

# Intra-seasonal variation in zooplankton availability, chick diet and breeding performance of a high Arctic planktivorous seabird

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**Abstract** Different phenological responses to climate changes by species representing preys and predators may lead to mismatch between functionally dependent components of an ecosystem, with important effects on its structure and functioning. Here, we investigate within-season variation in zooplankton availability, chick diet composition and breeding performance of a small planktivorous seabird, the little auk (*Alle alle*) in two large colonies in Hornsund and Magdalenefjorden, Spitsbergen, differing in synchrony of breeding (11-day vs. 22-day hatching period, respectively). Assuming similar zooplankton phenology and existing differences in duration of the little auk breeding period, we expected lower availability of the preferred food in the less synchronized colony in Magdalenefjorden and in consequence a negative effect on nestling body mass and survival. We found that in both colonies *Calanus glacialis* (copepodite stage CV) was the most important prey item in the chick diet making up 68–87 % of the biomass and energy of all prey items. The only exception was the end of the chick-rearing period in Magdalenefjorden, when contribution of this prey item was significantly lower (24–26 %). Thus, late breeders in Magdalenefjorden were apparently mismatched regarding *C. glacialis* CV availability. However, the hatching date did not affect birds fitness (reproductive output and chick pre-fledging mass) significantly. Results of our study indicate that little auks breeding on Spitsbergen can

respond to a wide range of environmental conditions and prey availabilities through the plasticity of their foraging behaviour, which may help them to maintain their optimum fitness level in changing and unpredictable environments.

**Keywords** Match–mismatch · Dovekie · *Calanus glacialis* · Breeding success · Chick growth · Spitsbergen

## Introduction

Inter- and intra-seasonal changes in environmental conditions and food availability often affect foraging behaviour and diet of animals including numerous bird species (e.g. Morrison et al. 1990; Watanuki et al. 1993; Charrassin et al. 1998; Jakubas and Manikowska 2011). Interpretation of changes in diet may differ between ecological groups. For generalists, it may indicate prey switching, i.e. increased predator selection for a particular prey species when it is abundant and decreased selection when it is scarce (e.g. Murdoch et al. 1975). For specialized predators, having strong, fixed preferences for a given prey type, regardless of its abundance (Charnov 1976), changes in diet may indicate a severe change in availability of the preferred prey, and this, in turn, may have serious negative consequences on the predator breeding performance. Thus, recognizing changes in diet of specialized predator within the breeding period may indicate changes in foraging conditions, especially in the case of predators breeding in seasonal environments. They schedule their most energy-demanding life-history events, such as reproduction to coincide with the peak of abundance of the preferred food. In many regions, however, climate changes shift annual cycles of multiple organisms (Parmesan and Yohe 2003; Root et al. 2003) and predators may respond differently

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than their prey. This may lead to mismatches between functionally dependent components of ecosystem with important effects on the structure and function of the whole ecosystem (Stenseth et al. 2002). The potential for mismatches between predator and prey dynamics is compounded for seabirds breeding in high latitudes. The Arctic is currently undergoing a dramatic climate change, with a twofold greater increase in temperature compared to the global increase (IPCC 2007). Moreover, high-latitude nesting seabirds have a limited time window to reproduce what may limit their ability to adjust the timing of breeding to shifts in peaks of food abundance (Svensson 1995; Shultz et al. 2009).

The little auk (or dovekie) (*Alle alle*) is a small, zooplanktivorous seabird breeding exclusively in the high Arctic. It is considered to be the most abundant alcid in the Palaearctic (Stempniewicz 2001). The female lays 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). Owing to the high cost of locomotion, both in the air (flapping flight) and in the water (underwater ‘flight’), the little auk’s foraging is believed to be energetically expensive (Gabrielsen et al. 1991; Konarzewski et al. 1993). To cover such high-energy demands, the little auk forages almost exclusively on copepods associated with cold Arctic waters (in the Spitsbergen area: *Calanus glacialis*, especially copepodite stage CV), which are larger and much richer in energy than their counterparts from warmer Atlantic waters (*C. finmarchicus*) (Weslawski et al. 1999; Karnovsky et al. 2003; Jakubas et al. 2007, 2011; Fort et al. 2010; Kwasniewski et al. 2010, 2012). The distribution of cold Arctic waters along the west coast of Spitsbergen varies spatially and seasonally (Walczowski and Piechura 2007), affecting the accessibility of the zooplankton species preferred by the little auk (Kwasniewski et al. 2012). Spatial and temporal variability in ice cover extent could lead to a mismatch between the timing of ice algal and/or phytoplankton blooms and the timing of reproduction and development of *C. glacialis* (Søreide et al. 2010). Ice breakup occurring too early or too late can cause a mismatch between primary and secondary producers (Leu et al. 2011). For instance, early ice breakup may shorten the ice algal bloom period and also the gap between ice algal and phytoplankton blooms and hence lead to poorer growth conditions for developing *C. glacialis* population (Leu et al. 2011; Daase et al. 2013). Those changes may have negative consequences for the entire lipid-based Arctic marine food web (Leu et al. 2011), including top predators such as little auks.

We aimed in this study to investigate within-season variation in zooplankton availability, chick diet composition and breeding performance of little auks breeding in

two large colonies on west Spitsbergen, in Hornsund and Magdalenefjorden. Both colonies are situated in the area where Atlantic, Arctic and glacial waters converge, mix and exchange (Saloranta and Svendsen 2001). The timing of ice retreat and peaks of pelagic phytoplankton bloom are similar in both areas [according to 10-year data for 1998–2007 (Ji et al. 2013) and sea ice data for the studied year (Norwegian Ice Service, <http://polarview.met.no/>)]. To our knowledge, there are no detailed data on zooplankton phenology of *C. glacialis* in the studied areas; however, given environmental conditions both studied areas probably represent Kongsfjorden phenological ice-free scenario (Daase et al. 2013). Therefore, we anticipated that *C. glacialis* CV abundance would also be similar in both colonies. However, given (1) descent of *C. glacialis* CV to deeper water starting at the beginning of August (Daase et al. 2013), (2) more prolonged breeding in Magdalenefjorden (hatching span: 25–32 days; Jakubas and Wojczulanis-Jakubas 2011) than in Hornsund (9–15 days; Stempniewicz 2001; Wojczulanis-Jakubas 2007) and (3) later start of breeding in Magdalenefjorden (Jakubas et al. 2013), we expected decreasing availability of the preferred food (*C. glacialis* CV) in Magdalenefjorden. As low abundance of this copepod may affect significantly energy content of the little auk chick meals (Jakubas et al. 2007), we expected that chick body mass and survival in the Magdalenefjorden colony would be lower than in Hornsund.

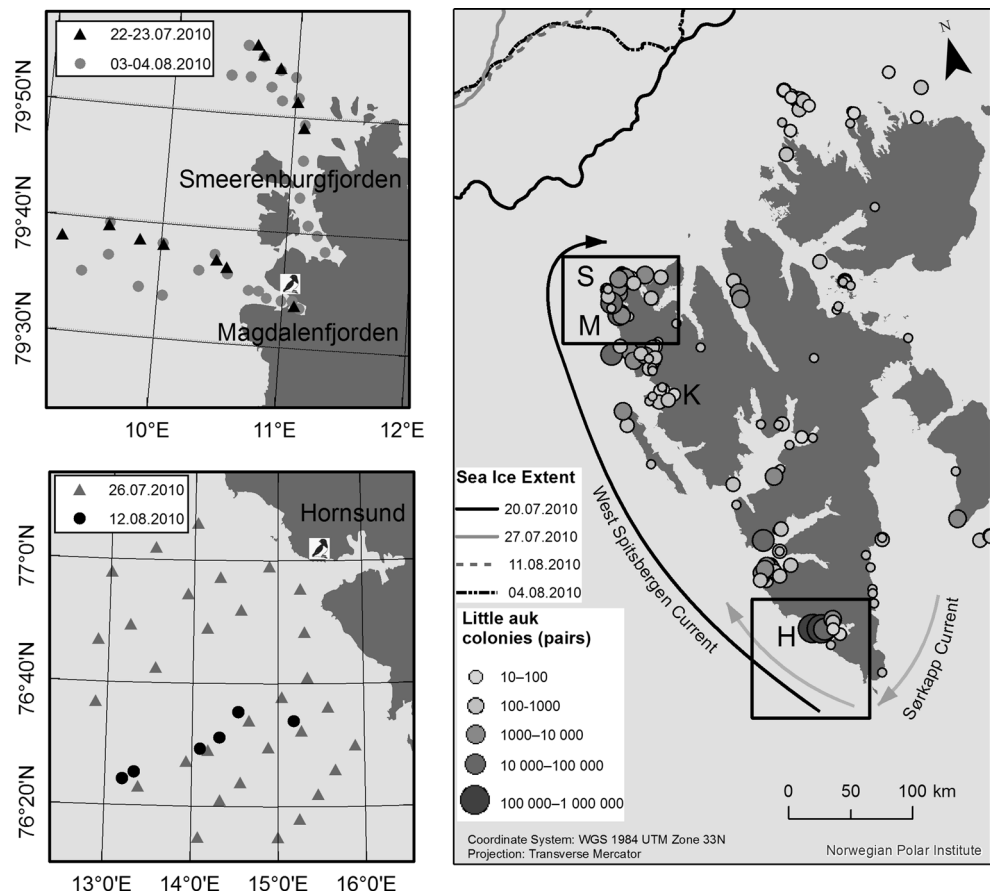
## Methods

### Study area

We carried out the study in two large little auk colonies in Hornsund (SW Spitsbergen; 77°00′N, 15°33′E) and Magdalenefjorden (NW Spitsbergen; 79°35′N, 11°05′E) in 2010 (Fig. 1). The two fjords are the main breeding areas of the little auk on Svalbard (Isaksen 1995). We studied the zooplankton community composition on known foraging grounds of little auks breeding in Hornsund (fjord and shelf zone) and Magdalenefjorden areas (fjord and shelf zone close to Magdalenefjorden and Smeerenburgfjorden) (Jakubas et al. 2011; 2012, 2013, 2014; Stempniewicz et al. 2013; Hovinen et al. 2014a) (Fig. 1).

The Hornsund area is influenced by both the coastal Sørkapp Current, carrying cold, less saline Arctic-type water from the northeast Barents Sea, and the West Spitsbergen Current (WSC), supplying warmer and more saline Atlantic waters from the Norwegian Sea (Piechura et al. 2001). In the vicinity of Magdalenefjorden, the WSC flows over the shelf slope and meets relatively cold and fresh Arctic water present there in the form of an

**Fig. 1** (Right) Study area with ocean current patterns in the Spitsbergen region (arrows; modified after Loeng and Drinkwater 2007), sea ice extent during food sample collection in Magdalenefjorden (based on ice maps from the Norwegian Ice Service; <http://polarview.met.no/>) and the locations and sizes of little auk colonies (circles; data of Norwegian Polar Institute). (Left) Close-up of the Magdalenefjorden (M), Smeerenburgfjorden (S) and Hornsund (H) areas (lower), showing zooplankton sampling sites (circles and triangles), and little auk colonies (the little auk icon); K Kongsfjorden



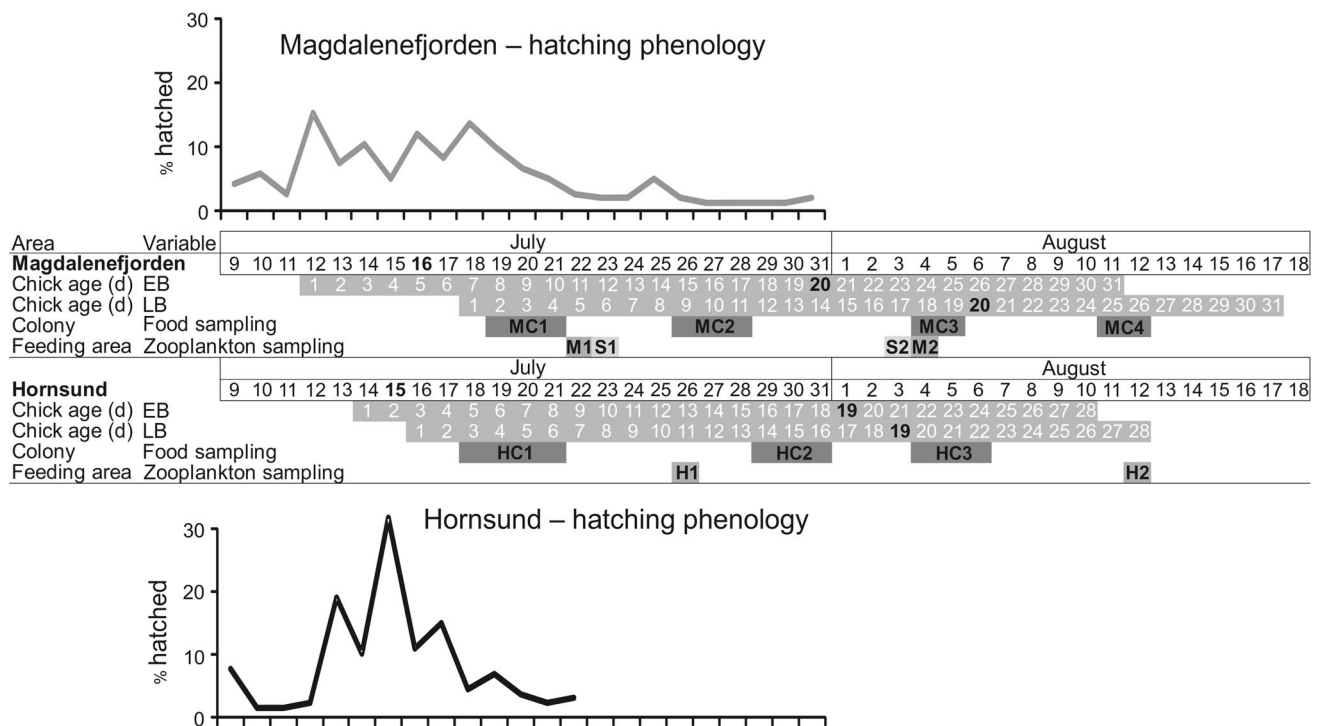
anticyclonic coastal current. The two water masses partly mix, creating a transitional zone of differing widths depending on the season (Daase et al. 2007; Walczowski and Piechura 2007; Trudnowska et al. 2012). Smeerenburgfjorden lies at the northern end of the cold coastal current that flows along the west coast of Spitsbergen, but it is also strongly influenced by the Svalbard Branch of WSC (Saloranta and Svendsen 2001; Walczowski et al. 2005), which carries warm, saline Atlantic water to the north of the island. During the little auk breeding season in the studied year, the marginal sea ice zone was located 110–190 km north off Magdalenefjorden, and there was no ice in the Hornsund area (Norwegian Ice Service; <http://polarview.met.no/>) (Fig. 1).

### Field work

We took the zooplankton samples from each of the distinguished little auk foraging grounds twice during the whole chick-rearing period—32 and 6 samples in the Hornsund area (hereafter H1–H2), 6 and 15 in the Magdalenefjorden area (M1–M2), and 6 and 15 in the Smeerenburgfjorden area (S1–S2) (for sampling dates—see Fig. 2). Sampling was carried out from the research

vessel *Oceania* (Institute of Oceanology, Polish Academy of Sciences), except for the first sampling in the Magdalenefjorden/Smeerenburgfjorden area (M1 and S1) that was done from the Norwegian research vessel *Lance* (Norwegian Polar Institute). Different number of samples collected in particular periods and sites were determined by weather conditions during the sampling and logistic reasons. A WP-2-type net with a 0.25-m<sup>2</sup> opening area (Tranter and Fraser 1968) and fitted with filtering gauze of 500 µm mesh size was hauled vertically from 50 m depth to the surface (considering maximal dive depth of 38 m attained by depth recorder equipped little auks, Karnovsky et al. 2011). We preserved the zooplankton samples in 4 % formaldehyde solution in borax-buffered seawater.

We took samples of the food loads from adult little auks carrying food to their chicks captured in the colony with mist nets or noose carpets. We caught birds in two colony patches in Magdalenefjorden estimated to 1100 and 5000 breeding pairs, respectively, and in one patch in Hornsund (estimated to 3240 breeding pairs; Keslinka et al., unpublished data). We gently scooped the food content out of the little auk's gular pouch with a small spoon and released the birds after 5–10 min of handling. We put each food load into a separate plastic container and preserved it in 4 %



**Fig. 2** Timing of data collection during the field work in Spitsbergen, 2010. The *graphs above and below the diagram* show the little auk hatching dynamics in Magdalenefjorden (*grey line, up*) and Hornsund (*black line, bottom*). *Bolded numbers in white bars* indicate median hatching dates at the whole colony scale. *The numbers in grey bars* denote the chick age for early (EB; 1–50 % of the hatching date distribution) and late (LB; 51–100 % of the hatching date distribution) breeders; *days marked in black in grey bars* indicate peak body

mass days in nests of early and late breeders (based on data from Table 7). Duration of chick presence in nests in Hornsund and Magdalenefjorden according to Harding et al. (2004) and Wojczulanis-Jakubas and Jakubas (2012), respectively. Codes for food sampling in colonies in Magdalenefjorden: MC1–MC4 and in Hornsund: HC1–HC3. Codes for zooplankton sampling in the little auks’ foraging areas in Magdalenefjorden: M1–M2, in Smeerenburgfjorden: S1–S2 for, and in Hornsund: H1–H2

formaldehyde solution in seawater. We collected food samples three times in Hornsund (hereafter HC1–HC3,  $N = 13, 23$  and  $13$ ) and four times in Magdalenefjorden (MC1–MC4,  $N = 23, 23, 19$  and  $23$ ) (for sampling dates—see Fig. 2).

To establish hatching dates, we inspected 126 nests in Hornsund and 128 in Magdalenefjorden. Active nests were found during incubation and checked every 2 day, starting from 2 d before the expected hatching date (estimated according to data from previous seasons) until we found a hatchling. Then, to investigate chick survival and chick growth, we monitored the nests ( $N = 78$  and  $94$  in Hornsund and Magdalenefjorden, respectively) starting from when the chicks were at age 14–15 days. We weighed chicks every 3 days until they disappeared from the nest at 21–31 day (Harding et al. 2004; Wojczulanis-Jakubas and Jakubas 2012). We did not capture the chicks for the first 2 weeks of their life to minimize disturbance and considered the hatched chicks that were not found at 14–15 days as dead. We weighed the chicks to the nearest 0.1 g using a 300 g OHAUS electronic balance. Many little auk nesting chambers are difficult to access and/or chicks are able to

escape from the main chamber when disturbed, which influenced particular sample sizes. Thus, sample sizes varied for hatching dynamic, survival and chick growth (Table 7).

**Data analyses**

We calculated zooplankton dry masses according to Kwasniewski et al. (2010) and literature therein. We calculated the energy estimates according to Harris et al. (2000).

We applied the following multivariate methods to investigate spatio-temporal variations in the qualitative and quantitative composition of zooplankton samples collected on the foraging grounds and from birds: (1) non-metric multidimensional scaling (nMDS), an indirect gradient analysis approach which produces an ordination based on a distance matrix explained by the Bray–Curtis similarity measure (Taguchi and Oono 2005), used to visualize similarity of foraging ground zooplankton communities and food load compositions (shown only for biomass); (2) analysis of group similarities (ANOSIM), a procedure



based on Bray–Curtis measure of similarity to test differences among groups (Clarke 1993); 3) the similarity percentage breakdown (SIMPER) procedure, to assess the average per cent contribution of individual items to the dissimilarity between objects in a Bray–Curtis dissimilarity matrix; significance of results was assessed by ANOSIM (Clarke 1993). Furthermore, we applied the nonparametric Kruskal–Wallis test to compare abundance, biomass and energy content of *Calanus glacialis* and all prey items combined between the samples from foraging grounds and from the little auk chick diet.

We deciphered and visualized spatial and temporal differences in the diet using a feeding strategy Costello diagram. It incorporates prey-specific abundance (i.e. the percentage a prey taxon comprises of all prey items in only those samples in which the actual prey occurs) and frequency of occurrence metrics to indicate prey importance, dominant or rare and the predator feeding strategy (specialist or generalist) (Costello 1990, modified by Amundsen et al. 1996).

To compare distribution of hatching dates between the colonies, we used Mann–Whitney *U* test. To compare chick growth between the colonies, we used the following variables: peak mass (the highest mass noted per chick), the day when the peak mass was achieved (Stempniewicz 1980) and pre-fledging mass (at 21–22 days). The peak and fledging masses have been found to be effective growth indicators (Zach 1988). Because the study was completed before majority of chicks fledged, we used in analyses pre-fledging mass.

To estimate the effect of colony, hatching date and their interaction on chick growth variables (i.e. peak mass, peak day mass and pre-fledging mass), we used general linear model (GLM). Nonsignificant interaction terms ( $P > 0.05$ ) were removed and analyses rerun including only colony and hatching date.

To investigate breeding success between the two colonies, we analysed chick survival up to 20 days (the number of 20-day-old chicks/number of chicks hatched; chicks that disappeared from the nest after 20 days were assumed to have fledged; Harding et al. 2004). We analysed data on chick survival using logistic regression starting with models that included hatching date as continuous independent variable, colony as the grouping variable, and the interaction between the colony and hatching date. If the interaction term was nonsignificant ( $P > 0.05$ ) in the first run, we removed it and rerun the analysis including only hatching date and colony terms.

To visualize differences in phenology between early and late breeders, we presented duration of chick presence in nests [according to Harding et al. (2004) in Hornsund and Wojczulanis-Jakubas and Jakubas (2012) in Magdalenefjorden] of early (chicks hatched on dates representing a

first half, i.e. 1–50 % of the hatching date distribution) and late (chicks hatched on dates representing a second half, i.e. 51–100 % of the hatching date distribution) breeders (Figs. 1, 5).

We performed nMDS, ANOSIM and SIMPER procedures using PAST 3.0 software (Hammer et al. 2001). We expressed results as similarities in nMDS and ANOSIM and as dissimilarities in SIMPER. All other analyses we conducted in STATISTICA 8.0 (StatSoft, Inc., Tulsa, Oklahoma, USA) and R software (R Core Team 2015).

## Results

### Zooplankton structure on the foraging grounds

In Magdalenefjorden, abundance and biomass of all zooplankton items combined during the first sampling in Magdalenefjorden (M1) were significantly higher compared to the second sampling (M2). M1 and M2 values were significantly lower compared to both Hornsund samplings (H1–H2), and last sampling in Smeerenburgfjorden (S2) (Table 1). In Magdalenefjorden, abundance and biomass of *C. glacialis* CV collected during the second sampling (M2) were significantly lower compared to the first one (M1), as well as to the second sampling in Hornsund (H2). In Hornsund, values recorded there during the second sampling (H2) were significantly higher compared to H1. In Smeerenburgfjorden, abundance and biomass of *C. glacialis* CV were similar in both samplings (Table 1; Fig. 3a).

The nMDS plot of similarity in zooplankton composition regarding its biomass showed no clear separation between various areas/dates; however, samples M2 and H2 generally clustered in two positions different from the rest of the samples (Fig. 3a). These samples were characterized by the lowest (M2) and the highest (H2) biomass of the little auk most important prey, *C. glacialis* CV (Table 1).

SIMPER procedure showed that samples from the little auk foraging grounds in the Magdalenefjorden (average within-group dissimilarity: abundance 82 %, biomass 77 %) and Hornsund areas (average within-group dissimilarity: abundance 78 %, biomass 83 %) were more dissimilar than the samples from Smeerenburgfjorden (average within-group dissimilarity: abundance 58 %, biomass 61 %) (Table 2). SIMPER also showed a high degree of zooplankton dissimilarity between the second sampling in Magdalenefjorden (M2) and all other sampling areas (abundance 79–93 %, biomass 78–93 %). Analyses also revealed a high degree of zooplankton dissimilarity between the two samplings in the Hornsund area (H1 and H2; biomass 83 %) and the second in the Smeerenburgfjorden area (S2; biomass 84 %) (Table 2).

**Table 1** Abundance (ind. m<sup>-3</sup>) and biomass (g m<sup>-3</sup>) of zooplankton from the foraging grounds of little auks in different periods of time in Hornsund (H1–H2), Magdalenefjorden (M1–M2) and Smeerenburgfjorden (S1–S2) in 2010;  $Q_1$ – $Q_3$ —percentiles 25–75 %

Variable	Code	All zooplankton items combined			<i>C. glacialis</i> CV		
		Median	$Q_1$ – $Q_3$	<i>N</i>	Median	$Q_1$ – $Q_3$	<i>N</i>
Abundance	H1	2039.5 <sup>a</sup>	1084.7–4604.9	32	16.0 <sup>a</sup>	0.0–34.7	32
	H2	5277.0 <sup>b</sup>	2562–10631	6	137.5 <sup>a,b</sup>	67–517	6
	M1	1575.7	876.2–1970.5	6	60.7 <sup>c</sup>	16.0–138.6	6
	M2	141.2 <sup>a,b,c</sup>	47.5–457	15	5.9 <sup>b,e</sup>	2.1–7.9	15
	S1	992.2	610.5–1306.8	6	42.4	28–64	6
	S2	1760.8 <sup>c</sup>	594.4–3689.8	15	21.4	9.4–34.6	15
Biomass	H1	163.5 <sup>a</sup>	121.1–374.1	32	9.9 <sup>a</sup>	0.0–21.5	32
	H2	1075.4 <sup>b</sup>	377.5–1505.1	6	85.3 <sup>a,b</sup>	41.5–320.6	6
	M1	174	118.6–247.8	6	37.6 <sup>c</sup>	9.9–86	6
	M2	27.8 <sup>a,b,d</sup>	10.7–76.8	15	3.6 <sup>b,c</sup>	1.3–4.9	15
	S1	110.5	74.5–223.4	6	26.3	17.4–39.7	6
	S2	129.6 <sup>d</sup>	56.9–273.2	15	13.2	5.8–21.5	15

Superscript letters represent differences among samplings based on Kruskal–Wallis ( $P < 0.001$ ) and post hoc Dunn tests: <sup>a,b</sup>  $P < 0.007$ , <sup>c</sup>  $P = 0.01$ , <sup>d</sup>  $P = 0.03$

The SIMPER analysis showed that *C. finmarchicus* CIII and CIV development stages contributed the most (24 and 39 %, respectively) to the observed pattern of dissimilarity in abundance. Stages CIV and CV of this copepod made substantial contributions (33 and 17 %, respectively) to the observed dissimilarities in biomass (Table 3).

### Chick diet composition

The nMDS plot of similarity in the diet composition (by biomass) showed no clear separation among colonies and dates. However, many MC4 samples were clustered in one group, different from the others (Fig. 3b). Generally, the diet samples from Hornsund were clustered more closely together than those from Magdalenefjorden (Fig. 3b). SIMPER procedure revealed that samples from the Magdalenefjorden colony were more dissimilar (average within-group dissimilarity: abundance 60 %, biomass and energy content 61 %) than those from the Hornsund colony (average within-group dissimilarity: abundance 29 %, biomass and energy content 30 %) (Table 4). SIMPER analysis also showed a high degree of dissimilarity in dietary composition between the last sample collected in Magdalenefjorden (MC4) and other samples (abundance: 79–83 %, biomass and energy content 82–85 %) (Table 4). SIMPER analysis showed that *C. glacialis* CV contributed greatly (59–64 %) to the observed dissimilarity in abundance, biomass and energy content among diet samplings. The sympagic amphipod *Apherusa glacialis* contributed 8 % to the observed dissimilarity in biomass and energy content (Table 3).

Comparison of abundance, biomass (dry mass) and energy content of *C. glacialis* CV in food samples revealed

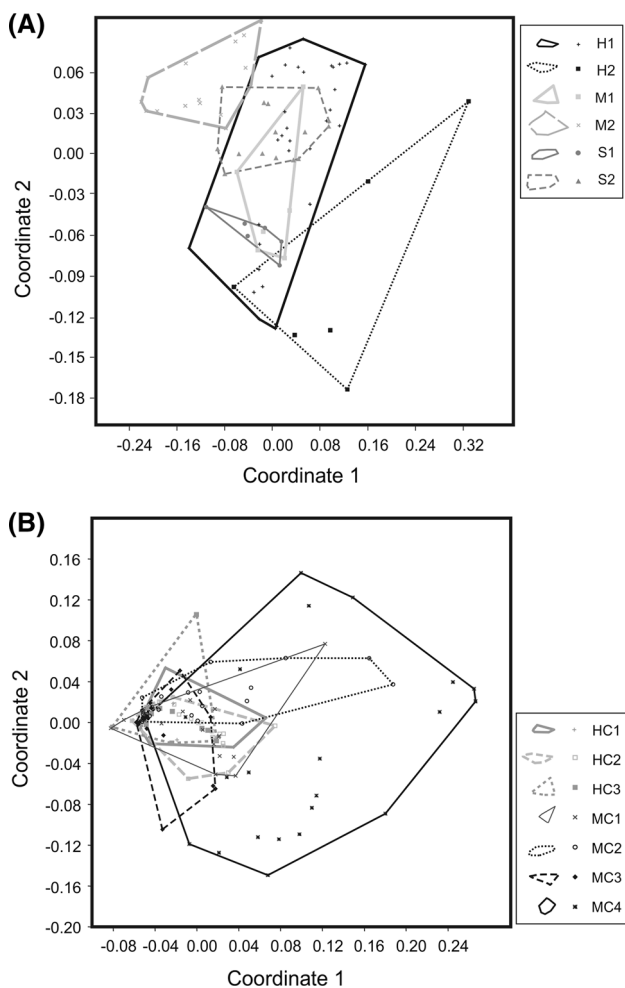
significantly lower values in MC4 compared to all other samplings. The medians were 46–58 times lower compared to earlier samplings in Magdalenefjorden and 45–65 times lower compared to Hornsund. In the case of all diet items combined, significant differences between MC4 and the majority of other samplings were recorded with median values 4–6 (abundance) and 2–3 times (biomass and energy) lower than in earlier samplings in Magdalenefjorden and 4–5 (abundance) and 2–3 (biomass and energy) times lower than in Hornsund (Table 5; Fig. 3b).

Dietary composition was generally similar in both colonies at all stages of the nestling period. *C. glacialis* CV was dominant prey, occurring frequently, and taken in great numbers (Fig. 4). Ancillary prey occurred in samplings MC2 and MC4 from Magdalenefjorden and included *A. glacialis*. The last sampling in Magdalenefjorden (MC4) was exceptional—there was no dominant prey species; the majority of prey items (including *C. glacialis* CV) were classified as being taken occasionally by most birds (Fig. 4).

The frequency of occurrence of *C. glacialis* CV in MC4 food loads was lower (24 % and 26 % in terms of biomass and energy, respectively) compared to other samplings (up to 87 %) (Table 6). *A. glacialis* made up 36 and 38 % of all prey items in terms of biomass and energy content, respectively (Table 6).

### Hatching phenology, chick survival and body mass

The distributions of hatching dates were similar in both colonies (Table 7; Fig. 2; Mann–Whitney *U* test,  $Z_{128, 126} = 1.73$ ,  $P = 0.08$ ) with median values on 15 and 16 July in Hornsund and Magdalenefjorden, respectively.



**Fig. 3** nMDS plots of Bray–Curtis similarities in the relative biomass of zooplankton taxa in **a** samples collected in the little auk foraging grounds in Magdalenefjorden (M1–M2) and Hornsund (H1–H2) shelf zones, in Smeerenburgfjorden (S1–S2) and **b** in the food samples collected from little auks in the colonies in Hornsund (HC1–HC3) and Magdalenefjorden (MC1–MC4) in 2010. Convex hulls contain all samples from one area/date

However, the hatching period in Magdalenefjorden lasted twice as long as in Hornsund (Table 7; Fig. 2).

In the logistic regression for chick survival up to 20 d, the hatching date x colony interaction term was insignificant ( $P = 0.94$ ). In analysis excluding the interaction, neither hatching date ( $P = 0.22$ ) nor colony ( $P = 0.81$ ) affected chick survival significantly. Chick survival up to 20 d was high (>95 %) and did not differ significantly between the two colonies (Table 7).

None of the GLM analyses (for peak body mass, pre-fledging mass and peak body mass age) revealed significant interaction between the hatching date and colony (all  $P > 0.29$ ). This indicates that the slopes relating those variables to hatching date did not differ strongly between the colonies. When we excluded the interaction term from the

**Table 2** Average percentage dissimilarity of zooplankton communities on the little auk foraging grounds in different periods of time in Hornsund (H1–H2), Magdalenefjorden (M1–M2) and Smeerenburgfjorden (S1–S2) in 2010 (SIMPER analyses; dissimilarity measure: Bray–Curtis) and summary of significance of differences assessment (ANOSIM; similarity measure: Bray–Curtis)

Code (N)	H1 (32)	H2 (6)	M1 (6)	M2 (15)	S1 (6)	S2 (15)
Abundance (ANOSIM $R = 0.37$ , $P = 0.0001$ )						
H1	–	78.4	59.0	86.4 <sup>a</sup>	63.6	56.5 <sup>b</sup>
H2	78.4	–	75.5	92.9 <sup>a</sup>	74.3	80.1
M1	59.0	75.5	–	82.3 <sup>a</sup>	43.8	50.3
M2	86.4 <sup>a</sup>	92.9 <sup>a</sup>	82.3 <sup>a</sup>	–	79.4 <sup>a</sup>	82.2 <sup>a</sup>
S1	63.6	74.3	43.8	79.4 <sup>a</sup>	–	58.5 <sup>c</sup>
S2	56.5	80.1 <sup>b</sup>	50.3	82.2 <sup>a</sup>	58.5 <sup>c</sup>	–
Biomass (ANOSIM $R = 0.35$ , $P = 0.0001$ )						
H1	–	82.6 <sup>a</sup>	62.3	81.4 <sup>a</sup>	66.6	57.6
H2	82.6 <sup>a</sup>	–	77.3	93.3 <sup>a</sup>	76.3	83.9 <sup>b</sup>
M1	62.3	77.3	–	77.2 <sup>a</sup>	47.0	56.9
M2	81.4 <sup>a</sup>	93.3 <sup>a</sup>	77.2	–	77.7 <sup>a</sup>	73.4 <sup>a</sup>
S1	66.6	76.3	47.0	77.7 <sup>a</sup>	–	61.2 <sup>c</sup>
S2	57.6 <sup>b</sup>	83.9	56.9	73.4 <sup>a</sup>	61.2 <sup>c</sup>	–

Superscript letters represent differences among samplings based on Bonferroni-corrected  $P$  values (ANOSIM): <sup>a</sup> 0.002, <sup>b</sup> 0.003, <sup>c</sup> 0.05

model, the colony affected significantly peak body mass ( $P = 0.002$ ); chicks in Hornsund were significantly heavier (by 7.1 g) compared to Magdalenefjorden (Table 7). Hatching date did not affect peak body mass significantly ( $P = 0.91$ ). Age at which the chicks gained peak body mass was affected significantly by the colony ( $P = 0.02$ ); chicks in Hornsund reached their peak body mass 1 day earlier than in Magdalenefjorden (Table 7). Hatching date did not affect peak body mass age significantly ( $P = 0.51$ ). The pre-fledging chick body mass was affected neither by colony ( $P = 0.25$ ) nor by hatching date ( $P = 0.84$ ) (Table 7).

### Discussion

To our knowledge, this is the first study investigating within-season variation in zooplankton availability, chick diet composition and breeding performance of zooplanktivorous little auks. Studies on changes in diet of zooplanktivorous seabirds may be especially informative, because they feed on organisms that respond relatively quickly and predictably to environmental variations (Bertram et al. 2001; Sydeman et al. 2001; Hipfner 2009).

Previous papers have shown that *Calanus glacialis* CV is the most important prey item for little auks breeding on Svalbard (Weslawski et al. 1999; Karnovsky et al. 2003; Kwasniewski et al. 2010; Jakubas et al. 2007, 2011, 2016,

**Table 3** Sources of variability in zooplankton composition (average percentage dissimilarity) in all foraging ground samples and chick diet samples (right) collected in 2010 according to the SIMPER analysis; only taxa with a contribution of (Contr.) >5 % are presented

Zooplankton items	Abundance		Biomass		Energy content	
	Average dissimilarity	Contr. (%)	Average dissimilarity	Contr. (%)	Average dissimilarity	Contr. (%)
Foraging grounds						
<i>C. finmarchicus</i> CV	5.9	8.2	11.9	16.7	–	–
<i>C. finmarchicus</i> CIV	28.2	39.4	23.4	32.9	–	–
<i>C. finmarchicus</i> CIII	17.4	24.3	5.6	7.9	–	–
<i>C. glacialis</i> CV			10.3	14.5	–	–
<i>C. glacialis</i> CIV	7.4	10.4	11.3	15.8	–	–
<i>C. glacialis</i> CIII	6.4	8.9	–	–	–	–
Chick diet						
<i>Apherusa glacialis</i>	–	–	4.1	8.3	3.8	7.7
<i>C. finmarchicus</i> CV	4.8	9.9	–	–	–	–
<i>C. glacialis</i> AF	–	–	2.9	5.7	3	6.1
<i>C. glacialis</i> CV	31.1	63.6	29.5	59.1	30	60.4
<i>C. hyperboreus</i> AF	–	–	–	–	2.5	5.1
<i>T. abyssorum</i> <5 mm	2.7	5.4	–	–	–	–

**Table 4** Average percentage dissimilarity of little auk chick diet composition (abundance, biomass and energy content) between samples collected in different periods of time in Hornsund (HC1–HC3) and Magdalenefjorden (MC1–MC4) in 2010 (SIMPER analyses; dissimilarity measure: Bray–Curtis) and summary of significance of differences assessment (ANOSIM; similarity measure: Bray–Curtis)

Code (N)	HC1 (13)	HC2 (30)	HC3 (23)	MC1 (23)	MC2 (23)	MC3 (19)	MC4 (23)
Abundance (ANOSIM $R = 0.18$ , $P = 0.0001$ )							
HC1	–	31.4	26.0	38.3	37.5	34.0	83.1 <sup>a</sup>
HC2	31.4	–	28.2	35.8	37.2	37.7 <sup>c</sup>	82.1 <sup>a</sup>
HC3	26.0	28.2	–	35.5 <sup>b</sup>	34.8 <sup>d</sup>	32.0 <sup>c</sup>	83.3 <sup>a</sup>
MC1	38.3	35.8	35.5 <sup>b</sup>	–	39.9	39.5	79.1 <sup>a</sup>
MC2	37.5	37.2	34.8 <sup>d</sup>	39.9	–	38.9	80.0 <sup>a</sup>
MC3	34.0	37.7 <sup>c</sup>	32.0 <sup>c</sup>	39.5	38.9	–	80.3 <sup>a</sup>
MC4	83.1	82.1 <sup>a</sup>	83.3 <sup>a</sup>	79.1 <sup>a</sup>	80.0 <sup>a</sup>	80.3 <sup>a</sup>	–
Biomass (ANOSIM $R = 0.17$ , $P = 0.0001$ )							
HC1	–	33.1	27.7	39.3	39.6	34.3	85.0
HC2	33.1	–	28.6	35.1	38.3	36.0	83.7 <sup>a</sup>
HC3	27.7	28.6	–	34.6 <sup>g</sup>	35.6 <sup>e</sup>	30.8	85.1 <sup>a</sup>
MC1	39.3	35.1	34.6 <sup>g</sup>	–	41.4	38.9	82.2 <sup>a</sup>
MC2	39.6	38.3	35.6 <sup>e</sup>	41.4	–	39.6	83.0 <sup>a</sup>
MC3	34.3	36.0	30.8	38.9	39.6	–	83.2 <sup>a</sup>
MC4	85.0	83.7 <sup>a</sup>	85.1 <sup>a</sup>	82.2 <sup>a</sup>	83.0 <sup>a</sup>	83.2 <sup>a</sup>	–
Energy content (ANOSIM $R = 0.17$ , $P = 0.0001$ )							
HC1	–	32.9	27.6	39.1	39.2	34.0	85.0
HC2	32.9	–	28.5	34.9	37.9	35.5	83.8 <sup>a</sup>
HC3	27.6	28.5	–	34.3 <sup>f</sup>	35.3 <sup>e</sup>	30.4	85.1 <sup>a</sup>
MC1	39.1	34.9	34.3 <sup>f</sup>	–	41.1	38.6	82.3 <sup>a</sup>
MC2	39.2	37.9	35.3 <sup>e</sup>	41.1	–	39.3	83.1 <sup>a</sup>
MC3	34.0	35.5	30.4	38.6	39.3	–	83.3 <sup>a</sup>
MC4	85.0	83.8 <sup>a</sup>	85.1 <sup>a</sup>	82.3 <sup>a</sup>	83.1 <sup>a</sup>	83.3 <sup>a</sup>	–

Superscript letters represent differences among samplings based on Bonferroni-corrected  $P$  values (ANOSIM): <sup>a</sup> 0.002, <sup>b</sup> 0.004, <sup>c</sup> 0.008, <sup>d</sup> 0.01, <sup>e</sup> 0.02, <sup>f</sup> 0.03, <sup>g</sup> 0.04



**Table 5** Comparison of abundance (ind. meal<sup>-1</sup>), biomass (dry mass) (mg meal<sup>-1</sup>) and energy content (kJ meal<sup>-1</sup>) of *C. glacialis* CV and all zooplankton items in food loads collected from adult little auks in different periods of time in the Hornsund (HC1–HC3) and Magdalenefjorden (MC1–MC4) colonies in 2010;  $Q_1$ – $Q_2$ —percentiles 25–75 %

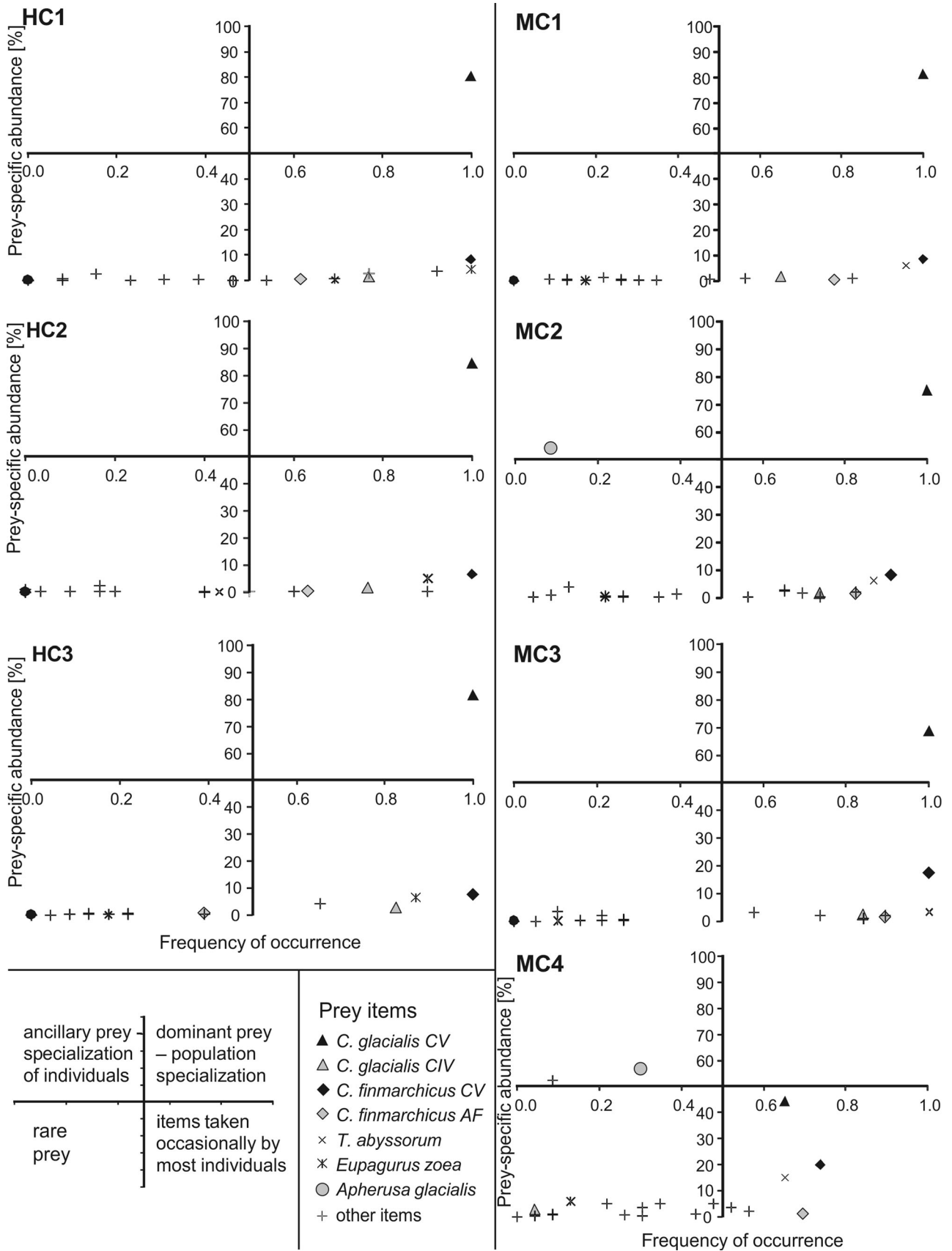
Variable	Code	All items combined			<i>C. glacialis</i> CV		
		Median	$Q_1$ – $Q_3$	<i>N</i>	Median	$Q_1$ – $Q_3$	<i>N</i>
Abundance	HC1	2266.0 <sup>a</sup>	2152–3295	13	2005.0 <sup>a</sup>	1605–2399	13
	HC2	1848.5 <sup>b,g</sup>	1330–2323	30	1455.0 <sup>b</sup>	1130–2060	30
	HC3	2390.0 <sup>c</sup>	1891–2858	23	1980.0 <sup>c</sup>	1620–2250	23
	MC1	1796.0 <sup>d</sup>	1005–2482	23	1440.0 <sup>d</sup>	778–2033	23
	MC2	1913.0 <sup>e</sup>	1539–2626	23	1500.0 <sup>e</sup>	1205–1980	23
	MC3	2702.0 <sup>f,g</sup>	2170–3146	19	1799.0 <sup>f</sup>	1495–2260	19
	MC4	433.0 <sup>a,b,c,d,e,f</sup>	272–679	23	31.0 <sup>a,b,c,d,e,f</sup>	0.0–133	23
	Biomass	HC1	1496.2 <sup>a</sup>	1286.4–1876.3	13	1243.3 <sup>a</sup>	995.2–1487.6
HC2		1114.9	779.1–1380.2	30	902.2 <sup>b</sup>	700.7–1277.4	30
HC3		1402.5 <sup>b</sup>	1102–1586.7	23	1227.8 <sup>c</sup>	1004.5–1395.2	23
MC1		1062.2	608.3–1426.1	23	892.9 <sup>d</sup>	482.4–1260.6	23
MC2		1284.8 <sup>c</sup>	1108.8–1504.7	23	930.1 <sup>e</sup>	747.2–1227.8	23
MC3		1513.4 <sup>d</sup>	1117.5–1705.4	19	1115.5 <sup>f</sup>	927.0–1401.4	19
MC4		559.3 <sup>a,b,c,d</sup>	195.7–1047.7	23	19.2 <sup>a,b,c,d,e,f</sup>	0.0–82.5	23
Energy content		HC1	44.9 <sup>a</sup>	38.5–55.5	13	37.2 <sup>a</sup>	29.8–44.5
	HC2	33.2	23.2–41.2	30	27.0 <sup>b</sup>	21.0–38.2	30
	HC3	41.9 <sup>b</sup>	32.9–47.5	23	36.8 <sup>c</sup>	30.1–41.8	23
	MC1	31.7	18.1–42.5	23	26.7 <sup>d</sup>	14.4–37.7	23
	MC2	37.9 <sup>c</sup>	32.6–44.9	23	27.8 <sup>e</sup>	22.4–36.8	23
	MC3	45.1 <sup>d</sup>	33.3–50.6	19	33.4 <sup>f</sup>	27.8–42.0	19
	MC4	15.2 <sup>a,b,c,d</sup>	5.3–29.1	23	0.6 <sup>a,b,c,d,e,f</sup>	0.0–2.5	23

Superscript letters represent differences among samplings based on Kruskal–Wallis ( $P < 0.001$ ) and post hoc Dunn tests: <sup>a, b, c, d, e, f</sup>  $P < 0.007$ , <sup>g</sup>  $P = 0.04$

Kidawa et al. 2015). Our study indicates that this preference is temporally consistent throughout the chick-rearing period. This prey item made up 68–87 % of all dietary components in terms of biomass and energy in both colonies during all the samplings in Hornsund and the first three in Magdalenefjorden. Only during the last diet sampling in Magdalenefjorden (MC4), contribution of *C. glacialis* CV was considerably lower (24 and 26 % in biomass and energy content, respectively), suggesting a mismatch of late breeders in this colony with the peak availability of the preferred prey item.

Considering similar ice conditions (i.e. lack of ice in close proximity of colonies) in both areas and high biomass of *C. glacialis* CV in zooplankton samples collected in Hornsund at the same time as MC4 chick diet sampling in Magdalenefjorden, one may expect similar *C. glacialis* CV availability for birds from both colonies, even late in the season. Although we have no data on zooplankton abundance in the little auk feeding grounds for the period of the last diet sampling in the Magdalenefjorden colony (MC4), our results suggest divergent patterns of *C. glacialis* CV availability in both studied areas throughout the little auk nestling period. Firstly, the biomass of that prey item found in the zooplankton samples collected in the Magdalenefjorden area (M2) 1 week before the last diet sampling

(MC4) was significantly lower than during the first sea sampling there (M1) (Fig. 5). Also, the biomass of *C. glacialis* CV in M2 sample was significantly lower than that found at the same phenological stage in the Hornsund area (H2) (Fig. 5). Secondly, we found an opposite pattern of changes in *C. glacialis* CV abundance and biomass between the first and second sea samplings in the two areas, with an increasing trend in Hornsund and decreasing one in Magdalenefjorden feeding grounds. This indicates a poor availability of this prey item at the end of chick-rearing phase in the latter colony during MC4 diet sampling suggesting mismatch of late breeders with peak availability of the preferred food. It suggests that abundance of *C. glacialis* CV throughout the little auk chick-rearing period might differ between areas despite similar winter and spring ice conditions determining the timing of ice algal and phytoplankton blooms and subsequently the timing of life-history events of this copepod (Daase et al. 2013). Differences in specific local conditions (e.g. temperature, timing of the onset and magnitude of the spring phytoplankton bloom) may affect development and recruitment of *C. glacialis* in both areas (Daase et al. 2013). Additionally, a study of fine-scale zooplankton vertical distribution performed at the turn of July and August 2010 revealed that in the shelf zone in Hornsund area the highest proportion of *C. glacialis* to *C.*



**Fig. 4** Costello diagrams, i.e. scatterplots of all little auk prey species according to their occurrence and prey-specific abundance in diet samples collected in different periods in Hornsund (HC1–HC3) and Magdalenefjorden (MC1–MC4) in 2010. *Lower left* Interpretation of the diagram according to Amundsen et al. (1996)

*finmarchicus* was found at the surface layer (depth of 0–10 m) contrary to the Magdalenefjorden area, where it was recorded considerably deeper (20–40 m) (Trudnowska et al. 2015). Moreover, autumn descent of *C. glacialis* CV to deeper water (<50 m) in Kongsfjorden (75 km south of

**Table 6** Abundance, biomass and energy content of the most common prey items in food samples (% in all samples) collected from adult little auks in the colonies in different periods of time in Hornsund (HC1–HC3) and Magdalenefjorden (MC1–MC4) in 2010 (>15 % bolded, ‘–’ denotes the lack of the prey item in the samples)

Relative...	HC1	HC2	HC3	MC1	MC2	MC3	MC4
<b>Abundance (%)</b>							
<i>Calanus finmarchicus</i> CV	8.1	6.4	7.4	8.4	7.9	<b>17.4</b>	<b>17.4</b>
<i>C. glacialis</i> AF	3.3	2.0	2.7	0.8	1.5	1.9	0.5
<i>C. glacialis</i> CV	<b>80.5</b>	<b>84.6</b>	<b>81.5</b>	<b>81.4</b>	<b>75.0</b>	<b>68.8</b>	<b>38.2</b>
<i>C. hyperboreus</i> AF	<0.01	–	<0.01	0.6	1.5	<0.01	2.6
<i>Themisto libellula</i>	0.2	0.1	0.0	5.7	7.5	4.1	13.7
<i>Th. abyssorum</i>	0.0	0.0	0.0	0.0	1.4	0.0	9.8
<i>Apherusa glacialis</i>	–	–	–	–	1.4	–	9.8
<i>Thysanoessa inermis</i>	0.2	0.1	<0.01	<0.01	<0.01	<0.01	0.9
<b>Biomass (%)</b>							
<i>C. finmarchicus</i> CV	2.8	2.3	2.7	3.1	2.5	6.9	3.8
<i>C. glacialis</i> AF	6.8	4.4	5.8	1.9	2.8	4.7	0.6
<i>C. glacialis</i> CV	<b>80.1</b>	<b>86.4</b>	<b>84.6</b>	<b>86.6</b>	<b>68.4</b>	<b>79.1</b>	<b>24.0</b>
<i>C. hyperboreus</i> AF	<0.01	–	<0.01	3.3	7.1	0.3	8.5
<i>Themisto libellula</i>	2.4	0.8	0.3	0.8	1.7	1.3	6.0
<i>Th. abyssorum</i>	0.2	0.1	0.1	1.6	5.0	3.3	3.6
<i>Apherusa glacialis</i>	–	–	–	–	7.8	–	<b>38.5</b>
<i>Thysanoessa inermis</i>	1.3	0.5	0.1	0.4	0.4	0.3	4.6
<b>Energy content (%)</b>							
<i>C. finmarchicus</i> CV	2.6	2.1	2.5	2.9	2.4	6.5	3.8
<i>C. glacialis</i> AF	7.2	4.6	6.1	2.0	3.0	4.9	0.7
<i>C. glacialis</i> CV	<b>80.6</b>	<b>86.8</b>	<b>84.9</b>	<b>87.1</b>	<b>69.9</b>	<b>80.0</b>	<b>25.9</b>
<i>C. hyperboreus</i> AF	<0.01	–	<0.01	3.4	7.4	0.3	9.4
<i>Themisto libellula</i>	2.2	0.7	0.3	0.7	1.5	1.2	5.8
<i>Th. abyssorum</i>	0.1	0.1	0.1	1.4	4.4	2.8	3.3
<i>Apherusa glacialis</i>	–	–	–	–	6.9	–	<b>36.1</b>
<i>Thysanoessa inermis</i>	1.2	0.5	0.1	0.4	0.3	0.3	4.6

**Table 7** Chick growth and breeding success in little auks breeding in the Magdalenefjorden and Hornsund colonies in 2010 (*N* number of nests studied, SD standard deviation,  $Q_1$ – $Q_3$ —percentiles 25–75 %)

Variable	Hornsund	Magdalenefjorden
<b>Hatching</b>		
Date—median,	15 July,	16 July,
$Q_1$ – $Q_3$ ( <i>N</i> )	14–17 July (126)	13–19 July (128)
Range (day)	11	22
<b>Breeding success variables</b>		
Chick survival up to 20 days ( <i>N</i> )	96 % (78)	96 % (94)
<b>Chick growth variables</b>		
Peak body mass (g)—mean ± SD ( <i>N</i> )	129.9 ± 9.2 (27)	122.8 ± 9.2 (50)
Peak body mass age (day)—mean ± SD ( <i>N</i> )	19 ± 1.7 (27)	20 ± 2.8 (50)
Pre-fledging body mass (g)—mean ± SD ( <i>N</i> )	122.3 ± 9.6 (22)	118.1 ± 11.1 (58)



large proportion of alternative energy-rich prey items like *Apherusa glacialis* or *Calanus hyperboreus*, which suggests that the little auks explored more distant foraging grounds. These prey items occur in substantial densities relatively far from Magdalenefjorden, in the marginal sea ice zone (ca 110–140 km from the colony at that time, Fig. 1) and in the open sea in the West Spitsbergen Current (Lønne and Gulliksen 1991; Scott et al. 1999; Arndt and Swadling 2006; Hop et al. 2006; Kwasniewski et al. 2010). The regular presence of the ice-associated amphipod *A. glacialis* in food samples from Magdalenefjorden has been reported earlier (Kwasniewski et al. 2010; Jakubas et al. 2011; Boehnke et al. 2015), and GPS tracking has confirmed that little auks forage repeatedly in the marginal sea ice zone (Jakubas et al. 2012, 2013). Such a switch between foraging grounds was not fully effective; the total energy content of the MC4 food loads was 2–3 times less than earlier samples from the same colony. Given the high costs of little auk locomotion and foraging (Gabrielsen et al. 1991; Konarzewski et al. 1993), it seems that frequent exploitation of distant feeding grounds over a longer time scale could be too costly for the parent birds. In the course of chick-rearing period, they normally reach such distant foraging areas only during infrequent long foraging trips (Jakubas et al. 2012).

In contrast to the planktivorous Cassin's auklet (in which decreased nestling growth and survival have been reported in 'mismatch' years with reduced prevalence and persistence of its primary prey, *N. cristatus* in nestling diets; Hipfner 2008), low-energy food with a very small proportion of the preferred *C. glacialis* CV delivered to chicks in Magdalenefjorden late in the season (MC4) did not adversely affect little auk nestlings. Peak body mass was higher in Hornsund; however, it was not affected by the hatching date. The pre-fledging body mass and chick survival up to 20 days were similar in both colonies and were not related to the hatching date. Given the advanced age of chicks of the late breeders' in Magdalenefjorden during the 'mismatched' MC4 sampling (25–26 days of life; Figs. 2, 5), they may have been little affected by the smaller quantity and inferior quality of food loads, since they were already in the phase of decreasing body mass after reaching the peak mass around 20 d of life (Stempniewicz 1980) and their energy requirements were relatively low at that stage of development (Konarzewski et al. 1993). Moreover, at that age little auk chicks usually have the highest fasting capacity owing to the considerable extra fat reserves they have built up (Taylor and Konarzewski 1989). However, worse quality and quantity of food delivered to chicks of late breeders late in the season may have affected their date of fledging. We have no data to verify it but slower chick growth rate in suboptimal food condition has been documented in the zooplanktivorous

Cassin's auklet (Bertram et al. 2001, Hedd et al. 2002) as well in the little auk in the studied colonies in previous seasons (chicks from Hornsund fledged earlier than in Magdalenefjorden; Jakubas et al. 2013).

Our results show that timing of breeding of little auks generally matched high availability of their preferred prey in both colonies in the year of this study, except for the late breeders in the Magdalenefjorden colony, which probably were mismatched during the late stage of chick-rearing period. Despite low-energy content of food delivered to chicks late in the season (during our last sampling) in Magdalenefjorden, reproductive output was not affected significantly by the hatching date. This confirms previous observations that little auks breeding on Spitsbergen can respond to a wide range of environmental conditions and prey availabilities through the plasticity of their foraging behaviour (Jakubas et al. 2007, 2011, 2013, 2016; Harding et al. 2009; Kwasniewski et al. 2010). The effectiveness of behavioural buffering may be affected by oceanographic conditions and colony location. Hovinen et al. (2014b) revealed that fledging probability was generally higher in Magdalenefjorden (range 0.91–1.0) with lower sea surface temperature (SST) than in Isfjorden (range 0.62–0.97) with higher SST, resulting in worse prey availability and quality in the little auk's foraging grounds. Location of colony in area offering alternative foraging grounds, which may be explored when the trophic conditions in the traditional foraging areas deteriorate, may determine the birds' ability to modify foraging strategy (Jakubas et al. 2012, 2016; Kidawa et al. 2015).

We are aware of some limitations of our study. Areas of at-sea sampling were chosen based on previous knowledge of little auks foraging grounds location, although we cannot exclude that birds sometimes would have foraged outside those traditional areas, e.g. in local temporary phenomena, like eddies enhancing productivity and concentration of zooplankton (Joiris and Falck 2011; Jakubas et al. 2013). Our limited data set based on one year and two zooplankton sampling replicates is insufficient for a comprehensive test of the match–mismatch hypothesis. The data presented here can, however, be treated as a pilot study contributing to the planning of a broad-scaled investigation covering several seasons and sites differing in oceanographic conditions and zooplankton/bird phenology. Nevertheless, our study has filled an evident gap in knowledge about within-season diet variation of the little auk and its preferred food availability in the high Arctic.

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