Little auks (*Alle alle*) breeding in a High Arctic fjord system: bimodal foraging strategies as a response to poor food quality?

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Abstract

The foraging behaviour of little auks (*Alle alle*) in the Bjørndalen colony on the western coast of Spitsbergen was studied during the breeding season 2005. The duration of foraging trips and contents of gular pouches were analysed. Quantitative zooplankton samples procured in the vicinity of the colony facilitated a comparison between gular pouch contents and the availability of prey species. Zooplankton and gular pouch samples were all sampled within a time window of approximately one week. Using the Bray–Curtis similarity index, we determined that little auks in this colony have a bimodal foraging strategy consisting of long and short foraging trips with two corresponding distinct diets. Short trips are most likely to be centred on areas within the Isfjorden complex, whereas the birds are most likely to use the long trips (of typically more than 10 hours) to reach areas off the continental slope where they are able to feed selectively on large, energy-rich food items such as *Calanus hyperboreus*. This bimodal foraging strategy may be a response to the low availability of nutrient-rich food close to the colony, which is insufficient to sustain both parents and chicks. Bimodal foraging trip strategies are well documented in many species in the Southern Ocean. This is the first study to show a similar feeding pattern in an Alcidae species in the Northern Hemisphere.

With more than one million breeding pairs, the little auk (*Alle alle*) is one of the most abundant seabirds on Spitsbergen (Isaksen & Gavrilo 2000). Little auks have been shown to feed selectively in areas dominated by Arctic water masses, where they mainly utilize the largest copepodite stages (CV and adults) of the calanoid copepod species *Calanus glacialis* (Mehlum & Gabrielsen 1993; Weslawski et al. 1994; Weslawski et al. 1999; Karnovsky et al. 2003). So far, studies of little auk foraging behaviour have been focused on birds that can choose to feed in either Arctic or Atlantic water masses, where they can select the energy-rich *C. glacialis* (Mehlum & Gabrielsen 1993; Weslawski et al. 1994; Weslawski et al. 1999; Karnovsky et al. 2003). Here we present a study of the foraging behaviour, diet and food availability of little auks breeding in a colony by a fjord on the western coast of Spitsbergen, which receives a variable influx of warm Atlantic water masses (Svendsen et al. 2002; Berge et al. 2005; Cottier et al. 2005), and which harbours the less energetically profitable *Calanus finmarchicus* (Falk-

Petersen et al. 2007). *C. finmarchicus* is probably too small and has an energetic value too low to sustain a breeding population of little auks (Nettleship & Evans 1985; Weslawski et al. 1999).

We studied little auks breeding in the colony at Bjørndalen (78°14′N, 15°19′E), which is 50 km from the mouth of Isfjorden (Fig. 1). Little auks arrive at the colony during April, establishing nests in the talus below steep rock faces. A pair lays a single egg in early to mid-June; the egg hatches 30 days later. Mean fledging is at 25–27 days (Stempniewicz 2001; Harding et al. 2004). Both parents participate in the brooding and feeding of the chick, but the female participates to a lesser degree in the late chick-rearing phase (Harding et al. 2004). On their foraging trips little auks store the catch in a gular pouch located below the beak. In the early phase of chick rearing, male and female birds in a colony in Hornsund, Spitsbergen, engaged in foraging trips that averaged 153 and 148 min in length, respectively (Harding et al. 2004). Later in the chick-rearing period these values increased to
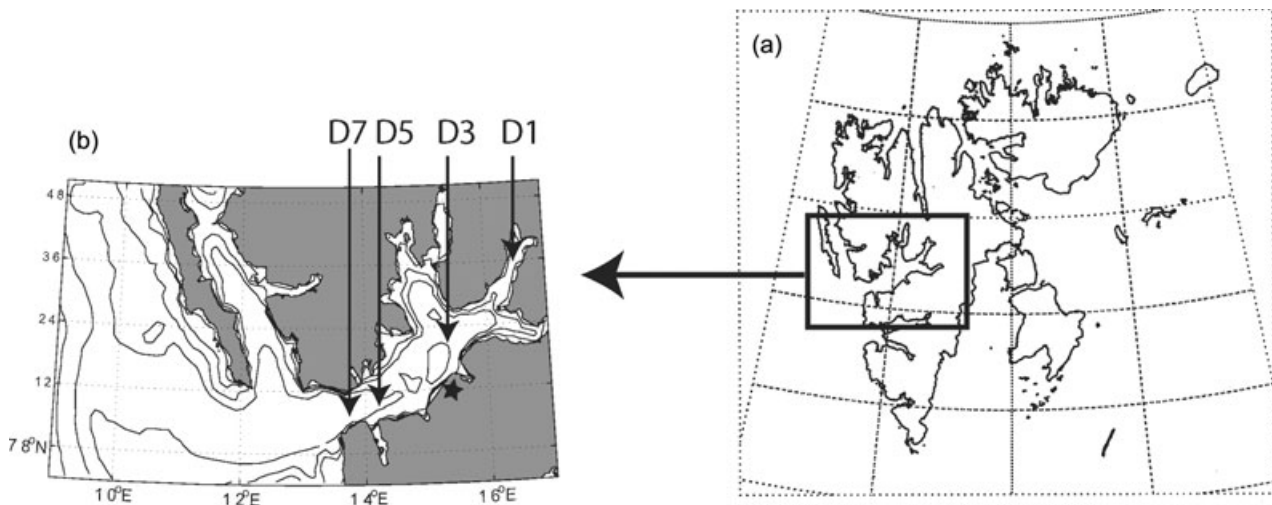
Fig. 1 (a) Svalbard and (b) Isfjorden, showing the sampling sites (D1–D7) along the Isfjorden transect. The star indicates the location of the Bjørndalen little auk colony.

155 min for males and 375 min for females, few of which delivered food to their chicks (Harding et al. 2004). The chicks require 262 kJ/day to grow normally, and this is estimated to be equivalent to four food loads per parent each day (Karnovsky et al. 2003; Kwasniewski et al. 2003).

Isfjorden is an open fjord on the western coast of Spitsbergen (Fig. 1) that is periodically strongly influenced by the influx of warmer Atlantic water masses (Berge et al. 2005; Cottier et al. 2005; Svendsen et al. 2002). As a result of the gradual modification of the vertical stratification in the fjord through mixing with warmer and fresher surface water, the front separating fjord and shelf water weakens and allows Atlantic water to penetrate into the fjord (Cottier et al. 2005). Episodic and rapid intrusion of Atlantic water can also appear in the autumn during periods with prevailing northerly winds, as a result of offshore Eckmann transport in the surface layer compensated by onshore subsurface transport of Atlantic water masses into the fjord (Berge et al. 2005). In effect, the fjord is mainly dominated by Arctic water during the winter, whereas there are large annual variations in the influx of warmer Atlantic water during summer. Predictable cold water masses are most prevalent in sill fjords where the sill effectively prevents mixing of water masses. As a result of the dominance of Arctic water masses and the presence of a sill, Billefjorden (40–55 km from the Bjørndalen colony) has been shown to retain a relatively large and stable population of the Arctic species *C. glacialis* (Arnkværn et al. 2005). In Isfjorden itself (Figs. 1, 2; stations D3–D7), which is regularly influenced by warmer Atlantic water masses, the same reliable standing stock of large and energy-rich food resources is

not to be expected. The shelf brake, offering another rich feeding ground (Falk-Petersen et al. 2007) is approximately 150 km away and is probably too far for frequent regular foraging trips.

Little auks breeding in Bjørndalen may be faced with low availability of preferred prey close to the colony, and abundant, energy-rich, preferred prey further away. Faced with the same spatial distribution of prey, blue petrels (*Halobaena caerulea*) in the Southern Ocean have a bimodal foraging trip pattern in which, it is hypothesized, food for chicks is procured on short trips, whereas longer trips are used for energetic self-maintenance (Weimerskirch et al. 2003). Given the poor foraging opportunities close to the Bjørndalen colony, we predict that little auks there have developed a similar bimodal foraging behaviour.

Material and methods

Zooplankton—net tows

Zooplankton were collected along a transect spanning the entire length of Isfjorden (Fig. 1) with two consecutive replicate standard WP-2 plankton net hauls (0.25 m^2 in area, mesh size 180 µm) at each of the four stations on 27 July 2005. As little auks only dive to 35 m (Falk et al. 2000) the nets were towed vertically from a depth of 50 m up to the surface. Attached to the nets was a salinity–temperature–depth (STD) unit (SD 204; SAIV A/S, Bergen, Norway) that measured the depth-specific temperature and salinity at each station. The sampling interval on the STD was set to 1 s^{-1}. Zooplankton samples were preserved in a 4% borax-buffered formaldehyde seawater
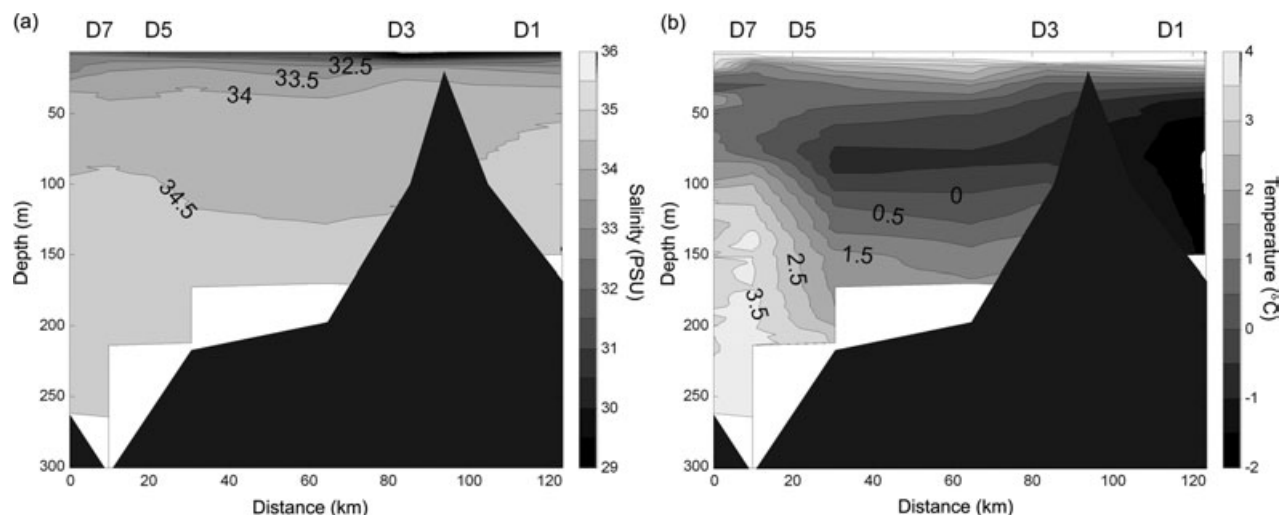
Fig. 2 (a) Salinity and (b) temperature profiles of Isfjorden on 27 July 2005. The four sampling stations are indicated at the top. Temperature and salinity plots were produced using the 1D interpolation function "interp1" of the MATLAB (v. 7.0.1; Mathworks Inc., Natick, MA, USA) software package, based on the four bottom-to-surface conductivity-temperature-depth casts. A rough outline of the bottom topography is represented in black.

solution. In the laboratory, samples were split using a simple box splitter down to fractions containing approximately 250 copepodites of *Calanus* spp. Based on these fractions, all *Calanus* specimens from copepodite stage (C1) to adult females (AF) were measured and identified on the basis of their prosome lengths, using size distribution tables that are well established for Svalbard waters (Kwasniewski et al. 2003). A Zeiss stereomicroscope was used for identification and counting. A 100% filtering efficiency of the WP-2 net was assumed, and the sampled seawater volume was calculated based on the wire length and the net opening area. Densities of the different *Calanus* stages are presented as the average between the two replicates (Fig. 3).

Foraging trip duration

Little auks were caught using a 9-m mist net placed perpendicular to the talus slope at the bottom of the study area. Birds caught in the net were immediately removed and all birds received three colour rings for later identification using binoculars. We also injected an 11×2 mm ID 100A passive integrated transponder (PIT) tag (EID Aalten BV, Aalten, the Netherlands) subcutaneously in the back of each bird's neck to be able to study their feeding behaviour. Using binoculars, we were able to find the probable nest entry holes of 10 nests. We equipped the 10 nest entry holes with tube-shaped PIT tag antennas that were hooked up to a Trovan® LID665 OEM PITtag decoder (EID Aalten BV; see Korslund & Steen 2006 for details). All other entrances were blocked. Each
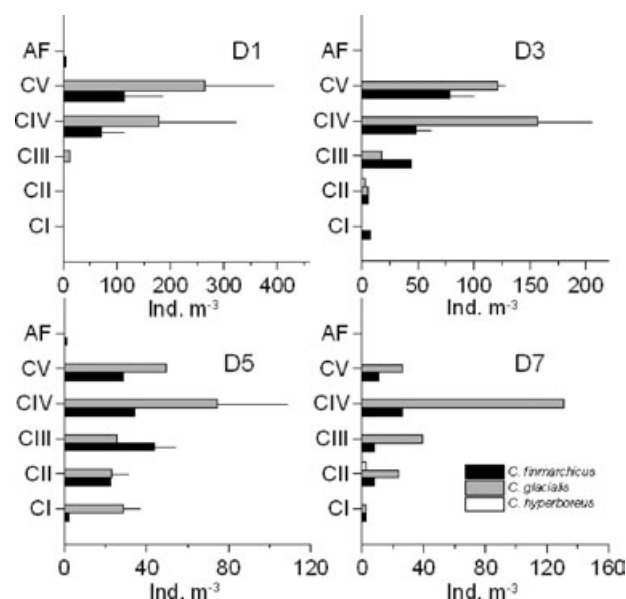
Fig. 3 Stage-specific abundance (calculated as number of individuals per m³) of the three species *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* at the four stations (D1, D3, D5 and D7) spanning the entire length of Isfjorden (see Fig. 1). Samples were taken on 27 July 2005. Scales on the *x*-axis differ in order to highlight the stage- and species-specific variations along the transect.

time a bird with a PIT tag passed through the antenna the time of passage and the bird's unique identification number was stored in the reader. Using this procedure we got reliable readings from four birds, two from the same entrance hole, between 23 July and 4 August 2005. All

summary statistics were calculated using raw trip time data from all four birds. Trips shorter than 10 min were regarded as movements around the nest entrance and were not used in the calculation of foraging trip times.

Using the times between two passages through the PIT tag antenna would give time spent either in the burrow or outside it. The time series with the longest times is probably time spent outside the burrow, as the chicks are homeothermic at 2–4 days (Harris & Birkehead 1985) and the study was undertaken late in the breeding season (see Results for details).

Zooplankton—gular pouches

Diet samples from the little auks were taken from 24 birds caught in the mist net in the study area. The contents of the gular pouches were carefully scooped out using a blunt spoon (three in late June and 21 between 21 and 23 July 2005). Although all visible prey items were removed from the gular pouches, we are not certain that the samples contain all food items the bird brought back to the colony. Hence, no quantitative conclusions can be drawn regarding total biomass of prey items in each food load. However, as the gular pouches were sampled without any bias towards specific prey items, relative frequencies of occurrence were calculated based on the raw data. A summary is presented in Table 1. The contents of the gular pouches were immediately transferred to small plastic beakers containing 70% ethanol and/or 4% borax-buffered formaldehyde seawater solution for preservation and later analysis. In the laboratory, the contents of the gular pouches were analysed in the same way as the net tow samples described above. The relative similarity of gular pouch contents was compared using the Bray–Curtis similarity index (Bray & Curtis 1957) and was displayed using the PRIMER software package. We used the square roots of the absolute numbers of each prey species in each of the gular pouch samples as variables to minimize the effect of large numbers and zeros.

Results

Zooplankton along the Isfjorden transect

Two replicates of the four stations along the Isfjorden transect (except station D6, for which only a single sample was available) were analysed (Fig. 3). The absolute number of *Calanus* spp. was highest at the innermost station (D1), whereas the relative frequencies of *C. glacialis* and *C. finmarchicus* remained approximately the same along the three inner stations, with roughly twice as many *C. glacialis* as *C. finmarchicus*. At all but the innermost station, copepodite stage CIV was present in higher

Table 1 Frequency of occurrence of different prey species in gular pouch contents from 24 little auks.

Species	Diets with 25% *C. hyperboreus* or less[a]		Diets with more than 25% *C. hyperboreus*[a]	
	Mean	SE	Mean	SE
Amphipoda sp.	0.001	0.001	0.000	0.000
Apherusa glacialis	0.000	0.000	0.003	0.002
Bivalvia larvae	0.004	0.004	0.000	0.000
Calanus finmarchicus CIII	0.000	0.000	0.000	0.000
Calanus finmarchicus CIV	0.002	0.002	0.004	0.004
Calanus finmarchicus CV	0.051	0.018	0.004	0.004
Calanus finmarchicus AF	0.004	0.001	0.000	0.000
Calanus glacialis CIII	0.000	0.000	0.000	0.000
Calanus glacialis CIV	0.006	0.002	0.007	0.007
Calanus glacialis CV	**0.571**	0.056	**0.144**	0.019
Calanus glacialis AF	0.018	0.002	0.008	0.004
Calanus hyperboreus CIV	0.003	0.002	0.018	0.008
Calanus hyperboreus CV	0.014	0.008	**0.407**	0.035
Calanus hyperboreus AF	0.007	0.003	**0.286**	0.052
Calanus sp.	0.052	0.010	0.080	0.022
Themisto abyssorum	**0.176**	0.048	0.029	0.021
Themisto libellulla	0.009	0.005	0.001	0.001
Themisto sp.	0.015	0.004	0.008	0.002
Thysanoessa furcilia	0.002	0.001	0.000	0.000
Thysanoessa longicaudata	0.032	0.010	0.001	0.001
Thysanoessa rachii	0.000	0.000	0.002	0.002
Thysanoessa sp.	0.019	0.004	0.002	0.002
Zoea larvae	0.005	0.003	0.002	0.002
Other[b]	0.009	0.002	0.006	0.004

[a] We have divided the data into two diet groups based on the similarity indexes: one group containing 25% or less *Calanus hyperboreus* ($n = 19$) and one group containing more than 25% *C. hyperboreus* ($n = 5$). The numbers in boldface indicate prey items that occur in 10% or more of the gular pouches.
[b] The category 'Other' consists of fish larvae, *Gammarus setosus*, *Gammarus wilkitzkii*, *Hyperoche medusarum*, *Ischyrocerus anguipes*, *Metridia longa* CIV, *Metridia longa* female, *Onisimus litoralis*, *Onisimus* sp., Ostracoda, *Pareuchaeta* sp., *Sagitta elegans* and unidentified Mollusca.

numbers than all other stages. The abundance of the largest copepodite stages of *Calanus hyperboreus* was very low along the transect, with a total of four specimens (CIV, CV and AF) encountered in all samples combined. According to the STD profiles along the same transect, the density front at the mouth of the fjord system had not yet broken down, and most of the fjord was still dominated by relatively cold Arctic water masses (Berge et al. 2005; Cottier et al. 2005). In the upper layers, however, freshwater run-off was locally dominant (Fig. 2), with possibly a marked impact on the small-scale distribution and abundance of the zooplankton.

Foraging trip times

The little auks showed a striking and repetitive pattern in their feeding trips, with a series of short trips followed by

one long trip (Fig. 4). We obtained continuous registration of foraging trip times of birds from three nests (20, 25 and 35) from 23 July to 3 August 2005. Both parents at nest 20 were registered, but only one gave high-quality registrations; data from the bird with low-quality registrations are not shown in Fig. 4. The chick in nest 25 hatched on 11 July, followed by chicks hatching in nest 35 on 17 July and in nest 20 on 18 July. The youngest chick was 5 days old at the start of the study and was already thermoregulatorily independent of its parents

(Harris & Birkehead 1985). Trips shorter than 10 min constituted 54 and 27% of the movements of both parents in nest 20, whereas they constituted 69 and 60% of the movements of birds in nests 25 and 35, respectively. The remaining trips showed a Poisson distribution pattern with an average of 89 (SE 3.4) min/trip when considering only trips shorter than 5 h, and an average of 675 (SE 43.1) min/trip when considering only trips longer than 5 h. If we use a cut-off point of 5 h we get a ratio of 5.15 short trips (≤5 h) to one long trip (>5 h)
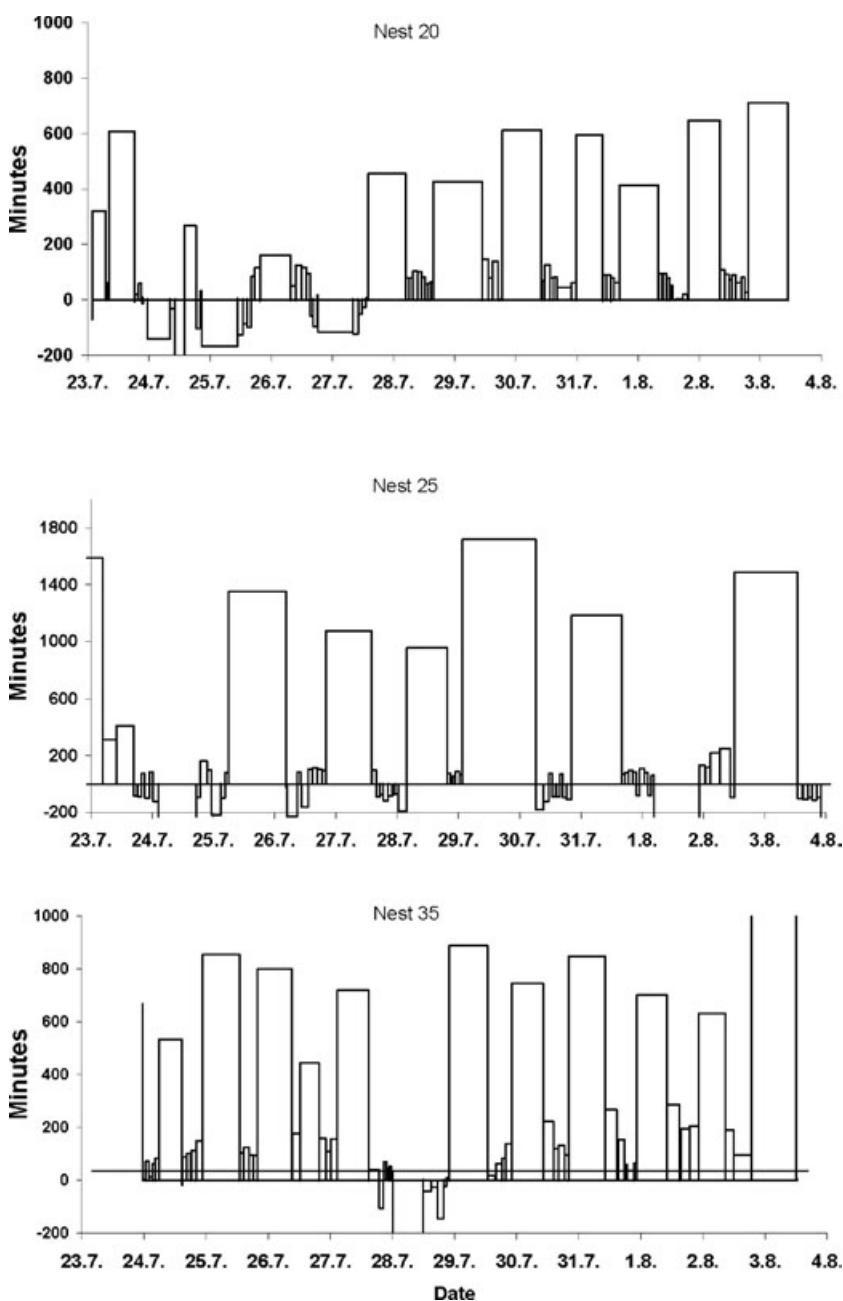
Fig. 4 Duration of foraging trips and time spent in the nest of parents from three nests (20, 25 and 35). Foraging trips are positive values and time in the nest are negative values. The height of each bar indicates time spent on a particular trip and the *x*-axis denotes the start and stop time of the trip.

using data from all trips and birds. We used 5 h as a cut-off because this duration was longer than the bulk of the short trips.

Chick diet

Gular pouch contents from 24 little auks were analysed and identified. In total, the average number of prey items in the gular pouches was 460 (SE 53.3), ranging from a minimum of 54 items up to 962 (except for one sample, diet sample #10, that contained approximately 2000 unidentified eggs). Among these, *Calanus* spp. were the dominant group of food items, although *Thysanoessa* spp. and *Themisto abyssorum* were also frequent (Table 1). Using the Bray–Curtis similarity index (Bray & Curtis 1957), we determined that the diet of the little auks was characterized by a group of five samples containing 25% or more *C. hyperboreus* (14, 17, 20, 22 and 24), and another group with either no or less *C. hyperboreus* (Table 1, Fig. 5). This separation into two diet groups is interesting as *C. hyperboreus* was hardly found in our net hauls in Isfjorden, and probably originates from outside the fjord (Falk-Petersen et al. 2007). Among the *Calanus* species, *C. glacialis* was the dominant species and, interestingly, CV stages were recorded nearly exclusively in the gular pouch samples. Only a few *C. glacialis* CIV were recorded, whereas there was a consistently low number of AF in most of the gular pouches. The birds that had high numbers of *C. hyperboreus* also had high numbers of *C. glacialis*. Low numbers of *C. finmarchicus* were recorded in most gular pouches. There also seemed to be a consistent pattern in that those gular pouches with low to medium numbers of *C. glacialis*
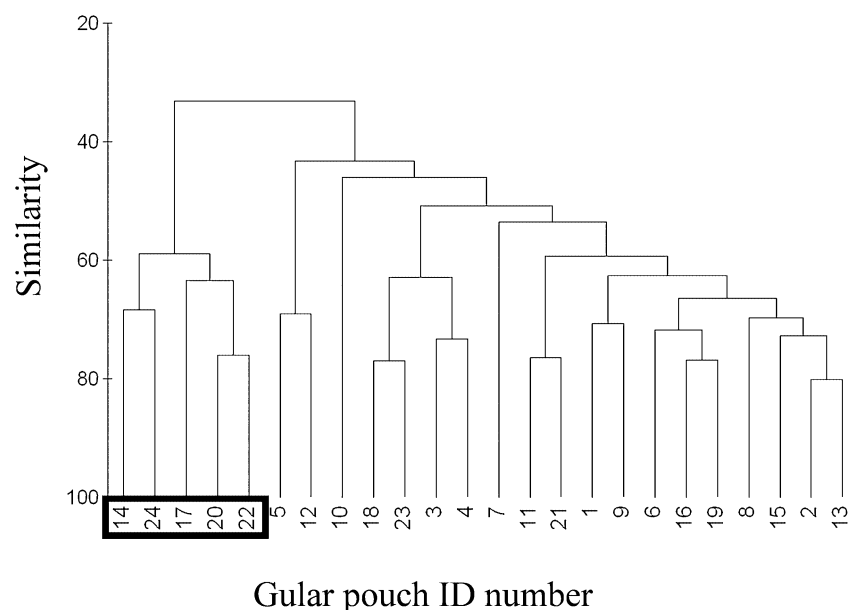
Trip times and diet

As shown above, analysing the PIT tag data revealed that little auks have short and long foraging trips at a ratio of 5.15 : 1. If the 24 gular pouch samples are taken to represent 24 trips, and if we apply the ratio of 5.15 : 1 to these 24 trips, we would expect 3.9 long trips and 20.1 short trips. Assuming that a sizeable quantity of *C. hyperboreus* in the gular pouch indicates that the bird has been feeding outside the Isfjorden complex, and hence has been on a 'long' foraging trip, the ratio between short and long trips based on diet is 3.8 short trips to 1 long foraging trip (19 short trips and 5 long trips). The similarity in the ratio of short and long trips from the PIT tag data to the ratio of the gular pouches having less than and more than 25% *C. hyperboreus* is striking, and is not significantly different (Fisher's exact test, $P > 0.9$). If we lower the cut-off point and use 5% *C. hyperboreus* instead of 25% as the dividing line between short and long trips, as deduced from the gular pouch contents, there were 16 short trips and 8 long trips—a ratio of 2 : 1, which is still not significantly different from the expected ratio based on the gular pouch samples ($P > 0.3$).

Discussion

Five of the 24 gular pouch contents from little auks breeding in Bjørndalen, Spitsbergen, contained large

and very few *C. hyperboreus* had the largest number of *T. abysorum* and krill, mainly *Thysanoessa longicaudata* (Table 1).

Fig. 5 Cluster diagram based on the Bray–Curtis similarity index, and produced with a group average linkage between the clusters. The gular pouches are divided into two major clades, one consisting of samples 14, 17, 20, 22 and 24 (outlined in the box) and one consisting of the remaining samples. Samples 14, 17, 20, 22 and 24 contain more than 50% *Calanus hyperboreus*.

quantities of *C. hyperboreus*, suggesting that the birds catch prey at two distinct locations. During long trips, averaging 11.5 hours, the little auks probably forage on the preferred prey *C. hyperboreus* (Pedersen & Falk 2001) at the shelf brake, about 150 km away from the colony. The short trips, on average 1.5 hours, are limited to the area close to the breeding colony, where they feed on *C. glacialis* (Table 1, Fig. 4).

Calanus species have a 2–5-year life cycle in the Arctic (Falk-Petersen et al. 2007). The energy needed for surviving the dark, unproductive polar night is collected during the productive part of the year, and is stored as lipids in oil sacs. The older stages of *Calanus* species contain oil sacs that can fill up most of the body cavity. The oil sac grows 2.8 times when the prosome length increases from 2.5 to 3.5 mm within the same *Calanus* species (Vogedes et al. unpubl. data). The size and energy content differ markedly between the species as well as between the stages (Scott et al. 2000; Falk-Petersen et al. 2007). For example, *C. glacialis* and *C. hyperboreus* are considerably larger than *C. finmarchicus*, and stage CV *C. glacialis* and *C. hyperboreus* contain approximately 10 and 25 times more energy (lipids) per individual, respectively, than *C. finmarchicus*.

The little auks in our study area seem to select nearly exclusively *C. glacialis* stage CV, although *C. glacialis* stage CIV are much more abundant at all stations except the station at the bottom of Billefjorden (D1). What is even more striking is that a substantial quantity of AF *C. glacialis* was found in the gular pouches, even though not a single AF was recorded in the net hauls. Five birds had high numbers of *C. hyperboreus* (CIV, CV, AF); these five birds also had moderate to high numbers of *C. glacialis* stages CV and AF. Along the transect that spanned the entire Isfjorden, only four *C. hyperboreus* individuals were recorded in the net hauls. *C. finmarchicus* was only recorded in low number in gular pouches despite its abundance in the fjord. From this we can deduce that the little auk is able to select two very specific zooplankters: the larger stages of *C. glacialis* and *C. hyperboreus* (mainly stage CV for both species). Although *C. glacialis* is common all over Isfjorden, *C. hyperboreus* is only found in significant numbers at the shelf break, approximately 150 km away from the nests (Falk-Petersen, pers. comm.). The higher energy demand for carrying out long foraging trips may be outweighed by the significantly higher energy content of *C. hyperboreus*. The co-occurrence of the highest number of *C. hyperboreus* and *C. glacialis* stage CV and AF in five of the birds suggest that these species occur together in dense concentrations on the shelf brake or the outer shelf. For the shorter trips within Isfjorden, the little auk probably feed on *C. glacialis*, *T. abysorum* and krill, which are known to be abundant in west Spitsbergen fjords (Hop et al. 2002; Kwasniewski et al. 2003).

Conclusion

We show for the first time a bimodal foraging trip pattern (Granadeiro et al. 1998; Weimerskirch et al. 2003) for an alcid species. This bimodal pattern is likely to be caused by a lack of suitable prey items close to the colony, forcing breeding little auks to also forage in distant areas. The long foraging trips are too infrequent to provide enough energy for the chicks (Karnovsky et al. 2003; Kwasniewski et al. 2003). Thus, our results support the hypothesis that the long foraging trips are likely to have evolved in order to replenish energy reserves for the adults, whereas the short trips mainly provide food for the chicks (Granadeiro et al. 1998; Weimerskirch et al. 2003). A flexible foraging strategy might have evolved in response to a highly variable environment, and further studies should focus on breeding performance relative to the ratio of short and long foraging trips. In good years, long trips should be short and more time should be spent on short foraging trips. In poor years the long trips should be longer, and there should be fewer short trips. Breeding performance should be negatively correlated to the average long trip length.

Acknowledgements

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