Foraging distributions of little auks *Alle alle* across the Greenland Sea: implications of present and future Arctic climate change

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ABSTRACT: The Arctic is undergoing widespread warming. In order to understand the impact of climate change on Arctic marine food webs, we studied the at-sea distribution of foraging little auks in contrasting conditions of the Greenland Sea. While the eastern side of the Greenland Sea has experienced recent warming, the western side is still dominated by cold, Arctic water in the East Greenland Current. We hypothesized that foraging little auks would be found in greatest abundance in cold Arctic waters bearing more lipid-rich prey, allowing them to deliver more energy-rich food to their chicks. To test our hypotheses, we made ship-borne bird observations and zooplankton tows, as well as analyses of chick meals at 2 little auk colonies adjacent to 3 distinct water masses in the Greenland Sea. Associated with the coldest water in the East Greenland Current, we found the highest concentrations of large *Calanus* copepods (*C. glacialis* and *C. hyperboreus*), as well as the highest concentrations of foraging little auks, indicating a relationship that is likely to be disrupted by increasing water temperatures. To assess potential future impacts of ocean warming, we used a coupled atmosphere–ocean global climate model (AOGCM) to predict Greenland Sea sea-surface temperatures over the study area at the end of the 21st century. Our results suggest that 4 of 8 little auk breeding colonies in the North Atlantic may be negatively impacted as temperatures exceed the thermal preferenda of large *Calanus*, which is the preferred prey of little auks during the breeding season.

KEY WORDS: At-sea observations · *Calanus* copepod · Climate model · East Greenland Current · Seabird · Little auk · Sea temperature · West Spitsbergen Current

INTRODUCTION

In recent years, the effects of climate change have been especially pronounced in the Atlantic sector of the Arctic. In the Greenland Sea, sea ice has declined and the eastern side has experienced large increases in temperature (Blindheim et al. 2000, Vinje 2001). These changes have been driven primarily by increased advection of warm, saline, Atlantic water into the Greenland Sea via the West Spitsbergen Current (WSC) (Aagaard et al. 1987, Walczowski & Piechura 2006, Fig. 1).
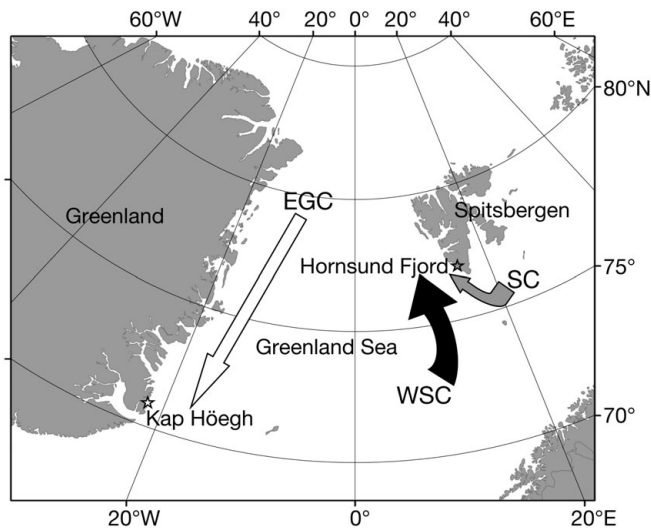
Fig. 1. Study area. Arctic-fed East Greenland Current (EGC, white arrow), Atlantic-fed West Spitsbergen Current (WSC, black arrow), and Arctic-fed Sørkapp Current (SC, grey arrow)

The Greenland Sea is made up of diverse water masses. Briefly, the WSC originates in the Atlantic Ocean and flows north alongside the cold Sørkapp Current (SC; Saloranta & Svendsen 2001). The SC also runs north along the west coast of Spitsbergen inshore of the WSC but advects cold, low salinity, Arctic water that originates northeast of the island (Swerpel & Zajaczkowski 1990; Fig. 1). The East Greenland current (EGC) is characterized by cold, low salinity water. It originates in the Arctic Ocean and flows south along the east coast of Greenland (Bourke et al. 1988; Fig. 1).

A different numerically dominant *Calanus* zooplankton species can be found in each of these water masses. The EGC primarily supports the large, lipid-rich copepod *Calanus hyperboreus* (Hirche 1997). The SC is dominated by medium-sized *C. glacialis* (Karnovsky et al. 2003). The WSC advects high densities of *C. finmarchicus*, which is the smallest, least lipid-rich species of the *Calanus* copepods, into the Greenland Sea (Scott et al. 2000, Karnovsky et al. 2003). Some *C. finmarchicus* are recirculated in the Greenland Sea and the Arctic Ocean and get mixed into both the SC and the EGC (Hirche & Kosobokova 2007).

Such marked differences shape regional food webs, and the distribution and ecology of planktivorous organisms, including marine mammals and seabirds. For instance, Karnovsky et al. (2003) found that little auks *Alle alle*, which are small planktivorous seabirds, responded strongly to the distribution of water masses and associated copepods on the east side of the Greenland Sea. Little auks breeding in Hornsund Fjord on

the southwest side of Spitsbergen foraged in the SC where they fed on energy-rich *Calanus glacialis* and avoided the WSC where the smaller *C. finmarchicus* was found in high densities (Karnovsky et al. 2003). In a similar fashion, Hunt & Harrison (1990) found that least auklets *Aethia pusilla* on King Island, Bering Sea, flew to feed in a water mass that had larger, more energy-rich prey.

Recent warming of the eastern sector of the Greenland Sea has been particularly pronounced in both the SC and the WSC. During the period 1965 to 1997, the SC has warmed by 1°C (Blindheim et al. 2000) and surface water temperature of the WSC increased by as much as 2°C (Hurrell 1995, Schlichtholz & Goszczko 2006). In contrast, the cold, low salinity water flowing from the Arctic Ocean appears to have been a relatively constant feature in the western sector (as summarized by Hop et al. 2006).

Little auks are the most abundant seabird species in the North Atlantic (80 million ind., estimated from Kampp et al. 1987, Isaksen & Gavrilo 2000, Egevang et al. 2003) and are an essential component of local marine food webs. They occur on both sides of the Greenland Sea (Spitsbergen and East Greenland) where the 2 populations experience the highly contrasting environments of the EGC and the SC/WSC. Comparison of these 2 populations allowed us to test the impact of warming in the Greenland Sea on their foraging conditions.

More specifically, our objectives were to (1) compare the at-sea distribution and abundance of little auks foraging in both the eastern and western sectors of the Greenland Sea, (2) assess the physical properties of the water masses where the birds did, and did not, forage, (3) determine the species composition, size and density of prey in the different water masses, (4) assess the impact of foraging in different water masses on chicks at colonies on either side of the Greenland Sea in terms of the energy they receive, and (5) model future temperature increases in the region and assess how it may impact the distribution of zooplankton species, with energetic implications for little auks.

Given the physical and biological properties of the different water masses, we hypothesized that there would be strong zonal differences in (1) the foraging distribution of little auks, (2) the composition of diets fed to chicks, and (3) the amount of energy delivered by little auk parents to their chicks. We predicted that birds foraging on the western side of the Greenland Sea would forage in the EGC on the largest calanoid copepod *Calanus hyperboreus*. On the eastern side, we predicted that little auks would forage in the SC and consume primarily the medium sized *C. glacialis* as in 2001 (Karnovsky et al. 2003). We predicted that the chicks being fed on the western side of the Green-

land Sea would receive more energy than chicks on the eastern side. With observations and modeling results, we sought to answer the question: Will future increases in warming in this region result in a northward progression in the ranges of copepod species, resulting in a lower-energy zooplankton community dominating waters adjacent to several massive little auk colonies?

To test our hypotheses, we studied little auks breeding at and foraging off 2 colonies, one on each side of the Greenland Sea, in summer 2005. The Kap Höegh little auk colony is located on the east coast of Greenland near Scoresbysund Fjord (78° 43′ N, 22° 38′ W), which is an area influenced by the EGC (Bourke et al. 1988; Fig. 1). The Hornsund Fjord colony is located on the west coast of Spitsbergen (77° 15′ N, 15° 22′ E), which is adjacent to the WSC and the SC (Aagaard et al. 1987, Karnovsky et al. 2003; Fig. 1).

Little auks are planktivorous seabirds that migrate to the Greenland Sea during their breeding season to feed in its productive waters. Throughout their range, during the breeding season little auks mainly feed their chicks with calanoid copepods of the genus *Calanus* (e.g. Roby et al. 1981, Weslawski et al. 1999a, Pedersen & Falk 2001, Karnovsky & Hunt 2002, Karnovsky et al. 2003, Karnovsky et al. 2008). Little auks are subsurface foragers that use their wings for underwater propulsion, diving to maximum depths of 35 m (Falk et al. 2000). They raise one chick during the breeding season and both males and females partake in feeding their chick. A pair of little auks feeds its chick ~5× d^{-1} (Stempniewicz 2001) and each food delivery can contain over 1000 prey items (Karnovsky et al. 2003). Adult little auks collect prey for their chick in a specialized gular pouch (Stempniewicz 2001), and chicks leave the colony when they reach 25 d of age on average (Harding et al. 2004).

The 3 aforementioned *Calanus* species (*C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*) present strong contrasts in size and energy content. Previous studies of gular pouch content have determined the size/stage range commonly taken by little auks: *C. finmarchicus* copepodid stage CV and adult females (AF); *C. glacialis* copepodid stage CIV, CV, and AF; *C. hyperboreus* CIV, CV, and AF (hereafter 'edible' *Calanus*; Węsławski et al. 1999a,b, Karnovsky et al. 2003). Scott et al. (2000) found that stage V of *C. hyperboreus* and *C. glacialis* copepodids contain 25× and 8× the lipid content of stage V *C. finmarchicus*, respectively.

Making this comparative study of the contemporary Greenland Sea, and modeling future copepod distributions based on predicted ocean temperature changes allowed us to gain insight into how present and future warming may impact Arctic marine food webs in the Greenland Sea.

MATERIALS AND METHODS

At-sea surveys. We conducted at-sea surveys adjacent to both Kap Höegh, eastern Greenland (hereafter: Greenland) and Hornsund Fjord in southwestern Spitsbergen (hereafter: Hornsund) in 2005. We conducted surveys when chicks at both colonies were ~15 d old during the mid-chick rearing period. We conducted the Greenland at-sea surveys aboard the sailboat RV 'Vagabond' (15.3 m) from 1 to 11 August, and the Hornsund surveys from 29 to 30 July aboard the sailboat RV 'Oceania' (48.9 m). Despite the slight differences in timing, both cruises were conducted during the same stage of chick rearing at each colony. We conducted surveys whenever the boats were underway and counted foraging little auks found in a 90° arc from directly in front of the boat out to one side (to 300 m) off the side with the best visibility (following the methods described by Karnovsky et al. 2003). Our survey track on the eastern side of the Greenland Sea was designed to cross the shelf break at 500 m depth and to repeat the surveys conducted in 2001 (Karnovsky et al. 2003). On the western side of the Greenland Sea, we designed our survey lines to make several zonal transects across the EGC. We counted all little auks that were sitting on the water because we considered these birds to be foraging instead of transiting (flying) to another foraging site. We recorded our observations directly into a computer. We calculated densities of foraging birds (number of sitting or feeding birds km^{-2}) along 3 km segments of the transect lines. We believe that the little auks seen during the at-sea surveys originated from the colonies adjacent to the survey areas because of the very short foraging trips that birds make to collect food for their chicks (Welcker et al. 2009b), and because in 2001, Karnovsky et al. (2003) found little auks foraging within 50 km of the Hornsund colony.

Zooplankton and physics sampling. To assess prey species and densities, we made vertical plankton net tows from 50 m depth using a WP-2 net with a 0.25 m^2 opening area (Tranter & Fraser 1968) and fitted with filtering gauze of 500 μm mesh size. The nets were fitted with a mechanical flow meter (General Oceanics, model 2030). The only difference in the sampling methods between the 2 sites was that a hand winch was used at the Greenland site whereas a mechanical winch was used at the Hornsund site. We preserved the zooplankton in 5% formalin and seawater buffered with borax and analyzed the samples under a dissecting microscope. We identified plankton to the species level and life stage whenever possible and measured taxa that varied in length. We calculated the densities (m^{-3}) of the edible *Calanus* species and stages. We used reported values of dry weights for *Calanus* spe-

cies and life stages (Karnovsky et al. 2003 and sources therein) and an energetic value estimate of 26 kJ g dry wt^{-1} (Węłsawski et al. 1994) to calculate the energy available to little auks in the different water masses.

To determine the physical characteristics of the water masses in the study area, we stopped surveys every 10 to 15 km to conduct conductivity-temperature-depth (CTD) casts (see locations of circles in Fig. 3). We used the water temperature and salinity obtained at 15 m depth in all analyses. We classified water masses as EG, WSC, or SC based on temperature, salinity, and location.

Chick diets and provisioning frequency. In order to compare the composition of prey taken by little auks at the 2 colonies, we used mist nets and noose carpets to catch adult little auks as they were returning to the colony with food in their gular pouch. Once caught, we gently scooped out the prey from their gular pouch using a small plastic spoon and preserved the meals in 5% formalin and seawater. We banded, measured and weighed the adults before they were released, and no bird was caught more than once. We counted and identified all chick diet items to the lowest possible taxon and estimated total energetic content, again using reported values of dry weights of the various taxa (Berestovskii et al. 1989, Mumm 1991, Hanssen 1997, Węłsawski et al. 1999a, Karnovsky et al. 2003) and an energetic value estimate of 26 kJ g dry wt^{-1} (Węłsawski et al. 1994). We only included complete diet samples in the analyses of the energetic content, percent composition and average number of prey items per food load. We calculated the percent composition by dividing the number of individuals of the taxon of interest by the total number of zooplankters collected for each colony.

We assessed the number of food loads chicks receive per day at both colonies by observing marked provisioning birds for 24 h during the mid-chick rearing period when chicks were ~10 to 15 d old (as in Welcker et al. 2009b). These observations were made during (Greenland) or just prior to (Hornsund) the oceanographic sampling. We caught provisioning birds in their nests or just outside of their nests with noose carpets. Each bird was marked on its breast feathers with a unique colour pattern and given a unique combination of coloured rings on their legs. We sat ~10 to 15 m from the nesting area for 24 h and recorded the frequency and timing of entry of the marked little auks into their nests with food for their chicks. A minimum of 2 observers collected these data simultaneously to ensure that all feeding events were recorded.

Spatial analysis and habitat associations. We compared the spatial distributions of ocean temperature, zooplankton abundance, and density of foraging little auks using ArcGIS. Bins of bird density were overlaid over a temperature raster (or krige) for the study area based on the temperatures measured at 15 m from the CTD casts. We repeated this process with zooplankton densities overlaid over the temperature raster.

Modeling the impact of future climate change. We used data from the continuous plankton recorder (CPR) to calculate the thermal preference of the 3 important *Calanus* species in the Nordic seas: *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* (Warner & Hays 1994, Beaugrand et al. 2007, Helaouët & Beaugrand 2007). The mean abundance per CPR sample of each of these copepod species was calculated for each temperature category (–2 to 25°C by 1°; see Fig. 7) using the International Comprehensive Ocean–Atmosphere Data Set (ICOADS 1 Degree) provided by NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (Woodruff et al. 1987).

To assess the potential impact of changes in sea surface temperature (SST) and water masses on little auk colonies by the end of the 21st century, data from the European Centre at Hamburg (ECHAM 4) were used in a coupled atmosphere–ocean general circulation model (AOGCM; Roeckner et al. 1996) with a horizontal resolution of 2.8° latitude and 2.8° longitude. Projections of monthly SST from 1990 to 2100 were based on scenario A2 (atmospheric pCO$_2$ of 856 ppmv by 2100; Intergovernmental Panel on Climate Change Working Group Report I 2001; see Beaugrand et al. 2008 for information on the nature of these data). In addition, we used SST and ice data (HadlSST 1.1) from 1990 to 2005 to examine the mean location of sea ice in relation to little auk colonies. These data had a spatial resolution of 1° longitude and 1° latitude and were based on *in situ* observations of SST and sea ice as well as satellite derived estimates (AVHRR for SST and SSMI for ice) as in Rayner et al. (2003).

RESULTS

We performed CTD casts and net tows at 25 stations adjacent to each colony. In Hornsund, these represented 9 WSC and 16 SC stations. In all, 9510 little auks were observed foraging in the waters off Hornsund in 128 three km transect segments, and 8584 in the waters off Greenland in 236 three km segments.

Water temperatures, zooplankton and foraging little auks

The distribution of ocean temperatures off Hornsund indicated the presence of 2 ocean currents with distinct temperatures (Fig. 2). Inshore was a mass of cold water that can be identified as the Arctic-fed SC, with tem-

peratures ranging from 2.4°C inshore to 5.5°C along the front with the WSC. Offshore was the Atlantic-fed WSC, with a temperature range of 5.5 to 9°C (Fig. 2). There were significantly higher densities of *Calanus* *finmarchicus* in the WSC than in the SC (1-tailed *t*-test p = 0.003) (Fig. 3, Table 1). Conversely, there were significantly higher densities of large *C. glacialis* in SC than in WSC water (1-tailed *t*-test p = 0.013) (Fig. 3,
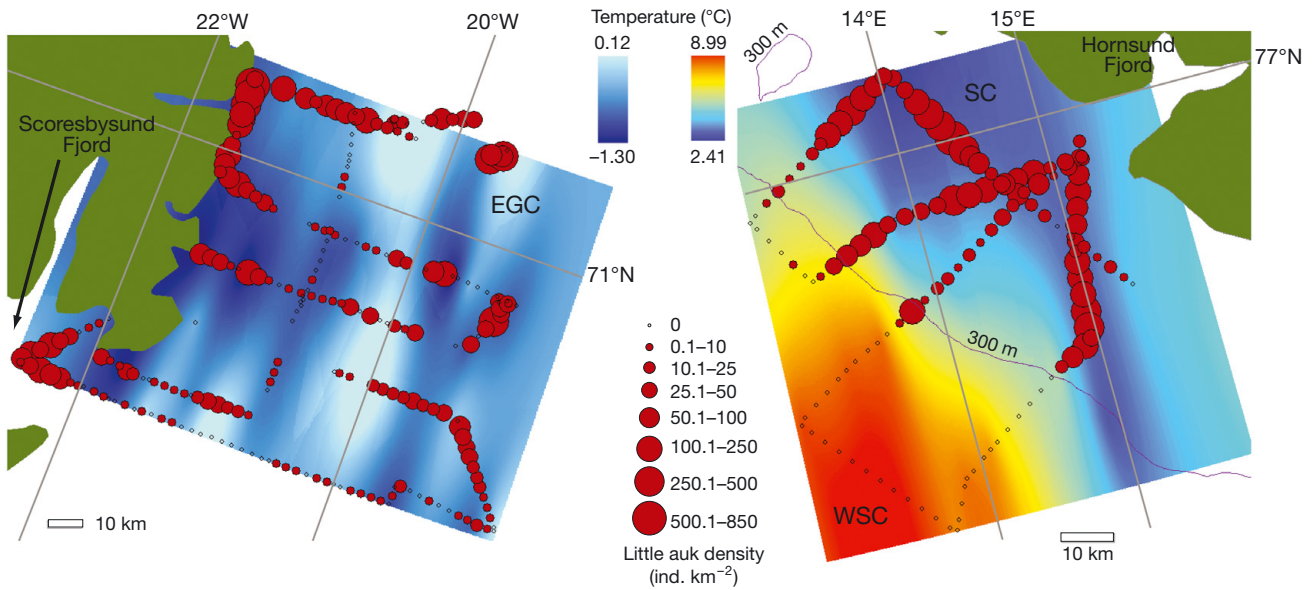

Fig. 2. *Alle alle.* Densities and distribution of foraging little auks in relation to water mass temperatures (measured at 15 m depth) adjacent to study colonies. Abbreviations are as in Fig. 1
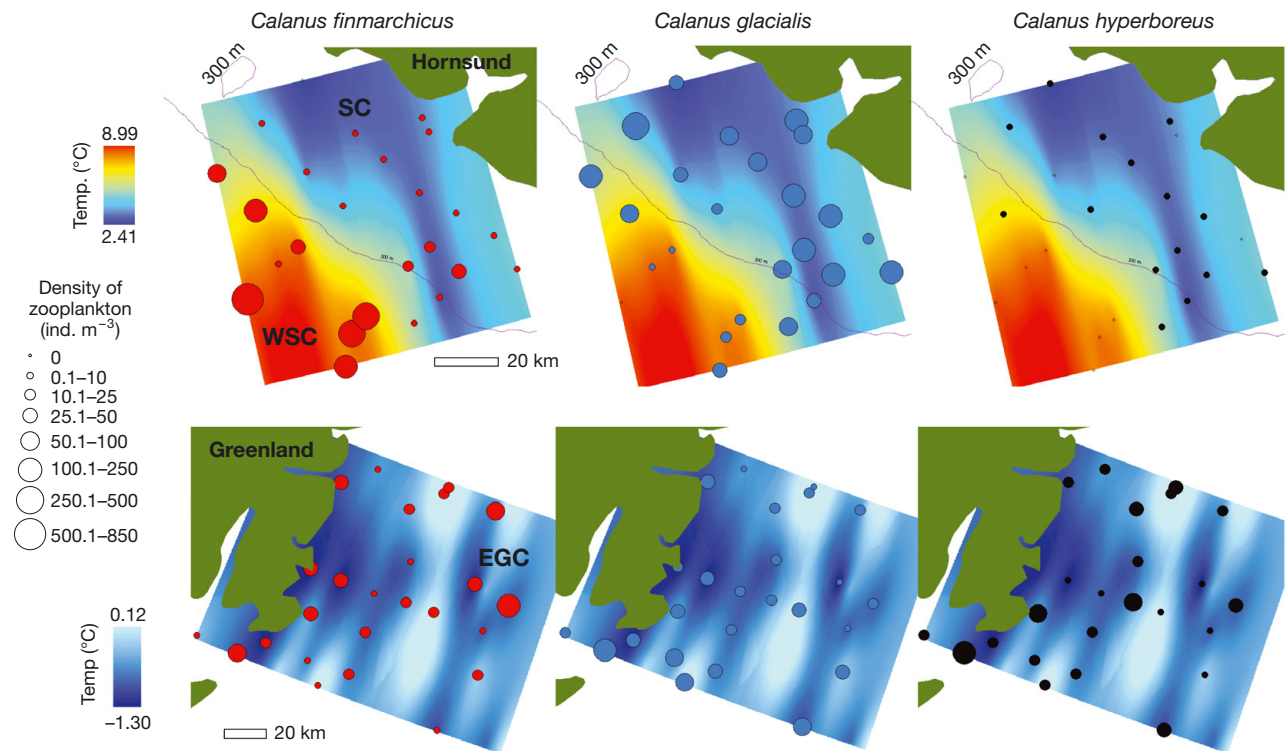

Fig. 3. *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. Densities and distribution in relation to water mass temperatures (measured at 15 m depth) adjacent to study colonies. Abbreviations are as in Fig. 1

Table 1). *C. hyperboreus* was present in low densities (Fig. 3, Table 1), and was also more closely associated with SC than with WSC water (1-tailed *t*-test p = 0.028). The highest densities of foraging little auks (max 778 ind. km^{-2}) were found associated with SC waters, and hence with high densities of *C. glacialis* (Figs. 2 & 3). Little auks were not found foraging where there were high densities of *C. finmarchicus.*

Unlike Hornsund's 2 distinct Arctic- and Atlantic-fed currents, the water temperatures off Greenland indicated a single very cold water mass, with a temperature range of –1.30 to 0.12°C (Fig. 2). The densities of *Calanus* species were more evenly distributed throughout the Greenland study area, and the densities of foraging little auks were not found to be associated with the presence of any one *Calanus* species. In general, zooplankton species and foraging little auks were evenly distributed throughout the sampling area, but with exceptionally high little auk densities occurring near the mouths of east Greenland fjords (Fig. 2). The waters off Greenland contained far higher numbers of edible *C. hyperboreus* than did either water mass near Hornsund (Table 1, Fig. 3).

The major energy source available to little auks in the SC was *Calanus glacialis*, whereas in the WSC, the majority of energy was in the form of *C. finmarchicus* (Table 1). In the EGC, both *C. glacialis* and *C. hyperboreus* contribute a large portion to the energy content of the water (Table 1). Overall, the total energy provided by edible (large size) life stages of *Calanus* species was highest in the WSC (mean ± SE, 1.38 ± 0.27 kJ m^{-3}, due largely to the high density of *C. finmarchicus*; Table 1).

Table 1. *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. Densities and energetics (means ± SEs) of edible large-stage copepods (*C. finmarchicus*: copepodid stage, CV, and adult females, AF); *C. glacialis*: stages CIV, CV, AF; *C. hyperboreus*: stages CIV, CV, AF) in 3 divergent water masses (WSC: West Spitsbergen Current, no. of tows = 10; SC: Sørkapp Current, no. of tows = 15; EGC: East Greenland Current, no. of tows = 25)

Species Water mass	Density in net tows (ind. m^{-3})	Range (ind. m^{-3})	Available energy (kJ m^{-3})
C. finmarchicus			
WSC	179.8 ± 82.2	3.3–849.6	1.11 ± 0.46
SC	7.9 ± 2.8	0.0–39.6	0.04 ± 0.01
EGC	26.1 ± 6.1	3.0–128.3	0.15 ± 0.05
C. glacialis			
WSC	36.1 ± 10.6	0.0–100.8	0.28 ± 0.08
SC	100.2 ± 17.8	15.6–258.3	0.78 ± 0.14
EGC	36.8 ± 7.0	1.8–162.0	0.40 ± 0.10
C. hyperboreus			
WSC	0.5 ± 0.3	0.0–3.6	0.00 ± 0.00
SC	1.3 ± 0.5	0.0–7.6	0.02 ± 0.01
EGC	28.5 ± 6.4	3.0–169.9	0.41 ± 0.12

Chick diets

We collected 27 complete chick meal samples in Greenland from 25 July to 7 August, and 33 in Hornsund (22 to 28 July & 1 August). Diet samples from the 2 sites contained similar numbers of food items (Greenland: 920 ± 88; Hornsund: 1010 ± 101; p = 0.516). The compositions of diet samples at the 2 colonies were similar in that they were both dominated by copepods of the genus *Calanus*; however, the relative contributions of *C. hyperboreus*, *C. glacialis*, and *C. finmarchicus* differed between the colonies. The chick diets at Greenland were dominated by *C. hyperboreus* (57.6%) and *C. glacialis* (32.3%) (Fig. 4), while food loads collected in Hornsund were overwhelmingly *C. glacialis* (86.7%), with *C. hyperboreus* being nearly absent from the diet (Fig. 4). *C. finmarchicus* occurred in low numbers in the diet, totaling 6.0% of the diet items in Greenland and 2.9% in Hornsund. Non-calanoid taxa represented 4.1% of total diet items in Greenland (of which *Apherusa glacialis* was the dominant species) and 9.8% in Hornsund (of which *Pagurus pubescens* zoea was dominant) (Fig. 4). The average energy in a chick meal did not differ between Hornsund and Greenland (Hornsund: 17.2 ± 1.4 kJ; Greenland 16.0 ± 1.2 kJ; 2-tailed *t*-test p = 0.531). We found no difference in the number of meals per day that little auk chicks in East Greenland received and that which chicks in Hornsund received (5 ± 1.1 and 3.5 ± 0.8 meals d^{-1} for Greenland and Hornsund, respectively; 2-tailed *t*-test p = 0.13).

Modeling results

The CPR survey data were collected south of the study area; however, the surveys spanned Atlantic water masses over the entire ocean temperature range encountered. We found that *Calanus finmarchicus* was preferentially located in waters that are 5 to 7°C, while the optimum temperature for *C. glacialis* and *C. hyperboreus* was much lower, at 0 to 2°C (Fig. 5). Neglecting areas that are ice-covered one or more months of the year, our modeled SSTs in the Nordic Seas for the period 1990 to 2005 matched well with observations (Fig. 6a,b). By extending this model into the late 21st century using current trends in levels of anthropogenic forcing (scenario A2), we project temperature increases across the entire little auk breeding range, with the greatest increases occurring in what are currently the coldest surface waters of the study area (Fig. 6c,d). By breaking these modeled results into 3 temperature ranges (≤3°C for the *C. glacialis* and *C. hyperboreus* thermal preferendum, ≥5°C for the *C. finmarchicus* thermal preferendum, and 3°C to 5°C for
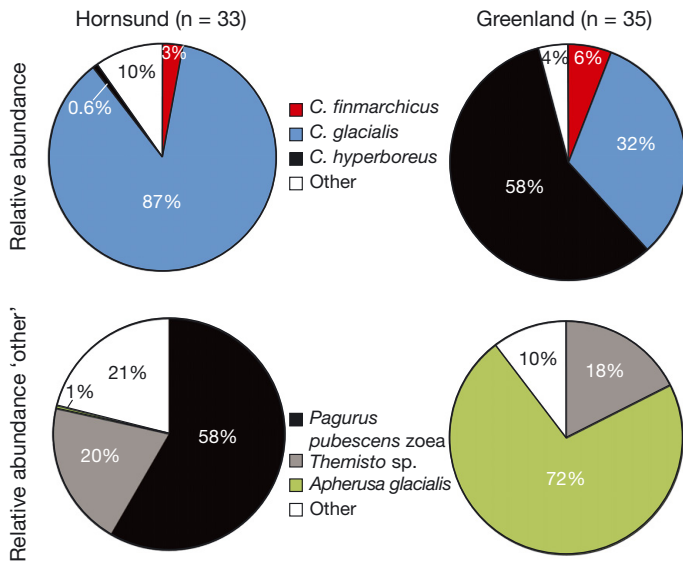
Fig. 4. *Alle alle*. Relative abundance (by number) of chick diet items. The upper pie charts represent all diet items, while the lower represent that fraction not consisting of *Calanus* copepods

the biogeographical boundary), we tailored the SST model expressly for the effects it may have on little auk populations during the peak of the breeding season, i.e. July, when foraging demands are at their highest. Toward the end of the 21st century, 4 of 8 major (>10 k breeding pairs) little auk colonies in the modeled area (Stempniewicz 2001) may face a shift from large/energy-rich to small/lean copepods (Fig. 7).

DISCUSSION

We identified marked differences in the physical and biological properties of water masses between and within our 2 study areas on opposite sides of the Greenland Sea. Cold, low salinity Arctic waters of the EGC and the SC contained more large, energy-rich copepods than warmer, more saline waters of the WSC. Contrary to our hypothesis, the WSC had the highest total energy available from copepods due to high densities of *Calanus finmarchicus*. However, this species represented only a small portion of the diet of little auk chicks (2.9% of diet items in Hornsund). Therefore, cold Arctic waters of the SC and the EGC are practically the most profitable waters to foraging little auks because they provide access to large, energy-rich copepods (Harding et al. 2009a and see below).

These oceanographic patterns were correlated with marked differences in the foraging distribution of little auks on each side of the Greenland Sea (Fig. 2). Off

Hornsund, birds largely restricted their foraging to the Arctic waters of the SC, confirming that their foraging preferences were associated with the abundance of *Calanus glacialis* rather than the total energy available from *Calanus* copepods in the water column. This pattern is consistent with results from at-sea surveys conducted in 2001 within the same zone (Karnovsky et al. 2003). In contrast, off East Greenland, little auks were found foraging throughout the study area, with high numbers at the mouths of east Greenland fjords (Fig. 2). This suggests the presence of mechanisms creating areas of higher concentrations of prey, by physical forcing or due to increased biological production in hydrographic fronts, between the fresh glacial runoff and the more saline, denser seawater.

On both sides of the Greenland Sea, adult little auks provisioning chicks primarily consumed the larger copepod species available: *Calanus glacialis* on the eastern side (although *C. finmarchicus* was more abundant nearby) and *C. hyperboreus* on the western side (although *C. glacialis* was equally abundant). On
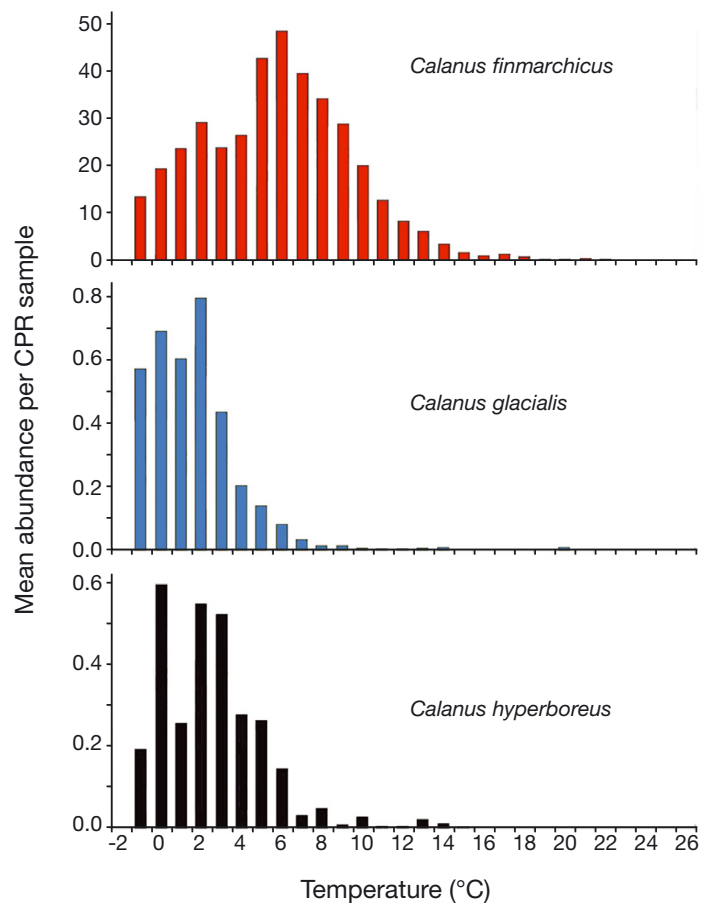

Fig. 5. *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. Thermal associations of the 3 species found in continuous plankton recorder (CPR) samples
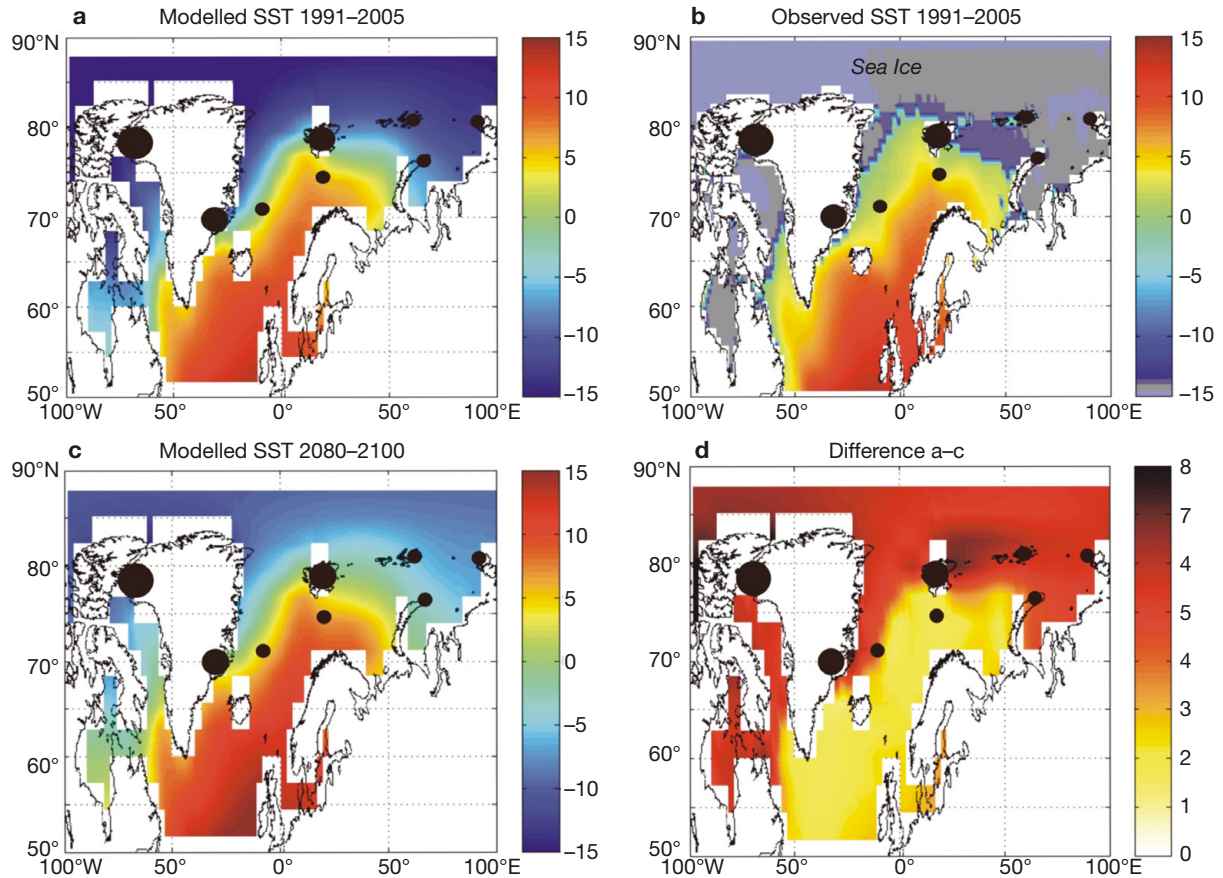
Fig. 6. Sea surface temperatures (SST) for the period 1990–2005 (modeled and observed data) and projected changes in SST for the period 2080–2100 (scenario A2). (a) ECHAM 4 skin temperature (SST) for the period 1990–2005. Note that sea ice is not represented. (b) Observed SST for the period 1990–2005 using Hadley (HadlSST 1.1) data. The last 3 colours in the colour scale represent areas covered by sea ice, for the period 1999–2005, as follows: dark lilac: < 1 mo yr^{-1} on average, grey: between 1 and 4 mo yr^{-1} on average, pale lilac: ≥ 4 mo yr^{-1} on average. (c) ECHAM 4 skin temperature (SST) for the period 2080–2100. Note that sea ice is not represented. (d) Differences (°C) in modeled skin temperature (SST) between the period 2080–2100 (c) and the period 1990–2005 (a). Black circles: Large colonies of little auks (Stempniewicz 2001). Largest circle (Northeast Greenland): 33 million breeding pairs, medium circles: 1 to 10 million pairs, and smallest circles: 10 000 to 1 million pairs
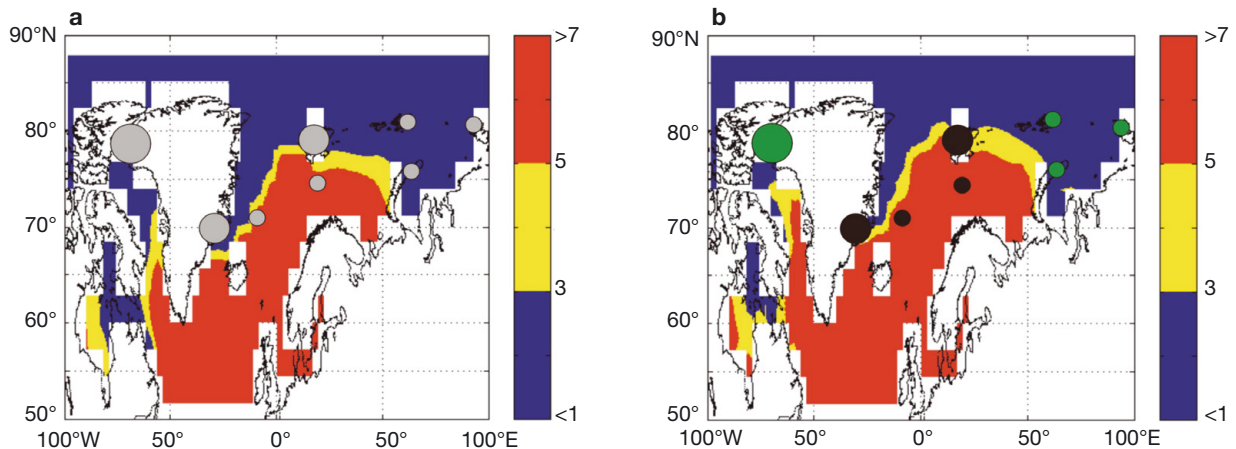

Fig. 7. Location of 3 water masses between 1990–2005 (a) and 2080–2100 (b) using ECHAM 4 A2 data for July. Water masses in red have temperatures >5°C and are therefore more likely to contain high proportions of *Calanus finmarchicus* (see Fig. 3). Water masses in blue have temperatures <3°C and are therefore more likely to contain high proportions of *C. glacialis* and *C. hyperboreus*. Water masses in yellow have temperatures ≥3°C and ≤5°C and represent the biogeographical boundaries. Grey circles: locations of colonies, black circles: little auk colonies that will likely be negatively impacted by future temperature increase, green circles: colonies that will remain within the preferred temperature range of their preferred prey over the modeled time frame. See Fig. 6 for the definitions of circle sizes

the eastern side of the Greenland Sea, the energy-rich WSC with high abundances of *C. finmarchicus* was well within the foraging range of little auks (only 50 km away from the colony). Brown (1976) reported finding little auks 100 to 150 km from their breeding colonies. Therefore, little auks clearly avoided areas where *C. finmarchicus* was the dominant prey.

Finally, contrary to our predictions, and despite the aforementioned prey differences, the amount of energy delivered to little auk chicks per meal did not differ between the 2 study colonies. Furthermore, there were no significant intercolony differences in the average number of prey items per chick diet. One explanation for this result is that the little auks foraging adjacent to the Kap Höegh colony took more *Calanus finmarchicus* to their chicks than did Hornsund little auks. In the EGC, *C. finmarchicus* was as abundant as *C. hyperboreus* (Table 1). Therefore, while the energy content of most of the prey (*C. hyperboreus*) was greater in the chick food loads at Kap Höegh, these birds also took higher numbers of the less energy-rich *C. finmarchicus.* We found no significant difference in the number of food deliveries between colonies; however, our observations were made for only 24 h on a small number of nests (Greenland 8, Hornsund 6).

Impacts of present oceanographic changes

Our results show that little auks from the Greenland Sea experience diverse foraging conditions, but are capable of providing similar amounts of energy to their chicks despite these contrasting abiotic and biotic conditions. The capacity to exert such plasticity has been demonstrated for a wide range of other seabird species confronted with environmental change (Golet et al. 2000, Hedd et al. 2002, Abraham & Sydeman 2004, Gall et al. 2006) and has also been demonstrated experimentally for little auks (Harding et al. 2009b). Nevertheless, there are indications that foraging conditions of little auks in the eastern part of the Greenland Sea are degrading rapidly. Since 2001, little auks foraging on the eastern side of the Greenland Sea (adjacent to Spitsbergen) have had variable diets (Jakubas et al. 2007, Moline et al. 2008), which could be associated with recent changes in the physical properties and distribution of the WSC and the SC and the zooplankton community these water masses support. Between 2001 and 2005, there has been a dramatic 7-fold decrease in the density of *Calanus glacialis* in the SC adjacent to Hornsund Fjord. In 2001, the density of *C. glacialis* in the SC was 716 ± 122 ind. m^{-3} (Karnovsky et al. 2003). In 2005, there were only 100 ± 18 ind. m^{-3} (n = 15; Table 1). Factors driving this decline are unclear, but may include

the onshore flow of warm water from the WSC into the SC, or declines in ice cover and/or currents favorable to *C. glacialis*. Despite the decline in densities of *C. glacialis*, this copepod was still the dominant species being carried back to chicks on the eastern side of the Greenland Sea. Hence, the threshold of minimal density of *C. glacialis* that would force little auks to feed on *C. finmarchicus* was not reached in 2005, but may well be reached in the future. Beyond a certain threshold of prey availability, Arctic waters may become unprofitable for foraging little auks, with consequences for their reproductive success and population dynamics. Although little auk parents have been shown to have flexibility in both their energy expenditure (Welcker et al. 2009a) and foraging behaviour (Welcker et al. 2009b, Karnovsky et al. unpubl.), life history theory predicts a limit to the additional reproductive costs breeders can accept, with parents prioritizing self-maintenance over increased provisioning effort when foraging costs become too high (e.g. Velando & Alonso-Alvarez 2003).

By comparing the zonal differences in water mass characteristics, zooplankton density, and distribution of foraging little auks, we gained insight into how increases in sea water temperature and consequently in the abundance of smaller prey may impact little auks. This spatial comparison allows us to understand how warming may impact little auks and other upper trophic predators that rely on Arctic copepods (e.g. the Arctic cod *Boreogadus saida*, which is a crucial link to Arctic upper trophic predators; Lønne & Gulliksen 1989).

Impact of future climate change

The distribution and strength of currents in the Greenland Sea and the interactions between them vary inter-annually (Loeng et al. 1997). They are also influenced by fluctuations of the North Atlantic Oscillation (NAO; Dickson et al. 2000). An increase in the influx of Atlantic water into the Arctic Ocean has been linked to a positive-phase NAO (Dickson et al. 2000). Since the 1960s, the NAO has been in a predominantly positive phase with exceptionally high magnitudes (Hurrell 1995). Although the NAO is a natural mode of climate fluctuation, it is possible that it has been influenced by anthropogenic factors, such that the positive phase has become increasingly common (Visbeck et al. 2001). Increased Atlantic flow into the Arctic Ocean may reduce the extent of the SC near Hornsund Fjord, and thus the densities of the preferred prey, *Calanus glacialis*.

Based on our SST modeling results and the optimal temperatures of the prey species involved, it is clear

that many little auk colonies in the Nordic Seas will face a shift towards a zooplankton community dominated by *Calanus finmarchicus* by the end of the 21st century. We predict a greater temperature effect (impacting more little auk colonies) later in the season, which is the time of late chick-rearing and most intensive foraging by little auk parents and fledglings. These findings mesh with predictions of Falk-Petersen et al. (2007) and Stempniewicz et al. (2007), who forecast that the eastern side of the Greenland Sea will become similar to the marine ecosystem off the west coast of Norway, with energy flow through *C. finmarchicus* to herring *Clupea harengus*, rather than through *C. glacialis* to little auks. In the North Sea, common murres *Uria aalge* suffered reproductive failure or had chicks fledge in poor body condition due to consumption of prey with low calorie content (Wanless et al. 2005). Climate change has forced a number of high latitude top predators to switch to sub-optimal prey, which has induced declines in adult body mass, chick fledging mass, adult survival, and reproductive success (as reviewed by Österblom et al. 2008). In a similar fashion, declines in Atlantic cod *Gadus morhua* L. in the North Sea are linked to shifts in the *Calanus* copepod community from *C. finmarchicus* to *C. helgolandicus* associated with warming temperatures (Beaugrand et al. 2003). Further investigations are required to determine the exact threshold of levels of large copepod availability below which little auks will not be able to compensate via foraging plasticity, and will experience a reduction in chick and/or adult survival.

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