breeding in Greenland overwinter off Newfoundland while part of birds breeding in Svalbard cross the North Atlantic to overwinter off southwest Greenland (Fort et al. 2013). Krill, *Themisto* spp. and capelin made up between 99 and 100 % of the wet weight of the proventricular content on the three sampling locations in all months except near Cape Farwell in December when copepods and shrimps together constituted 14 %. Some (likely few) concentrations of copepods can be found off southwest Greenland until December within the diving range (the upper 50 m) of the little auk, but they seems to be of minor importance, at least in coastal areas.

Krill and Themisto were found with roughly the same frequency, but the meal size of krill was often considerably larger, making krill the most important prey by weight in all areas. Fish were also important, but most often found as bones or otholiths (late stages of digestion) unlike crustaceans that were found in more evenly frequencies in the various stages of digestion (Table 2). This indicates that fish are digested faster than the crustaceans, which would underestimate their importance. The difference might, however, also occur because the exoskeleton makes crustaceans that have been stripped for muzzle and fat appears less digested than a fish in the same condition. Fish only became the dominating prey in Nuuk during February (Fig. 1), and when that happened, the average weight of the

proventricular content dropped to 47 % of the average weight in January when krill was the main prey and the average weight of the birds decreased from 170 to 157 g.

Fort et al. (2010a, b) found that isotopic $\delta^{15}N$ signatures of blood samples from little auks caught during summer in east Greenland and off Nuuk in January were similar. Our study, however, show that the winter prey off Nuuk is very different from the summer prey off east Greenland, which mainly consisted of Calanoid copepods. The similarity in $\delta^{15}N$ signatures across seasons in spite of feeding differences can possibly be caused by overlap in feeding ecology of the Calanoid copepods, krill and *Themisto* spp. The two dominating krill species *M. norvegica* and *T. raschi* feed on phytoplankton during summer supplied with more detritus during winter (Mauchlin and Fisher 1969), and the feeding spectrum of *T. raschii* can range over several trophic levels of the pelagic food web (Agersted et al. 2011). Krill will on average feed on a higher trophic level than copepods and that was also found in (Hansen et al. 2012), who measured stable isotope values from both groups sampled off southwest Greenland. However, they found large differences in stable isotope values along a north–south gradient in copepods, and also on a smaller inshore–offshore scale in the Nuuk area with >2 ‰ difference in $\delta^{15}N$ values in the same species. During winter, little auks can occupy relatively wide areas of several thousand square kilometers (Fort et al. 2012), and even small shifts in feeding location may quickly be reflected in shifting blood isotope values. These circumstances make stable isotopes an inadequate tool to distinguish between copepods and krill in the diet of predators in these waters. It could nevertheless be used at a regional or large spatial scale to investigate changes in trophic status over time when birds use a wider spectrum of prey (Karnovsky et al. 2008; Fort et al. 2010b).

A recent study show that *C. finmarchicus* are abundant within the range of little auks during December–January in some frontal zones between sub-Arctic and boreal waters and that many little auks are foraging in these areas (Fort et al. 2012). Such concentrations of large *Calanus* during winter has, however, never been documented off southwest Greenland or in other Arctic waters that are not close to the boreal zone. Our study shows that krill, *Themisto* spp. and capelin provide the food base for the little auk during winter in the coastal part of some of their main winter habitats in the Arctic. This is new and important insight into the forage ecology of the species. More studies are, however, needed to determine offshore diet and annual variation in order to get a more complete picture of the winter diet of these birds.

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