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Foraging closer to the colony leads to faster growth in little auks

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ABSTRACT: Knowledge of foraging behaviour is essential to understand both the ecological roles of seabirds and the constraints acting upon them in marine ecosystems. Here, we investigated foraging trips of a small planktivorous alcid, the little auk *Alle alle*, using miniature GPS loggers. We performed the study in 2 large breeding colonies in west Spitsbergen (Hornsund and Magdalenefjorden) with contrasting oceanographic conditions (Arctic and Atlantic environments, respectively). Generally, in both locations little auks foraged in areas with low sea surface temperature (Arctic-type water, marginal ice zone, and frontal zones) where preferred zooplankton are commonly abundant. In the Arctic environment (Hornsund), birds foraged significantly closer to the colony (up to 60 km) compared to up to 150 km in the Atlantic environment (Magdalenefjorden). Hatching and breeding success and chick survival up to 20 d as well as chick body mass parameters were similar in both studied colonies. However, chicks in the Arctic environment (Hornsund) achieved both peak body mass and fledging age earlier, suggesting faster chick growth than in the Atlantic environment (Magdalenefjorden). The importance for breeding little auks of nearby cold water foraging grounds may make them sensitive to predicted climate change with serious negative consequences for body condition, future survival and breeding success.

KEY WORDS: Zooplanktivorous alcid · Foraging range · Zooplankton · *Calanus glacialis* · Parental efforts · Breeding success · Chick growth · Spitsbergen

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INTRODUCTION

Macro-scale fluctuations of oceanographic conditions (e.g. North Atlantic Oscillation, El Niño Southern Oscillation) as well as mesoscale and local processes (e.g. sea ice dynamics, sea current distribution, upwelling strength and spread, atmospheric blocking) affect marine food webs, including changes in species composition and shifts in their phenology (Stenseth et al. 2003). In consequence, top predators such as seabirds may experience temporal and/or spatial changes in food availability that affects their breeding success, body condition and survival (e.g. Kitaysky & Golubova 2000, Harding et al. 2003, Adams et al. 2004, Sydeman et al. 2006, Moline et al. 2008, Gaston et al. 2009, Shultz et al. 2009).

Central place foraging seabirds (i.e. birds which forage at remote locations, but consistently return to the colony to deliver food to chicks; Weimerskirch 2002) may be particularly sensitive to changes in marine environment. Thus, knowledge of foraging behaviour of the seabirds is essential to understand both their ecological roles and constraints acting upon them in marine ecosystems (Monaghan 1996, Wilson et al. 2002). A Global Positioning System

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(GPS) tracking system with loggers attached to individuals is one of the most efficient methods of studying seabird foraging behaviour (Daunt et al. 2003, Garthe et al. 2007, Grémillet et al. 2004, Wilson et al. 2002). The latest miniaturization of the GPS loggers (~5 g) allows them to be used even on small seabirds (e.g. <200 g).

Here, we investigated the foraging behaviour of a small alcid (120 to 180 g), the little auk (or dovekie) *Alle alle* while provisioning chicks in West Spitsbergen, off the northern coast of Norway, using miniature GPS loggers. The little auk is a zooplanktivorous seabird that breeds colonially in the high Arctic and is considered the most abundant alcid in the Palearctic (Stempniewicz 2001). Little auk females lay a single egg annually in a nest usually situated under boulders in mountain scree. Both partners incubate the egg, then brood (for the few first days) and feed the chick (Stempniewicz 2001). Due to the high cost of locomotion, both in the air (flapping flight) and in the water (underwater 'flight' during diving), little auk foraging is believed to be energetically expensive (Gabrielsen et al. 1991, Konarzewski et al. 1993). To cover such high energetic demands, little auks forage almost exclusively on planktonic crustaceans, focusing on copepods associated with cold Arctic waters, which are larger and much richer in energy than their counterparts from warmer Atlantic waters (Karnovsky et al. 2003, 2010, Jakubas et al. 2007, 2011, Kwasniewski et al. 2010). In areas situated relatively close to the marginal sea ice zone, sympagic fauna (mainly *Apherusa glacialis*) can contribute considerably to the little auk diet composition (e.g. Kwasniewski et al. 2010). The distribution of cold Arctic waters along the west coast of Spitsbergen varies spatially and seasonally (e.g. Walczowski & Piechura 2007), affecting the accessibility of the zooplankton items preferred by little auks (Kwasniewski et al. 2012).

Some aspects of foraging behaviour (foraging trip duration, diving characteristics) has been recently studied intensively in little auks (Steen et al. 2007, Harding et al. 2009, Welcker et al. 2009, Wojczulanis-Jakubas et al. 2010, Jakubas et al. 2011, Karnovsky at al. 2011). The ranges of foraging trips have been indirectly estimated to be between 130 and 219 km (total distance covered) based on the mean flight duration of parent birds equipped with time-depth recorders (TDRs) (Welcker et al. 2009). However, the exact routes and location of foraging areas are largely unknown. The recent, pioneering study on GPS-equipped little auks (Jakubas et al. 2012) documented that little auks rearing chicks in the colony in NW Spitsbergen are able to reach the marginal sea ice zone situated >100 km from the colony. The marginal sea ice zone is an attractive foraging ground due to its abundant amphipods and copepods (Arndt & Swadling 2006), resulting in high concentrations of little auks in the Greenland Sea (Joiris 2000).

We aimed to compare ranges of foraging trips and location of feeding grounds of little auks breeding in 2 colonies in West Spitsbergen characterized by contrasting oceanographic conditions. To understand little auk foraging behaviour in given conditions, we investigated oceanographic and trophic parameters of the feeding grounds: sea-ice distribution, sea surface temperature (SST) and zooplankton distribution. We also studied how foraging behaviour of birds from studied colonies affected the breeding success and chick growth rate. We expected that (1) range of foraging trips would be shorter in Arctic than in Atlantic-influenced environments, (2) birds would search for foraging areas with favourable zooplankton items associated with cold Arctic-type waters or marginal sea ice zone, (3) different foraging conditions would influence the chick growth rate and breeding success.

MATERIALS AND METHODS

Study area

We carried out the study in 2 large little auk colonies at Ariekammen slopes in Hornsund (SW Spitsbergen; 77° 00′ N, 15° 33′ E) and at a moraine of Buchannbreen glacier and Alkekongen slopes in Magdalenefjorden (NW Spitsbergen; 79° 35′ N, 11° 05′ E) in 2011 (Fig. 1). Both studied fjords are the main breeding areas of little auks on Svalbard (Isaksen 1995).

The Hornsund area is influenced by both coastal Sørkapp Current, carrying cold, less saline Arctic-type water from the northeast Barents Sea and the West Spitsbergen Current (WSC), providing warmer and more saline Atlantic waters originating from the Norwegian Sea (Piechura et al. 2001, Cottier et al. 2005). In the vicinity of the Magdalenefjorden colony, the WSC flows on the shelf slope and meets relatively cold and fresh Arctic water present there in form of an anti-cyclonic coastal current. The 2 water masses partly interfere, creating a transitional zone of differing widths according to the seasons (Daase et al. 2007, Walczowski & Piechura 2007, Trudnowska et al. 2012). The marginal sea ice zone is permanently

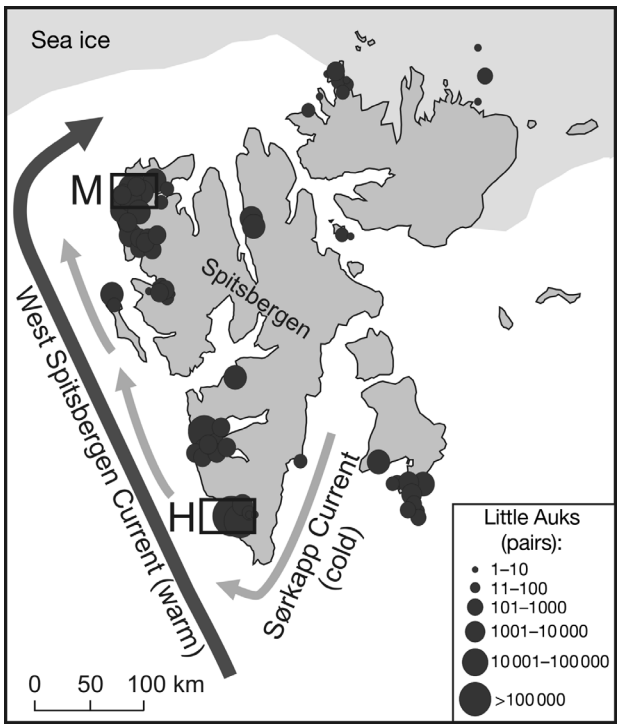

Fig. 1. Study area with ocean current patterns in the Spitsbergen region (arrows, modified after Loeng & Drinkwater 2007), sea ice extent in July 2011 (area permanently covered by close and very close ice; light grey area) and the locations and sizes of little auk colonies (grey circles, modified after Isaksen & Gavrilo 2000). Rectangles: colonies studied (H: Hornsund; M: Magdalenefjorden)

situated ca. 100 km north off Magdalenefjorden (Fig. 1). In the Hornsund area, sea ice is present only in some seasons depending on atmospheric and oceanic processes (Jakubas et al. 2007, Kwasniewski et al. 2012).

GPS tracking

We used miniature GPS loggers (ECOTONE PATRON EP-3.1 and EP-3.3, size including battery and potting 40 × 17 × 9 mm). Up to 1000 GPS fixes can be stored in the logger memory. The time of day and GPS position were recorded every 15 min (Hornsund) or 20 min (Magdalenefjorden). We chose the logger type following the recommendation from a previous study (Jakubas et al. 2012): it was the lightest GPS logger available on the market during the study (4.4 to 4.9 g) and equipped with remote data transmission (to minimize the bird's stress related to recapture). Field tested accuracy of the GPS receiver was ± 20 m. Sampling started 24 h after (Magdalenefjorden) or immediately after (Hornsund) starting the logger (i.e. up to 2 hours before logger attachment). The time between recorded fixes can vary depending on the time spent by the bird under water (satellite signal unavailable).

We attached the GPS loggers to the bird's central back feathers using LOCTITE 4860 cyanoacrylate glue (Henkel) at approximately the midpoint of the centre line of the body. We positioned the logger by fishing line (diameter 0.5 mm) covered with cyanoacrylate glue, looped (but not tightened) around the bird's neck. The logger mass (including attachment, 4.9 to 5.4 g) was equivalent to 2.8 to 3.5% of body mass of equipped individuals (mean body mass ± SD of the adults equipped with loggers in Hornsund: 159.0 ± 8.86 g, n = 12; birds in Magdalenefjorden were not measured).

To download data from the loggers, we used a remote data transmission system. Loggers had a radio link for data download and GPS activity control. Base stations were installed in the colonies and downloaded data from loggers automatically each time birds with loggers were within range of the base station (up to 800 m). To save the battery, base station switched off GPS loggers while they were within the download range of the base station. GPS loggers were activated automatically when birds were out of base station signal range.

We caught the birds in the nest chambers during the pre-hatching (Magdalenefjorden) and early chick-rearing (Hornsund and Magdalenefjorden) period in 2011. Instrumenting little auks at those stages gives the highest probability of recapture (and GPS logger retrieval) because during that time birds stay in the nest for longer periods of time to incubate the egg and brood the chick. We released the birds back into the nest after no more than 10 min of handling. The egg or chick was kept warm in a cotton bag during the parent handling.

We attached GPS loggers to 13 ind. in Hornsund (including 1 ind. that we equipped twice with 2 different loggers) and 23 ind. in Magdalenefjorden. In total, we obtained records from 10 ind. in Hornsund and 9 ind. in Magdalenefjorden. Of these, data series from 6 birds in Hornsund and 2 birds in Magdalenefjorden were too short for analysis and we excluded them from further analysis. Thus, in total, we analysed 5 trips from 4 birds in Hornsund and 9 trips from 7 birds in Magdalenefjorden (Table 1). The effect of GPS loggers on parent birds and their chicks is described in Appendix 1.

We obtained the following data from the GPS loggers: (1) geographical positions; (2) the total distance

Table 1. *Alle alle*. Characteristics of recorded foraging trips of GPS logger equipped little auks breeding in Hornsund and Magdalenefjorden. Identification numbers beginning with H and M represent Hornsund and Magdalenefjorden, respectively. **Bold**: 2 trips for the same individual. Period: prior hatching (prh) and chick rearing (chr). Trip status indicates completeness of the trip (n–C: first record was n km from the colony and last record was in the colony; C–n: first record was in the colony and last record was n km from the colony; n–n: first and last records were n km from the colony). Negative chick age values: days before hatching

ID	Total distance (km)	Max distance (km)	Trip status	Trip duration (h)	Period	Chick age (d)	Date of trip
H5	146	61	Whole trip	19.3	chr	1	14 Jul
H11	123	51	(7–51)	–	chr	1	13–14 Jul
H12	143	54	(C–27)	–	chr	6	17–19 Jul
H19	164	60	Whole trip	18.7	chr	1	13–14 Jul
H19	112	61	(10–38)	–	chr	2	14–15 Jul
M1	425	139	Whole trip	42.8	chr	3[a]	19–20 Jul
M5	269	129	(129–C)	–	prh	–3	19–20 Jul
M8	182	86	(86–C)	–	chr	2	19–20 Jul
M8	314	133	(C–20)	–	chr	3	20–21 Jul
M14	332	150	(150–C)	–	chr	1[a]	23–25 Jul
M22	190	93	(C–21)	–	chr	1[a]	24–25 Jul
M24	198	92	(75–C)	–	prh	–2	19–20 Jul
M24	265	126	Whole trip	16.5	prh	–1	20–21 Jul
M5′	375	136	(C–3)	37.9	prh	–3	19–22 Jul

[a]Exact hatching date unknown, age of chick estimated based on the chick's appearance.

travelled (km), as the sum of the distances (km) between all GPS positions along each individual's track; (3) maximum straight-line distance from the colony to the distal point reached on each foraging trip; (4) trip duration, defined as the time an individual left the colony to the time it returned; (5) mean travel speed (km h^{-1}), determined as the distance between 2 consecutive neighbouring GPS locations divided by the time interval between recorded locations; (6) momentary flight speed (km h^{-1}) recorded by GPS loggers (only values >10 km h^{-1} were considered — see point 7, below); (7) stationary positions (hereafter called 'foraging areas'), defined as the positions with mean travel speed ≤10 km h^{-1}; such stationary positions suggest foraging behaviour, as low transit speeds are commonly considered as an indicator of swimming or foraging behaviour of marine predators (Nel et al. 2001, Grémillet et al. 2004, Awkerman et al. 2005, Weimerskirch et al. 2005, 2006, Simmons et al. 2007, Kotzerka et al. 2010). Due to inherent errors of GPS, there are some errors in momentary speed calculation (D'Este et al. 1999). Thus, we decided to distinguish stationary positions based on mean travel speed, not momentary speed.

Due to small sample size and low number of replicated trips (i.e. trips performed by the same individual) we decided to not include individuals as a random effects term in inter-colony comparison. We calculated simple non-parametric Mann-Whitney *U*-tests.

Kernel analyses were performed to determine high density aggregations (hotspots) for the stationary (foraging) positions of tracked birds. Hotspots (main foraging areas) were delimited by >40% kernel density contours. Kernel analyses were performed using ArcGIS v. 9.2.

Remote sensing

To evaluate environmental conditions on the foraging grounds, we analyzed SST and sea ice extent (i.e. position of the marginal sea ice zone) in periods when GPS-tracked individuals performed foraging trips. The MODIS Aqua SST data (NASA Ocean Color Web) was used in our study. We chose the Level 3, 4 km binned data product consisting of an average from all retrieved 'good' SST data acquired during daytime 3 or 8 consecutive days as the most representative for the purpose of this study. From these results we extracted the sub satellite points related to the locations of bird observation and used in analyses. The sea ice extent was visualized based on the 4 km resolution data from The National Environmental Satellite, Data, and Information Service (NESDIS), as a part of National Oceanic and Atmospheric Administration (NOAA/NESDIS/OSDPD/SSD 2004). Visualized ice corresponded to very close and close ice. Due to heavy cloudiness, we were only able to prepare complete SST maps for the following peri-

ods: 25 to 27 July 2011 for the Hornsund area and 19 to 21 July and 25 to 27 July 2011 for the Magdalenefjorden area. However, those dates corresponded fairly well to the dates of recorded flights of GPS-equipped little auks (Table 1). For the sea ice extent, we prepared the maps for 14 July 2011 in the Hornsund area and in 21 July 2011 in the Magdalenefjorden area.

Zooplankton and hydrology studies

We carried out the zooplankton sampling simultaneously with hydrological measurements in the sea area adjacent to the little auk colony in Hornsund (West Spitsbergen Shelf, WSS) corresponding with previously investigated little auk feeding grounds (Karnovsky et al. 2003, 2010, Kwasniewski et al. 2010, Jakubas et al. 2011). The sampling was performed from the Institute of Oceanology of Polish Academy of Sciences research vessel Oceania between 27 and 29 July 2011.

To examine *in situ* oceanographic variables such as hydrology (temperature, salinity), zooplankton and phytoplankton concentration in the little auks foraging grounds, we used a sampling platform equipped with CTD (SBE 911plus, Seabird Electronics), laser optical plankton counter (LOPC; Brooke Ocean Technology) and fluorometer (Seapoint Sensors). The platform was towed horizontally along investigated transects at a speed of 4 knots at 25 m depth in the Hornsund area. Specifications of LOPC measurements and further data processing are described in detail in Trudnowska et al. (2012).

We presented the plankton size structures for a few selected transects representing different hydrological regimes (Atlantic, Frontal Zone, Arctic, or eddy) (see Fig. 8). Two distinct water masses of Arctic ($T \leq 1$°C, salinity < 34.4) and Atlantic ($T > 2$°C, salinity > 34.4) origin (Piechura et al. 2001, Cottier et al. 2005, Schlichtholz & Houssais 2002) were separated by a hydrological front, the position of which is generally correlated with bathymetry associated with the shelf edge (Saloranta & Svendsen 2001). The frontal zone in our study was indicated by a temperature gradient of 5°C (see Fig. 8). The eddy observed in the Hornsund area was characterized by 3°C higher SSTs and 0.4 higher salinity than the surrounding water.

We performed 3 zooplankton net catches in the Arctic-type waters in the Hornsund area to supply salinity LOPC mapping with complementary taxonomical information. Since the LOPC was towed at 25 m depth, we used net catches taken vertically at 20 to 30 m depth intervals with a multiple plankton sampler (Hydrobios, mesh size 180 µm, mouth opening 0.25 m^2). We performed quantitative and qualitative sample examinations in the lab following Harris et al. (2000). We identified *Calanus* spp. and individual copepodid stages based on the criteria given in Kwasniewski et al. (2003). We expressed zooplankton abundance in units of ind. m^{-3} using filtered water volume estimated by the net flow meter.

The size range of 1.6 to 2.5 mm equivalent spherical diameter (ESD) was defined for the older copepodid stages of *Calanus* spp., mainly the CV Stage of *C. glacialis*, which — among other prey — is targeted by little auks breeding in both studied colonies (Kwasniewski et al. 2010, Jakubas et al. 2011). Its frequency in the total plankton abundance was calculated separately for different water masses.

Breeding success and chick body mass

As logger instrumentation may affect breeding parameters of little auks negatively (see Appendix 1, Kidawa et al. 2012), we used nests of control birds unburdened by loggers to compare breeding success and chick growth between colonies.

To establish hatching date in both colonies, we checked all nests every 2 d, starting from 2 d before expected hatching date (based on the egg-laying data and a 29 d incubation period, Stempniewicz 1981) until we found a hatchling. Then, we monitored nests starting when the chicks were at age 14 to 15 d and weighed them every 3 d until they disappeared from the nest at 21 to 31 d (Wojczulanis-Jakubas & Jakubas 2012).

We compared the following chick body mass variables between the colonies: peak mass (the highest mass noted per chick), fledging mass (the last mass measured before the chick's departure from the colony) and mass recession (difference between peak and fledging mass, after Stempniewicz 1980, Konarzewski & Taylor 1989). We also compared the day when peak mass was achieved and the day of fledging (the last presence in the nest). The peak and fledging masses have been found to be effective growth indicators, even more so than the widely used growth-curve analysis (Zach 1988). As we were not able to catch all chicks during each visit, the sample sizes were different for particular body mass variables.

To compare breeding success between both colonies, we analyzed hatching success (no. hatched

chicks per no. monitored eggs), breeding success up to 20 d (no. 20 d old chicks per no. monitored eggs), and chick survival up to 20 d (no. 20 d old chicks per no. hatched chicks). We assumed that chicks that disappeared from the nest after 20 d had fledged (Harding et al. 2004).

We performed all statistical analyses in STATISTICA v. 8.0. To present the distribution pattern of sea temperatures in the Hornsund area, we used interpolated horizontal mapping in Ocean Data View software (Schlitzer 2011).

RESULTS

Foraging trip range and speed

Total distance covered by logger-equipped individuals from Hornsund during one foraging trip (median [Me] = 143 km) was significantly lower compared to Magdalenefjorden (Me = 269 km; Mann-Whitney *U*-test, $U < 0.0$, $p = 0.003$). Also, maximal straight-line distance from the colony was lower in Hornsund (Me = 60 km) than in Magdalenefjorden (Me = 129 km; Mann-Whitney *U*-test, $U < 0.0$, $p = 0.003$) (Table 1, Fig. 2).

Momentary speed was similar in both studied colonies (Hornsund: Me = 53 km h^{-1}, min.–max. = 11–80 km h^{-1}, n = 32; Magdalenefjorden: Me = 43 km h^{-1}, min.–max. = 11–91 km h^{-1}, n = 66; Mann-Whitney *U*-test, $Z = -1.49$, $p = 0.14$). Little auks spent only 14 and 27% (Hornsund and Magdalenefjorden, respectively) of their foraging trips engaged in flight. The remaining part of the time budget consisted of stationary positions (presumably foraging and resting; speeds ≤10 km h^{-1}). Distribution of mean travel speeds differed between the colonies (Fig. 3; Kolmogorov-Smirnov test, $D = -0.61$, $p < 0.025$). Values of mean travel speed recorded in Hornsund (Me = 25 km h^{-1}, min.–max. = 11–60 km h^{-1}, n = 38) were lower than in Magdalenefjorden (Me = 33 km h^{-1}, min.–max. = 11–71 km h^{-1}, n = 130; Mann-Whitney *U*-test, $Z = 2.29$, $p = 0.02$). In Hornsund, mean travel speed was higher during outgoing flights compared to return flights (Mann-Whitney *U*-test, $U = 5.09$, $p = 0.004$, n = 6 outgoing, 12 incoming, for 2 individuals with the whole trip recorded, combined) (Fig. 4). Birds from Magdalenefjorden traveled with similar mean travel speed both during ongoing and return flights (Mann-Whitney *U*-test, $U = 18.0$, $p = 0.21$, n = 5 outgoing, 12 incoming, for 2 individuals with the whole trip recorded, combined) (Fig. 4).

In Magdalenefjorden, parameters of flights performed during the pre-hatching (n = 4) and chick-rearing (n = 5) period were similar (Mann-Whitney *U*-test, total distance covered, $p = 1.00$; maximal distance from the colony, $p = 0.71$).

Distance from colony to foraging areas

Foraging areas (stationary positions) of birds from Hornsund were situated closer to the colony (Me = 43 km, min.–max. = 2–61 km) compared to Magda-

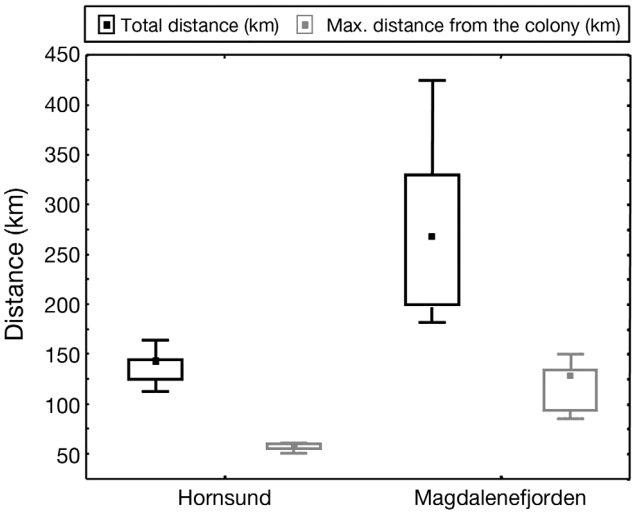

Fig. 2. *Alle alle*. Total distance covered by GPS-equipped little auks and their maximal distance from the colony in Hornsund (n = 5 trips) and Magdalenefjorden (n = 9 trips). Points show the median distance covered, boxes represent the 25 to 75% quartiles, and whiskers the minimum and maximum distance

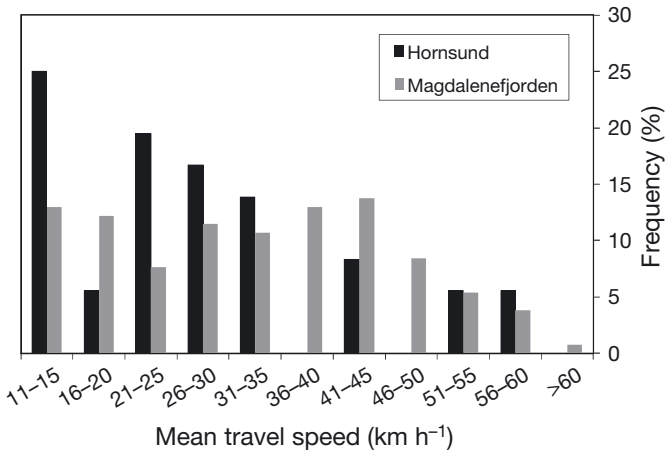

Fig. 3. *Alle alle*. Distribution of little auk mean travel speeds recorded by GPS data loggers during the breeding season. Flight speeds ≤10 km h^{-1} representing stationary positions are not depicted (see 'Materials and methods')

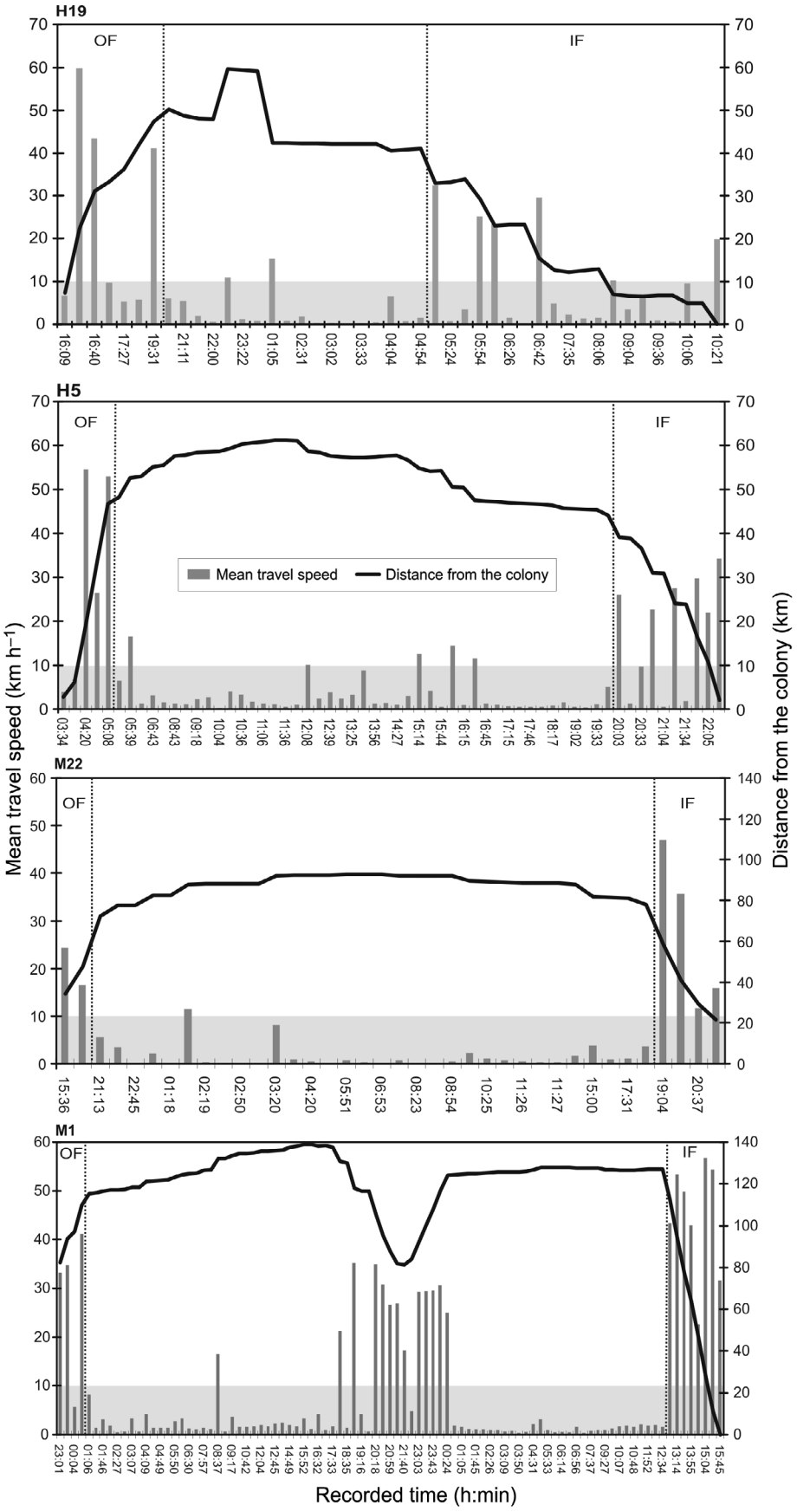

Fig. 4. *Alle alle*. Typical ranges of mean travel speed (bars) and distance from the colony (line) of GPS-equipped individuals. Grey shading: speeds ≤10 km h^{-1}, considered as staying at foraging areas. Right and left parts of graph separated by dotted lines indicate outgoing (OF) and incoming (IF) flights. IDs—H: Hornsund; M: Magdalenefjorden

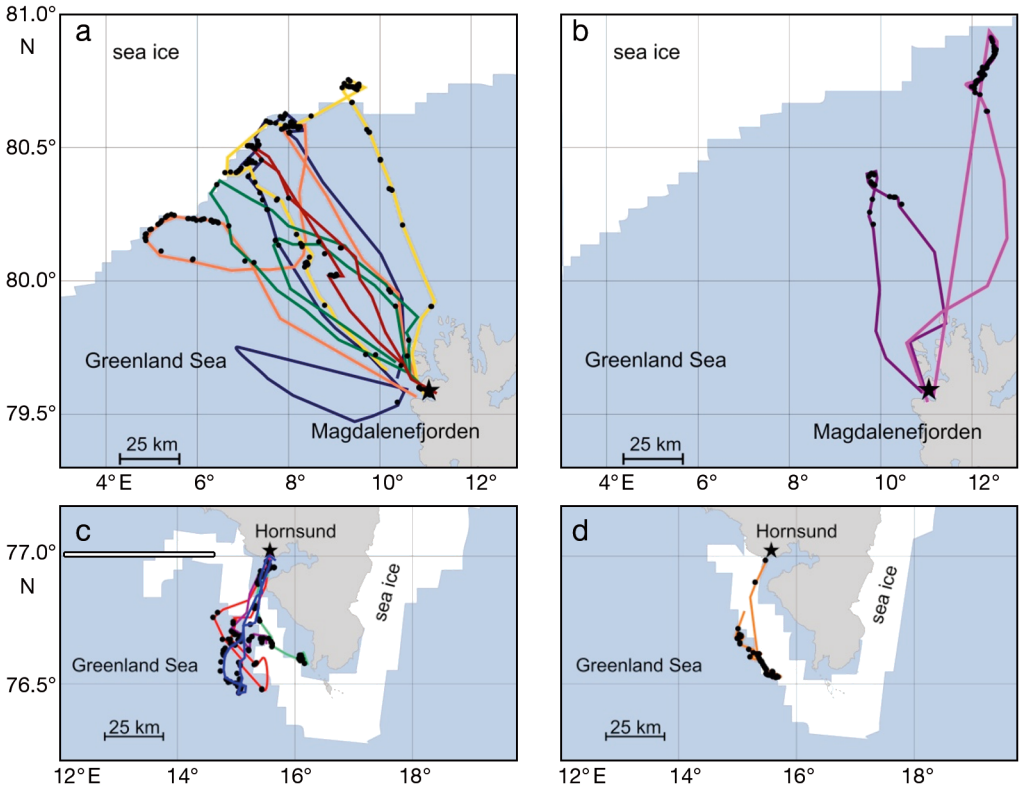

Fig. 5. *Alle alle*. Trips of individuals (represented by different colours) breeding in Hornsund and Magdalenefjorden. (a) 7 trips from 19 to 22 July and sea ice range on 21 July, (b) 2 flights from 23 to 25 July and sea ice range on 24 July, (c) 4 trips from 13 to 15 July and sea ice range on 14 July, (d) 1 trip from 17 to 19 July and sea ice range on 18 July. Black points: foraging positions of GPS-equipped individuals; stars: breeding colonies

lenefjorden (Me = 126 km, min.–max. = 1–149 km; Mann-Whitney *U*-test, $Z = 17.5$, $p < 0.001$, n = 227, 364). More than half of foraging positions of birds from Hornsund (59%) were located between 26 and 50 km from the colony whereas most positions of little auks from Magdalenefjorden (53%) were between 126 and 150 km from the colony.

Table 2. Sea surface temperature (SST) median values (parentheses: 25th to 75th percentiles) at flight positions and in foraging areas of GPS-logger-equipped little auks *Alle alle* from colonies in Hornsund in Magdalenefjorden. Flight logging from Hornsund took place between 13 and 19 July 2011. n, n: no. of foraging and flight positions, respectively

SST date / area	SST (°C)		Mann–Whitney *U*–test	
	Foraging areas	Flight positions	*Z* (n, n)	p
25–27 July/ Hornsund	1.7 (1.6–2.2)	1.6 (1.5–1.9)	1.76 (206, 37)	0.08
19–21 July/ Magdalenefjorden	0.5 (–0.2–2.1)	2.6 (1.1–3.1)	–7.17 (253, 109)	<0.0001
25–27 July/ Magdalenefjorden	0.7 (0.5–1.0)	2.2 (1.9–2.5)	–4.96 (102, 13)	<0.0001

Foraging habitat characteristics

Birds from both colonies foraged mainly in the marginal ice zone, which during our survey was situated much further from the Magdalenefjorden area (Fig. 5). In Magdalenefjorden, SST values in the foraging areas were significantly lower compared to flight positions (Table 2, Fig. 6).

In Hornsund, SST values in both foraging areas and flight positions were similar (Table 2, Fig. 7). The areas in the Hornsund shelf covered by zooplankton studies were situated in the transitional zone between cold (Arctic origin) and warm (Atlantic origin) water masses. The co-existing Atlantic and Arctic realms on the WSS are characterized not only by differences in water temperature and salinity but also by different zooplankton assemblages, both in terms of abun-

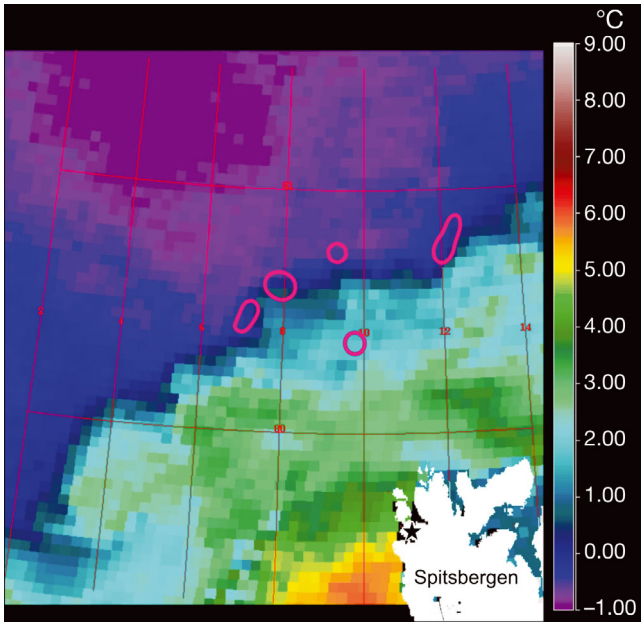

Fig. 6. *Alle alle*. Main foraging areas (magenta circles) of all GPS-equipped little auks from the colony in Magdalenefjorden (black star) represented by >40% kernel density contours and MODIS sea surface temperature 3-day composite image (4 km resolution) of the West Spitsbergen area for 19 to 21 July 2011

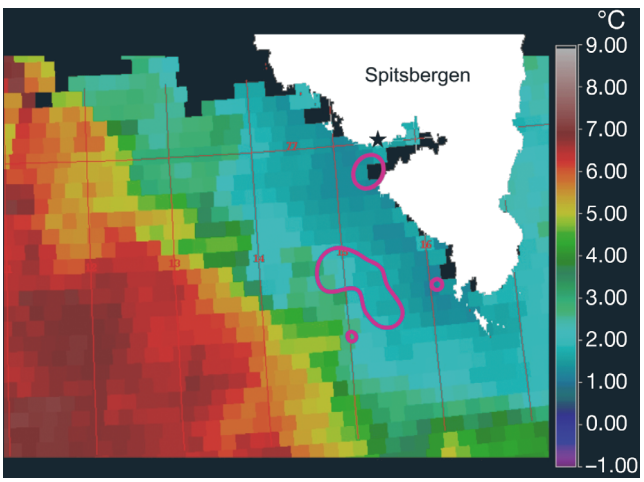

Fig. 7. *Alle alle*. Main foraging areas (magenta circles) of all GPS-equipped little auks from the colony in Hornsund (black star) represented by >40% kernel density contours and MODIS sea surface temperature 3-day composites image (4 km resolution) of the West Spitsbergen area for 25 to 27 July 2011

dance and species composition. (Table 3, Fig. 8). Warm Atlantic-type waters contain numerous (Table 3) but very small (Me = 0.4 mm ESD) mesozooplankton and were separated from cold Arctic-type waters by the frontal system, which was indicated by temperature gradient and the co-occurrence of 2 mesozooplankton fractions. The small zooplankton fraction occurring in Arctic waters was represented mainly by *Cirripedia* spp. larvae, *Pseudocalanus* spp., *Oithona similis*, Copepoda nauplii and younger stages of *Calanus* spp. The second mode consisted mainly of older life stages of *Calanus* spp., mainly *C. glacialis* (70%). Additionally, we detected an eddy characterized by the presence of large zooplankton, most probably *C. glacialis* Stage CIV-V (Fig. 8).

During the sampling campaign from 27 to 29 July, the highest abundance and frequency of zooplankton in the size range 1.6 to 2.5 mm ESD (prey size corresponding to *Calanus glacialis* Stage CV preferred by little auks) was found in the eddy and Arctic-type waters (Table 3). Frontal Zone and Atlantic-type waters were significantly less abundant in *C. glacialis* (Table 3). Foraging positions of birds were located mainly in cold Arctic-type waters. Birds generally avoided areas with higher temperatures and a corresponding low abundance of large zooplankton items (Fig. 8).

Breeding success and chick growth parameters

All breeding variables (hatching success, breeding success and chick survival up to 20 d) in control nests were similar in both studied colonies (Fisher exact tests, $p > 0.05$) (Table 4).

Mean date of chick hatching in Hornsund was significantly earlier than in Magdalenefjorden (on average 4 d; see Table 5). Peak body and fledging mass as well as body mass recession were similar in chicks from both colonies. Peak body mass and fledging occurred on average 1 d earlier in Hornsund compared to Magdalenefjorden. Mean fledging date in Hornsund was on average 6 d earlier than in Magdalenefjorden (Table 5).

DISCUSSION

Using miniature GPS data loggers, we determined exact locations of foraging areas and foraging ranges of little auks from 2 main little auk breeding aggregations on Spitsbergen situated in different oceanographic regimes. Results from Hornsund are presented for the first time. Data for Magdalenefjorden confirm results of our earlier study (Jakubas et al. 2012) and provide more details on feeding ground location and foraging trip ranges. In contrast to previous studies, where location of foraging grounds was

Table 3. Properties of different marine environments in the Hornsund area based on LOPC-CTD-F platform measurements between 27 and 29 July 2011 at a depth of 25 m. *Calanus glacialis* Stage CV identified as zooplankton items in size range 1.6–2.5 mm equivalent spherical diameter. Q_1–Q_3: quartiles 25–75%. All values differed significantly among environments (Kruskal-Wallis tests, $p < 0.0001$, post-hoc Dunn test, $p < 0.02$) except for those in *italics*

Environment type		Temperature (°C)	Salinity (PSU)	Total zooplankton abundance ($\times 10^3$ ind. m^{-3})	*C. glacialis* CV Abundance (ind. m^{-3})	*C. glacialis* CV Frequency (%)
Arctic-type waters	Median	0.0	33.0	31	49.3	0.1
	Q_1–Q_3	−0.3–0.2	32.5–33.3	24–48	0.0–148.5	0.0–0.4
	n	5323	5323	5323	5323	5323
Frontal Zone	Median	*3.9*	*34.1*	98	0.0	0.0
	Q_1–Q_3	2.5–4.2	33.8–34.2	57–140	0.0–45.8	0.0–0.1
	n	2215	2215	2215	2215	2215
Atlantic-type waters	Median	6.2	34.9	132	24.3	0.0
	Q_1–Q_2	5.8–6.8	34.7–35.1	92–182	0.0–75.9	0.0–0.0
	n	6665	6665	6665	6665	6665
Eddy	Median	*2.5*	*33.9*	49	402.6	1.1
	Q_1–Q_3	2.1–2.7	33.8–33.9	31–64	182.3–1395.5	0.5–3.0
	n	184	184	184	184	184

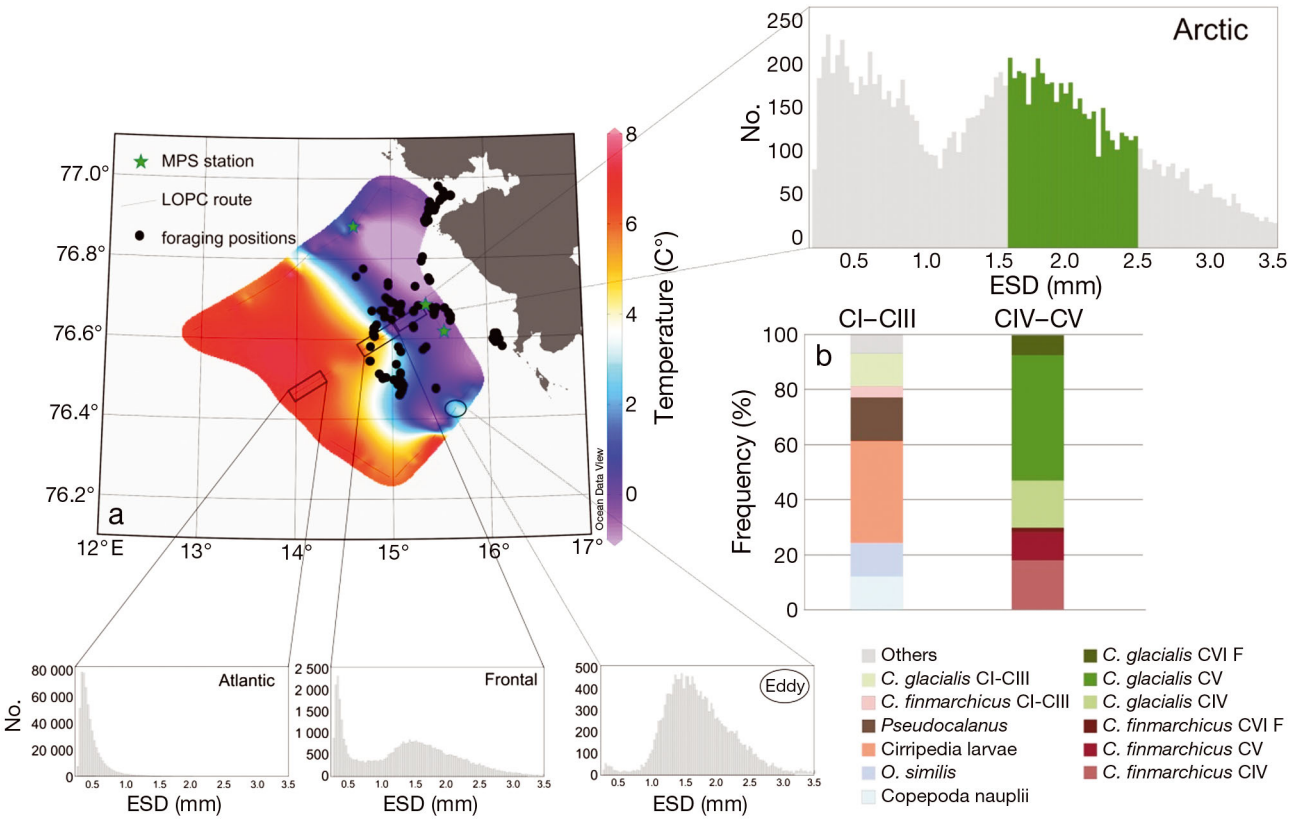

Fig. 8. (a) Water temperature at 25 m depth in the Hornsund area. Black dots: foraging sites of GPS-equipped little auks *Alle alle*. Inset bar graphs detail zooplankton size structure (ESD: equivalent spherical diameter) of selected Atlantic, Frontal, and Arctic-type waters, and an eddy with large zooplankton (Eddy). Green bars in Arctic-type waters: size range of *Calanus glacialis*. (b) Relative abundance of zooplankton taxa (in size range of *C. glacialis* and *C. finmarchicus* stages CI to CIII and CIV to CV based on net zooplankton catches

estimated indirectly based on analyses of flight duration, food load composition, at-sea distribution of foraging birds of unknown origin and status, and recorded temperature (e.g. Karnovsky et al. 2003, 2010, 2011, Welcker et al. 2009), here we present actual foraging areas of little auks from particular colonies and characterized actual environmental conditions in those areas.

Table 4. *Alle alle*. Hatching success, breeding success and chick survival (all in %; parentheses: number of nests) up to 20 d (unhatched eggs excluded from the chick survival, included in breeding success) in Hornsund and Magdalenefjorden. Data from Hornsund from Jakubas & Wojczulanis-Jakubas (2013)

Colony	Hatching success	Breeding success up to 20 d	Chick survival up to 20 d
Hornsund	92 (147)	84 (103)	96 (89)
Magdalenefjorden	98 (45)	83 (42)	85 (41)

Little auks from both sites used cold water in the marginal sea ice zone as their feeding grounds. Birds from Magdalenefjorden performed foraging trips to more distant foraging areas compared to Hornsund. That result was expected, as foraging trip duration in Magdalenefjorden was reported to be longer than in Hornsund in previous studies (Kwasniewski et al. 2010, Jakubas et al. 2011). The analysis of SST values at stationary and flight positions in Magdalenefjorden area shows that birds generally flew over warmer water to reach remote areas in the marginal ice zone. In the Hornsund area, little auks flew over the coastal ice belt to reach foraging areas in the marginal ice zone. For SST, the closest time for which we were able to obtain data was a period 7 to 14 d later than recorded flights and 3 to 4 d later than sea ice disappeared from the Hornsund area (i.e. 23 July 2011; sea ice maps of Norwegian Meteorological Institute). Thus, temperatures recorded both at flight and foraging positions were higher than zero. However, even those elevated SST values in the foraging areas of little auks (median 1.7°C), measured 3 to 4 days after ice disappearing, were lower than temperatures recorded in the Hornsund area by TDR loggers attached to birds in a different breeding season, when sea ice was not present in this area (average temperature of the water in which the birds dived was 4.2°C; Karnovsky et al. 2011). This indicates remarkable inter- and intra-annual variability of oceanographic conditions on the foraging grounds of little auks in the Hornsund area. Calculated theoretical maximum foraging distance from the colony based on mean flight times for Hornsund (129 km; Welcker et al. 2009) may suggest further foraging flights in years with high influx of warm Atlantic-type waters when food conditions are suboptimal in close foraging areas. Indeed, the 8 yr study (2001–2008) in the Hornsund area confirmed that oceanographic conditions (water temperature and salinity, ice conditions), zooplankton composition and abundance as well as chick diet composition and energy content varied significantly and in an alternating pattern within a range above the threshold that could pose a threat to offspring provisions (Kwasniewski et al. 2012).

Our study provides data of momentary and mean travel speeds of little auks. According to the present results, assumed flight speed of little auks (72 km h^{-1}) used to estimate foraging range based on visual observations and TDR data (Welcker et al. 2009), or to model the relationship between body mass and flight costs (Harding et al. 2009), is too high. Momentary speed measured directly in the field in Magdalenefjorden (60 km h^{-1}; L. Iliszko unpubl. data) and estimated for other alcids (60–70 km h^{-1}; Bradstreet & Brown 1985) are closer to results presented in this study.

Lower mean travel speeds in Hornsund may be explained by closer location of foraging areas and higher proportion of local flights within the foraging area. In contrast, birds from Magdalenefjorden performed >100 km flights over less attractive warmer waters, which may explain their higher mean travel speed. Birds from Hornsund traveled at higher mean speed during outgoing flights compared to return flights possibly because they flew quickly over the coastal ice belt to reach foraging ground in the marginal sea-ice zone.

Table 5. *Alle alle*. Mean ± SD hatching dates and chick growth parameters in the little auk colonies in Hornsund and Magdalenefjorden (parentheses: number of chicks). Data from Hornsund from Jakubas & Wojczulanis-Jakubas (2013)

Parameter	Hornsund		Magdalenefjorden		Student *t*-test *t*	p
Hatching date	15 Jul ± 3.0 d	(69)	20 Jul ± 2.7 d	(34)	7.5	<0.0001
Peak body mass age [d]	19 ± 2.3	(67)	20 ± 2.3	(30)	2.2	0.03
Peak body mass [g]	130 ± 9.0	(67)	126 ± 11.4	(30)	–1.7	0.08
Fledging body mass [g]	118 ± 10.0	(65)	114 ± 11.1	(32)	–1.6	0.12
Body mass recession [g]	12 ± 6.7	(63)	13 ± 6.9	(28)	0.7	0.49
Fledging age [d]	24 ± 1.8	(69)	25 ± 1.7	(32)	4.1	<0.0001
Fledging date	08 Aug ± 3.2 d	(69)	14 Aug ± 2.8 d	(32)	8.7	<0.0001

In this study, we characterized the oceanographic and biological environments near the large colony of little auks in Hornsund. The results are concordant with data reported in earlier studies in the same regin (Karnovsky et al. 2003, 2010, Kwasniewski et al. 2010, 2012, Jakubas et al. 2011). Owing to co-occurrence of cold Arctic and warmer Atlantic sea currents, the Hornsund area offers little auks various zooplankton communities:

Arctic-type with large copepods, Atlantic-type with very abundant but small organisms, and a mixture in the transitional zone. The locations of the majority of foraging positions in the Hornsund area corresponded to Arctic-origin water masses and frontal zones. This pattern is consistent with results from at-sea surveys conducted in 2001 and 2005 (Karnovsky et al. 2003, 2010) and 2009 and 2010 (Stempniewicz et al. 2013) within the same area. Relationships between water mass characteristics and zooplankton size spectra are extremely important for little auks, for which there appears to be a prey size threshold (Weslawski et al. 1999, Kwasniewski et al. 2010). An eddy observed in the study area was characterized by the presence of large zooplankton and higher temperature. Some of the recorded foraging positions were located close to the eddy. Eddies can cause upwelling or downwelling of the water, and in consequence, upwelling of nutrients in the wider area (Joiris & Falck 2011). Thus, recorded positions of GPS-equipped individuals may have matched the area with large copepods. The importance of hydrological phenomena such as fronts, ice edges and eddies (enhancing productivity and concentration of plankton; Labat et al. 2009) to foraging seabirds including little auks has already been stressed (Lønne & Gabrielsen 1992, Hunt 1997, Ainley et al. 1998, 2005, Russell et al. 1999, Bost et al. 2009, Joiris & Falck 2011).

We have no simultaneous zooplankton data from the marginal sea-ice zone situated in NW Spitsbergen, where GPS-equipped little auks from Magdalenefjorden foraged. However, it is well-known that this area is rich in the sympagic amphipod *Apherusa glacialis* and Arctic copepod *Calanus glacialis* (Lønne & Gulliksen 1991, Lønne & Gabrielsen 1992, Błachowiak-Samołyk 2008). Studies from Magdalenefjorden from 2007 to 2008 revealed that 5 to 18% of collected food loads consisted almost exclusively of *A. glacialis* (Kwasniewski et al. 2010, Jakubas et al. 2011). This sympagic amphipod contributed substantially to total prey biomass in little auks shot in the marginal ice zone around Svalbard (Lønne & Gabrielsen 1992, Mehlum & Gabrielsen 1993). Low number of foraging positions of birds from Magdalenefjorden in the close shelf zone may have resulted from suboptimal feeding conditions due to the high proportion of Atlantic copepods in the zooplankton community (Kwasniewski et al. 2010, Jakubas et al. 2011). In such conditions, searching for the preferred food items, such as *C. glacialis*, among abundant but less favored *C. finmarchicus*, may require more time and energy-demanding foraging (Kwasniewski et al. 2010).

Since little auks adopt a bimodal foraging strategy, alternating long trips with several consecutive short trips (Steen et al. 2007, Welcker et al. 2009, Wojczulanis-Jakubas et al. 2010), one may expect that GPS tracking to reveal both types of trips. However, in our study, majority of flights represented long trips (considering distances and estimated duration). The possible explanation of the unimodal pattern observed in our study is the fact that little auks at the end of incubation and at the beginning of the chick-rearing period (brooding) probably do not have such high energy demands as during later stages of the chick-rearing period. As both partners share the incubation and chick brooding duties equally (Stempniewicz & Jezierski 1987, Wojczulanis-Jakubas et al. 2009) and only one of them is present in the colony, the unimodal pattern of trip length probably represents normal behaviour of little auks during those stages of the breeding period. Data from birds equipped with temperature loggers during late incubation in Magdalenefjorden in 2009 also indicate a unimodal pattern of foraging trips (D. Jakubas unpubl. data). Similar intra-seasonal variation in patterns of foraging trip length was found in the wandering albatross *Diomedea exulans* (Weimerskirch et al. 1993). This procellariform performs unimodal trips during incubation and brooding (early chick-rearing) periods and adopts a bimodal strategy when the chick is left alone in the nest. On the other hand, the unimodal pattern of trip length may have been caused by unnatural behavior of instrumented birds (in Magdalenefjorden resulting in lower chick survival and body mass recession compared to control birds) and/or low sample size. A study comparing performance of unburdened and logger-burdened little auks revealed that both groups of birds adopted a bimodal strategy, although burdened individuals performed shorter but more frequent long foraging trips (Kidawa et al. 2012). Thus, this bias, along with a relatively small sample size, might have affected the pattern of foraging trips observed in the present study. Further investigations into this subject are needed.

Our results show that inter-colony differences in distances covered by chick-rearing little auks did not affect breeding success. Chicks from both colonies gained similar body mass, but at different rates — peak body mass and fledging in Hornsund occurred one day earlier than in Magdalenefjorden. This confirms an earlier finding from the same colonies (Jakubas et al. 2011) that despite a greater parental effort of birds from Magdalenefjorden (direct observations showed longer foraging trips), body mass of chicks was similar in both colonies. However, a

slower chick growth rate in seasons with suboptimal food conditions has been documented in the zooplanktivorous Cassin's auklet *Ptychoramphus aleuticus* (Bertram et al. 2001, Hedd et al. 2002). Thus, the reaching of peak body mass and fledging at an older age in Magdalenefjorden may suggest lower quality and quantity of delivered food compared to Hornsund (reported earlier by Kwasniewski et al. 2010). However, considering the interval of nest controls during the chick-rearing period (2 d), a one day difference in peak body mass and fledging should be interpreted with caution.

The results of our study emphasize the importance of highly productive areas (marginal ice zone, Arctic-type water masses) as foraging areas for little auks. The stronger influx of Atlantic water in the Arctic Ocean (meaning lower abundance of *Calanus glacialis*), and the reduction in ice extent (meaning longer distance to sympagic amphipods and worsening conditions for *C. glacialis* reproduction and development) that are projected to occur with climate change may result in the shortage of preferred prey species in the foraging areas within a 'cost-effective' distance from the colony (IPCC 2007, Hop et al. 2006, Piechura & Walczowski 2009, Kwasniewski et al. 2012). Thus, little auks may be forced to fly longer distances to reach colder feeding areas where their preferred prey is still abundant, causing increased energetic demands with serious negative consequences for daily time budget of adults, their colony attendance, body condition, future survival and breeding success (e.g. Hamer et al. 1993, Golet & Irons 1999). The southernmost little auk populations in Iceland and south Greenland have already collapsed following the 19th century shift in sea currents and plankton dispersal (Stempniewicz 2001).

On the other hand, recent studies revealed that little auks breeding on Spitsbergen are able to respond to a wide range of environmental conditions and prey availabilities, via plasticity of their foraging behaviour, allowing them to maintain their fitness levels (Jakubas et al. 2011, Grémillet et al. 2012). Moreover, spatial and seasonal variability in little auk diets (Fort et al. 2010) may allow them to adapt to expected climate changes by feeding on novel zooplankton species, which may extend their distributions to the North Atlantic as a result of global warming (Fort et al. 2010).

Detailed knowledge of foraging ecology of pelagic seabirds is still scarce, as their foraging activity is difficult to observe. Only recently, usage of modern technologies such as GPS tracking, satellite remote sensing, automatic high-resolution platforms equipped with advanced sensors, and moored stations, enables fast mapping of zooplankton abundance and community size-structure simultaneously with hydrological conditions in the investigated foraging areas. Future applications of these powerful new technologies promise many valuable insights into the foraging strategies of pelagic seabirds, including small-sized species such as the little auk.

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Appendix 1. Assessment of the effects of GPS loggers

We assessed potential effects of GPS loggers on breeding little auks by (1) monitoring the chick survival in nests of instrumented individuals and (2) comparing breeding success and chick growth variables between nests of instrumented and non-instrumented parents.

Chick survival in nests of instrumented individuals. We monitored nests with GPS-equipped individuals 2 and 4 d after attachment. In total, we took off loggers from 3 birds in Hornsund and 3 in Magdalenefjorden. Of instrumented birds recaptured, 2 birds in Hornsund and 1 in Magdalenefjorden had lost their loggers. In all nests of those logger-free birds, we found live chicks during 2 consecutive visits after logger attachment. We were not able to observe 8 logger equipped individuals in Hornsund; during 2 consecutive visits we found live chicks in 7 nests and a dead chick in 1 nest. In Magdalenefjorden, we were not able to observe 19 logger-equipped individuals. However, during 2 consecutive visits after logger attachment, we found live chicks in 6 nests and dead chicks in 6 nests. We have no information about 3 birds which had inaccessible nests (very deep nest chambers).

Chick survival and growth of instrumented and non-instrumented parents. To assess the influence of devices on chick survival and growth we compared measured variables between nests with GPS equipped parents and control nests. In Hornsund, chick survival up to 20 d was similar in nests of instrumented (78%, n = 9) and control birds (96%, n = 89; Fisher's exact test, p = 0.09). In Magdalenefjorden, however, chick survival up to 20 d in nests of instrumented birds was significantly lower (50%, n = 14) than in control birds (85%, n = 41; Fisher's exact test, p = 0.01). In Hornsund, chick body mass variables were similar in nests of instrumented (n = 7) and control (n = 81) parents (Mann-Whitney *U*-test, Hornsund: peak body mass, p = 0.17; fledging mass, p = 0.68, body mass recession, p = 0.37). In Magdalenefjorden, fledging mass was similar in both types of nests (Mann-Whitney *U*-test, p = 0.64). However, all chicks in nests of burdened parents (n = 5) gained peak body mass only at fledging. Thus, their body mass recession (median = 0 g) was significantly lower than in control birds (median = 13 g, n = 28) (Mann-Whitney *U*-test, $U = 5.08$, p = 0.001).

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