

Zooplankton phenology may explain the North Water polynya's importance as a breeding area for little auks

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ABSTRACT: The little auk *Alle alle* is the most abundant seabird in the North Atlantic, and >80 % of the global population breeds along Greenland's shores of the North Water (NOW) polynya region. We questioned why the NOW is such an important little auk breeding area, and hypothesized that the key factor may involve chick feeding opportunities. We studied the oceanography, and the distribution and abundance of little auks and their zooplankton prey between 73 and 78.5°N in August 2015, and concurrently sampled little auk chick diets. Zooplankton in the diet were dominated by *Calanus hyperboreus* and *C. glacialis*, but biomasses, community compositions and depth distributions differed across the latitudinal range. Little auk chicks were mainly fed *Calanus* spp. between 3 and 5 mm. Within the foraging range of the breeding colonies, areas where phytoplankton was concentrated in patches in the water column were important for the foraging distribution of little auks, and increasingly so at shorter distances from the colonies. In the NOW region, in contrast to other areas in Baffin Bay, high abundances of large *Calanus* spp. are present within little auk diving range both in spring/early summer and in late summer during the little auk chick-rearing period. We conclude that this unusually long and continuous presence of suitable prey items in the surface waters, covering the full little auk breeding cycle, is the main reason why the NOW region, under current climate conditions, is the most important little auk breeding area globally.

KEY WORDS: Little auk · *Alle alle* · Zooplankton · Phytoplankton · Arctic · *Calanus* · Baffin Bay · North Water polynya

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INTRODUCTION

For centuries, some Arctic marine areas have been known to be particularly productive biologically, and to sustain large populations of fish, marine mammals and seabirds (Deming et al. 2002, Heide-Jørgensen et al. 2007, Lydersen et al. 2014). Identification of such hot spots and the mechanisms controlling their productivity and ecosystem dynamics are critical

when assessing the vulnerability of ecosystems to climate change and other human impacts. The high-Arctic North Water (NOW) region is a particularly productive area, and it contains the world's largest breeding population of little auk *Alle alle*, a zooplanktivorous diving alcid weighing approximately 160 g. The little auk is the most abundant seabird in the North Atlantic, and about 33 million pairs, corresponding to >80 % of the global population, breed

along 325 km of Greenland's shores in the NOW region (Boertmann & Mosbech 1998, Kampp et al. 2000, Egevang et al. 2003).

We used the little auk population in the NOW region to study the dynamics of a marine ecosystem that maintains very large colonies of a seabird that is a central-place forager during chick rearing. The Ashmole's Halo hypothesis for colonial seabirds predicts that foraging range increases with colony size, ultimately leading to a decline in reproductive success due to intraspecific competition (Ashmole 1963, Gaston et al. 2007). The hypothesis has general empirical support (e.g. Elliot et al. 2009), though factors other than intraspecific food competition, such as bathymetry, oceanographic features and interspecific food competition (with e.g. fish), are important for the distribution of lucrative and popular food patches (Amélineau et al. 2016, Bertram et al. 2017, Wilkinson et al. 2018). For large seabird colonies to exist, there must be a high prey density within the birds' foraging range, and the birds must be able to find the prey to feed their chicks. In a typical high-Arctic marine system there is a spring peak in the surface waters of both phytoplankton and zooplankton following ice melt (Daase et al. 2013). However, the crucial time of chick rearing is much later than the spring peak. We predict that the presence of large zooplankton in the surface layers at this time are important for the distribution of little auk colonies.

The genus *Calanus* is key among zooplankton in the Arctic (Falk-Petersen et al. 2007) and a main prey for the little auk (Steen et al. 2007, Karnovsky et al. 2008, Frandsen et al. 2014). *Calanus* spend the winter at depth in hibernation, and arrive in the surface layers in spring to feed on the phytoplankton and fill their lipid stores for the following winter. When they leave the surface layer, the zooplankton community becomes dominated by smaller species, and often the biomass is much lower (Madsen et al. 2001a, Møller et al. 2006). The timing of their descent to deeper waters is crucial to their predators. Visual predators, like many fish species, depend on the light in the surface waters (Langbehn & Varpe 2017), and seabirds like the little auk can only dive to 50 m, thus to these predators, *Calanus* are only accessible when they are still in the surface layers.

Smith Sound in Northern Baffin Bay (see Fig. 1) is a very productive area (Michel et al. 2015) with great importance to many seabirds and marine mammals, and it has been identified as an area of particular ecological and biological significance (Barber et al. 2001a, Christensen et al. 2012). The main reason for its high productivity is the presence of the NOW

polynya. Typically, an ice arch forms during winter in the southern part of Kane Basin, blocking inflow of drift ice from the Polar Sea, and strong northerly winds sweep the area south of the ice arch free from the new ice that continuously forms on the sea surface. The open water and the recurring formation of new sea ice increases the seawater density, which sinks and entrains circulation and upwelling of water (Melling et al. 2001). The permanently open water and low sea ice cover allow phytoplankton blooms to start much earlier than in surrounding areas (Ringuette et al. 2002, Tremblay et al. 2006). Accordingly, the abundance of the dominant zooplankton genus *Calanus* is higher in the NOW than in the nearby non-polynya area of Barrow Strait, with recruitment of young copepods starting 1.5 to 3 mo earlier in the NOW (Ringuette et al. 2002). The distribution and production of plankton is influenced both by local production and by the circulation of water masses. Water from the Arctic Ocean flows into the polynya from the north through Nares Strait, where it mixes with southern waters deriving from a northwest flowing branch of the West Greenland Current (Bâcle et al. 2002, Tremblay et al. 2002). The eastern, Greenlandic part of the NOW is significantly more productive than the western part (Klein et al. 2002), probably due to a broad relatively shallow shelf and stronger influence and advection of nutrients from the West Greenland Current.

Due to the special importance of the NOW in spring and early summer, much effort has been invested in studying the physical processes and primary/secondary production that occurs during this period (Deming et al. 2002). However, for little auks, the period later in the summer—from mid-July to mid-August, when they feed their chicks and prepare for southward migration—may be more critical. At this time, each pair has to bring in ca. 9 meals of lipid-rich copepods each day to raise their single chick (Welcker et al. 2009, Frandsen et al. 2014, Mosbech et al. 2017). To procure these meals, they frequent foraging grounds up to 100 km or more from their breeding colonies and dive intensively as deep as 50 m (Jakubas et al. 2013, A. Mosbech et al. unpubl. data). Previously, the little auk has been estimated to be responsible for more than 90 % of the carbon flux to seabirds in the NOW (Karnovsky & Hunt 2002); however, those estimates were based on sampling in the western part of the NOW, i.e. not covering the waters in proximity to the little auk colonies. Although not assessed directly, studies of little auk carbon demands during summer suggest that the area close to the Greenlandic coast is very important, and that zoo-

plankton abundance there has to be very high to sustain the little auk's energy requirements (Karnovsky & Hunt 2002).

In this paper, we sought to determine why the NOW is such an important breeding area for the little auk. To address this question, we investigated physical oceanography, vertical and horizontal distribution and biomass of phytoplankton and zooplankton, as well as the at-sea densities of foraging little auks in northern Baffin Bay and eastern Smith Sound (73 to 78.5° N) during early August 2015. To evaluate the importance of different zooplankton species to the chicks, we sampled chick meals in adjacent colonies. We hypothesized that the main reason why the NOW is such an important breeding area for the little auk is that suitable prey are available within diving range of the birds throughout the whole summer, as opposed to most other high-Arctic marine areas, where primary and secondary production are concentrated in short-lived blooms.

MATERIALS AND METHODS

Sampling and survey effort

The study was carried out off the Greenland coast in August 2015. Three areas were sampled (hereafter referred to as north, middle and south) with the HDMS 'Ejnar Mikkelsen' from the Danish Navy (1 to 8 August 2015, middle and northern area) and the RV 'Sanna' from the Greenland Institute of Natural Resources (10 to 15 August 2015, southern area) (Fig. 1). In the southern area, corresponding to eastern Baffin Bay, we sampled 11 stations off Upernavik (between ~73 and 74° N). In the middle area, which covers northwestern Melville Bay and the southern extension of the NOW (between ~75.3 and ~76.3° N), 27 stations were sampled. In the northern area, encompassing Smith Sound in the northern part of the NOW, 13 stations were sampled (between ~76.6 and 78.5° N). The stations were laid out on linear transects, generally with 10 km spacing between stations. The transects cut across gradients in bathymetry, many traversing shelf and shelf-break, extending into deep waters. In the north and middle areas, which correspond to the breeding range of the little auk, the transects were specifically designed to cross gradients in the density of foraging auks, assuming that the birds undertake directional trips from their colonies to the offshore foraging areas as shown by Amélineau et al. (2016). Thus, based on the positions of breeding colonies (Boertmann & Mosbech 1998), the transects extended

perpendicularly from coasts where the little auks breed. In the middle area, the transects reached 100 km from the coast, almost encompassing the maximal foraging range recorded for little auks breeding in the NOW (Mosbech et al. 2018). On one transect (A, and later, T), the stations were sampled twice on 3–4 and 11–12 August. Physical variables and zooplankton were sampled at the stations; little auk counts were made between the stations.

Hydrography

Salinity and temperature were measured with a Seabird CTD (SBE19-2V), to the bottom of the NOW from R/V 'Sanna' and to 150 m depth from HDMS 'Ejnar Mikkelsen'. The CTD on the HDMS 'Ejnar Mikkelsen' also carried a WetLabs ECO FLNTU fluorometer. Data were plotted using the statistical software R (R Development Core Team 2016).

Phytoplankton

At each station, water was sampled at 5, 20, 30, 50 and 100 m from HDMS 'Ejnar Mikkelsen' and at 10, 20 and 50 m from RV 'Sanna'. Chlorophyll *a* (chl *a*) was measured in duplicate by filtering 250 ml of water through GF/F filters. Filters were extracted in 5 ml of 96 % ethanol for 24 h (Jespersen & Christoffersen 1987), and fluorescence was measured on a Turner Trilogy fluorometer (before and after HCl addition) calibrated against a chl *a* standard. The fluorescence from the CTD on HDMS 'Ejnar Mikkelsen' was calibrated using the measured chl *a* values and, in the depth range of 0 to 50 m, chl *a* was integrated using the calibrated profiles. Since chl *a* measurements from the RV 'Sanna' were only made at 3 depths, peaks in chl *a* may not have been captured, and integrated values were therefore not calculated for the southern area covered by that vessel.

Zooplankton

At each station, 2 samples were taken with a 60 µm WP2 net (0.25 m²; UNESCO 1968); one from 0 to 50 m and one from just above the bottom (max. depth 750 m) to the surface. Sampling was carried out both day and night. Samples were preserved in buffered formalin (4 % final concentration). For copepods, individuals were counted, and species/genera, stage and sex were identified. *Calanus hyberboreus* were

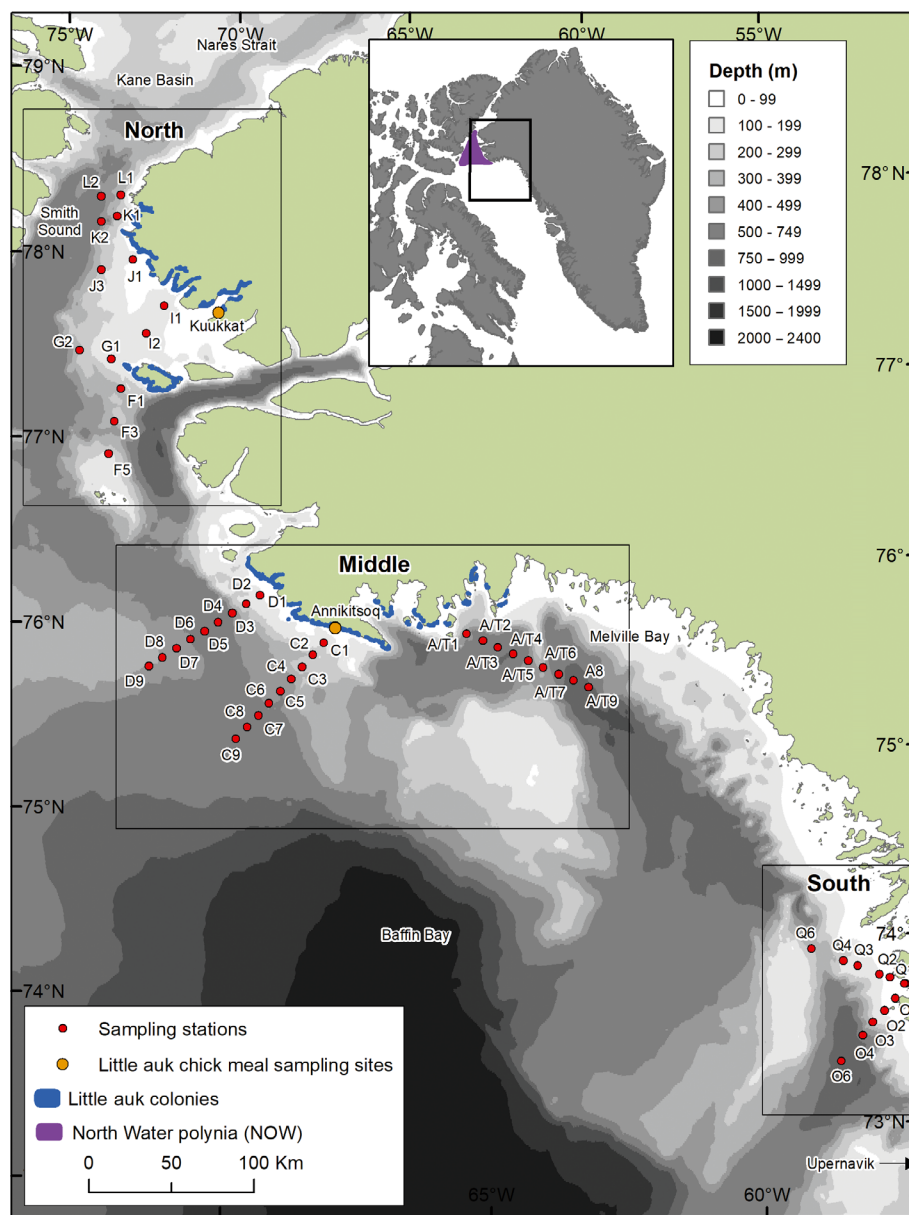


Fig. 1. Study area, indicating the positions of sampling stations, distribution of little auk breeding colonies and sites where little auk gular pouch samples were collected. Also shown are the 3 sub-areas used in the data analyses. The southern area corresponds to eastern Baffin Bay (~73–74°N); the middle area covers north-western Melville Bay and the south-eastern extension of the North Water (NOW)/Smith Sound (~75.3–76.3°N); the northern area corresponds to north-eastern part of NOW/Smith Sound (~76.6–78.5°N). On the overview map, the solid purple area represents the approximate late winter/early spring extent of the NOW polynya

identified to species for copepodite stages CIII–CVI, while *C. finmarchicus* and *C. glacialis* were identified to species for CV and CVI based on prosome length (Swailethorp et al. 2011, Nielsen et al. 2014). All smaller stages were only identified to genus. Prosome length was measured for 10 individuals in each species/stage group in all samples. Biomass of copepods was calculated using length to C-weight regressions from the literature (Klein Breteler et al. 1982, Hirche & Mumm 1992, Sabatini & Kjørboe 1994, Hygum et al. 2000, Madsen et al. 2001, Satapoomin et al. 2004). Non-copepod zooplankton groups were identified to genus or species and counted; their total lengths were measured.

Multivariate analysis of *Calanus* community structure

The copepod community structure was investigated by non-metric multidimensional scaling (NMDS) ordination (Oksanen et al. 2011). The sample units were *Calanus* copepodite and adult abundances at the different stations in the 0 to 50 m depth range. Pairwise distances among samples were calculated using the Bray-Curtiss dissimilarity index (or Steinhaus dissimilarity index) as the community dissimilarity measure. Bray-Curtis distances are well-suited for analysis of ecological data and regarded as good for detecting gradients (Oksanen

et al. 2011). Since the data range was very large, the raw abundances were square-root transformed and then submitted to Wisconsin double standardization (each species is divided by its maximum and each sample by its total). The NMDS analysis is an iterative process, and the best solution is that with the lowest stress (highest goodness-of-fit). In order to support the interpretation of the results from the NMDS, environmental vectors of average temperature (10 to 50 m), average salinity (10 to 50 m), integrated chl *a* (0 to 50 m) and latitude were fitted onto the ordination. The vectors show the directions of gradients, and the lengths of the arrows are proportional to the correlation between the variable and the ordination. Statistical significance of the environmental variables was assessed on the basis of permutation tests (999 permutations; Oksanen et al. 2011). The analyses were done using the ‘vegan’ package (Oksanen et al. 2011) in R (R Development Core Team 2016).

Little auk observations

Little auks were counted on the transects between sampling stations. We used a survey protocol developed specifically for seabird observations in Greenland waters (Johansen et al. 2015), which is based on European Seabird at Sea (ESAS) procedures (Tasker et al. 1984, Webb & Durinck 1992). Birds were counted within a 300 m wide strip on one side of the track line of the ship, using flocks of birds (with flock size) as the sighting unit. Birds observed on the sea surface (e.g. foraging/resting) were attributed to specific distance bands subdividing the strip (0–50, 50–100, 100–200 and 200–300 m), whereas flying birds were simply recorded within the 300 m strip using the snapshot technique (Tasker et al. 1984). Due to our focus on foraging, only birds observed on the sea surface were included in the statistical analyses.

When observing birds from a ship, detection probability tends to decrease with distance from the ship, and often factors such as flock size, weather conditions and sea state are also important. Distance sampling methods make it possible to model detection probability as a function of perpendicular distance from the track line of the ship and other co-variables (Buckland et al. 2001), and we used Distance v.6.2 software (Thomas et al. 2010) to evaluate different detection functions (uniform, half-normal, hazed rate and negative exponential) for our little auk data. Based on Akaike’s information criterion corrected for

small sample size (AIC_c), we selected a hazard rate detection function and used it to calculate the abundance of little auks on the sea surface within a 300 m \times 4 km rectangle around each sampling station.

Little auk chick meal samples

Contemporaneous with the ship survey, meals brought in from the sea by little auk adults to their chicks in a small sub-lingual pocket (gular pouch) were collected in the breeding colonies Kuukkat ($n = 12$; collected 7 to 10 August 2015) and Annikitsq ($n = 20$; collected 29 July to 1 August 2015) in the northern and middle areas, respectively (Fig. 1). The birds were caught with noose carpets fabricated from chicken wire and fishing line, and the chick meals were gently extracted using a small paintbrush with rubber tip (extraction time < 2 min). In the field, the meals were weighed on an electronic scale (accuracy: 0.01 g), the proportion of the gular pouch content collected was assessed (10 to 100%), and the samples were stored in 4 % formalin. In the lab, zooplankton from the samples was processed as described above, although copepod stages were only assessed as adults or copepodites.

We used Ivlev’s selectivity index to evaluate the prey selectivity of little auks. This index is calculated from the proportion of a size/species group in the diet (r) and the corresponding proportion in the *in situ* plankton samples (p): $(r - p)/(r + p)$. Positive values indicate selection, whereas negative values indicate avoidance (Ivlev 1961).

Colony effect on little auk at-sea distribution

As a result of the central-place foraging strategy of little auks during the breeding season, and their significant cost-of-flight values, distances to and sizes of nearby colonies likely influence at-sea densities. Even if prey distributions were homogenous, we would expect a strongly aggregated distribution of foraging birds near breeding colonies. Analysis of the coupling between little auks and their prey must account for this ‘colony effect.’ Following Renner et al. (2013), we quantified colony effect by:

$$\text{ColEf}_i = \sum_{c=1}^n \frac{s_c}{d_{i,c}}$$

where ColEf_i is the colony effect at station i , s_c is the size of colony c , and $d_{i,c}$ is the distance between station i and colony c . Thus, the colony effect at a given

station is the colony-size-weighted, inverse distance to colony, summed over all (n) colonies. Breeding numbers are not available for little auk colonies in northwest Greenland, so we used the areas of the colonies from the mapping of Boertmann & Mosbech (1998) as a proxy. As little auks are reluctant to fly over land, we used distance over sea, rather than Euclidian (direct) distance, when calculating colony effect.

Analyses of the spatial coupling between little auks and prey density

We tested the hypothesis that little auk spatial distribution at sea is explained by colony effect ('ColEf') in combination with the availability of suitable prey within diving range. Based on the contents of the chick meal samples (see 'Results'), we used the total abundance of zooplankton >3 mm in the upper 50 m at our sampling stations as a measure of prey availability ('Zoo3mm'). We further speculated that areas where prey are concentrated in patches at certain depths (as opposed to being evenly distributed in the diving range) are more attractive to little auks due to reduced foraging costs. We did not have a direct measure of the degree of vertical patchiness of zooplankton in the upper 50 m. However, we used the coefficient of variation (CV) of phytoplankton in the upper 50 m ('PhyCV'; obtained from the CTD) as a proxy, based on the assumption that zooplankton follow their phytoplankton prey.

Using a model-selection approach (Burnham & Anderson 2002), simple linear models were applied to investigate the influences of ColEf, Zoo3mm and PhyCV on the number of little auks observed on the sea surface within the 300 m \times 4 km rectangles around our sampling stations. Initially, all variables, including the response, were log transformed to approach normal distributions and homogeneity of variances. The global model included all explanatory variables and all first order interactions between explanatory variables. All combinations of explanatory variables were tested, whereas first order interactions were only included if the main effects were also part of the model. AIC_c was used to select the most parsimonious model(s) (Burnham & Anderson 2002). Models were ranked relative to the model with lowest AIC_c, and Δ AIC_c was calculated as the difference in AIC_c values relative to this best model. Models with Δ AIC_c < 2 were identified as candidate models, but for general information we also report diagnostics (Δ AIC_c, multiple R^2 , and direction of

slope [sign]) for univariate models of the 3 explanatory variables. The modelling was carried out for the northern and middle areas separately, and for those areas combined. Stations in the southern area were not included due to absence of little auks (see 'Results'). All calculations were done using the multi-model inference package 'MuMIn' (Bartón 2016) in R (R Development Core Team 2016).

RESULTS

Hydrography

At all stations, a distinct surface mixed layer was seen, but it was generally thinner in the middle and southern areas (<30 m) than in the northern area (<50 m). (Fig. 2). Below this surface layer, the northern area had salinity values >33, increasing with depth, and generally temperatures below 0°C. In the middle and southern areas, the salinity pattern was similar to that in the northern area, whereas temperature increased with depth to ~2°C at 150 m.

In all 3 areas, the surface layer had lower salinity and higher temperatures than the deeper parts of the profile, except for the 2 northernmost transects in Smith Sound (K and L), where the surface layer temperature stayed below 0°C. At the stations farther south in Smith Sound (transects G, I and J), the temperature in the surface layer was 3 to 5°C. At the stations in the middle area (transects A, C and D), temperatures in the surface layer were as high as 9°C and salinity as low as ~26. In the southern area (transects O and Q), the surface layer was slightly deeper than in the middle area. Here, salinity was always above 30 and temperature below 7.5°C. On transect A/T, which was sampled twice, there was a slight deepening of the surface layer between the 2 visits.

Phytoplankton

In the northern area, chl *a* was found in the upper 50 m and the concentration generally decreased with depth without pronounced peaks. The concentrations were below 5 μ g chl *a* l⁻¹, except for the northernmost stations (Stns K2, L1 and L2), where a maximum value of 8 μ g l⁻¹ was reached (Fig. 2). In the middle area, surface concentrations were low, but distinct peaks were seen in the profiles, and the patchiness (CV of chl *a*) was generally highest there.

Peaks were generally located just under the surface layer at ~30 to 50 m depth. There, the chl *a* concentration reached 20 to 30 $\mu\text{g l}^{-1}$. In the southern area, no CTD fluorescence measurements were made, but the few Niskin bottle samples taken at specific depths showed low surface concentrations and higher concentrations deeper in the water column.

As a consequence of the high sub-surface concentrations in the middle area, the integrated chl *a* biomass was generally higher there than farther north. Only the 4 northernmost stations (in transects K and L) had similar high values (Fig. 3).

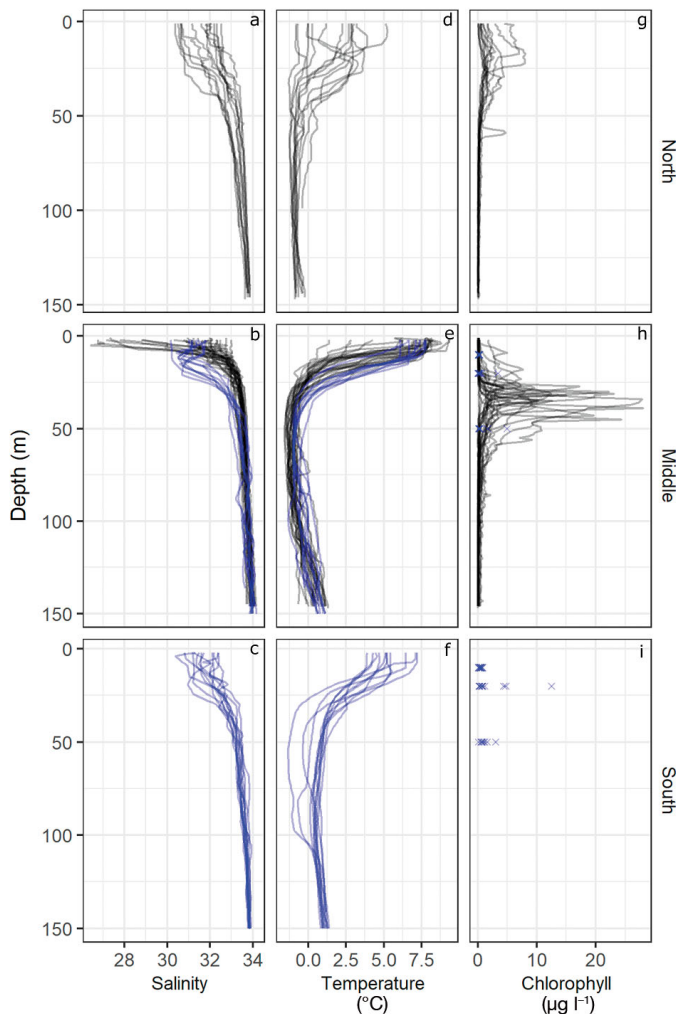


Fig. 2. (a–c) Salinity, (d–f) temperature and (g–i) chl *a* as a function of depth at sampling stations in the 3 sub-areas of the study. Black and blue lines: the HDMS 'Ejnar Mikkelsen' and RV 'Sanna' surveys, respectively. On one transect (A/T), the stations were sampled twice: on 3 and 4 August by HDMS 'Ejnar Mikkelsen', and on 11 and 12 August by RV 'Sanna'. Blue crosses: measured chl *a* samples from the RV 'Sanna' survey

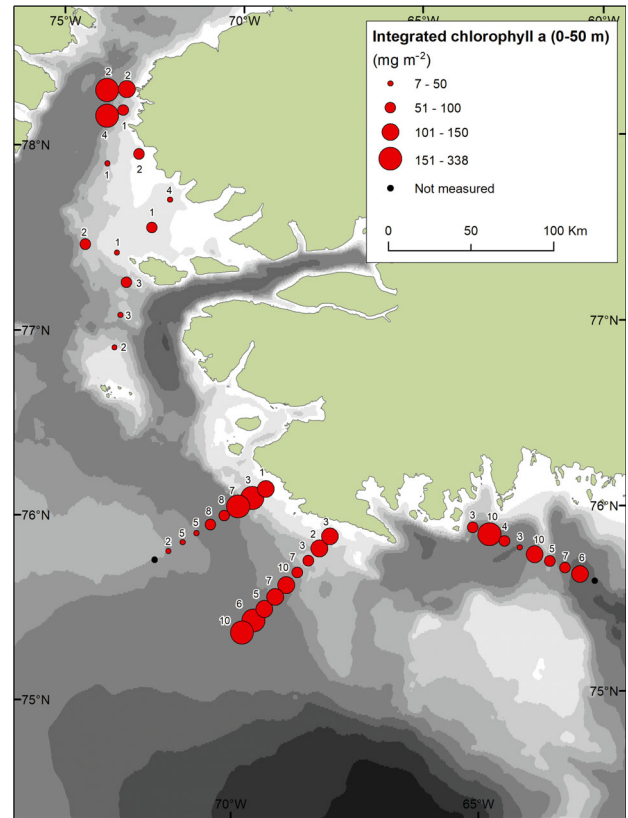


Fig. 3. Integrated chl *a* in the upper 50 m of the water column at the sampling stations (mg m^{-2}). Number associated with each station: coefficient of variation (CV) of chl *a* in the upper 50 m of the water column at the stations, multiplied by 10^4

Copepods

The total biomass of copepods in the water column was not consistently different between the 3 sub-areas (Fig. 4b). However, in the northern area, most of the copepods had left the surface waters as resting stages, and at most stations <10 % of the biomass was found in the upper 50 m (Fig. 4a vs. b). In the middle and southern areas, copepod biomasses in the upper 50 m were much higher, and a larger proportion of the total biomass remained in the surface layer. Especially at stations close to the coast, the majority of the copepods were sometimes found in the upper 50 m, although distributions were quite variable. At the stations farthest from the coast, around 20 % of the copepod biomass was in the upper 50 m, resembling the depth distribution in the northern area.

Calanus spp. dominated the copepod biomass at all stations, particularly in the upper 50 m (mean \pm SD: $88 \pm 11\%$) (Fig. 4). Other abundant genera were *Pseudocalanus* spp., *Oithona* spp., *Triconia* spp. and

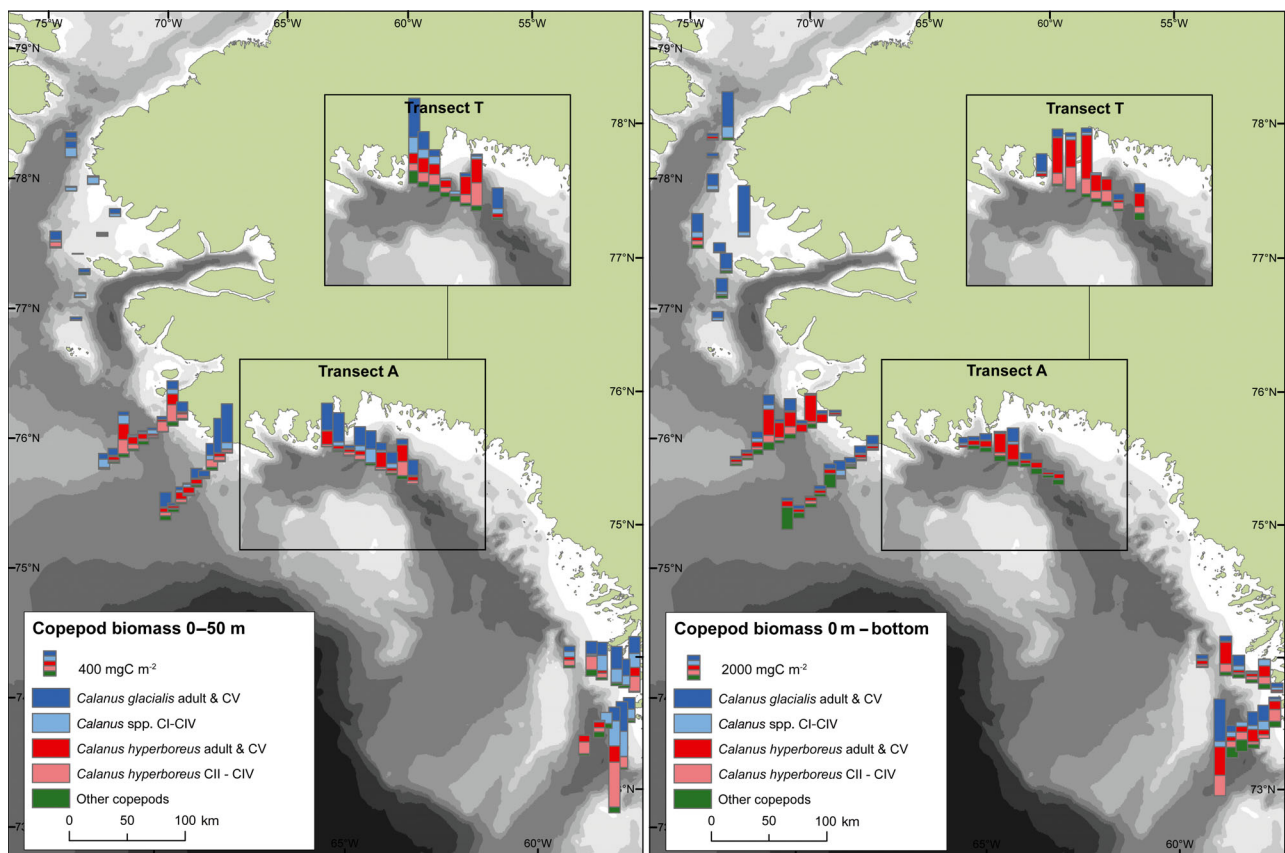


Fig. 4. Biomass of copepods in (a) the upper 50 m of the water column and (b) the whole water column (mg C m^{-2}). Transect A/T was sampled twice: on 3 and 4 August (main map) and on 11 and 12 August (map insert). Note the different scales used to depict biomasses in (a) and (b)

Metrida longa. The distribution of copepods within the size range fed to little auk chicks (i.e. >3 mm; results for little auk meal samples below), resembled the general copepod biomass distribution due to the dominance of large *Calanus* specimens (Fig. 5).

The *Calanus* community composition was distinctively different among the sampled areas (Fig. 4). NMDS ordination analysis resulted in a goodness-of-fit $R^2 = 0.977$ (stress = 0.152) (Fig. 6). Temperature, salinity, latitude and depth vectors were significant (permutations test, $p < 0.05$) on the ordination. Integrated chl *a* was not significant (permutations test, $p = 0.09$) and is not mentioned further in this analysis. *Calanus hyperboreus* copepodite and adult stages were located in the direction of the depth and salinity vectors, and in the opposite direction from the latitude vector, indicating that the relative abundance of this species was highest to the south in more saline waters of greater depth. In contrast, the *Calanus* spp. stages only identified to genus (labelled calCI-calCIV in Fig. 6) were relatively more abundant in

shallow waters in the north. With respect to this variation, *C. glacialis* copepodite and adult stages took a middle position. However, males and females of this species were relatively more abundant in cold waters. When the sample units were colour-coded according to geographical area (Fig. 6), it becomes evident that the pattern was largely driven by a stark contrast between the middle area, dominated by *C. hyperboreus*, and the northern area, where the copepodite stages constitute a larger proportion of the *Calanus* community. The southern area was positioned in between, indicating resemblance to the middle area more than the northern one.

Little auk chick meal samples compared to *in situ* zooplankton samples

In the chick meal samples, which were evaluated in the field to have been completely collected (90 to 100 %), the average (\pm SD) number of prey items per

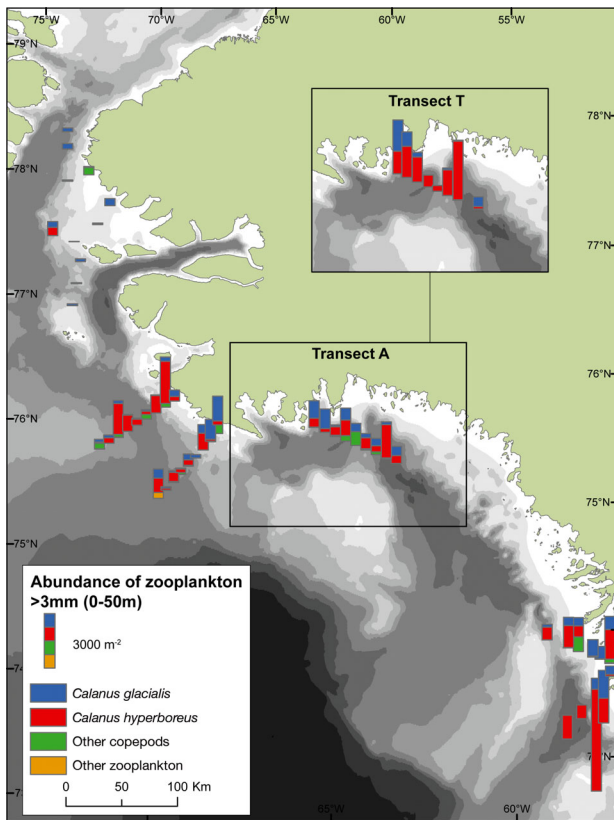


Fig. 5. Abundance of zooplankton with prosome length >3 mm in the upper 50 m of the water column at the sampling stations (ind. m⁻²)

meal was 978 ± 589 and 773 ± 319 for the colonies in the northern and middle areas, respectively (Fig. 1), and the average weight of a prey item was $308 \mu\text{g C}$.

The majority of the zooplankton specimens found in the gular pouches of little auks were *C. hyperboreus* with prosome lengths between 3 and 5 mm (88 and 71 % in the north and middle areas, respectively), followed by *C. glacialis* in the same size range (7 and 17 % in the north and middle areas, respectively). *Calanus* >3 mm from the net samples were determined to be *C. glacialis* CV-VI and *C. hyperboreus* CIII-IV. The chick meal samples collected in the middle area also contained some amphipods of larger sizes (Fig. 7).

Compared to the average size and taxon distributions at the sampling stations, there were clearly more *C. hyperboreus* in the chick meal samples. Ivlev's selectivity index was positive for *C. hyperboreus* 3 to 5 mm in both areas, indicating they were selected (Table 1). In the northern area, Ivlev's index was also positive for *C. hyperboreus* 5 to 7 mm, while in the middle area there was a selection for *C.*

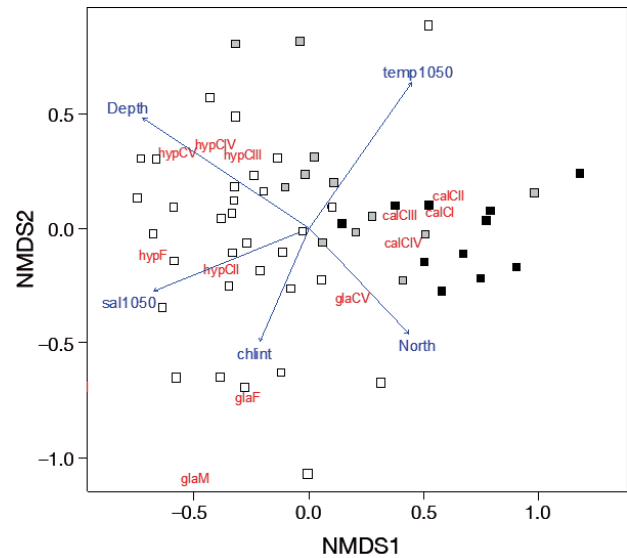


Fig. 6. Non-metric multidimensional scaling (NMDS) ordination analysis of the copepod community structure in the upper 50 m of the water column (*Calanus* copepodite and adult abundances). Environmental vectors of temperature (average 10 to 50 m depth: 'temp1050'), salinity (average 10 to 50 m depth: 'sal1050'), integrated chl *a* (0 to 50 m depth: 'chlnt'), latitude ('north') and bottom depth ('depth') are fitted onto the ordination. White squares: stations in the middle sub-area; black squares: northern sub-area; grey squares: southern sub-area

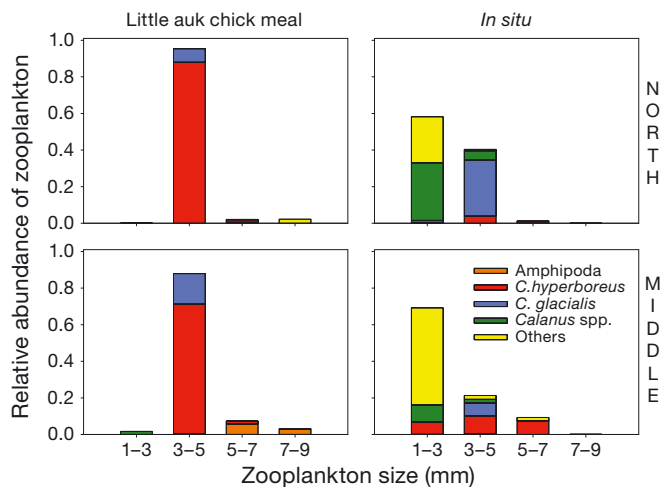


Fig. 7. Relative abundance of zooplankton across different taxa and length (mm) categories in the gular pouch samples from little auks and *in situ* in the upper 50 m of the water column at the sampling stations in the northern and middle area, respectively

glacialis 3 to 5 mm. Ivlev's selectivity index was also positive for amphipods in both areas. However, this may or may not be correct, since the net we used cannot be assumed to collect all amphipods. For all other groups, Ivlev's selectivity index was negative.

Table 1. Ivlev's selectivity indices for size and taxon distributions of prey selected by little auks from colonies in the north and middle sub-areas (see Fig. 1). nd: no data

	Zooplankton size (mm)		
	3–5	5–7	7–9
Middle			
Others	−0.99	−0.90	−0.28
<i>Calanus</i> spp.	−0.69	−1.00	nd
<i>C. glacialis</i>	0.41	−1.00	nd
<i>C. hyperboreus</i>	0.76	−0.67	nd
Amphipoda	−0.13	1.00	1.00
North			
Others	−0.95	−0.53	0.87
<i>Calanus</i> spp.	−1.00	nd	nd
<i>C. glacialis</i>	−0.61	−1.00	nd
<i>C. hyperboreus</i>	0.92	0.23	nd
Amphipoda	0.21	1.00	0.79

Little auk distribution

During the systematic seabird survey, 876 km of transect line was covered and a total of 56 322 little auks were observed (Fig. 8). Of these, 23 903 were recorded at the sea surface foraging and/or resting, and 32 419 were observed in flight between breeding colonies and at-sea foraging areas. Little auks were totally absent on the transects in the southern area, corresponding to the lack of breeding colonies there, whereas in the middle and northern area little auks were observed on all transects. Based on distance-sampling methods, estimated densities of little auks on the sea surface in the vicinity of our sampling stations ranged between 3 and 1518 ind. km^{−2} (Fig. 8). Particularly in the northern area, where most stations were relatively close to the breeding colonies, high densities of little auks were observed on the sea surface, specifically on the shelf. In the middle area, the highest at-sea densities were recorded farther offshore, at and immediately beyond the shelf break. On transect A, density was high in conjunction with a pronounced underwater ridge separating 2 deep basins. It is important to note that the transects generally started approx. 10 km from the coast, so that potential near-shore foraging areas were not covered by the survey.

Coupling between little auks and their prey

Table 2 summarizes the attempt to model the number of little auks at the sea surface based on the colony effect (ColEf), total abundance of zooplankton >3 mm in the upper 50 m (Zoo3mm), coefficient of

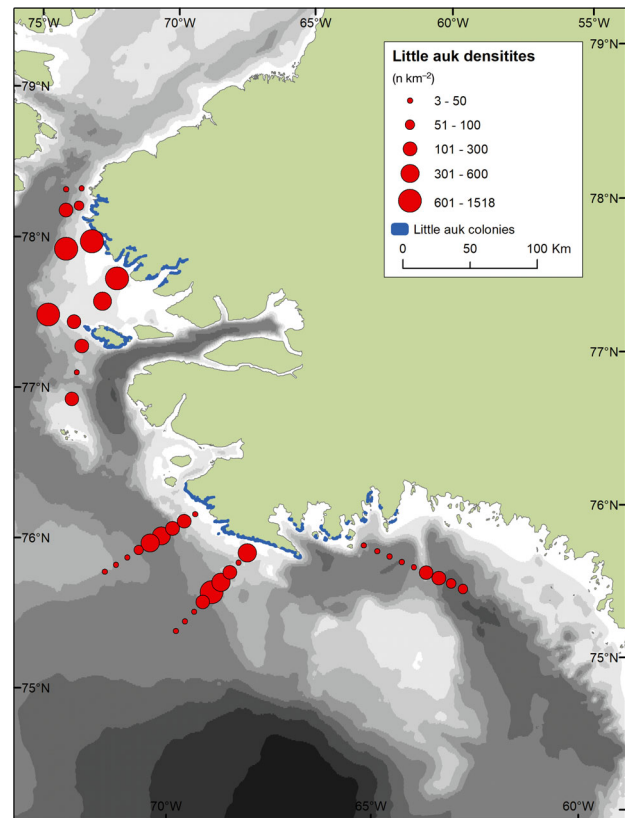


Fig. 8. Density of little auks (ind. km^{−2}) on the sea surface in the vicinity of the sampling stations, estimated by means of distance sampling methods

variation of phytoplankton in the upper 50 m (PhyCV), and the first order interactions among these explanatory variables. For each of the 3 data sets—northern area, middle area and those combined—only 2 candidate models remained after model selection based on $\Delta AIC_c < 2$. In the northern area, the most parsimonious model was the intercept, implying that the best description was simply the overall mean with no influence of any explanatory variables. However, a model involving a positive correlation with ColEf ($R^2 = 0.27$) was also among the candidates. For the middle area, the most parsimonious model included ColEf and PhyCV, with little auk numbers being positively related to both. The other candidate model for this area included the same main effects plus their interaction. The interaction implies that the relationship between little auk numbers and PhyCV is dependent on ColEf, with the little auks' positive response to PhyCV growing stronger close to breeding colonies (Fig. 9). The 2 candidate models for the middle area had multiple R^2 values of 0.52 and 0.54. Similarly to the middle area, the most parsimonious model of both areas combined included ColEf and

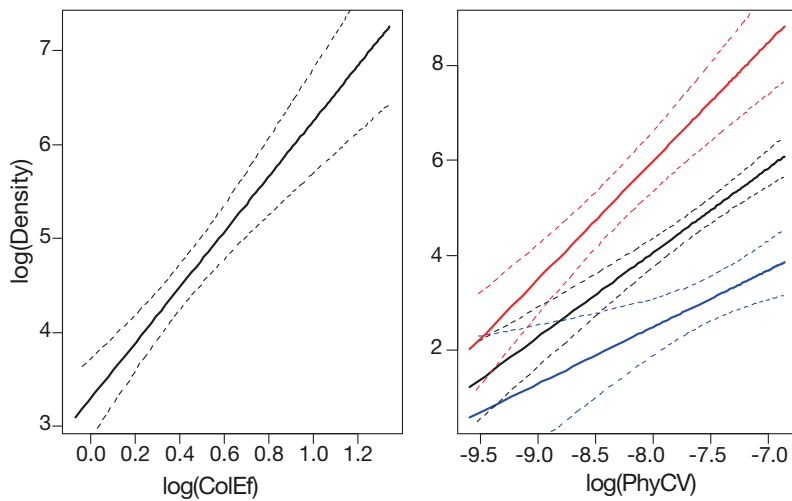


Fig. 9. Relationships between little auk at-sea density and colony effect (ColEf) and phytoplankton coefficient of variation in the upper 50 m (PhyCV), predicted from the candidate model ColEf + PhyCV + ColEf:PhyCV for the middle area (see Table 2). Left panel: response of little auk at-sea density to ColEf under the average value of PhyCV recorded at the sampling stations, and over the data range of ColEf covered at the stations. Right panel: response of little auk at-sea density to PhyCV under the minimum (blue), average (black) and maximum (red) value of ColEf covered at the sampling stations, and over the data range of PhyCV recorded at the stations. All confidence intervals (dashed lines) are based on 1 SE

PhyCV. Beside ColEf and PhyCV, the other candidate model for the combined area also included Zoo3mm. Little auk numbers were positively correlated with ColEf and PhyCV in both candidate models for the combined area, but they appeared to be negatively correlated with Zoo3mm in the candidate model with lower R^2 . Although the candidate models for the middle and the combined area resembled

each other, multiple R^2 values for the combined area were somewhat lower (0.30 and 0.33), reflecting the contrasts between the northern and middle areas.

DISCUSSION

Plankton distribution

This study documented high abundance of large *Calanus* during late summer in the upper waters of northern Baffin Bay and eastern Smith Sound (73 to 78.5° N), where an estimated 33 million little auk pairs breed. It was previously found that biomass of *Calanus* is high (up to 3200 mg C m⁻²) during spring in this area (Ringuette et al. 2002, Saunders et al. 2003). While that accords with findings from other Arctic areas, e.g. Disko Bay farther south in West Greenland (69° N) (Madsen et al. 2001, Swalethorp et al. 2011), the high biomass we record in the northern Baffin Bay (up to 3000 mg C m⁻²) in late summer is remarkable compared to areas further south

where the large *Calanus* have left the surface waters at this time of the year (Fig. 10). Since little auks feed their chicks *Calanus* from mid-July to mid-August, high biomass of large *Calanus* in the surface water during late summer is crucial to them. In general, species of *Calanus* have flexible phenology across the Arctic, varying in relation to different physical and biological environments (Daase et al. 2013). The timing

Table 2. Results of modelling little auk at-sea density as a function of colony effect (ColEf), abundance of zooplankton >3 mm in the upper 50 m (Zoo3mm) and phytoplankton coefficient of variation in the upper 50 m (PhyCV), plus all first order interactions. Both response and explanatory variables were subjected to log transformation. For each model and subset of data (sub-area), the difference in Akaike's information criterion corrected for small sample size (ΔAIC_c) values relative to the best model (ΔAIC_c), as well as multiple R^2 and direction of slope (sign) for the respective variables are reported. The most parsimonious models (candidate models) for each sub area were selected based on $\Delta AIC_c < 2$. See also Fig. 9 for a plot of one of the candidate models for the middle area

	Middle area			North area			North + middle area		
	ΔAIC_c	R^2	Sign	ΔAIC_c	R^2	Sign	ΔAIC_c	R^2	Sign
Univariate									
ColEf	15.0	0.02	+	0.5	0.27	+	4.3	0.15	+
Zoo3mm	14.7	0.03	–	3.5	0.04	+	8.2	0.05	+
PhyCV	7.7	0.27	+	3.4	0.05	–	9.9	0.01	–
Candidate models ($\Delta AIC_c < 2$)									
ColEf + PhyCV	0.0	0.52	++	0.0	0.00		0.0	0.30	++
ColEf + PhyCV + ColEf:PhyCV	1.8	0.54	+++	0.5	0.27	+	0.7	0.33	++–

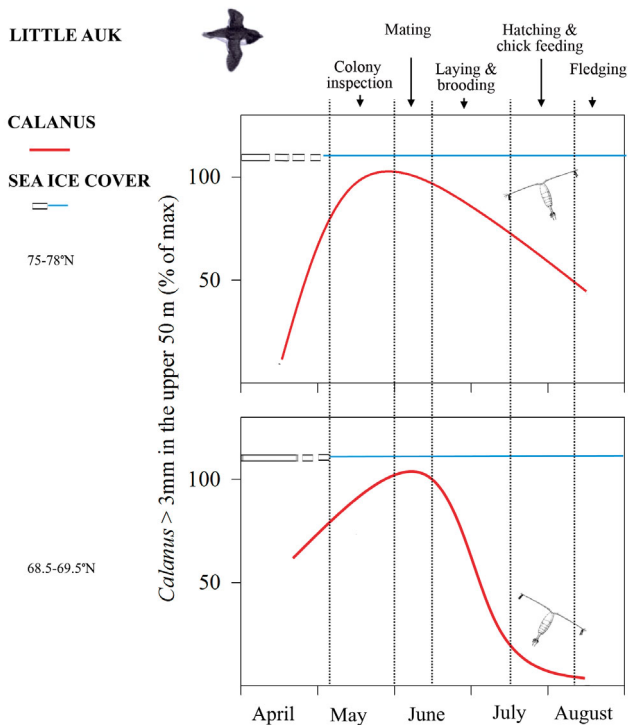


Fig. 10. Conceptual diagram of the abundance of large *Calanus* in the upper 50 m of the water column in the North Water (NOW) polynya (75 to 78°N) and Disko Bay (68.5 to 69.5°N), and sea ice cover and current breeding phenology of little auks in the NOW. Based on data from Barber et al. (2001), Madsen et al. (2001), Saunders et al. (2003), Hansen et al. (2006), this study and Mosbech et al. (2018)

of zooplankton populations are of great importance to their predators, and climate-induced shifts can lead to reduced breeding success, e.g. as shown for Cassin's auklets feeding on the copepod *Neocalanus cristatus* (Mackas et al. 2007, Bertram et al. 2017)

Water circulation may partly explain the distinctly different *Calanus* biomass levels and community compositions in our northern and middle/southern areas, with dominance of *C. glacialis* in north and *C. hyperboreus* farther south. Baffin Bay is influenced by inflow from the Arctic Ocean through 4 gateways, all of which contain shallow sills allowing for exchange of only upper water layers (Michel et al. 2015). Our northern area receives water through Nares Strait and this may contribute to the dominance of *C. glacialis*, which is typically distributed along the Arctic shelves (Falk-Petersen et al. 2009). That is particularly the case to the north of Nares Strait. A north-moving branch of the West Greenland Current influences the middle and southern areas. That flow from the south is constrained by the 500 m isobath across the entrance to Smith Sound Canyon

(Bâcle et al. 2002). The inflow may contribute to the higher biomass of *C. hyperboreus*, which is generally associated with deeper water (Falk-Petersen et al. 2009). Samples taken during May in 1998 to the west of our northern area, and thus from an area with greater water depths than our stations there, had more equal contributions of *C. glacialis* and *C. hyperboreus* (Ringuette et al. 2002) than what we found. However, it is not possible to separate the impacts of season and bathymetry.

Different life history timing of *Calanus* along the west coast of Greenland may also influence the observed patterns. Before their descent to deep waters, *Calanus* need to build up substantial lipid reserves for overwintering (Hirche 1997, Falk-Petersen et al. 2009). However, the upper water where food is plentiful is often where predation risk is greatest. In the northern portion of our study area (77 to 78.5° N), in Smith Sound, phytoplankton concentration was generally low, except for the 4 northernmost stations. At the same time, predation pressure was high due to the numerous little auks breeding in this area, and possibly other predators as well, e.g. polar cod *Boreogadus saida* and amphipods (Fortier et al. 2001). Thus, it could be that the highest fitness for *Calanus* spp. in that area may require early descent from the upper water column. In the Norwegian Sea, the first *C. finmarchicus* descend to the diapause habitat as early as June despite sufficient food for a second generation seemingly present in the surface waters. This has been interpreted as a strategy to avoid predation by herring (Kaartvedt 2000, Varpe & Fiksen 2010). Diel vertical migration (DVM) may also be a strategy to avoid predators (Fortier et al. 2001), but our sampling was not designed to test if DVM was taking place due to continuous daylight in the northern and middle area. However, the pattern that *Calanus* had left the upper water column in our northern sub-area was consistent across both day and night samples. In the northern sub-area, the sea ice disappears earlier than in the middle and southern sub-areas, and therefore *Calanus* may reach sufficient lipid reserves for descent earlier there. Farther south, in our middle and southern areas where phytoplankton is still abundant, it may be favourable for *Calanus* to remain longer in upper layers despite the predation risk, especially because early season food stocks presumably are lower than in the NOW proper due to greater ice cover during spring/early summer. Lipid stores of *Calanus* copepodites would therefore also be lower here in August than further north. Still farther south, in Disko Bay (69° N), conditions also seem to favour an early descent, since low abundance of

Calanus is found in the upper 50 m in August compared to the spring (Madsen et al. 2001). Potentially, the early bloom in Disko Bay (Madsen et al. 2001), compared to that in the northern Baffin Bay (Mei et al. 2002), allows *Calanus* copepodites to build up sufficient lipid stores for early descent to their overwintering depths.

The prey of little auks

We found that a very high proportion of the little auk chick meals consisted of *Calanus* in the size range 3 to 5 mm. This corresponds to *C. glacialis* stage CV/adults and *C. hyperboreus* stage CIII/CIV. Larger *C. hyperboreus* (i.e. stage CV/females, which are 5 to 7 mm) were not abundant in the chick meal samples, although they were present at most stations, at least in our middle area. Thus, even though little auks can feed on much larger prey items (Boehnke et al. 2015, Karnovsky et al. 2008), they seem to focus on a specific size range when selecting prey for their chicks—a range not including the largest and most energy-rich *C. hyperboreus* and not including the smaller prey items. The absence of the smaller prey may be attributable not as active avoidance, but simply a reflection of lower detection probability of smaller prey items during visual search. Decreased light at depth will further decrease catch efficiency of visual predators (Stempniewicz et al. 2013, Varpe et al. 2015). Older stages of *Calanus* are often found deeper in the water column than younger stages (Daase et al. 2008, Darnis & Fortier 2014, Trudnowska et al. 2015). If this was the case during our survey, the older stages would require more effort for the birds to catch, perhaps contributing to their under-representation in the gular-pouch samples compared to the *in situ* samples.

Although the little auk displays flexible foraging behaviour (Grémillet et al. 2012), preference for *C. glacialis* and *C. hyperboreus* over the smaller *C. finmarchicus* has often been found (Karnovsky et al. 2003, Harding et al. 2009, Frandsen et al. 2014). Little auks have been shown to prefer Arctic waters with abundant large zooplankton, and to invest time and effort in flying to foraging areas far from the colonies (Jakubas et al. 2013). Foraging in areas dominated by larger zooplankton may be more energy efficient (Karnovsky et al. 2011). In our study, the largest *Calanus* species, *C. hyperboreus*, was positively selected (although not its largest stages). In the middle area, the allocation between *C. glacialis* and *C. hyperboreus* in the gular-pouch samples matched

their relative abundance in the *in situ* samples, when considering only the size range selected for by the little auks (3 to 5 mm). In the northern area, however, the relative abundance of *C. hyperboreus* was much greater in the gular-pouch samples than in the net hauls, where it was almost absent at most stations. These data suggest that the birds were strongly selective; either by discriminating between species/sizes, or by flying to areas dominated by *C. hyperboreus* that were not well-sampled by us, or both. In other areas, similar discrepancies between diet and estimated food availability have often been ascribed to spatial heterogeneity of the zooplankton (Steen et al. 2007, Vogedes et al. 2014).

Our picture of little auk feeding patterns was obtained from studying gular-pouch samples, representing the diet given to the chicks during late chick rearing (approx. 2 to 15 d before assumed fledging), whereas we have no data describing the diet of little auk adults. However, analyses of stomach contents and stable isotopes of adult little auks in the NOW suggest that they also depend mostly on *Calanus* during summer (Karnovsky et al. 2008). In autumn, after chick rearing is over, the diet of the adults has been shown to change to amphipods and small polar cod (Karnovsky et al. 2008). In the West Greenland wintering area, little auk diet is dominated by krill *Thysanoessa* spp. and amphipods *Themisto* spp. (Rosing-Asvid et al. 2013).

Little auk distribution and coupling to prey distributions

In accordance with our hypothesis, our linear models showed that little auk at-sea densities were positively related to colony effect (high densities close to many and/or large breeding colonies) and to vertical patchiness of phytoplankton within their diving range (PhyCV in the upper 50 m). This was true for our middle area, and for the middle and northern areas combined, whereas the northern area itself only had colony effect amongst the candidate models. This probably reflects the different situations in those areas during the survey. The northern area was characterized by lack of pronounced vertical peaks of chl *a*, and much of the zooplankton there (~90%) had descended beyond the little auk diving range. Especially in the middle area, where pronounced phytoplankton peaks were detected at ~30 to 50 m, the combination of colony effect and phytoplankton CV yielded a strong model of little auk at-sea distribution patterns ($R^2 = 0.52$). The most parsimonious

model for the middle area included only these 2 variables, but the other candidate model, which also included their interaction, has more logical appeal ($\Delta AIC_c = 1.8$; $R^2 = 0.54$): the relationship between little auk density and phytoplankton CV depends on the level of colony influence. The response of little auks to vertical patchiness of phytoplankton grew more positive in proximity to many and/or larger breeding colonies. During the breeding season, little auks are central-place foragers, and as we have seen from the lack of little auks on the transects in our southern area, their at-sea distribution is constrained to regions adjacent to breeding colonies. It makes sense that vertical patches of phytoplankton, and the concentrations of prey items assumed to be associated with the patches, would only matter to the little auks within foraging range of the breeding colonies (approx. 100 km). The relationship is stronger at distances closer to the colony with lower flight costs. In a similar way, we would expect the relationship to grow stronger with decreasing depth of the prey patches due to lower diving costs and more light available for visual searches (Langbehn & Varpe 2017), whereas prey patches approaching the limit of the little auk diving range would be less attractive.

Contrary to our expectations, the biomass of suitable prey items within little auk diving depth (zooplankton >3mm in the upper 50 m) was generally found to be an unimportant explanatory variable. In the univariate models, it explained very little of the variance in little auk distribution patterns ($R^2 < 0.05$ for both areas), and it only formed part of one candidate model (for the combined area). In that instance, it added only slight explanatory power to the model comprising colony effect and PhyCV (not enough to make up for the cost of the extra parameter), and it entered with a negative sign. Thus, if prey density had any effect, little auk density appeared to be negatively correlated with the biomass of suitable prey within their diving range. This may have to do with the significant predation pressure the little auks can exert on their prey. The degree of prey concentration/dispersion within the upper 50 m that the little auks can access may also be significant. The little auk has the highest metabolic rate of any alcid of their size (Gabrielsen et al. 1991), and they probably depend on very dense prey concentrations both horizontally and vertically (Harding et al. 2009). Thus, the abundance of prey integrated through the upper 50 m (the variable we could measure with our net hauls) likely only achieves significance if the prey items are actually concentrated somewhere within that vertical range. We do not have a direct measure

of this, but we speculate that the reason why phytoplankton variability in the upper 50 m proved to be such a good predictor of little auk distribution patterns (when combined with colony effect) in our study relates to the fact that it indirectly reflects prey concentrations in all 3 dimensions.

Why is the NOW polynya region such an important breeding area for little auks?

In West Greenland, little auk colonies are almost completely restricted to north of 75° N and west of 60° W, corresponding to our northern and middle areas. However, zooplankton data from our southern area suggest that abundances of suitable prey items within little auk diving range are just as great there in August. South of the NOW polynya, in north-eastern Baffin Bay, however, the ice cover during late spring/early summer (Barber et al. 2001a) presumably delays the initiation of the phytoplankton spring bloom and the associated zooplankton abundance. That potentially constrains access to prey when the birds first arrive for the breeding season in early May. Even farther south, e.g. in Disko Bay, the sea ice disappears in May, and the spring zooplankton abundance there is as high as in the NOW, including plenty of large *Calanus* (Ringuette et al. 2002, Swalethorp et al. 2011) (Fig. 10). So why are little auk colonies not common in Disko Bay? Absence of the right substrate for nesting (scree with a particular boulder size) may be a limitation, just as the higher precipitation and resulting snow cover may present a problem for the onset of the breeding season. The snow has to melt before little auks can establish nests in the scree. However, differences in zooplankton phenology may also be a controlling factor. In August, when the little auks are heavily dependent on large *Calanus* for feeding their chicks, these copepods have already left the surface layers of Disko Bay for diapause deeper than the birds' diving range (Fig. 10). On the Canadian side of Baffin Bay, and even the Canadian side of the NOW, little auk colonies are also absent. Here, sea ice remains until mid-summer (Tang et al. 2004), and even though large *Calanus* are present in the surface waters off Baffin Island in September (Kjellerup et al. 2015), the productive season is short and probably starts too late for the little auks. The world's second largest little auk breeding population is found in East Greenland in close association with the Scoresbysund polynya (Kampp et al. 1987), which, like the NOW, also secures a long productive season.

Thus, the reason for exceptional concentration of little auk breeding populations along the Greenlandic shores of the NOW may be that primary production, and the associated abundance of zooplankton, starts early and is maintained throughout the summer, supporting the full breeding cycle of the birds. This holds under current climate conditions. In the future, changing ice cover, temperature and stratification may alter the phenology, abundance and composition of phytoplankton and zooplankton, in both spring and summer. How such changes emerge will be crucial for the success of little auks (Stempniewicz et al. 2007). A warmer climate may also result in northward propagation of other zooplankton predators, like capelin *Mallotus villosus* (Rose 2005, Ingvaldsen & Gjøsæter 2013). An increase in visual zooplankton predators may increase selection against the large zooplankton species (Langbehn & Varpe 2017). This could lead to a zooplankton community with lower abundance of the large *Calanus* species, on which the little auk breeding population of the NOW is clearly heavily dependent.

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