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ORIGINAL ARTICLE

Parental efforts of an Arctic seabird, the little auk *Alle alle*, under variable foraging conditions

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Abstract
Observed large-scale changes in climate and oceanography, which are especially pronounced in the Arctic, represent profound challenges for upper trophic predators. Knowledge about the extent to which marine predators are able to adjust to environmental variability is essential in order to assess the impact of changing oceanic conditions on the Arctic ecosystem. The main goal of this study was to investigate the impact of oceanographic conditions that varied on an inter-annual and inter-colony basis on the foraging and breeding strategy of a zooplanktivorous alcid, the little auk *Alle alle*. The study was conducted in two little auk breeding colonies in Spitsbergen (Hornsund and Magdalenefjord) located in different hydrographical regimes in two contrasting seasons (2009 and 2010). This article provides a comprehensive study linking a number of variables describing foraging ground quality, measured directly at sea, with the birds' foraging strategy, parental efforts, body condition and survival of nestlings. The analyses revealed that under conditions of high water temperature and a low proportion of the preferred food item, *Calanus glacialis*, in relation to less energetically profitable *Calanus finmarchicus* in the little auks' foraging grounds, birds increased the overall duration of their foraging trips and decreased the frequency of chick feeding. The resulting lower calorific value of food delivered daily to the chicks entailed reduced chick survival. We might expect that further ocean warming would impair the time and energy budget of parent birds and, in consequence, the breeding success of the little auks.

Key words: *Alcidae, breeding success, trip duration, oceanographic variability, zooplankton*

Introduction

During chick-rearing, seabirds that breed on land and forage at sea have to devote a considerable amount of their time and energy to forage for themselves and provide food for their chicks. Life-history theory predicts that parental effort is adjusted so that the costs and benefits of current reproduction are balanced to maximize lifetime reproductive success (Ricklefs 1977; Stearns 1992). Nonetheless, trade-offs may appear when food is limited (Stearns 1992). Under conditions of high temporal and spatial variability in marine food supplies (e.g. Richter 1994; Falk-Petersen et al. 2007; Loeng & Drinkwater 2007), selection should favour a flexible

breeding effort (Erikstad et al. 1998). Indeed, some seabird species are able to buffer food shortages by adjusting foraging behaviour and time allocation (e.g. Litzow & Piatt 2002; Smout et al. 2013). However, species with specialized feeding habits or energy-demanding food-search techniques have less flexibility and are more prone to breeding failures (e.g. Frederiksen et al. 2006; Piatt et al. 2007; Bond et al. 2011, 2012). In any case, foraging beyond a certain threshold of prey availability may have negative consequences for birds' reproductive success and population dynamics.

The little auk, *Alle alle* (Linnaeus, 1758), a zooplanktivorous Arctic seabird (Stempniewicz 2001),

exhibits one of the highest mass-specific daily energy expenditures among seabirds (Gabrielsen et al. 1991). Owing to its small wing area and subsequent high wing loading, both in the air (flapping flight) and in the water (wing-propelled diving; Stempniewicz 1982; Gabrielsen et al. 1991), foraging is energetically expensive. Also, the energy demands of the chick are much higher than those of other seabird chicks of similar body size (Konarzewski et al. 1993). High energy demands force little auks to focus on energy-rich calanoid copepods that are associated with cold Arctic waters, such as *Calanus glacialis* Jaschnov, 1955 (Falk-Petersen et al. 1990, 2009; Karnovsky et al. 2003, 2010; Wojczulanis et al. 2006; Jakubas et al. 2007, 2011). Studies in west Spitsbergen have shown that little auks fed their chicks mainly with large *C. glacialis* (copepodid stage CV), while smaller and less energetically profitable *Calanus finmarchicus* (Gunnerus, 1770) and younger life stages of *C. glacialis* were avoided, even if they were equally or more abundant in the foraging grounds (Karnovsky et al. 2003; Jakubas et al. 2007, 2011; Kwaśniewski et al. 2010, 2012; Vogedes et al. 2014).

The composition of zooplankton communities is closely linked to oceanographic conditions (i.e. the distribution of Atlantic and Arctic water masses), with species of different size and energetic value adapted to the characteristics of different water masses (Scott et al. 2000; Beaugrand et al. 2002; Falk-Petersen et al. 2007; Błachowiak-Samołyk et al. 2008). The proportion of *C. glacialis* CV in relation to other zooplankters may reflect the quality of foraging conditions for planktivorous seabirds (Kwaśniewski et al. 2010; Stempniewicz et al. 2013).

During the chick-rearing period little auk parents adopt a dual foraging strategy, alternating long trips with several consecutive short trips (Steen at al. 2007; Welcker et al. 2009a; Wojczulanis-Jakubas et al. 2010). Long foraging trips are primarily devoted to self-feeding, while the short ones are performed to maximize chick-feeding rates (Jakubas et al. 2012; Welcker et al. 2012). The flexibility of foraging trip duration and chick-feeding frequency may serve as an important mechanism enabling little auks to adjust their foraging strategy and breeding effort to fluctuations in food availability. Previous studies demonstrated that with increasing water mass temperature, the overall time spent foraging by little auks tended to increase (Jakubas et al. 2007, 2011; Welcker et al. 2009a; Kwaśniewski et al. 2010; Grémillet et al. 2012). For all these reasons, the little auk constitutes a particularly interesting species to test hypotheses about the relationship between environmental conditions, foraging behaviour and breeding success. However, a comprehensive study linking a number of variables characterizing foraging

ground quality, measured directly at sea, with the birds' foraging strategy, parental efforts, body condition and nestling survival is lacking.

We hypothesized that under poor foraging conditions, i.e. high water temperature and low proportion of the preferred *C. glacialis* to *C. finmarchicus* in the foraging grounds, little auk parents would prioritize their own energetic demands. We expect that they would change their foraging strategy by increasing the overall duration of foraging trips, decreasing the frequency of short foraging trips (in relation to long foraging trips), and consequently decreasing the frequency of chick feeding. Accordingly, the growth and survival of their chicks might be impaired, while the body mass of adult birds might remain unaffected. To verify these predictions, we investigated the response of little auks to the foraging conditions that varied on an inter-annual and inter-colony basis, which constituted a natural experiment for the presented hypothesis.

Methods

Study area

The study was carried out in an area with large breeding aggregations of little auks on Spitsbergen (Isaksen 1995), on the Magdalenefjord (Høystakken and Alkekongen mountain slopes; 79°35′N, 11°05′E) and Hornsund Fjord (Ariekammen mountain slope; 77°00′N, 15°33′E; Figure 1). The oceanographic data were collected on the west Spitsbergen shelf at stations
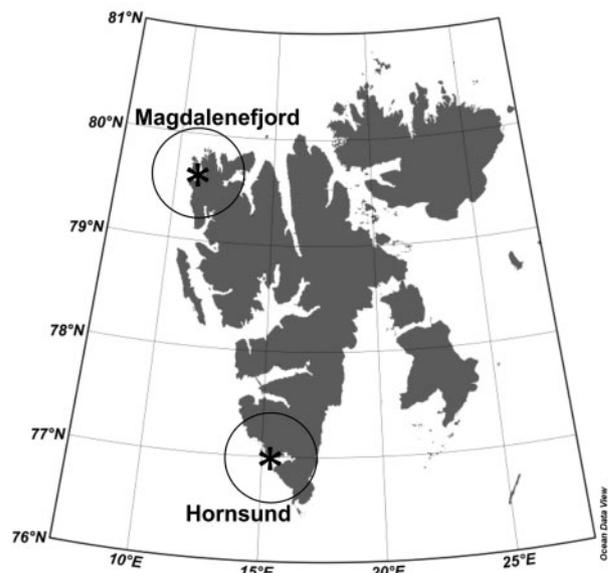

Figure 1. Study area with the locations of the little auk *Alle alle* colonies in Magdalenefjord (upper asterisk) and Hornsund (lower asterisk) within a 50 km radius from each site (black circles). The map was prepared using Ocean Data View software (Schlitzer 2011).

located within a 50 km radius from each colony (Figure 1). The sampling area corresponded well to the little auks' core foraging area at sea, determined from at-sea direct observations (Karnovsky et al. 2003, 2010; Stempniewicz et al. 2013) and the actual foraging position of GPS-equipped individuals (Jakubas et al. 2013). Data concerning the foraging grounds, food delivered to chicks, parental efforts and adult body mass were collected between 24 July and 4 August, in 2009 and 2010. The sampling period corresponded to the mid-chick-rearing period (chicks at age 10–18 days, determined by median hatching dates in each colony and season). To obtain the median date of hatching, chick body mass and survival, little auks' nests were monitored from late incubation and continuing to the fledging period (i.e. between 10 July and 10 August in 2009 and 2010).

The two study areas are characterized by different hydrographical regimes. The Hornsund area is influenced largely by the coastal Sørkapp Current carrying cold, less-saline Arctic-type waters from the northeast Barents Sea in addition to the West Spitsbergen Current, which transports warm saline Atlantic waters from the Norwegian Sea (Piechura et al. 2001; Cottier et al. 2005). In the Magdalenefjord area, the West Spitsbergen Current predominates on the shelf slope (Saloranta & Svendsen 2001). Additionally, a marginal sea ice zone is situated relatively close (about 100 km north) to the Magdalenefjord colony (Jakubas et al. 2012, 2013).

Fieldwork

Measurements and sampling at sea were carried out by the research vessel 'Oceania' (Institute of Oceanology, Polish Academy of Sciences). Temperature and salinity in the foraging grounds of the little auks were measured with a FastCat CTD (Sea-Bird Electronics) producing profiles of the upper 50 m of the water column and the averaged values for the layer were analysed. To sample zooplankton, a WP-2 net with a 0.25 m^2 opening fitted with 500 μm mesh was used. The net was hauled vertically from a depth of 50 m to the surface and the zooplankton sample was preserved in 4% formaldehyde–seawater solution, buffered with borax. Sampling was conducted at 10 and 11 stations in Hornsund (in 2009 and 2010, respectively) and at 15 stations in Magdalenefjord in each season.

To collect the chick diet samples, adult birds were randomly captured in the colony using a mist-net or noose-carpets. Only birds with the gular pouch full of food were considered. The content of the pouch was gently scooped out with a small plastic spoon. Each food load was put in a separate plastic box and preserved in 4% formaldehyde–seawater solution. In total, 30 food samples were collected from each colony and season.

In order to record the chick feeding frequency and the duration of foraging trips, 25 and 33 birds in Hornsund and 42 and 41 birds in Magdalenefjord in 2009 and 2010, respectively, were captured in their nests or in the colony using a mist-net or noose-carpets and marked (individual combinations of colour rings and colour dye on the birds' breasts). Two 24 hour continuous observations of all marked birds were performed in each colony and season (except for Hornsund in 2009, where only one observation was performed). The observed birds nested in close proximity, allowing two observers to follow all birds. The presence of the birds was monitored continuously and all departures and arrivals with/ without food of the marked individuals were recorded.

All adult birds caught in the colony (in total, 71 and 124 birds in Hornsund and 145 and 101 in Magdalenefjord in 2009 and 2010, respectively) were weighed using a PESOLA® balance (± 1.0 g) and measured (head–bill length) using callipers (± 0.1 mm). Small blood samples (20 μl) for DNA-based sex identification were collected from the brachial vein (following the procedure described in Owen 2011). Each sample was stored in 1 ml of 96% ethanol. Birds were released after about 10 min of careful handling without any harm.

To study chick survival, 81 and 137 little auk nests were monitored in Hornsund and 157 and 152 in Magdalenefjord in 2009 and 2010, respectively. Every 2–3 days, the nests were checked for nestling presence/absence. Additionally, 33 and 18 chicks in Hornsund and 17 and 19 chicks in Magdalenefjord in 2009 and 2010, respectively, were weighed every 3 days from the age of 14–15 days until fledging.

Laboratory work

All zooplankton samples collected at sea and chick diet samples were examined following the procedures described in Kwaśniewski et al. (2010). *Calanus* spp. were identified to species and developmental stage (copepodid) based on the description given in Kwaśniewski et al. (2003). Other zooplankton was identified to the lowest possible taxonomic level, and the body length of each individual was measured for the purpose of biomass calculations.

DNA for sexing was extracted from coagulated blood (after ethanol evaporation) using a Blood Mini Kit (A&A Biotechnology, Gdynia, Poland). CHD-gene based analyses were performed with the primer pair F2550 and R2718 according to Griffiths et al. (1998) using a 50°C annealing temperature for the polymerase chain reaction (PCR). The sex

differences in the PCR products were clearly visible under UV light when the fragments were separated on a 2% agarose gel and stained with ethidium bromide.

Data analysis

The analyses of zooplankton in foraging areas and diet samples were done with regard to dry biomass (Barrett et al. 2007), which was calculated using standard biomass estimates for individual prey items (Berestovskii et al. 1989; Richter 1994; Karnovsky et al. 2003). Data for the most numerous copepods (*Calanus glacialis* and *C. finmarchicus*) were presented separately for copepodid stage CV (hereafter CV) and younger copepodid developmental stages (hereafter CIII–IV) combined with adult females (hereafter AF). Data for the less numerous *Calanus hyperboreus* Krøyer, 1838 were presented for the copepodid stages CIV–V combined with adult females. Other zooplankton in the foraging grounds included taxa other than *Calanus* spp. (e.g. the amphipod *Themisto*, *Pagurus pubescens* Krøyer, 1838 larvae, Pisces larvae). Energetic values of food loads were calculated using published estimates of the different taxa according to Kosobokova (1980), Węsławski & Kwaśniewski (1990) and Węsławski et al. (1999a, 1999b).

Distance-based permutational multivariable analysis of variance (PERMANOVA; Anderson 2001) based on the Bray–Curtis similarity measure was applied to analyse: (1) little auks' foraging grounds (variables presented in Table I, excluding the proportion *C. glacialis* CV to *C. finmarchicus* CV) and (2) food loads delivered to chicks (variables presented in Table II), with colony and season as categorical predictors and the interaction between the two (colony × season). Each term in the analysis

was tested using 9999 random permutations of the appropriate units. PERMANOVA is largely unaffected by heterogeneity for balanced designs, while for unbalanced designs it is sensitive to heterogeneity (Anderson & Walsh 2013). Thus, in order to compare the foraging grounds (unbalanced design) variables were ln-transformed to remove heterogeneous variances. Analysis of food delivered to chicks (balanced design) was performed on untransformed data. Non-metric multidimensional scaling (nMDS) analysis based on the Bray–Curtis similarity measure (Taguchi & Oono 2005) was performed to visualize similarities in foraging ground variables (untransformed data; Figure 2) and food-load composition (not shown); the similarity percentage (SIMPER) procedure was used to calculate the average similarities between samples from the two colonies and seasons.

The overall duration of foraging trips (period between departure and arrival at the colony), daily chick-feeding rate per parent per 24 h, and mean daily calorific value of food delivered by a single parent bird (daily chick-feeding rate × mean calorific value of food) were compared between the colonies and seasons (categorical predictors, with interaction between them) using a two-way factorial ANOVA. A Tukey's test was used in *post-hoc* pairwise comparisons. The duration of foraging trips was ln-transformed in order to meet normality assumptions (Quinn & Keough 2002). Because the distributions of foraging trips did not meet the bimodality assumptions (Wyszomirski 1992), trips were not classified as either short or long following the cut-off value method (Welcker et al. 2009a). However, foraging trips lasting up to 120 min were considered 'short' (corresponding to the mean duration of short trips estimated by Welcker et al. (2009a) for four

Table I. Foraging grounds. Temperature, salinity and biomass of zooplankton species in the upper 50 m layer at sampling stations in little auks' *Alle alle* foraging grounds in Hornsund and Magdalenefjord during the mid-chick-rearing period in 2009 and 2010 (see text for details).

	Hornsund				Magdalenefjord			
	2009 (*n* = 10)		2010 (*n* = 11)		2009 (*n* = 15)		2010 (*n* =15)	
	Me	Q1–Q3	Me	Q1–Q3	Me	Q1–Q3	Me	Q1–Q3
Temperature (°C)	2.9	2.7–3.1	3.6	3.6–3.7	6.1	5.8–6.3	4.7	4.3–5.2
Salinity (PSU)	33.4	33.3–33.6	33.0	33.0–33.4	34.2	33.9–34.6	33.7	33.3–34.4
Calanus glacialis CV (mg/m^3)	21.1	9.8–27.9	24.8	16.5–39.7	23.2	7.9–38.0	25.8	8.3–36.4
C. glacialis CIII–IV, AF (mg/m^3)	34.5	21.7–54.6	92.5	38.6–120.0	11.2	4.3–17.0	19.0	6.6–33.8
C. finmarchicus CV (mg/m^3)	2.2	1.4–3.2	10.3	2.6–38.8	62.8	36.5–114.1	29.7	16.6–59.9
C. finmarchicus CIII–IV, AF (mg/m^3)	2.2	1.1–5.4	12.2	6.8–75.4	100.3	51.2–125.5	80.9	65.0–124.9
C. hyperboreus CIV–V, AF (mg/m^3)	0.0	0.0–0.0	0.3	0.3–1.1	0.1	0.0–1.0	1.3	0.8–4.0
Other zooplankton (mg/m^3)	2.4	1.1–3.9	13.5	10.6–44.7	2.4	1.5–3.5	4.2	3.6–5.7
Proportion *C.g.*CV to *C.fin.*CV	7.8	4.6–14.7	2.6	0.4–10.1	0.5	0.1–0.6	0.8	0.3–1.4

Me, median; Q1–Q3, quartiles 25–75%; CIII–IV, CV, copepodid stages of *Calanus* spp; AF, adult females of *Calanus* spp.

Table II. Food delivered to chicks. The zooplankton biomass in the little auk *Alle alle* food loads collected during the mid-chick-rearing period in Hornsund and Magdalenefjord in 2009 and 2010 (see text for details).

| | Hornsund | | | | Magdalenefjord | | | |
| | 2009 (*n* = 30) | | 2010 (*n* = 30) | | 2009 (*n* = 30) | | 2010 (*n* = 30) | |
	Me	Min.–max.	Me	Min.–max.	Me	Min.–max.	Me	Min.–max.
Calanus glacialis CV (mg/meal)	753.3	12.4–1494.2	902.1	186.0–1953.0	800.1	0.0–1249.9	1064.9	6.2–1748.4
C. glacialis CIII–IV, AF (mg/meal)	80.3	4.5–613.4	27.1	0.0–161.3	0.6	0.0–19.8	44.0	5.2–549.2
C. finmarchicus CV (mg/meal)	37.5	2.1–121.9	23.5	4.3–64.2	127.3	0.0–233.5	39.1	0.0–186.2
C. finmarchicus CIII–IV, AF (mg/meal)	5.8	0.0–21.4	2.3	0.0–14.1	1.4	0.0–22.6	5.6	0.0–52.2
C. hyperboreus CIV–V, AF (mg/meal)	0.0	0.0–6.6	0.0	0.0–11.4	14.5	0.0–1215.4	11.4	0.0–803.5
Apherusa glacialis (mg/meal)	0.0	0.0–16.0	0.0	0.0–0	0.0	0.0–684.6	0.0	0.0–1304.5
Themisto abyssorum (mg/meal)	2.1	0.0–234.4	0.4	0.0–6.6	1.0	0.0–62.8	37.9	0.0–222.9
T. libellula (mg/meal)	0.9	0.0–1091.1	4.0	0.0–58.7	0.0	0.0–30.1	0.0	0.0–99.5
Pagurus pubescens (mg/meal)	35.7	0.0–492.0	25.6	0.0–332.1	0.0	0.0–55.6	0.0	0.0–3.9
Pisces larvae (mg/meal)	0.0	0.0–41.9	0.0	0.0–26.5	0.0	0.0–10.6	0.0	0.0–86.6

Me, median; Min.–max., minimum and maximum values; CIII–IV, CV, copepodid stages of *Calanus* spp; AF, adult females of *Calanus* spp.

little auk colonies) and their frequencies were compared between the two colonies and seasons by the χ^2 test (with Bonferroni correction in the case of multiple pairwise comparisons). The Pearson correlation coefficient was used to test the relationship between ln-transformed duration of foraging trips and: (1) foraging ground variables (ln-transformed data), (2) chick-feeding rate performed by each bird.

The body mass of adults corrected for body size was compared using ANCOVA with the head–bill length as a covariate (García-Berthou 2001;

Moya-Laraño et al. 2008), three categorical predictors (colony, season and sex) and the interaction between them. The sex of adult birds was used as a predictor, because adult females were found to be lighter than males during a part of the breeding period (Wojczulanis-Jakubas et al. 2012). The head–bill length correlated with body mass (Pearson correlation coefficient, $r_{439} = 0.38$, $P < 0.001$). In chicks, the peak body mass and the chick age when peak body mass was achieved were compared between the colonies and breeding seasons (categorical predictors, with
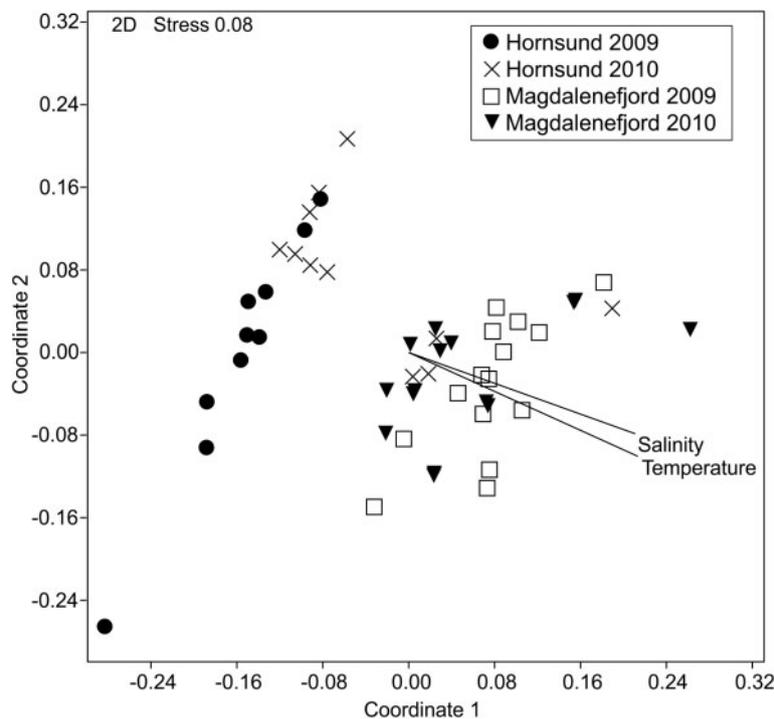

Figure 2. The nMDS plot based on the Bray–Curtis similarities in the biomass of zooplankton species with temperature and salinity in the upper 50 m layer at sampling stations in the little auks' *Alle alle* foraging grounds in Hornsund and Magdalenefjord during the mid-chick-rearing period in 2009 and 2010 (see text for details).

interaction between the two) using two-way factorial ANOVA. These variables are considered to be effective growth indicators (Zach 1988; Jakubas et al. 2013). Chick survival up to 20 days was examined (number of 20-day-old chicks/number of chicks hatched), because chicks that disappeared from the nest after 20 days were considered to have fledged (Harding et al. 2009; Welcker et al. 2009b; Wojczulanis-Jakubas & Jakubas 2012). Chick survival up to the 20th day was compared between the two colonies and seasons by the χ^2 test with Yates correction, and χ^2 tests with Bonferroni correction in pairwise comparisons. The statistical analyses were performed using PAST 3.0 software (Hammer et al. 2001; PERMANOVA, nMDS and SIMPER) and STATISTICA 10.0 (ANOVA, ANCOVA, Pearson correlation coefficient and χ^2 test). The critical alpha level was 0.05.

Results

Foraging grounds

The conditions in the foraging grounds differed significantly between the colonies and seasons in terms of all studied variables (hydrography and zooplankton biomass; Table I). Two-way PERMANOVA revealed that the foraging ground variables were significantly affected by colony ($F_{1,51}$ = 31.7, $P < 0.001$), season ($F_{1,51}$ = 7.8, $P < 0.001$), as well as the interaction, colony × season ($F_{1,51}$ = 7.9, $P < 0.001$). Even though the biomass of *Calanus glacialis*

CV was similar, the proportion of *C. glacialis* CV to *C. finmarchicus* CV varied between colonies and seasons (Table I). In both seasons studied, the water temperature was lower and the proportions of *C. glacialis* CV to *C. finmarchicus* CV were higher in the foraging ground in Hornsund compared to Magdalenefjord (Table I). However, temperature, salinity and the contribution of *C. finmarchicus* in Hornsund waters were higher in 2010 than in 2009, whereas in Magdalenefjord the opposite trend was observed, as all these variables were higher in 2009 than in 2010 (Table I). The nMDS ordination of biomass of zooplankton categories (with temperature and salinity as the environmental data) showed that the foraging ground in 2009 in Hornsund differed from the same site the following season and from both seasons in Magdalenefjord (Figure 2). The Bray–Curtis similarity index estimated for foraging ground variables revealed greater inter-annual similarity in Magdalenefjord (66%) than in Hornsund (54%; Figure 2). The average inter-colony similarity of foraging ground variables was lower in 2009 (38%) than in 2010 (51%; Bray–Curtis similarity index; Figure 2).

Food delivered to chicks

Two-way PERMANOVA revealed that food delivered to chicks differed significantly between colonies ($F_{1,120}$ = 11.2, $P < 0.001$) and seasons ($F_{1,120}$ = 4.8, P = 0.002), and the interaction colony × season was
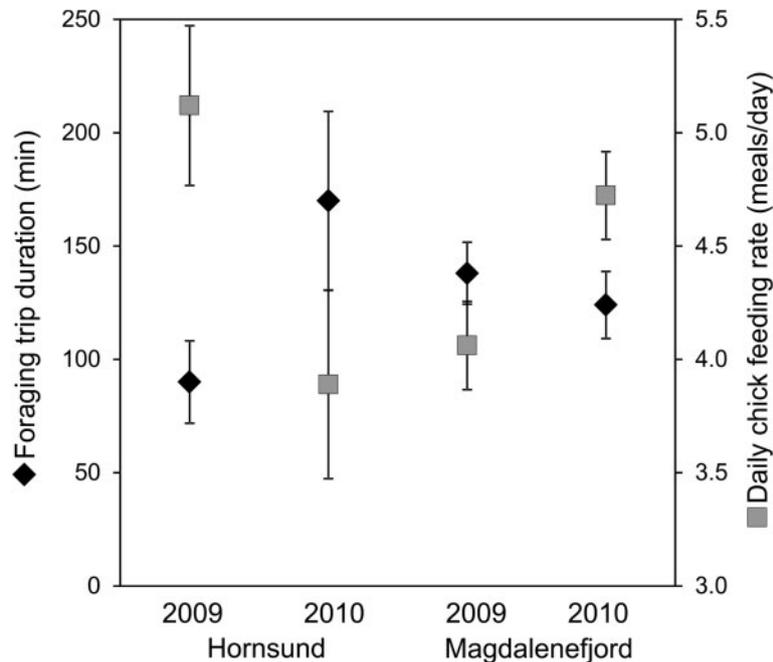

Figure 3. Foraging trip duration (means ± standard errors indicated by black diamonds; scale on the left *y*-axis) and daily chick feeding rate (means ± standard errors indicated by grey squares; scale on the right *y*-axis) of little auks *Alle alle* in Hornsund and Magdalenefjord in 2009 and 2010 (see text for details).

Table III. Relationship between duration of the little auk *Alle alle* foraging trips and variables describing the foraging grounds in the vicinity of the little auks' colonies (within a 50 km radius) in Hornsund and Magdalenefjord in 2009 and 2010 (Pearson correlation coefficient; significant correlations ($P < 0.05$) shown in bold).

Foraging ground variables	r	t	df	P
Water temperature (°C)	**0.51**	**3.81**	49	**< 0.001**
Salinity (PSU)	0.24	1.61	49	0.11
Calanus glacialis CV (mg/m^3)	0.08	0.49	49	0.63
C. glacialis CIII–IV, AF (mg/m^3)	0.10	0.73	49	0.47
C. finmarchicus CV (mg/m^3)	**0.54**	**4.14**	49	**< 0.001**
C. finmarchicus CIII–IV, AF (mg/m^3)	**0.48**	**3.87**	49	**< 0.001**
Other zooplankton (mg/m^3)	**0.52**	**4.29**	49	**< 0.001**
Proportion *C.g.*CV: *C.fin.*CV	**−0.42**	**−2.96**	49	**0.005**

CIII–IV, CV, copepodid stages of *Calanus* spp; AF, adult females of *Calanus* spp.

also significant ($F_{1,120} = 2.8$, $P = 0.03$). In both colonies in both seasons, *Calanus glacialis* CV was the main component of food loads (Table II). The biomass of *C. finmarchicus* CV was the highest in Magdalenefjord in 2009. Some taxa were specific to season or colony, such as *Pagurus pubescens* larvae, which constituted a considerable biomass of food loads in Hornsund, *C. hyperboreus* and *Apherusa glacialis* (Hansen, 1888), which were delivered to chicks mainly in Magdalenefjord and *Themisto abyssorum* Boeck, 1870, which occurred largely in Magdalenefjord in 2010. *Themisto libellula* (Lichtenstein in Mandt, 1822) was present in each colony and season, but its contribution was low (Table II). The Bray–Curtis similarity index revealed that the

average inter-annual similarity of food loads in Hornsund was 66%, while in Magdalenefjord it was 55%. The average inter-colony similarity of food loads in 2009 was 52%, while in 2010 it was 65%. The mean total energy content of food loads differed between seasons (ANOVA, $F_{1,120} = 9.17$, $P = 0.003$), but not between colonies (ANOVA, $F_{1,120} = 0.66$, $P = 0.42$); also, the effect of the interaction (colony × season) was insignificant (ANOVA, $F_{1,120} = 3.7$, $P = 0.06$; mean ± SD values in Hornsund in 2009: 31.0 ± 8.5 kJ and 2010: 33.0 ± 12.7 kJ; in Magdalenefjord in 2009: 28.7 ± 10.8 kJ and 2010: 37.9 ± 10.4 kJ).

Parental efforts

The overall duration of foraging trips performed by little auks was significantly affected by the interaction colony × season (ANOVA, $F_{1,825} = 23.4$, $P < 0.001$; Figure 3) and season (ANOVA, $F_{1,825} = 15.1$, $P < 0.001$), but the single effect of colony was insignificant (ANOVA, $F_{1,825} = 2.2$, $P = 0.14$). Trips performed by birds in Hornsund in 2009 were significantly shorter compared to the following season and to both seasons in Magdalenefjord (*post-hoc* Tukey's tests, $P < 0.001$; Figure 3). The overall trip duration positively correlated with water temperature and the biomass of smaller and less energetically profitable *Calanus finmarchicus* (copepodid stages: CV and CIII–IV, AF) in the foraging grounds. On the other hand, the overall trip duration decreased with the increasing proportion of the preferred food item, *C. glacialis* CV to *C. finmarchicus* CV, in the foraging grounds (Table III). The frequency of short
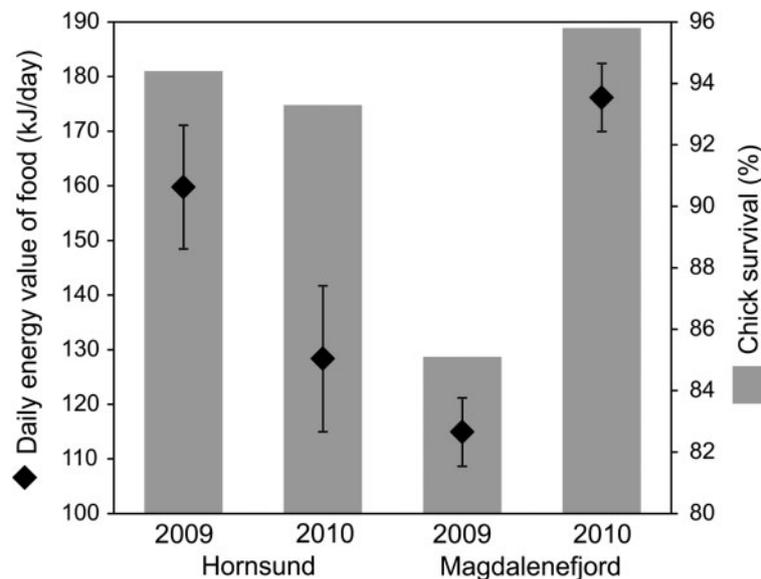

Figure 4. Daily energy values of food delivered by one parent bird to the chick (means ± standard errors indicated by black diamonds; scale on the left *y*-axis) and chick survival up to the 20th day (grey columns; scale on the right *y*-axis) of little auks *Alle alle* in Hornsund and Magdalenefjord in 2009 and 2010 (see text for details).

trips (lasting $\leq$ 120 min) differed between colonies and seasons (χ^2 test, $\chi^2 = 27.5$, df = 3, $P < 0.001$). In Hornsund, short trips were performed more frequently in 2009 (68% of all foraging trips) compared to 2010 (33%; χ^2 test with Bonferroni correction, $\chi^2 = 17.8$, df = 1, $P < 0.001$). In Magdalenefjord, the frequency of short trips was similar in the two seasons (i.e. 42% in 2009 and 48% in 2010; χ^2 test with Bonferroni correction, $\chi^2 = 2.9$, df = 1, $P = 0.09$). Considering the inter-colony differences, short trips were significantly more frequent in Hornsund compared to Magdalenefjord in 2009 (χ^2 test with Bonferroni correction, $\chi^2 = 21.8$, df = 1, $P < 0.001$), but in 2010 the inter-colony differences were insignificant (χ^2 test with Bonferroni correction, $\chi^2 = 3.9$, df = 1, $P = 0.05$).

The daily chick-feeding rate was significantly affected only by the interaction colony $\times$ season (ANOVA, $F_{1,208} = 9.6$, $P = 0.02$). The *post-hoc* pairwise comparison tests showed the daily chick-feeding rate in Hornsund in 2009 was significantly higher than in Magdalenefjord in 2009 (*post-hoc* Tukey's test, $P = 0.04$, Figure 3), while the other pairwise comparisons were insignificant (*post-hoc* Tukey's tests, $P > 0.05$). Single effects of colony or season as categorical predictors were not significant (ANOVA, $P > 0.05$; Figure 3). Similarly, the daily energy value of food delivered by one parent was significantly affected only by the interaction colony $\times$ season (ANOVA, $F_{1,208} = 22.3$, $P < 0.001$; Figure 4). The *post-hoc* pairwise comparison tests showed that the daily energy value of food in 2009 was significantly higher in Hornsund than in Magdalenefjord (*post-hoc* Tukey's test, $P < 0.001$), but in 2010 the situation was reversed (*post-hoc* Tukey's test, $P < 0.001$; Figure 4). Moreover, in Magdalenefjord the daily energy value of food was significantly higher in 2010 than in 2009 (*post-hoc* Tukey's test, $P < 0.001$; Figure 4). Other pairwise comparisons were insignificant (*post-hoc* Tukey's tests, $P > 0.05$). Furthermore, the mean trip duration calculated for each bird negatively correlated with its chick-feeding rate (Pearson correlation coefficient, $r = -0.62$, $t = -11.1$, df = 205, $P < 0.001$).

Adult body mass

The ANCOVA revealed that adult body mass was significantly affected by sex ($F_{1,431} = 6.8$, $P = 0.01$) and head–bill length ($F_{1,431} = 45.3$, $P < 0.001$). However, the effect of colony, season, and all of the interactions: colony $\times$ season, season $\times$ sex, colony $\times$ sex, and finally, colony $\times$ season $\times$ sex were insignificant ($F_{1,431} = 3.82$, $P = 0.05$; $F_{1,432} = 0.36$, $P = 0.55$; $F_{1,432} = 0.25$, $P = 0.61$; $F_{1,432} = 0.16$, $P = 0.69$; $F_{1,432} = 0.05$, $P = 0.82$; $F_{1,432} = 0.49$,

$P = 0.48$, respectively). The adult body mass corrected for body size was similar in little auks in both colonies and seasons (mean $\pm$ SE values in Hornsund in 2009: 162.3 $\pm$ 1.2 g ($n = 71$) and 2010: 162.4 $\pm$ 0.9 g ($n = 124$); in Magdalenefjord in 2009: 163.8 $\pm$ 0.8 g ($n = 145$) and 2010: 164.9 $\pm$ 0.9 g ($n = 101$)).

Chick body mass and survival

The peak body mass was similar in chicks in both colonies (ANOVA, $F_{1,86} = 3.3$, $P = 0.07$) and seasons (ANOVA, $F_{1,86} = 1.7$, $P = 0.20$); also, the interaction colony $\times$ season was insignificant (ANOVA, $F_{3,86} = 1.0$, $P = 0.33$). The chick age when peak body mass was achieved differed between colonies (ANOVA, $F_{1,86} = 6.9$, $P = 0.01$), but the effects of season and the interaction colony $\times$ season were insignificant (ANOVA, $F_{1,86} = 0.1$, $P = 0.77$ and $F_{3,86} = 2.3$, $P = 0.14$, respectively). Chicks achieved their peak body mass earlier (in terms of age) in Hornsund compared to Magdalenefjord (mean $\pm$ SD values in Hornsund in 2009: 19.0 $\pm$ 2.0 day ($n = 33$) and 2010: 18.0 $\pm$ 2.0 day ($n = 18$); in Magdalenefjord in 2009: 20.0 $\pm$ 3.0 day ($n = 17$) and 2010: 20.0 $\pm$ 2.0 day ($n = 19$)).

The highest chick survival was recorded in Hornsund in 2009 and in Magdalenefjord in 2010, while the lowest was observed in Magdalenefjord in 2009 (Figure 4). The overall differences between the two colonies and two seasons were significant (χ^2 test with Yates correction, $\chi^2 = 8.7$, df = 3, $P = 0.03$; Figure 4). However, in pairwise comparisons significant differences occurred only between the lowest (in Magdalenefjord in 2009) and highest chick survival (in Magdalenefjord in 2010; χ^2 test with Bonferroni correction, $\chi^2 = 6.0$, df = 1, $P = 0.01$; Figure 4).

Discussion

The present study, conducted in two contrasting seasons in two colonies located in different hydrographical regimes, demonstrated the flexibility of the little auks' foraging strategy and parental effort in response to the variable foraging ground quality, considering water temperature, salinity and zooplankton structure. In general, the little auks' foraging grounds in the vicinity of the Hornsund colony had more Arctic characteristics and, consequently, a higher contribution of the preferred food item, *Calanus glacialis*, in relation to the less energetically profitable *Calanus finmarchicus*, compared to the foraging grounds in the vicinity of the Magdalenefjord colony (Table I; Kwaśniewski et al. 2010; Jakubas et al. 2011). However, in Hornsund the

impact of Atlantic-origin waters was greater in 2010 than in 2009 (Table I; Walczowski et al. 2012), while in Magdalenefjord the situation in the study seasons was reversed, as the water temperature was higher in 2009 than in 2010 (Table I; Trudnowska et al. 2012). In both study areas, in the season with the stronger impact of Atlantic waters (i.e. Hornsund in 2010 and Magdalenefjord in 2009) the little auks adopted a similar strategy – they increased the overall duration of their foraging trips and decreased the frequency of short trips. This resulted in a lower frequency of chick feeding, lower daily energy value of food delivered to the chick, and finally, reduced chick survival. The peak body mass of chicks (studied on a smaller number of chicks than the survival rate) was similar in both seasons and colonies. A substantial decrease in chick body mass was observed in chicks with one of the parent birds artificially burdened (with clipped feathers or attached logger; Harding et al. 2009; Kidawa et al. 2012) when the feeding frequency was considerably reduced (two feedings per parent daily; Kidawa et al. 2012). Under those experimental conditions, the little auk parents were certainly much more burdened compared to the individuals experiencing the natural decrease in foraging ground quality observed here. Nonetheless, chicks achieved their peak body mass at an older age in the Magdalenefjord colony, where the foraging conditions were generally less favourable compared to Hornsund in both study seasons. Slower chick growth rates in seasons with suboptimal food conditions were also documented in the zooplanktivorous Cassin's auklet *Ptychoramphus aleuticus* (Pallas, 1811) (Hedd et al. 2002).

The lengthening of foraging trip duration under poor foraging conditions may suggest that little auks spent more time foraging under suboptimal food conditions or, alternatively, it may suggest the birds reached remote foraging locations where they could find better food sources. The first explanation may refer to inter-annual changes within one colony. Searching for preferred food items, such as *C. glacialis*, among very abundant but less-favoured *C. finmarchicus* requires more time and energy from little auks (Kwaśniewski et al. 2010, Stempniewicz et al. 2013). A study by Karnovsky et al. (2011) showed that birds foraging in low-quality waters spent more time underwater and made more 'searching' dives before flying to a different spot. Moreover, birds in poor local foraging conditions increased their diving effort, as indicated by longer dives with slower ascent rates and shorter resting times (Brown et al. 2012). The second explanation, concerning different distances to the foraging grounds, probably refers to the inter-colony variation in foraging trip duration. Data obtained by little auks tracked with GPS loggers

confirm much more distant foraging locations during the long-lasting trips of little auks breeding in Magdalenefjord compared to Hornsund (Jakubas et al. 2012, 2013).

This study demonstrates that little auks adjust their parental efforts in response to variable foraging ground quality. Welcker et al. (2012) suggested that undertaking less-frequent short foraging trips (in relation to long trips) under less-favourable foraging conditions suggests a focus on the self-maintenance of adult birds. Given their high nutritional demands, under conditions of limited resource availability parent little auks decrease their energy expenditures (indicated by the doubly labelled water method; Welcker et al. 2009b). The inter-annual and inter-colony variations in the foraging strategy of parent little auks observed in this study, without accompanying changes in their body mass, seems to support the hypothesis that under conditions of poorer quality and/or availability of food, parent little auks safeguard their own energetic demands, probably in order to maximize their lifetime reproductive success.

Furthermore, it seems that colony-specific features (e.g. the presence/absence of remote but still available high-quality foraging grounds that can be utilized by birds when conditions deteriorate) may determine the birds' foraging strategy and their ability to modify it. Therefore, the inter-annual comparison made in two contrasting seasons within one colony could deliver much more valuable information about the impact of oceanographic conditions on the little auks' parental efforts than a single inter-colony comparison. This spatio-temporal comparison gives a comprehensive view of the little auk's foraging and breeding strategy and may provide a better understanding of the responses of polar marine organisms to progressive ocean warming.

Seabirds are relatively well adapted to coping with a highly variable environment. High adult survival and the capacity to spread their breeding attempts over a long lifetime are probably a part of the adaptive strategy of long-lived species, which allows them to overcome periods of low breeding success (e.g. Chastel et al. 1993). Little auks display a range of behavioural plasticity that allows them to maintain a relatively high breeding success in face of oceanographic variability. Nonetheless, low-quality environmental conditions experienced during the developmental stage may have long-lasting consequences for chick survival and future reproductive outcome. Even if little auks are currently able to buffer the consequences of climate change in the North Atlantic, such abilities could not extend indefinitely (Grémillet et al. 2012).

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