



Foraging effort does not influence body condition and stress level in little auks

Dariusz Jakubas^{1,*}, Marta Głuchowska², Katarzyna Wojczulanis-Jakubas¹,
Nina J. Karnovsky³, Liliana Keslinka¹, Dorota Kidawa¹, Wojciech Walkusz^{2,4},
Rafał Boehnke², Małgorzata Cisek², Sławomir Kwaśniewski², Lech Stempniewicz¹

¹University of Gdańsk, Department of Vertebrate Ecology and Zoology, Legionów 9, 80-441 Gdańsk, Poland

²Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland

³Pomona College, Department of Biology, 175 W. 6th St., Claremont, California 91711, USA

⁴Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

ABSTRACT: In conditions of deteriorating food availability, seabirds may maximize their breeding success by increasing reproductive effort, which compromises body condition, stress level, survival, and future reproductive success. We studied a small planktivorous alcid, the little auk *Alle alle*, in 2 breeding colonies in west Spitsbergen, Norway (Hornsund and Magdalenefjorden) with contrasting oceanographic conditions (Arctic and Atlantic environments, respectively). We hypothesized that the chick diet composition and parental foraging effort differs between these colonies, which results in intercolony variation in body mass and stress level of both adults and chicks. We found differences in sea temperature and salinity (both lower in Hornsund) and the abundance of Atlantic copepod *Calanus finmarchicus* (3.6 times less abundant in Hornsund) between foraging areas. Birds from both colonies foraged selectively on *Calanus glacialis* CV. Composition, total biomass and energy content of food loads were similar in both colonies, though food delivered to nestlings in Magdalenefjorden was more diverse. The frequency of feeds was also similar in both colonies. Parent little auks in Magdalenefjorden, however, performed longer foraging trips than in Hornsund (medians 183 vs. 124 min). Longer foraging trips suggest that these birds traveled longer distances to find abundant prey at the marginal sea ice zone and/or spent more time foraging close to the colony but in poorer foraging areas. Despite increased parental efforts in Magdalenefjorden, body mass and stress levels of adults and chicks were similar in both colonies. This suggests that little auks from northwest Spitsbergen did not reach a threshold requiring prioritization of self-maintenance over chick provisioning.

KEY WORDS: Little auk · Diet composition · Parental efforts · Body mass · Stress level

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INTRODUCTION

Seabirds are top consumers in marine food webs, and studying them offers opportunities to detect and assess the biological effects of variability and changes in physical parameters of the marine ecosystem (Syde- man et al. 2001, Diamond & Devlin 2003). In conditions of deteriorating food availability, seabirds may maximize reproductive success by increasing breeding efforts and investing as much as possible in their off-

spring. Alternatively, individuals may have a fixed level of parental investment in a given reproductive period and may not invest above a given threshold that will negatively affect self-maintenance (Stearns 1992, Sæther et al. 1993, Navarro & González-Solís 2007). Provisioning behavior is generally considered to be a good measure of the breeding efforts of parents. In cases where the time and energy budgets of breeding adults are flexible, i.e. adjusted according to offspring energy demands and environmental conditions of the

*Email: biodj@univ.gda.pl

breeding season, parents can increase the rate of chick provisioning by lengthening foraging flights to reach more distant food resources or spending more time foraging at suboptimal feeding grounds (e.g. Hamer et al. 1993, Montevecchi 1993, Kitaysky 2001a, Weimerskirch et al. 2001, Litzow & Piatt 2003). Each of these strategies could be costly in time and energy and may compromise adult survival and future reproductive success (Stearns 1992, Roff 1992, Golet et al. 2004). Lower body masses observed in parent birds foraging in poor food conditions are often attributed to a loss of endogenous reserves associated with increased reproductive demands (Ricklefs 1983, Nur 1984, Golet & Irons 1999, Williams et al. 2007). Thus, body reserves can provide information on local food supplies and, accordingly, have been suggested as an indicator of marine resources (Cairns 1987, 1992, Montevecchi 1993). Some studies (Gaston & Jones 1989, Moreno 1989, Gaston & Perin 1993, Harding et al. 2009a), however, suggest that a lower body mass during chick-rearing is not a consequence of stress, but may result from programmed intrinsic processes of adaptive adjustment for reduced flight costs and increased foraging efficiency. Moreover, body mass is affected by a variety of components of individual state, which complicates the interpretation of changes (Ots et al. 1998). One possible way to interpret changes in body mass and determine whether foraging conditions exert an effect on individuals is to make a second, independent measure of body condition. Acute and chronic stressors, such as starvation, lead to an elevation of corticosterone level (Kitaysky et al. 2007, Davis et al. 2008). This corticosteroid is also secreted after depletion of fat reserves and stimulates metabolism based on amino acid mobilized mostly from muscle protein (Veiga et al. 1978, Cherel et al. 1988). Corticosterone level can provide information on the stress status of individuals in relation to the abundance of their food (Kitaysky et al. 2007). The ratio of the heterophils and lymphocytes (H:L ratio) is known to increase as a response to various stressors including food deprivation and can be directly related to corticosterone levels (Ots & Hórák 1996, Ruiz et al. 2002, Davis et al. 2008). This response is detectable within hours following an exposure to a stressor (Ots & Hórák 1996, Ruiz et al. 2002, Davis et al. 2008). Thus, the H:L ratio is not affected by stress associated with animal handling and blood sampling and is generally more reliable than corticosterone level as an indicator of avian stress (Davis et al. 2008). Strong inter-annual variation has been demonstrated in the H:L ratio, with higher values during seasons with adverse food conditions (Plischke et al. 2010).

The effects of maladjustment of parental provisioning to the offspring energy demands are well documented. Chicks exposed to deteriorating food condi-

tions exhibit lower body mass (e.g. Litzow et al. 2002, Suryan et al. 2002, Gaston & Hipfner 2006), elevated corticosterone level (e.g. Golet et al. 2000, Kitaysky et al. 2001b, Kitaysky et al. 2003) and a subsequent increase in H:L ratio (e.g. Hoi-Leitner et al. 2001, Suorsa et al. 2004, Lobato et al. 2005).

The little auk *Alle alle* is a small, zooplanktivorous seabird that breeds colonially in the high Arctic and is considered the most abundant alcid in the Palaearctic (Stempniewicz 2001). Little auks are socially monogamous with long-term pair bonds. They lay a single egg annually which is incubated by both sexes. Nests are mainly situated under boulders in mountain scree. Both partners brood (for the few first days) and feed the chick for 25 to 27 d (Stempniewicz 2001, Harding et al. 2004). Due to the high cost of locomotion in little auks, both in the air (flapping flight) and in the water (underwater 'flight' during diving), foraging is believed to be energetically expensive (Gabrielsen et al. 1991, Konarzewski et al. 1993, Stempniewicz 2001). To cover their extremely high energetic demands (Gabrielsen et al. 1991, Konarzewski et al. 1993), little auks focus mainly on energy-rich planktonic organisms associated with cold Arctic waters—mostly the large copepods *Calanus glacialis* and/or *C. hyperboreus*. They also take the smaller and energetically less profitable counterpart, *C. finmarchicus*, which is associated with Atlantic waters but in smaller amounts than the former 2 species (Mehlum & Gabrielsen 1993, Weslawski et al. 1999, Planque & Batten 2000, Pedersen & Falk 2001, Karnovsky et al. 2003, Wojczulanis et al. 2006). Hence, we expected little auks to be sensitive to changes in the availability of their preferred prey items induced by the distribution of Arctic and Atlantic waters. A recently observed increase in the influx of warm Atlantic waters (Schauer et al. 2004, Piechura & Walczowski 2009) that bring boreal zooplankton species closer to breeding colonies affected breeding little auks on NW Spitsbergen negatively through increasing parental efforts (Kwasniewski et al. 2010). The influence of increased parental investments on body condition or stress level, however, has not been assessed. It is essential to consider the physiological reaction of birds to their actual food conditions to understand the true costs of behavioral adaptation to environmental variability.

The aim of this study was to compare food availability, chick diet and provisioning, as well as the body mass and stress level of parents and chicks of little auks in 2 colonies with foraging areas that have contrasting oceanographic conditions—Arctic and Atlantic environments. We hypothesized that: (1) chick diet quality and quantity differ between colonies, reflecting the oceanographic conditions in the foraging areas; (2) parental efforts (chick feeding rate and for-

aging trip duration) of little auks are higher in Atlantic than in Arctic-influenced environments; (3) different parental effort influences the body mass and stress level in adults and/or chicks.

MATERIALS AND METHODS

Study area. Data on chick diet, parental effort, adult and chick body condition and stress level were collected in 2 large little auk breeding colonies at Ariekammen slopes in Hornsund (SW Spitsbergen; 77° 00' N, 15° 33' E) and at Høystakken and Alkekongen slopes in Magdalenefjorden (NW Spitsbergen; 79° 35' N, 11° 05' E) (Fig. 1). These areas are the main breeding areas of little auks on Svalbard (Isaksen 1995). Zooplankton samples and hydrological data were collected on the shelf areas of Hornsund and Smeerenburgfjorden and inside both fjords (Fig. 1), i.e. in the areas that correspond with known foraging areas of little auks from Hornsund (Karnovsky et al. 2003, 2010) and Magdalenefjorden

(D. Jakubas pers. obs). These 2 areas represent different oceanographic conditions. The sea shelf in the vicinity of Hornsund is typically under the influence of 2 main currents — the coastal Sørkapp Current, which carries cold, less saline Arctic water, and the West Spitsbergen Current (an extension of the Norwegian Atlantic Current), which transports warmer, more saline Atlantic water (Piechura et al. 2001, Cottier et al. 2005). Smeerenburgfjorden is located at the northern end of the cold coastal current that flows along the west coast of Spitsbergen, but it is also strongly influenced by the Svalbard Branch of the West Spitsbergen Current (Saloranta & Svendsen 2001, Walczowski et al. 2005), which carries warm and saline Atlantic water to the north of the island.

Study period. This study was conducted in July to August 2008 (Table 1). Data were collected during the early (chick age of 1 to 7 d), mid (8 to 20 d) and late (>20 d) phases of the little auk chick-rearing period and reflect stages of chick development. During the early phase, chicks have minimal energy demands; they are brooded by their parents and stay inside the

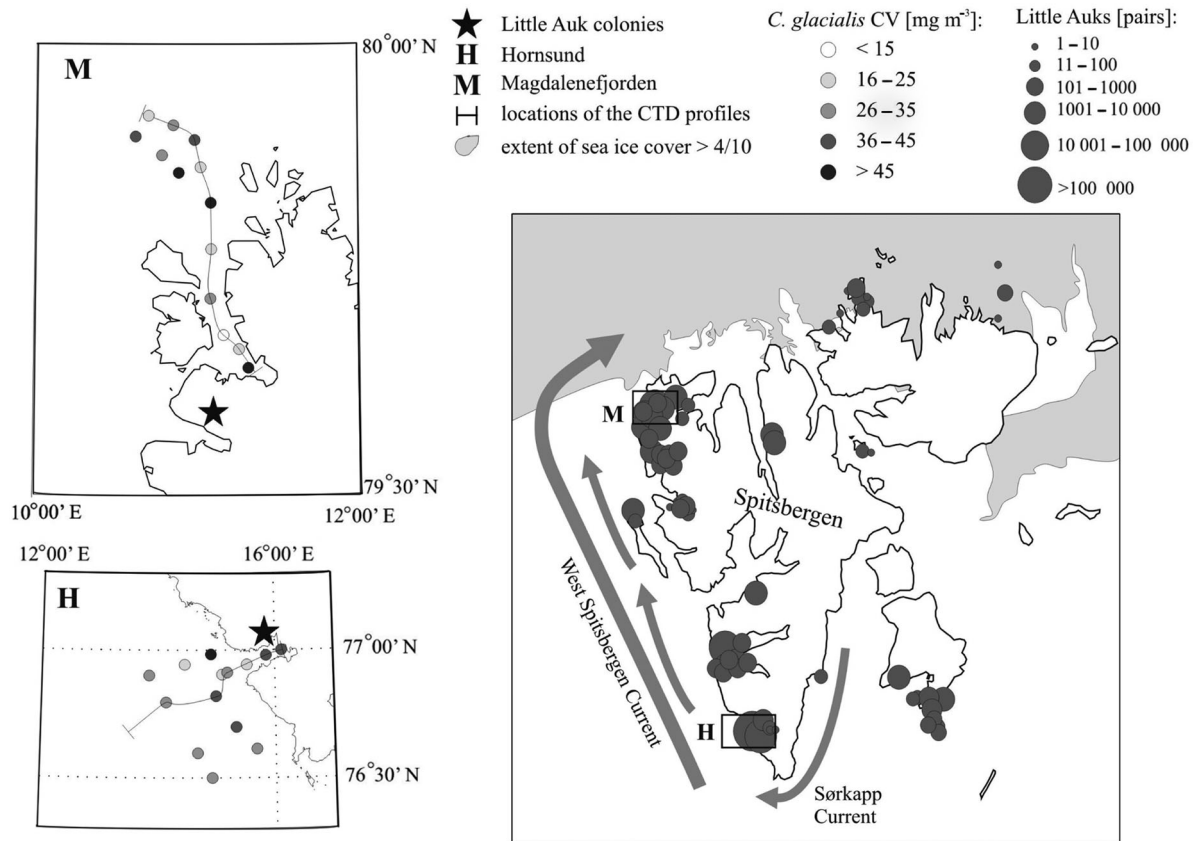


Fig. 1. (Right) Study area with ocean current patterns in the Spitsbergen region (arrows, modified after Loeng & Drinkwater 2007), sea ice extent (grey area, based on ice maps of Norwegian Meteorological Institute, www.met.no for 1 August 2008) and the locations and sizes of little auk *Alle alle* colonies (grey circles, modified after Isaksen & Gavrilov 2000). (Upper left) Close-up of the Magdalenefjorden-Smeerenburgfjorden area (M) with zooplankton sampling sites (circles; shading indicates *Calanus glacialis* CV biomass), the CTD profiles (lines) and little auk colony in Magdalenefjorden (star). (Lower left) Same data for the Hornsund area (H)

Table 1. Timing of data collection during field work carried out at the 2 study sites in Spitsbergen, 2008. Phase: phase of chick-rearing period

Type of data collected	Hornsund		Magdalenefjorden	
	Date	Phase	Date	Phase
Sea temperature and salinity, zooplankton composition	28–30 Jul	Mid	4–5 Aug	Mid/late
Chick diet	13–19 Jul	Early	24–27 Jul	Early
	31 Jul to 1 Aug	Mid	1–3 Aug	Mid
			9–12 Aug	Late
Adult body condition and stress level	31 Jul to 1 Aug	Mid	1–3 Aug	Mid
	11 Aug	Late	9–12 Aug	Late
Chick body condition and stress level	18–26 Jul	Early	22 Jul to 11 Aug	Early
	31 Jul to 8 Aug	Mid	28 Jul to 14 Aug	Mid
No. of feeds 48 h ⁻¹ and duration of foraging trips	4–6 Aug	Mid/late	3–5 Aug	Mid/late

nest. The mid phase comprises the period of maximal energy needs since chicks reach peak weight and intensively exercise their wings outside the nest chamber. During the late phase, prior to fledging, chicks lose body mass and female parents cease caring for chicks (Konarzewski et al. 1993, Stempniewicz 2001, Harding et al. 2004).

Hydrography. Hydrographic measurements were taken with a SBE 49 FastCAT probe (Sea-Bird Electronics) that recorded temperature, salinity, and pressure at zooplankton stations in the Hornsund and Smeerenburgfjorden areas (Fig. 1, Table 1). The data collected were averaged vertically every 0.5 m. Illustration of temperature and salinity distribution with depth was performed using selected stations located on transects (Fig. 2). Interregional comparisons of water parameters were conducted using stations localized only on the shelf. Depth distributions of temperature and salinity across the shelf were plotted with Surfer 8 (Golden Software).

Zooplankton collection. Zooplankton samples were collected in little auks foraging areas during the chick-rearing period (Table 1): 14 samples adjacent to and inside Hornsund fjord and 13 samples on the shelf off and in Smeerenburgfjorden (Fig. 1). Sampling was carried out from the IO PAS research vessel *Oceania* using a WP-2 type net with 0.25 m² opening area (Tranter & Fraser 1968) and fitted with filtering gauze of 500 µm mesh size. The net was towed vertically from the depth of 50 m to the surface and the collected zooplankton was preserved in 4% formaldehyde solution in seawater, buffered with borax.

Chick diet samples collection. Samples of the diet were taken from adult little auks transporting food to their chicks. The birds were captured randomly in the colony with mist-nets or noose-carpets. Food content was gently scooped out of the little auk's gular pouch with a small spoon. At the same time body condition of

the birds was examined (see 'Body condition and stress level' below) and they were released after 5 to 10 min of handling. Each food load was put in a separate plastic container and preserved in 4% formaldehyde solution. In total, 55 diet samples were collected in Hornsund and 69 were collected in Magdalenefjorden. Collection of chick meals was performed during early, mid (both colonies) and late (Magdalenefjorden) phases of chick-rearing (Table 1).

Parental effort (chick feeding rate and foraging trip duration). Feeding frequency and foraging trip duration of parent little auks were calculated based on 48 h non-stop observations performed in each colony on individually marked little auk parents (39 in Hornsund and 46 in Magdalenefjorden) when the chicks were 18 to 22 d old, at the end of the mid and the beginning of the late phase of chick-rearing (Table 1). Breeding birds were caught in nest crevices or on noose-carpets during early chick-rearing and marked with unique colour marks on breast feathers and a combination of colour rings. In addition, nest entrances of the monitored birds were labeled. The time of nest exit and departure from the colony, time of arrival at the colony, bird food status (with full gular pouch or not), and the time of nest entering were noted for each marked bird during the whole watch. Entering the nest with a full gular pouch and leaving it with an empty one was considered a chick feeding. The time between the last observation of the individual bird in the colony and its next appearance with a filled gular pouch was considered a foraging trip. The number of feeds and duration of foraging trips are presented as median values calculated per parent bird per 48 h.

Body condition and stress level. To assess body condition and stress level of adults and chicks, size-adjusted body mass and leukocyte proportion (H:L ratio) were applied. Adult breeders with full gular pouches caught in the colony for food sampling were ringed and

measured. Head-bill length (distance from the back of the head to the tip of the bill) was measured to the nearest 0.1 mm with dial callipers. All adults were weighed to the nearest 1.0 g using a 300 g PESOLA spring balance. A small blood sample (ca. 10 to 20 μ l collected from the brachial vein) was taken from each bird for calculation of leukocyte proportion. The blood sample was smeared on a microscopic slide immediately after collection and stored dry until staining. Adults were measured and blood sampled when the chicks were 17 to 19 and 26 to 28 d old (mid and late phases of chick-rearing period). The chick-rearing phase at adult capture was calculated based on the median hatching date for a group of nests inspected every 2 d (61 in Hornsund and 71 in Magdalenefjorden).

Chicks were weighed to the nearest 0.1 g using 300 g OHAUS electronic balance and blood was sampled. Leukocyte proportion was calculated in 2 age categories: 4 to 7 and 14 to 17 d old, which corresponded to early and mid phases of their development. The age of chicks was known because nests with weighed chicks were checked regularly (every 2 d) after hatching.

Laboratory analyses. All zooplankton samples collected at sea in the foraging areas or from adult little auks at the colonies were identified following the procedure described in Kwasniewski et al. (2010). Zooplankton from the genus *Calanus* were identified to species and developmental stage in accordance with Kwasniewski et al. (2003). Other zooplankton organisms were identified to the lowest possible taxonomic level, and their length was measured for the purpose of biomass calculations.

The blood smears were stained using the May-Grünwald-Giemsa method. The proportion of different types of leucocytes (lymphocytes, heterophils, monocytes, eosinophils and basophils) was assessed on the basis of an examination of 100 leucocytes under oil immersion (1000 \times magnification).

Data analyses. Water of temperatures $\geq 3.0^{\circ}\text{C}$ recorded in depth layers between 5 and 50 m was considered to be of Atlantic-type (Loeng 1991, Piechura et al. 2001, Cottier et al. 2005). To compare the compositions of food samples between the Hornsund and Magdalenefjorden colonies, multivariate methods (nMDS; Bray-Curtis similarity coefficients) were applied for standardized food load data (PRIMER v6 software; Clarke & Warwick 2001). Based on the predominant (>50%) composition of the food loads, 3 different groups of samples were distinguished: '*Calanus glacialis*', '*Calanus hyperboreus*' and '*Apherusa glacialis*'.

To compare the quantitative composition of food loads between breeding colonies we used food loads from the same phase of the chick-rearing period with similar sample sizes and only those for which we were certain as to their completeness, i.e. '*Calanus glacialis*'

type samples collected during the mid chick-rearing period (Hornsund $n = 17$, Magdalenefjorden $n = 18$). All food samples were used to present relative abundance of prey in the food delivered to chicks.

Data for the most numerous copepods (*Calanus glacialis* and *C. finmarchicus*) are presented separately for copepodid stage CV and other stages (including only copepodid stages III, IV and VI females [hereafter CIII-IV and AF] due to selectivity of the WP2/500 zooplankton net). Copepodid stage CV is the most numerous stage of *C. glacialis* in little auk food samples (Karnovsky et al. 2003, 2010, Kwasniewski et al. 2010). Copepodid stage CV of *C. finmarchicus* is the smallest 'edible' *Calanus* for little auks. Younger copepodid stages and adults of this species are rarely found in food samples (Karnovsky et al. 2003, 2010). Data for the less numerous *Calanus hyperboreus* are presented for all developmental stages combined.

Energetic value of food loads were calculated from abundance data by applying published individual estimates of energy content for individual zooplankton organisms (Kosobokova 1980, Percy & Fife 1981, Anger et al. 1983, Hay et al. 1991, Mumm 1991, Hansen 1997, Weslawski et al. 1999, Karnovsky et al. 2003, Wojczulanis et al. 2006).

To study little auk prey selectivity, a χ^2 -test-based selectivity V-index (Pearre 1982) was calculated using the total abundance for prey species or copepodid stage in food loads and in zooplankton samples from foraging areas. In the case of less abundant prey items (in all zooplankton samples), C-index was calculated (V-index with incorporated Yates' correction; Pearre 1982). The V-index is a useful measure of prey selection because it is zero-valued for no selection, is fairly robust as regards the effect of rare species in the community, and is statistically testable (Pearre 1982). Selectivity indices were calculated only for prey items present in zooplankton and food samples from both studied areas. The prey selectivity index was calculated only for food samples collected during the mid chick-rearing period as zooplankton sampling in the feeding grounds was also performed at that time. All food samples collected then represented '*Calanus glacialis*' type.

Due to the absence or very low numbers of monocytes, basophils and eosinophils in most of the blood smears, only percentages of heterophiles and lymphocytes and H:L ratios are presented in tables and considered in statistical analyses. Percentage of heterophiles and lymphocytes and H:L ratios were presented as median and quartile values since they were not normally distributed. We normalized the data using an arcsin square-root transformation (Zar 1999), prior to comparing those parameters between the colonies in adults and chicks by Student's *t*-test.

Total time spent by little auks on foraging trips per 48 h was calculated by multiplying the median number of feeds per parent by median foraging trip duration. Foraging trips of up to 2 h were considered 'short', and corresponded to mean duration of short trips reported for 4 little auks colonies (Welcker et al. 2009a).

Due to a high degree of head-bill length and body mass overlap between little auk males and females (Jakubas & Wojczulanis 2007) and small sample sizes for one sex category, the data for both sexes were pooled together. Also, due to a small number of known-sex chicks, the data for both sexes were also combined.

We adjusted body mass of adults to body size, using analysis of covariance (ANCOVA) with the head-bill length as a covariate (García-Berthou 2001). We chose this measure to represent the adult individual body size due to a significant correlation between this parameter and body mass at the mid (Pearson correlation coefficient, $r_{47} = 0.41$, $p = 0.003$) and late ($r_{35} = 0.41$, $p = 0.01$) phases of chick-rearing. The relationship of several other body-size parameters with body mass was not significant. The chicks were measured only in one colony. Thus, only chick raw body mass was compared between the colonies.

All 2×2 χ^2 tests when at least one cell of the table had an expected count < 10 were calculated with Yates' correction (Zar 1999). All statistical analyses were done in Statistica 8.0.

RESULTS

Oceanographic conditions on the foraging grounds

In July to August 2008, mean sea temperature and salinity values recorded at the shelf stations (both in depth layers 5–10, 11–20, 21–30, 31–40, 41–50 m and averaged over 5–50 m depths) were significantly lower near Hornsund than near Smeerenburgfjorden (Student's t -test, $p < 0.001$), except for depth layer 40 to 50 m, where the salinity in both areas was similar (Student's t -test, $t_{165} = 1.27$, $p = 0.21$). In the Hornsund area, the Atlantic-type water occurred over the shelf slope and westward, while the shelf itself was occupied by cooler and fresher waters, most likely associated with the flow of the Sørkapp Current (Fig. 2). In Smeerenburgfjorden area, Atlantic-type waters were present over the whole fjord and shelf area at all stations, and, in particular, the studied depth layers (Fig. 2).

Zooplankton structure on the foraging grounds

Calanus sp. made up 92% of the total net zooplankton abundance in both regions. In Hornsund, *C. glacialis* was the most abundant zooplankton (9% stage CV and 56% stages CIII-CIV and AF of total zooplankton abundance), while *C. finmarchicus* was repre-

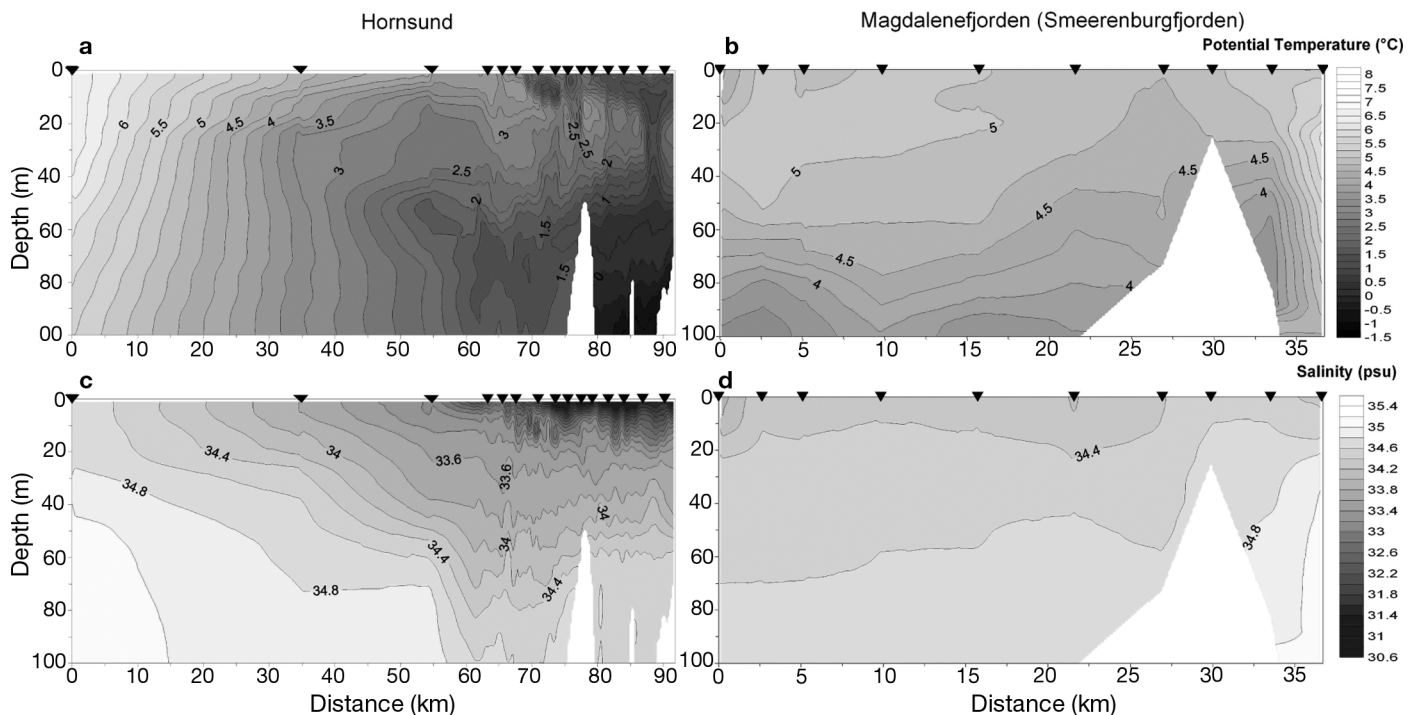


Fig. 2. Temperature and salinity distributions in July 2008 in the foraging ground of little auks *Alle alle* breeding in (a,b) Hornsund and (c,d) Magdalenefjorden (Smeerenburgfjorden). Black triangles show locations of the CTD measurements. Distance was measured from the most distant station westward from the shelf to the innermost station situated in the fjord

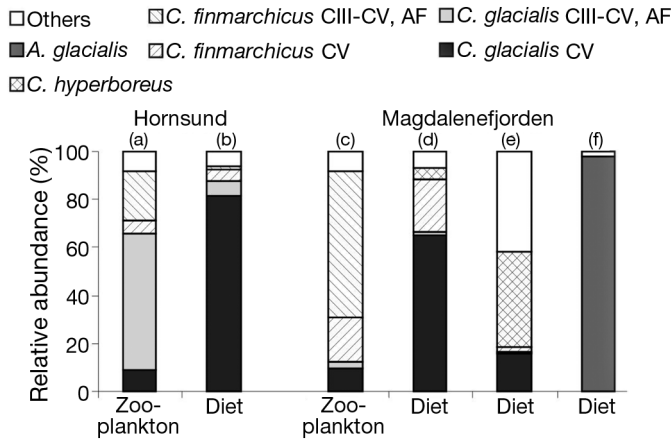


Fig. 3. Relative abundance of zooplankton taxa in (a) Hornsund (n = 14) and (c) Magdalenefjorden (Smeerenburgfjorden) (n = 13) feeding grounds compared with relative abundance of prey in the food delivered to little auk *Alle alle* chicks in Hornsund: (b) '*Calanus glacialis*' type (n = 54), and Magdalenefjorden (d) '*Calanus glacialis*' types (n = 53), (e) '*Calanus hyperboreus*' types (n = 8), and (f) '*Apherusa glacialis*' types (n = 7) colonies. CIII-IV, CV: copepodid stages of *Calanus* zooplankters; AF: copepodid stage VI females of *Calanus* zooplankters

sented by 6% stage CV and 20% by the other considered stages (CIII-CIV and AF). In Smeerenburgfjorden, *C. finmarchicus* was more important (18% stage CV and 61% stages CIII-CIV and AF). The contribution of *C. glacialis* in this area was lower, particularly because the proportion of stages CIII-CIV and AF was only 3%. However, the proportion of copepodid stage CV was the same as in Hornsund (9%) (Fig. 3a,c).

Abundance of zooplankton was similar on the little auks foraging grounds close to Hornsund (median 512 ind. m⁻³) and in Smeerenburgfjorden (median 456 ind. m⁻³) (Table 2). The abundance of the little auks preferred prey, *Calanus glacialis* CV, was similar in both areas (Table 2). In Smeerenburgfjorden, *C. fin-*

marchicus CV and *C. finmarchicus* CIII-IV and AF were significantly more numerous (3.6-fold for all stages combined) than in Hornsund. In contrast, *C. glacialis* CIII-IV and AF was 4-fold less numerous in Smeerenburgfjorden than in Hornsund. The abundance of other zooplankton species was similar in both foraging areas (Table 2). The proportion of abundance of *C. glacialis* CV abundance to all other zooplankton was 1:10 in both foraging areas (χ^2 test, $\chi^2_1 = 0.36$, p = 0.55).

Chick diet composition

The nMDS ordination of the food load samples for relative abundance of the food items showed that samples from Hornsund colony were more similar to each other (average within-group similarity 80%, PRIMER SIMPER procedure) than to samples from Magdalenefjorden colony (average similarity 56%). Food samples of '*Calanus glacialis*' type constituted 98% of samples collected in Hornsund and 77% of samples collected in Magdalenefjorden (Fig. 4). Food samples of '*Apherusa glacialis*' and '*Calanus hyperboreus*' types were found only in Magdalenefjorden and made up 10 and 12%, respectively, of all food loads collected there. The contents of 2 gular pouches were exceptional (Fig. 4), containing predominantly *Pagurus* sp. larvae (Hornsund) and *Thysanoessa inermis* (Magdalenefjorden). In all food samples of '*Calanus glacialis*' type, copepodid stage CV was the most important prey item, comprising 82 and 68% of the total abundances in Hornsund and Magdalenefjorden colonies, respectively (Fig. 3b,d). *Calanus finmarchicus* CV was found in 4% of samples from Hornsund and in 21% from Magdalenefjorden. The contribution of other prey items was lower — *C. glacialis* CIII-IV and AF: 6% in Hornsund, 2% in Magdalenefjorden; *C. hyperboreus*: 5% in Magdalenefjorden, 0.2% in Hornsund; *C. finmarchicus*

Table 2. Abundance (ind. m⁻³) of zooplankton taxa in feeding areas of little auks *Alle alle* in Hornsund (n = 14) and Magdalenefjorden-Smeerenburgfjorden (n = 13) area. Q₁-Q₃: quartiles 25–75%; CIII-IV, CV: copepodid stages of *Calanus* zooplankters; AF – copepodid stage VI females of *Calanus* zooplankters. Inter-regional comparison: Mann-Whitney U-test

	Abundance (ind. m ⁻³)				Interregional comparison	
	Hornsund		Magdalene-Smeerenburg		Z	p
	Median	Q ₁ -Q ₃	Median	Q ₁ -Q ₃		
<i>C. glacialis</i> CV	42	27–58	51	39–67	–0.82	0.409
<i>C. glacialis</i> CIII-IV and AF	272	189–375	13	6–21	4.39	<0.001
<i>C. finmarchicus</i> CV	20	10–43	84	63–111	–3.91	<0.001
<i>C. finmarchicus</i> CIII-IV and AF	80	44–136	326	138–476	–3.42	0.001
<i>C. hyperboreus</i>	<1	0–1	<1	0–1	0.17	0.865
Other prey items	35	24–55	44	28–62	–0.75	0.452
Total zooplankton	512	383–583	456	357–718	–0.19	0.846

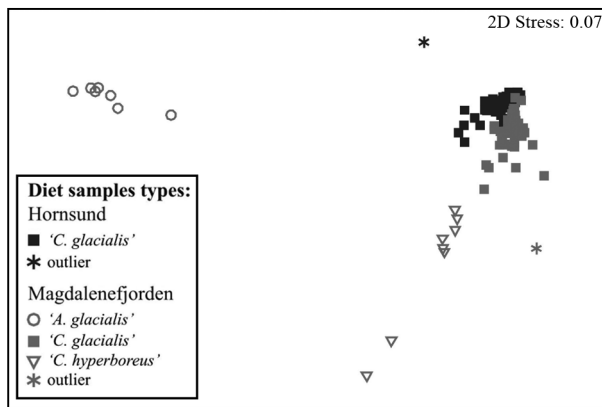


Fig. 4. *Alle alle*. nMDS plot of Bray-Curtis similarities in the relative abundances of prey items (*A.* = *Apherusa*, *C.* = *Calanus*) in the food samples collected from little auk chicks in Hornsund ($n = 55$) and Magdalenefjorden ($n = 69$) colonies

CIII-IV and AF: 2% in Hornsund and 1% in Magdalenefjorden (Fig. 3b); remaining items made 6% of the total abundance in both colonies.

In the '*Calanus glacialis*' type food samples collected during the mid chick-rearing period, the number of prey items per food load was significantly higher in Magdalenefjorden than in Hornsund (Table 3). The number of the most important prey item (*C. glacialis* CV), however, was similar in both colonies. Little auks from Magdalenefjorden fed chicks significantly more *Calanus finmarchicus* CV and *Calanus hyperboreus* than did birds from Hornsund. Abundance of other prey items was similar in both colonies (Table 3). The proportion of *C. glacialis* CV in relation to all other prey items was significantly higher in Hornsund (6:1) than in Magdalenefjorden (2:1); χ^2 test, $\chi^2_1 = 2869.7$, $p < 0.0001$). However, the total biomass and energy content of food loads of '*Calanus glacialis*' type collected in both colonies were similar (Table 3).

Prey selectivity

All selectivity indices for prey items analyzed were significant ($p < 0.003$) except for *Calanus hyperboreus* ($p = 0.08$) and *C. glacialis* CIII-IV and AF ($p = 0.23$) in Magdalenefjorden. Little auks from both colonies generally showed similar prey preferences. *C. glacialis* copepodid stage CV was the most positively selected prey item by little auks from both colonies ($V = 0.68$ in Hornsund and $V = 0.43$ in Magdalenefjorden) (Fig. 5). *C. glacialis* CIII-IV and AF were the most negatively selected (avoided) in Hornsund ($V = -0.60$) and not selected in Magdalenefjorden ($V = -0.01$). Stages CIII-IV and AF of Atlantic-water *C. finmarchicus* were avoided by birds from both colonies ($V = -0.30$ in Hornsund and $V = -0.70$ in Magdalenefjorden). *C. finmarchicus* CV ($V = -0.04$ in Hornsund and $V = 0.05$ in Magdalenefjorden) and *C. hyperboreus* ($C = -0.01$ in Hornsund and $C = 0.01$ in Magdalenefjorden) were neither selectively chosen nor avoided by little auks (Fig. 5).

Parental efforts

Chick feeding rate (no. of feeds per parent per 48 h), was similar in Hornsund (median: 7, Q_1 - Q_3 : 4–9, $n = 39$) and Magdalenefjorden (median: 7, Q_1 - Q_3 : 4–8, $n = 40$; Mann-Whitney *U*-test, $Z = 0.57$, $p = 0.55$). Duration of foraging trips performed by little auks in Magdalenefjorden (median: 183, Q_1 - Q_3 : 120–332 min, $n = 235$) was significantly longer than in Hornsund (median: 124, Q_1 - Q_3 : 89–274 min, $n = 212$; Mann-Whitney *U*-test, $Z = -3.92$, $p < 0.001$) (Fig. 6). In Hornsund, birds performed short trips (≥ 2 h) more frequently (48%) compared to Magdalenefjorden (26%; intercolony comparison long vs. shorter trips: χ^2 test, $\chi^2_1 = 21.73$,

Table 3. Comparison of abundance (ind. meal⁻¹), biomass (dry mass) (mg meal⁻¹) and energy (kJ meal⁻¹) of little auk *Alle alle* food loads from Hornsund ($n = 17$) and Magdalenefjorden ($n = 18$) colonies (diet samples of '*Calanus glacialis*' type, mid chick-rearing period). Q_1 - Q_3 : quartiles 25–75%; CIII-IV, CV: copepodid stages of *Calanus* zooplankters; AF: copepodid stage VI females of *Calanus* zooplankters. Intercolony comparison: Mann-Whitney *U*-test

	Abundance (ind. meal ⁻¹)				Intercolony comparison	
	Median	Median	Median	Median	Z	p
<i>C. glacialis</i> CV	1440	1048–1680	1343	1055–2075	-0.30	0.766
<i>C. glacialis</i> CIII-IV and AF	51	32–69	37	17–90	0.87	0.381
<i>C. finmarchicus</i> CV	40	20–80	483	310–708	-4.85	<0.001
<i>C. finmarchicus</i> CIII-IV and AF	9	7–16	25	8–40	-1.45	0.146
<i>C. hyperboreus</i>	<1	0–1	<1	0–5	-3.44	0.001
Other prey items	65	33–115	28	7–64	1.84	0.064
Total abundance	1584	1209–1836	2156	1609–2820	-2.36	0.018
Total biomass (mg meal ⁻¹)	976	730–1132	1053	782–1462	-1.06	0.291
Total energy (kJ meal ⁻¹)	29	22–34	31	23–43	-0.99	0.322

$p < 0.0001$; Fig. 6). Parent birds from Magdalenefjorden spent significantly more time per 48 h on foraging trips (1281 min bird⁻¹) compared to Hornsund (868 min bird⁻¹; χ^2 test, $\chi^2_1 = 57.58$, $p = 0.001$).

Body mass and stress level of adults

Body mass corrected for body size (head-bill length as a covariate) of little auks was similar in Hornsund and Magdalenefjorden at the mid phase of chick-rearing (respective mean \pm SE values 159.8 \pm 1.96 and 163.0 \pm 2.29 g; ANCOVA, $F_{1,46} = 88.4$, $p = 0.99$). A similar pattern was observed at the late phase (Hornsund: 169.1 \pm 3.54 g; Magdalenefjorden: 161.4 \pm 2.15 g; $F_{1,34} = 2.31$, $p = 0.14$). Body size (head-bill length), not colony ($p > 0.05$), had a significant effect on body mass at the mid ($F_{1,46} = 9.75$, $p = 0.003$) and late ($F_{1,34} = 6.29$, $p = 0.02$) phases of chick-rearing. The number of heterophils and lymphocytes per 100 leukocytes and H:L ratio were similar in adults in Hornsund and Magdalenefjorden, both at the mid and late phases of chick-rearing (Table 4).

Body mass and stress level of chicks

Body mass of chicks did not differ significantly between colonies in Hornsund and Magdalenefjorden

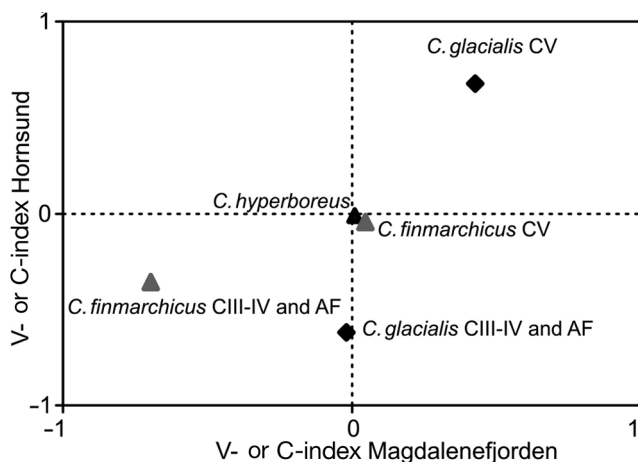


Fig. 5. *Alle alle*. Prey selectivity V-indices of little auks breeding in Magdalenefjorden plotted against those in Hornsund. Positive values indicate selectivity, negative values, avoidance, and zero, no selection. For *C. hyperboreus*, C-indices are presented (V-indices with incorporated Yates' correction). CIII-IV, CV: copepodid stages of *Calanus* zooplankters; AF: copepodid stage VI females of *Calanus* zooplankters

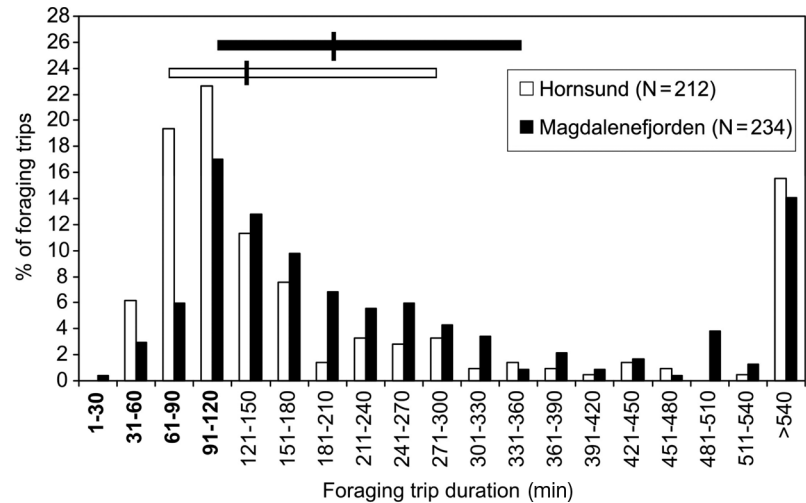


Fig. 6. *Alle alle*. Distribution of foraging trips duration of parent little auks from breeding colonies in Hornsund (vertical white bars) and Magdalenefjorden (vertical black bars) at the turn of mid and late phases of chick-rearing (chicks at age 18 to 22 d) in 2008. Horizontal bars indicate interquartile ranges and vertical lines indicate medians of foraging trip duration. Values in **bold** (≥ 120 min) indicate short foraging trips

both at the early (mean \pm SD, n = sample size) (Hornsund, 52.8 \pm 11.30 g, $n = 14$; Magdalenefjorden, 57.9 \pm 9.42 g, $n = 32$) (Student's t -test, $t_{44} = 0.99$, $p = 0.33$) and mid (Hornsund, 118.8 \pm 11.88 g, $n = 33$; Magdalenefjorden, 115.3 \pm 10.08 g, $n = 37$) (Student's t -test, $t_{68} = 1.32$, $p = 0.19$) phase of development. The number of heterophils and lymphocytes per 100 leukocytes and H:L ratio were similar in chicks from both colonies at the early and mid stages of their development (Table 5).

DISCUSSION

The effects of temporal and spatial variation in prey availability on chick diet composition, energetic content of food, and parental efforts (frequency of feeds and duration of foraging trips) in little auks have been previously documented (Jakubas et al. 2007, Welcker et al. 2009a, Wojczulanis-Jakubas et al. 2010, Kwasniewski et al. 2010, Karnovsky et al. 2010). Harding et al. (2009a,b), and Welcker et al. (2009b) investigated the effects on body mass and corticosterone level in parents and chicks. However, those studies were based on artificially burdened individuals (with transmitters or clipped feathers) and it is difficult to match the artificial burden to specific environmental conditions. In contrast, our comparison takes advantage of a natural experiment and allows the assessment of natural bird reactions to the specific, real environmental and food conditions. Such knowledge may be crucial for creating reliable scenarios of complex animal response to climate change.

Table 4. *Alle alle*. Percentages of heterophils, leucocytes and heterophil:lymphocyte (H:L) ratios in adult little auks caught at 2 stages of the chick-rearing period. Q₁-Q₃: quartiles 25 to 75%. Intercolony comparison (arcsin square root transformed data): Student's *t*-test

Parameter	Hornsund			Magdalenefjorden			Intercolony comparison		
	Median	Q ₁ -Q ₃	n	Median	Q ₁ -Q ₃	n	df	<i>t</i>	p
Mid phase (age 17 to 19 d)									
Heterophils (%)	60	53–68	30	66	61–72	21	1,49	-1.85	0.07
Lymphocytes (%)	35	29–42	30	31	25–36	21	1,49	1.38	0.36
H:L ratio	1.7	1.2–2.3	30	2.2	1.8–2.9	21	1,49	-1.44	0.16
Late phase (age 26 to 28 d)									
Heterophils (%)	60	53–64	10	59	41–65	28	1,36	0.66	0.51
Lymphocytes (%)	37	30–42	10	40	34–57	28	1,36	-0.95	0.35
H:L ratio	1.6	1.3–2.1	10	1.4	0.7–1.9	28	1,36	0.59	0.56

Table 5. *Alle alle*. Percentages of heterophils, leucocytes and heterophil:lymphocyte (H:L) ratios in little auk chicks at early and mid phases of growth. Q₁-Q₃: quartiles 25 to 75%. Intercolony comparison (arcsin square root transformed data): Student's *t*-test

Parameter	Hornsund			Magdalenefjorden			Intercolony comparison		
	Median	Q ₁ -Q ₃	n	Median	Q ₁ -Q ₃	n	df	<i>t</i>	p
Early phase (age 4 to 7 d)									
Heterophils (%)	42	34–47	14	46	33–53	32	1,44	0.55	0.59
Lymphocytes (%)	57	52–66	14	55	48–66	32	1,44	-0.54	0.59
H:L ratio	0.7	0.5–0.9	14	0.8	0.5–1.1	32	1,44	-0.78	0.44
Mid phase (age 14 to 17 d)									
Heterophils (%)	45	37–54	33	53	43–58	37	1,68	1.66	0.10
Lymphocytes (%)	54	44–62	33	45	39–56	37	1,68	-1.66	0.10
H:L ratio	0.9	0.6–1.3	33	1.2	0.8–1.5	37	1,68	-1.79	0.08

Diet composition and food condition in foraging areas

Different oceanographic conditions in the 2 foraging areas most likely account for the higher abundance of all stages of Atlantic *Calanus finmarchicus* and lower abundance of *C. glacialis* CIII-IV and AF in the Magdalenefjorden-Smeerenburgfjorden area (impacted by warm Atlantic waters), compared to Hornsund (influenced by cold Arctic waters). However, the abundance of the little auks preferred prey, *C. glacialis* CV, was similar in both areas at the time of our study. Despite differences in zooplankton composition in foraging areas and in chick diet composition (higher proportion of all other prey items in Magdalenefjorden), the abundance of preferred *C. glacialis* CV was similar in food samples from both colonies. Further, the total biomass and energy content of the most typical '*Calanus glacialis*' food samples were similar in Hornsund and Magdalenefjorden. Positive values of selectivity indices confirm that little auks elect *C. glacialis* CV and avoid smaller prey items (Karnovsky et al. 2010, Kwasniewski et al. 2010). However, in Magdalenefjorden, chick diet was more taxonomically diverse, where 22% of the meals represented '*Apherusa glacialis*' and

'*Calanus hyperboreus*' types. These types of food loads were absent in samples from Hornsund. These prey taxa occur in substantial densities relatively far from Magdalenefjorden (Hop et al. 2006). The persistent presence of the ice-associated pelagic amphipod *A. glacialis* (Hop et al. 2000, 2006, Arndt & Swadling 2006), reported earlier from the same colony by Kwasniewski et al. (2010), strongly suggests that little auks from Magdalenefjorden are able to forage regularly in the marginal sea ice zone. The longer duration of foraging flights recorded in Magdalenefjorden, compared to Hornsund, supports this suggestion. A pioneering study on little auk foraging using GPS tracking confirmed that some breeding adults from Magdalenefjorden reached the marginal sea ice zone up to 100 km from their colony (Jakubas et al. in press). Considering the high cost of foraging in adult little auks, the low proportion of energy delivered to the chick (15% of the energy gathered by the parent, Konarzewski et al. 1993), and the time that little auks spent on foraging trips, it is unlikely they are able to travel to distant foraging areas during each trip. They probably fly to the sea ice only occasionally, possibly during long foraging trips, as food-provisioning little auks exhibit a bimodal foraging strategy and alternate

long trips with several consecutive short trips (Steen et al. 2007, Welcker et al. 2009a, Wojczulanis-Jakubas et al. 2010). The frequency of short foraging trips (reflecting probably closer foraging, Welcker et al. 2009a) was lower and the duration of all foraging trips was longer in Magdalenefjorden than in Hornsund. This may suggest that the closest foraging areas explored by birds from Magdalenefjorden were further away from the colony, compared to the Hornsund area. Moreover, the longer time spent on foraging trips in Magdalenefjorden may be explained by the fact that little auks had to devote more time feeding selectively on their preferred larger-sized and energy-rich copepod prey, because the abundance of the smaller, less profitable *C. finmarchicus* was 3.6 times higher in Smeerenburgfjorden than on the Hornsund shelf.

Food conditions, body condition and stress level

Our study and a comparison of Hornsund and Greenland little auks (Karnovsky et al. 2010) showed that despite distinct differences in oceanographic conditions on foraging areas and duration of foraging trips, little auks from the colonies we compared provided chicks with food of similar quality and quantity and with similar frequency. These results were not expected as a comparison of Hornsund and Magdalenefjorden performed in 2007 (Kwasniewski et al. 2010) revealed that, despite similar abundance of the preferred prey of little auks, *Calanus glacialis* CV, in the foraging areas, little auks from Magdalenefjorden brought food loads of lower biomass and energy content with lower abundance of *C. glacialis* CV compared to Hornsund. Also foraging trip duration was longer and feeding frequency higher for birds from Magdalenefjorden (Kwasniewski et al. 2010). Results of the present study indicate that birds from both colonies provided chicks with food of similar quality and quantity and with similar frequency. As a consequence, the body mass and stress level of chicks did not differ between the colonies. Also body mass and stress level of adults, although they spent more time foraging at Magdalenefjorden, were similar in both colonies. Experimental studies on little auk parents with clipped flight feathers have shown that both adult and chick body conditions and stress level can be negatively affected by increasing flight costs (Harding et al. 2009a,b). Also, in some other seabirds, adults in unfavorable food conditions reduce their own body reserves and deliver less food to their offspring (e.g. Weimerskirch et al. 2001, Gaston & Hipfner 2006). In black-legged kittiwakes *Rissa tridactyla* and common guillemots *Uria aalge* (Piatt et al. 2007), however, as well as in little auks, no relationship between adult

body condition and food condition has been found. The responses of particular species/populations to worsening environmental conditions may be noticeable after crossing the critical threshold above which costs of increasing parental efforts become too high. As many relationships between parameters of seabird biology and food supply are not linear, many seabirds perform well as binary indicators that signal changes from good to bad feeding conditions and vice versa (Reid et al. 2005, Montevecchi 2007, Piatt et al. 2007). Our results indicate that little auks from Magdalenefjorden did not reach the critical threshold of prioritizing self-maintenance over chick provisioning in the season studied. Nevertheless, longer trips performed by birds from Magdalenefjorden exploiting warm-water foraging grounds confirm that foraging trip duration is the parameter that varies continuously with food availability (Piatt et al. 2007) and it may be a good indicator of foraging conditions.

Flexibility in the parental efforts

Results of our study confirm previous observations (Jakubas et al. 2007, Harding 2009a, Karnovsky et al. 2010, Kwasniewski et al. 2010) that little auks have some ability to adjust their reproductive effort in a given breeding attempt. The novel finding here is that they are able to adapt to the suboptimal environmental conditions without visible signs of stress. The flexibility in parental efforts probably depends on the actual local food availability and initial condition of breeding birds, and hence may differ among populations and seasons (Harding et al. 2009a). Lower fledgling mass and elevated corticosterone levels in little auk chicks of parents with experimentally increased flight costs suggests that stressed adults may have reached a threshold of prioritizing self-maintenance over increased provisioning effort when foraging costs become too high (Velando & Alonso-Alvarez 2003, Harding et al. 2009a). The question remains whether oceanographic and foraging conditions create such a threshold in natural, not experimental conditions. Foraging beyond a certain threshold of prey availability will have negative consequences for little auks' reproductive success and population dynamics. Such a threshold was apparently reached by the southernmost little auk breeding populations in south Greenland and Iceland, which collapsed following a shift in sea currents and plankton distribution in the 19th century (Stempniewicz 2001, Stempniewicz et al. 2007).

Sea surface temperature modelling, based on an Intergovernmental Panel on Climate Change scenario, predicts that half of the major little auk colonies in the Nordic Seas will face a shift towards a zooplankton

community dominated by the smaller, less profitable *Calanus finmarchicus* by the end of the 21st century (Karnovsky et al. 2010). It is expected that the Hornsund area will experience severe changes due to a strong influx of Atlantic water which may reduce the extent of cold coastal current (Sørkapp Current) and thus the densities of the little auk preferred prey, *C. glacialis* (Karnovsky et al. 2010). Predicted reduction in ice thickness and extent in the Arctic Ocean (IPCC 2007, Hop et al. 2006, Piechura & Walczowski 2009) may also severely impact little auks from Magdalenfjorden area by limiting the possibility of foraging on distant, food-abundant foraging areas in the marginal sea ice zone. Little auks will also be impacted if the expected continuous warming of the water masses and new phytoplankton bloom regime in the Arctic Ocean north of Svalbard causes an ecosystem shift from today's *C. glacialis/C. hyperboreus*-based energy transfer favourable to little auks to a *C. finmarchicus*-based food chain (Falk-Petersen et al. 2007). On the other hand, spatial and seasonal variability in little auk diets (Karnovsky et al. 2008, 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).

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