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Multi-colony tracking reveals potential threats to little auks wintering in the North Atlantic from marine pollution and shrinking sea-ice cover.

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Running title: sensitive hotspots for vulnerable seabirds

ABSTRACT

Aim Extensive development of human activities in combination with ocean warming are rapidly modifying marine habitats in the Arctic and North Atlantic regions. In order to understand the potential impacts on marine biodiversity, there is an urgent need to determine distributions and habitat preferences of potentially vulnerable species, and to identify sensitive hotspots that might require particular protection. Our aims were to track one of the most abundant seabirds of the world, the little auk (*Alle alle*) to provide a large, meta-population scale overview of its non-breeding distribution, and to document potential threats to this species from human activities and other environmental changes.

Location Arctic North Atlantic.

Methods Using light-level geolocators, we investigated the 2010/11 non-breeding distribution of 65 little auks from four major colonies distributed throughout the Arctic North Atlantic. Bird distribution during the moulting, wintering and pre-breeding periods was compared with (1) the extent of the marginal ice zone and (2) the areas covered by the main shipping lanes, and oil and gas activity licences.

Results We identify several hotspots for this species, including two key areas located in the Greenland Sea and off Newfoundland. Crucially, we show that some of these hotspots overlap extensively with areas of intensive human activities, including oil and gas extraction and shipping. As little auks, which spend the major part of their time on the sea surface, are extremely vulnerable to marine pollution, our results emphasize the risk associated with the projected expansion of these activities.

Main conclusions We conclude that management of further human enterprises in the Arctic needs to be based on more thorough risk assessment, requiring a substantial improvement in our knowledge of the distribution of sensitive species.

Keywords: *Alle alle*, conservation biogeography, geolocators, non-breeding distribution, oil pollution, seabird

INTRODUCTION

North Atlantic and Arctic marine habitats are changing rapidly, reflecting the combined effects of climate change and anthropogenic activities (ACIA 2004; AMSA 2009; AMAP 2011). These changes are, in turn, bound to have important impacts on marine biodiversity, regionally affecting community structure and dynamics (Pauly et al. 1998; Reid et al. 2000; Beaugrand et al. 2010; Gilg et al. 2012). In this context, there is a pressing need to improve our understanding of species-environment interactions, and individual responses to environmental variability, in order to predict consequences of habitat modification and anthropogenic pressure for their survival and population dynamics. Such investigations are often constrained by our limited knowledge of species distribution in these remote regions, yet the latter is a pre-requisite for effective prediction of future impacts.

Seabirds are an essential component of marine ecosystems, including in the North Atlantic and Arctic, where they are highly abundant (Barrett et al. 2006). They exert a strong predation pressure on lower trophic levels and therefore play a key role in marine food webs (Karnovsky & Hunt 2002; Brooke 2004; Barrett et al. 2006). Despite this ecological importance, many seabirds are threatened, exposed to the impacts both of climate change and anthropogenic activities, and their protection is a major concern (Butchart et al. 2004; Croxall et al. 2012). For instance, the rapid decrease of multi-year ice extent in the Arctic Ocean might restrict feeding habitats for some species and lead to a general northward shift in distribution (Gilg et al. 2012). The retreat of sea ice is also opening new shipping routes and increasing opportunities for extractive industries, targeting hydrocarbons, sea-floor minerals and unexploited fish stocks (AMSA 2009), thereby increasing the risk of oil pollution and incidental mortality of seabirds at sea. Determining seabird movements and distribution is therefore of pivotal importance in order to define sensitive areas requiring particular

attention with respect to recent and future development of human activities (McFarlane Tranquilla et al. 2013). This will also provide essential information for predicting the impacts of environmental modification on the Arctic seabird community.

In this study, we investigate the non-breeding distribution of the little auk (*Alle alle*), a small (150g) and abundant [>80 million individuals (Egevang et al. 2003)] high-Arctic seabird. Initial investigations showed that during their non-breeding season, little auks concentrate within particular hotspots located in the Greenland Sea and in the northwest Atlantic. There, millions of birds become exposed to local environmental perturbations (Mosbech et al. 2012; Fort et al. 2012a). Although valuable, both these studies focused on a single population located on the east coast of Greenland. However, little auks are widely distributed in the North Atlantic, with a breeding distribution that extends from the eastern Canadian coast to the Russian Arctic (Gaston & Jones 1998). Areas used by non-breeding birds might differ among populations, reflecting regional differences in oceanography and habitat preferences. Recent studies of other seabirds emphasise the importance of considering such variability for an adequate assessment of relative risks associated with human activities (Frederiksen et al. 2012; McFarlane Tranquilla et al. 2013). Similarly, only by carrying out large-scale investigations at the meta-population level will it be possible to identify the key non-breeding areas for little auks and to assess the potential future impacts of anthropogenic and other environmental change.

Using miniaturised bird-borne technology, the present study therefore aimed to (1) define the overall non-breeding distribution, and key moulting and wintering hotspots of adult little auks at a meta-population scale, and (2) document potential threats to this species from human activities (associated with oil or gas extraction, and shipping) and other environmental changes.

METHODS

Study sites

The non-breeding distribution of little auks was investigated in 2010/11 by tracking birds from colonies in northwest Greenland, east Greenland, Spitsbergen and Bjørnøya (Bear Island), hereafter referred to as NWG, EG, SP and BI, respectively (see Fig. 1 and Appendix S1 in Supporting Information for details). These four colonies represent the largest known breeding aggregations for little auks, world-wide, and cover most of the occupied range in the Arctic sector of the North Atlantic (Stempniewicz 2001). Non-breeding locations were estimated for a total of 65 birds using geolocators (Global Location Sensors or GLS) deployed in summer 2010 and retrieved in the following season (see Appendix S1 for details). Adult birds were captured at all colonies using noose carpets or by hand in their nest crevices, weighed and fitted with a GLS from the British Antarctic Survey (BAS, UK), mounted on a metal or plastic leg ring. Birds were released after <10 minutes of handling. Recaptures followed the same procedure. Four different models of GLS were used: Mk14, Mk18L, Mk12 and Mk10B (1.0-1.5g; all <2% of birds' body mass). During recapture, a small amount of blood was collected for subsequent molecular sexing.

To determine potential impacts of logger deployment, resighting rates of birds fitted with loggers in 2010 were compared with those of control birds (un-instrumented) in 2008 and 2009. Control adult little auks were captured following the same methods as instrumented birds and individually marked with a color ring. The following years, 61% and 57% of these birds were recaptured, respectively. These recapture rates of control little auks are similar to those obtained for equipped birds between 2010 and 2011 (Appendix S1). Only at SP was the rate lower, which was related to site-specific conditions and limited recapture effort precluding the recapture of all resighted birds. In addition, body mass of little auks at the time of logger deployment was compared with that

recorded when the device was retrieved the following year. We observed no significant difference (t -test: $t = -1.34$, $df = 137$, $p = 0.18$; means 2010 vs 2011: NWG: 147g vs 144g, EG: 152g vs 156g, SP: 167g vs 168g, BI: 156g vs 155g). This suggests that there was no substantial effect of the GLS on body condition.

Light-level data analyses

Light-level data were extracted from GLS loggers, linearly corrected for clock drift and processed with a threshold method (Wilson et al. 1992) using the BASTrak software package (BAS, Cambridge). We used threshold light intensity of 10, an angle of sun elevation of -3.0° , and applied the compensation for movements. The angle of sun elevation was determined following a two-step procedure: (1) a first range of possible angles was selected by visually inspecting locations derived from a variety of elevation angles and by considering that little auks do not occur inland during the non-breeding period. (2) The angle of sun elevation was then chosen following the ‘Hill-Ekstrom calibration’ method (Lisovski et al. 2012), assuming similar average shading intensity for the entire study period. This method was shown to provide the most accurate latitude estimations (Lisovski et al. 2012). Contrary to the ‘in-habitat calibration’, it can be used when no information is available for long periods from birds from a known location (e.g. at the breeding site; see Frederiksen et al. 2012), and is therefore suitable for high-Arctic marine species that breed in constant daylight areas. The method consisted of plotting estimated latitudes over time using a range of sun elevation angles (see above), and selecting the angle that minimized the variance of latitudes around the equinox periods.

Kernel analyses were performed to determine high density aggregations (hotspots) for the tracked birds during three distinct periods of the non-breeding season: (1) fall - 15 August to 15 September, the post-breeding period when this species is assumed to moult (Mosbech et al. 2012); (2) winter -

December and January, when birds are assumed to occupy their main wintering range (Fort et al. 2012a); and (3) spring - April, when little auks are thought to migrate back to their breeding site. Hotspots were delimited by the 50% kernel density contours. Kernel analyses were performed using the Animal Movement extension to ArcView 3.2 (ESRI) (Hooge & Eichenlaub 1997) with the bandwidth parameter (h factor) determined by least-squares cross validation, and a cell size of 50km. Results were mapped using ArcMap 10 (ESRI, Redlands, CA, USA). The first locations in the immediate post-breeding period were not always available starting 15 August, particularly for birds from SP and BI. Indeed, the constant daylight at high latitudes during summer precludes the calculation of geographic coordinates, and the date of first points therefore depended on colony latitude and the timing of latitudinal movements by the tracked birds.

Distribution of sea ice and human activities

Little auk distribution during the three distinct periods in the non-breeding season (see above) was compared with: (i) the extent of the marginal ice zone (10% ice concentration) on the 1 September 2010, 18 December 2010 and 15 April 2011, respectively, obtained from the NOAA National Ice Center (http://www.natice.noaa.gov/products/products_on_demand.html), (ii) the area covered by oil and gas activity licences for exploration, production and significant discovery off Newfoundland and Nova Scotia on the 15 February 2013, issued by the Canada-Newfoundland & Labrador Offshore Petroleum Board and Canada-Nova Scotia Offshore Petroleum Board, and (iii) the main shipping lanes off Newfoundland.

RESULTS

Little auk non-breeding distribution

Non-breeding little auks adopted different strategies according to their colony of origin, with only slight differences observed between sexes (Appendix S2). After breeding, tracked birds from NWG all moved south to a relatively small area in the northwest of the Davis Strait, where they remained from mid-August to mid-September (Figs. 1A and 2). In October, they continued their southward migration to reach the wintering area off Newfoundland in early December (Figs. 1B and 2), which was occupied for >3 months before the start of their northward migration (Fig. 2). In April, birds were still in the northwest Atlantic, in similar areas to those used during winter (Fig. 1C).

Birds from EG and SP spent the post-breeding period (probably moulting) in broadly the same area in the Greenland Sea (Fig. 1A). Three birds from SP adopted a different movement pattern, travelling east after the breeding season to spend several weeks in the Barents Sea south of Franz Josef Land (Fig. 1A). In mid-October, birds from EG migrated ~3000 km to the southwest, and reached their winter quarters off Newfoundland in early December (Figs. 1B and 2). Thus, their winter distribution overlapped extensively with that of birds from NWG. After three months, birds from EG returned north towards their colony (Fig. 2). In April, most were off the northeast coast of Iceland, and the remainders were further south in the North Atlantic (Fig. 1C). Unlike Greenlandic birds, tracked individuals from SP adopted two different movement patterns in winter; four of them (44%) moved west to spend the winter in the marginal ice zone south of the Davis Strait, and the rest (66%) remained in the Greenland Sea off the northern coast of Iceland (Fig. 1B). In April, all birds from SP were resident in the Greenland Sea (Fig. 1C).

After breeding, birds from BI all moved eastward into the Barents Sea, dispersing along the ice edge between south Spitsbergen and Novaya Zemlya (Fig. 1A). At the end of September, they moved west towards their winter quarters. Like birds from SP, those from BI divided into two

groups during autumn migration. Three birds (14%) crossed the North Atlantic to waters off southwest Greenland, 2900 km from their colony, where they stayed for almost four months until early March (Figs. 1B and 2). All others (86%) spent the winter in the Greenland Sea and along the northern coast of Iceland, in a similar area to that occupied by birds from SP during the same period.

Use of the marginal ice zone by little auks

The only little auks tracked from Greenland that appeared to use the marginal ice zone were birds from EG during the immediate post-breeding period. In contrast, the distribution of birds from both SP and BI overlapped considerably with the sea ice edge. In September, when little auks are assumed to moult, individuals from both SP and BI occupied an area located along the marginal ice zone in the Greenland Sea and the Barents Sea, respectively (Fig. 1A). Similarly, during winter, the northern limit of the main area occupied by little auks from SP and BI in the Greenland Sea was along the marginal ice zone (Fig. 1B). Birds from SP that overwintered in the Davis Strait were also close to the sea ice limit, as were the majority of birds from SP and BI in April (Fig. 1C).

Little auk distribution and human activities off Newfoundland

During winter and spring, the hotspots for Greenlandic birds (NWG and EG in winter and NWG in spring) included large areas off Newfoundland where offshore oil industry licenses have been issued. Indeed, both production and significant discovery license blocks are located entirely within the winter and spring hotspots used by the tracked birds. Exploration licenses, which might result in future production activities, also occupied a large part of the birds' core distribution (6% and 11% of EG and NWG winter hotspots respectively, and 7% of NWG spring hotspots; Fig. 3). Moreover, major shipping routes off Newfoundland transect the hotspots used by Greenlandic birds (Fig. 3).

DISCUSSION

Thanks to the rapid development of miniaturized geolocators over the last decades, the tracking of non-breeding seabirds has become a major field of research, including several recent studies of North Atlantic species (Frederiksen et al. 2012; Fort et al. 2012b; Magnúsdóttir et al. 2012). A main objective of these investigations has been to identify the hotspots at sea where large concentrations of seabirds occur, and to assess whether they need particular attention for the conservation of threatened species.

Our results supplement these investigations and provide for the first time a multi-colony overview of the non-breeding movements and distribution of little auks, for which very little information was available (but see Mosbech et al. 2012; Fort et al. 2012a). Despite past ringing effort, there are few ring recoveries of little auks away from colonies, probably because most birds die at sea in remote areas (Lyngs 2003). This lack of information is unfortunate since little auks, the most abundant seabirds of the North Atlantic, play an essential role in this ecosystem (Karnovsky & Hunt 2002) and are highly sensitive to environmental perturbation (Robertson et al. 2006; Wilhelm et al. 2007; Karnovsky et al. 2010). By the use of geolocators, we show that this species can perform large-scale movements during the non-breeding season, typically travelling up to 3500 km to reach the wintering grounds (Fig. 2). This confirms that non-gliding seabirds with high energetic costs of flight such as alcids (Pennycuik 1987) can perform long migrations to reach profitable wintering grounds (Guilford et al. 2011, Fort et al. 2013, McFarlane Tranquilla et al. 2013). This is important, as it shows that birds breeding in Svalbard reach the Canadian and the south-eastern coast of Greenland, which was unsuspected for this small species until our study. Our findings also highlight the existence of common areas used by different little auk populations during the same time periods. The Greenland Sea is one of two important regions, occupied by birds from East Greenland and

Spitsbergen (EG and SP) during fall (immediate post-breeding period) when moulting occurs, by both populations (SP and BI) from Svalbard during winter, and by birds from Spitsbergen (SP) during spring. The other crucial area are the waters east of Newfoundland, where all Greenlandic birds (NWG and EG) overwintered. Over 30 million pairs, almost the entire population of little auks from Greenland, breed in the Thule district on the west, and Scoresby Sund on the east (where NWG and EG birds were sampled); the remainder (a small minority) breed in the Uppernavik District (Stempniewicz 2001; Egevang et al. 2003). Therefore, tens of millions of individuals most likely spend the bulk of the non-breeding season within a rather concentrated area off Newfoundland, highlighting the key importance of this region for little auks. While there were strong suspicions that, with its high winter productivity (Fort et al. 2012a), waters off Newfoundland constituted a significant wintering ground for North Atlantic seabirds (e.g. Fifield et al. 2009, Gaston et al. 2011), it was not appreciated that the Greenland Sea might also be a major destination for non-breeding birds. The latter should now be confirmed at a community scale by combining multi-species tracking studies with at-sea surveys to determine the importance of this region for Arctic seabirds in general. Indeed, there is an increasing realization that large-scale multi-colony studies are required for widely distributed species in order to consider potential variation in non-breeding strategies among populations. These provide a more comprehensive overview of seabird distribution, and highlight biodiversity and resource hotspots that might be included in protected area networks (Grémillet & Boulinier 2009, Magnúsdóttir et al. 2012).

By focusing on four of the largest colonies located around the North Atlantic in areas where >90% of the global population is estimated to breed (Stempniewicz 2001; Egevang et al. 2003), we are confident that highlighted hotspots reflect the general non-breeding distribution for adult little auks. Moreover, our results are corroborated by previous investigations performed over three additional years at the EG colony (Mosbech et al. 2012; Fort et al. 2012a; Fort et al. unpublished).

Nevertheless, further studies focused on additional colonies (e.g. the Russian populations), more individuals, and several years are needed to confirm whether these non-breeding hotspots are used consistently, and whether they are representative of the entire little auk population. Furthermore, we emphasize that hotspots identified in this study only represent the distribution of breeding little auks. Although size limitations, and the difficulties involved in ensuring long-term attachment without deleterious effects, currently preclude the use of satellite-transmitters on little auks, additional investigations will have to be performed to determine if juveniles, immatures or non-breeders occupy similar areas to breeding adults during the non-breeding period.

Non-breeding little auks and sea ice

Recent studies suggested the importance of sea ice for little auks when it occurs in proximity to their colony (e.g. Jakubas et al. 2012), perhaps because it provides a particular source of prey such as sympagic amphipods (Fort et al. 2010) from which birds might benefit. Our findings suggest that the marginal ice zone also might be a key habitat for some little auk populations during the non-breeding season. Indeed, the distribution of birds from both study colonies in Svalbard overlapped closely with the location of the ice edge, year-round, particularly in the Greenland Sea, the Barents Sea and the southwest Davis Strait. However, our data do not allow us to assess whether the ice edge is specifically targeted by little auks or whether it merely represents a physical barrier constraining their northern distribution. These results have implications for our understanding of environmental pressures on little auks, and for investigations of the effects of future climate change. Recent studies suggested that during summer, climate change will affect the energy budgets, breeding success and distribution of many seabirds and other vertebrates in the Arctic (Gilg et al. 2012). These modifications will partly be due to a change of the sea ice extent that might allow access to new breeding and feeding sites, or modify prey availability (see Gilg et al. 2012 and

references therein). Here, we speculate that the predicted decrease in sea ice extent will also have a major effect on little auks during their non-breeding season. It will open new, potentially suitable wintering habitats in the Greenland Sea, or force individuals relying on the sea ice edge as feeding grounds to move northwards, following its retreat. In all cases, it is highly likely that the predicted reduction of sea ice will affect the distribution of little auks from Svalbard by modifying their winter habitat.

Human activities as a potential threat for Arctic seabirds

Seabirds from the alcid family are known to spend a large proportion of their time outside the breeding season in contact with the water surface, either resting or diving (Gaston & Jones 1998; Mosbech et al. 2012). During that time, they are therefore very sensitive to marine pollution, particularly oil spills resulting from illegal discharges from shipping, or accidental discharges from both shipping and oil and gas exploitation (Wiese & Robertson 2004; Wilhelm et al. 2007; Hedd et al. 2011). Here, we show that a major proportion of the global population of little auks (most likely millions of birds; see above) winters off Newfoundland within an area where the level of current and projected human activities, and therefore oil-related risks, are high. With its strategic shipping lanes and several offshore oil production platforms, the waters off Newfoundland are some of the most vulnerable areas in the sub-Arctic (Halpern et al. 2008). Recent studies involving bird-borne technology or at-sea surveys indicate that several seabird species gather in this region during winter in huge numbers, including common guillemots (*Uria aalge*), Brünnich's guillemots (*U. lomvia*), kittiwakes (*Rissa tridactyla*) and little auks (Fifield et al. 2009, Hedd et al. 2011; Frederiksen et al. 2012; McFarlane Tranquilla et al. 2013; this study); and chronic oil pollution from shipping has been shown to have significant deleterious effects on these species, killing thousands of individuals each year (Wiese & Robertson 2004). In the case of little auks, the combination of little apparent

variability in migration strategies (e.g. only one hotspot observed for all tracked birds from Greenland) and a relatively concentrated distribution might enhance this sensitivity, and hence even a single-point, small-scale pollution event could be detrimental to huge numbers of birds. Accordingly, little auks are among the species worst affected by oil spills in the North Atlantic (Heubeck 2006; Robertson et al. 2006). In addition to pollution around platforms, little auks might also be sensitive to the artificial light (including flares) generated by oil exploitation activities, which attract seabirds like little auks, increasing the risk of collisions with man-made structures and hence mortality (Wiese et al. 2001). For little auks, the main regions occupied during winter are located where the daylight period is short and light levels extremely low, and hence the attractiveness of artificial lights might be especially high. The fishing industry is also expected to expand in the Arctic with the opening of new fishing grounds as the seasonal extent of sea ice declines. While this might become a major threat to piscivorous seabirds by increasing the risk of accidental bycatch (Hedd et al. 2011), this should have limited impact on little auks during winter.

Crucially, seasonal overlaps between the marine industries (shipping and oil extraction) that are the source of oil pollution and seabird hotspots will almost inevitably increase in the Arctic, as sea ice retreats and human activities rapidly expand northwards. The predicted reduction of sea ice extent (IPCC 2007) will increase the number of days that existing Arctic shipping lanes are used, and open other routes (AMSA 2009; Fig. 4). Oil exploration, which has already expanded throughout the North Atlantic sector of the Arctic (Fig. 4), will certainly result in the deployment of additional oil platforms. In this context, it is essential to understand the large-scale distribution of seabirds, particularly as hotspots for these species are usually indicative of high resource availability and wider biodiversity, which should be protected before the establishment of new human industries. Additional efforts to define seabird habitat preference are also essential to investigate how a

warming climate could change the distribution of biodiversity and resource hotspots, because conservation strategies will need to cope with probable long-term changes in the overlap with, and hence pressure from, human industries. Seabird distribution can be related to specific environmental factors such as prey availability or temperature regimes (Fort et al. 2012a). Changes to oceanographic conditions as the climate warms (e.g. Beaugrand et al. 2002, 2010) could therefore cause a major redistribution of both prey and predator (Gilg et al. 2012). The conservation of their key feeding grounds and the establishment of stringent management strategies that reflect the pivotal role of seabirds within the ecosystems of the Northern Atlantic are of critical importance, as recently highlighted by several international initiatives by the Arctic Council and the International Maritime Organization (e.g. Arctic Council 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Deployment details

Appendix S2 Comparison of the distribution of male and female little auks

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BIOSKETCH

Jérôme Fort is post-doctoral researcher at Aarhus University, Denmark. Using a multidisciplinary approach, his main research activity aims to improve our understanding of the impact of global change on the Arctic seabird community.

Author contributions: J.F., B.M., H.S., D.G. and A.M. conceived the ideas; R.A.P. provided tracking devices and advice on geolocation processing; all authors (but R.A.P.) contributed to the collection of data; J.F. analysed the data; J.F., B.M., H.S., D.G., J.W., R.A.P., K.L.J and A.M. wrote the paper.

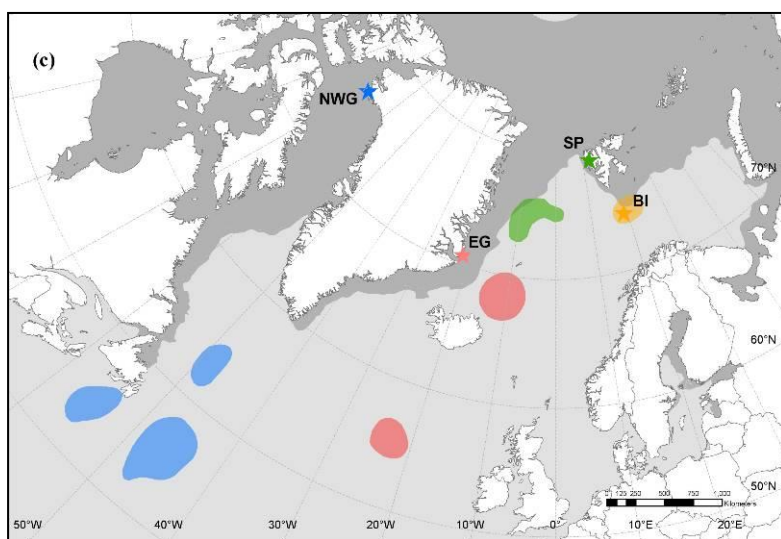
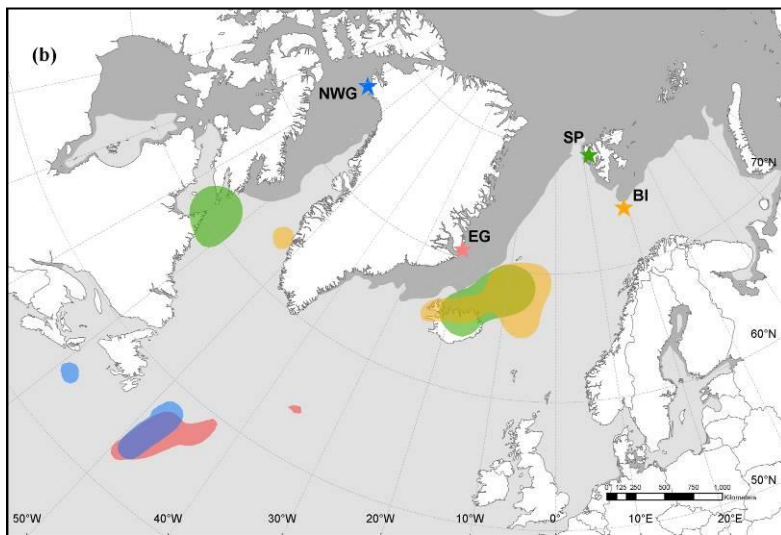
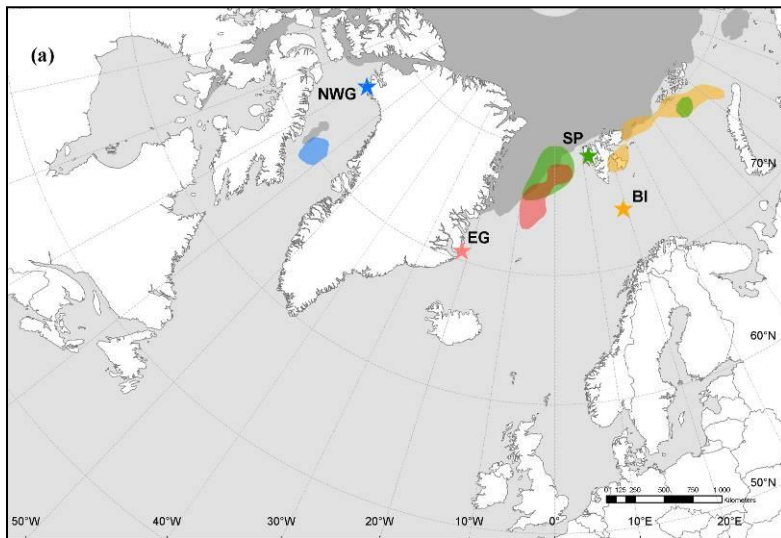


Fig. 1. Main areas occupied by little auks (*Alle alle*) in the 2010/11 non-breeding season, represented by 50% kernel density contours. (a) moulting (15 August – 15 September) distribution, (b) winter (December-January) distribution, (c) spring (April) distribution. On each map, colored stars represent the breeding colonies where birds were equipped, with the same color used for kernel density contours for that colony. The dark grey area indicates the extent of the marginal ice zone on 1 September 2010, 18 December 2010 and 15 April 2011. Ice data are from NOAA National Ice Center. Map projection: equidistant conic.

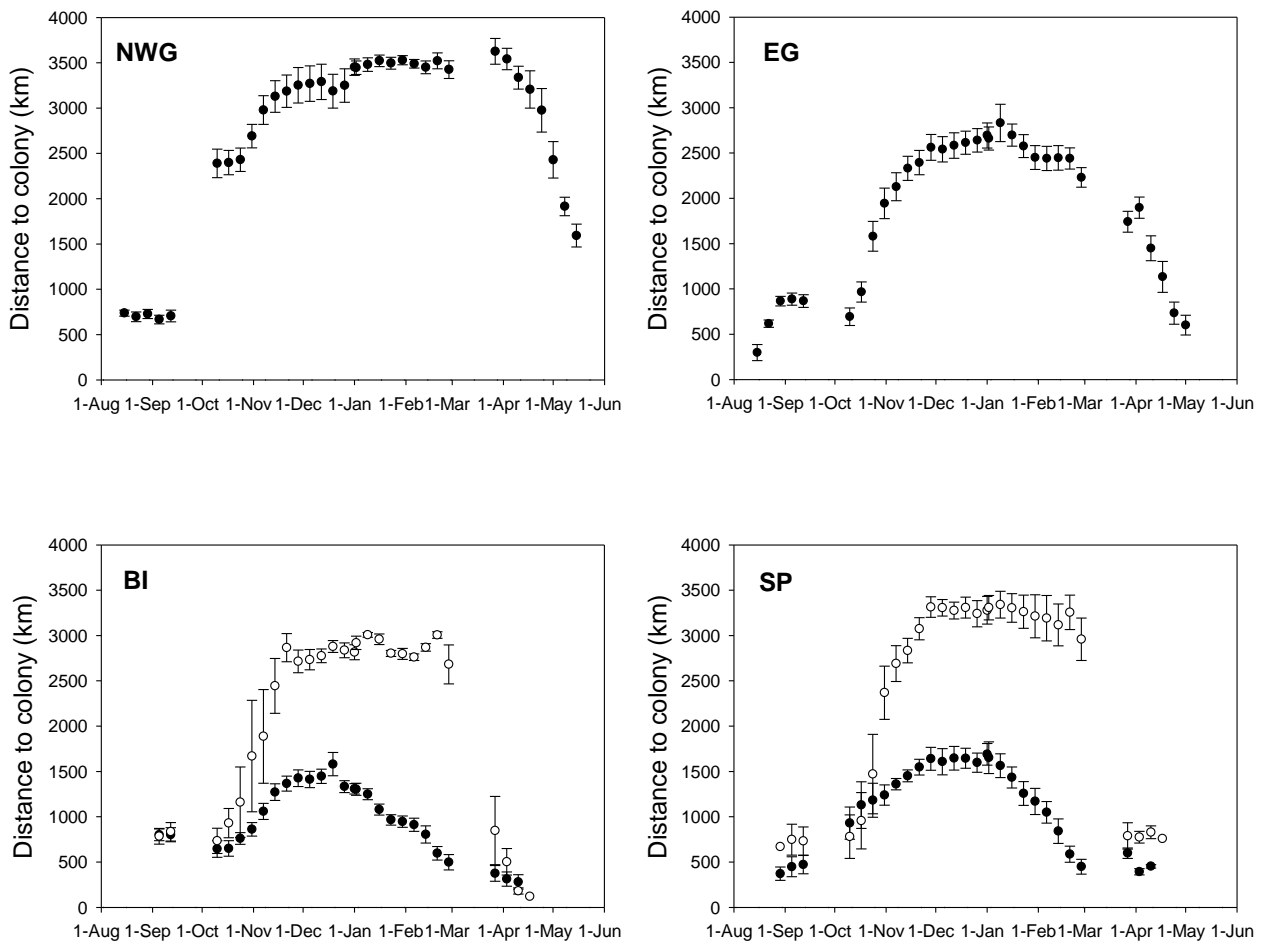


Fig. 2. Weekly distance (mean (SE), km) to the colony of origin for tracked little auks (*Alle alle*) from each of the four study sites. For SP and BI, black-filled circles represent weekly distance to colony of birds wintering in the Greenland Sea, and open circles represent birds wintering off the west coast of Greenland (see results). Data around equinox periods (from 15 September 2010 to 15 October 2010 and from 01 March 2011 to 01 April 2011) were excluded.

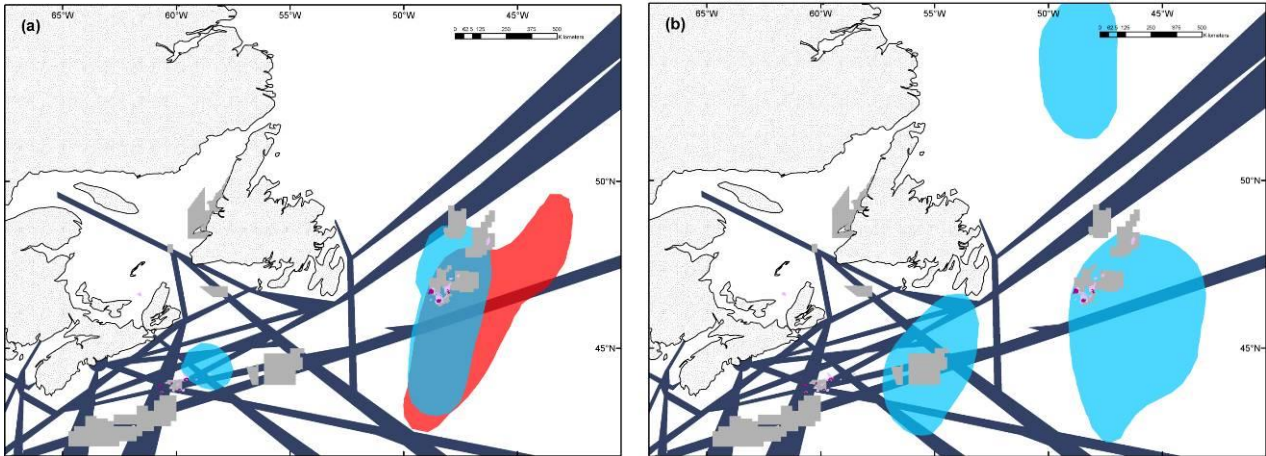


Fig. 3. Distributions in (a) winter (December 2010 and January 2011), and (b) spring (April 2011) of tracked little auks (*Alle alle*) from NWG (light blue) and EG (red) in relation to human activities off Newfoundland. Hotspots in bird distributions are the 50% kernel density contours. Production (purple), Significant Discovery (pink) and Exploration (light grey) license blocks were provided by the Canada-Newfoundland & Labrador Offshore Petroleum Board. Main shipping lanes (dark blue) are adapted from Lock et al. (1994). Map projection: Mercator.

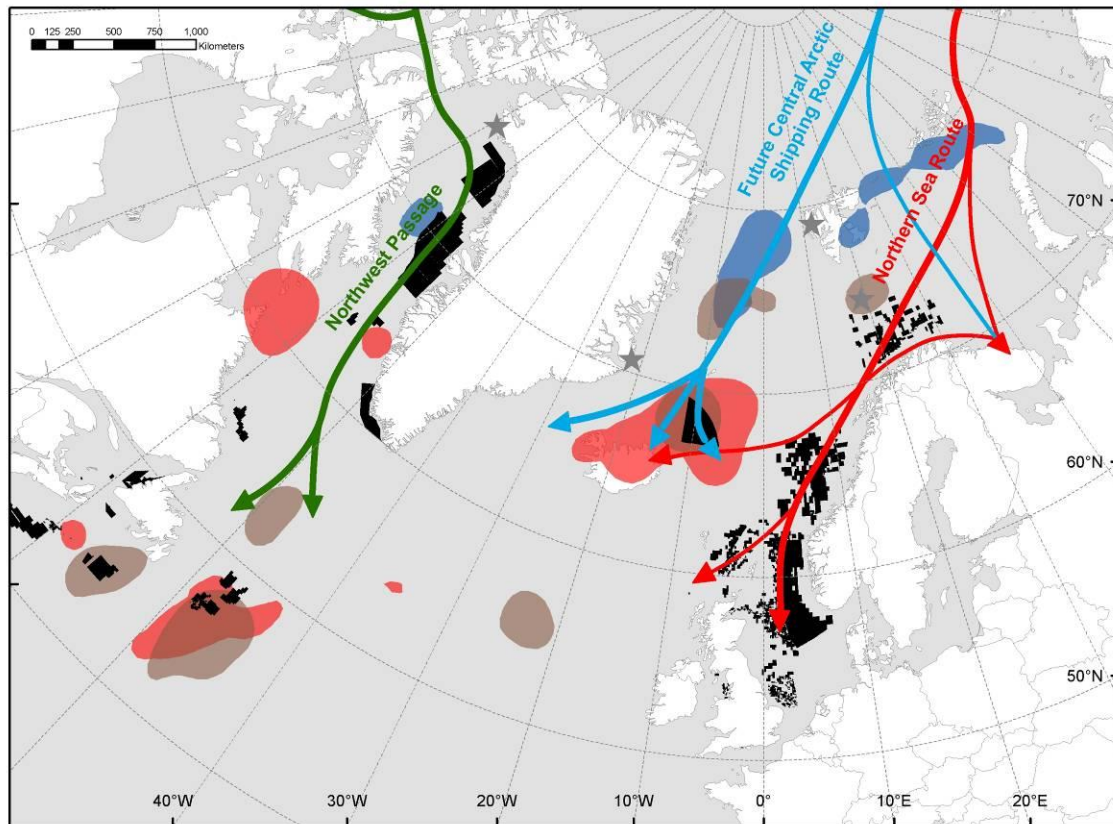


Fig. 4. Overlap between the non-breeding distribution of tracked little auks (*Alle alle*) and the development of future human activities in the Arctic (oil/gas activities and shipping routes). Little auk hotspots are defined by kernel 50% density contours in autumn (15 September/15 August – blue kernels), winter (December and January – red kernels) and spring (April – brown kernels). Black areas represent licensed exploration blocks in Canada (Newfoundland, Labrador and Nova Scotia), Iceland, Greenland, United Kingdom, Norway and Faroe Islands. License positions were provided by the Canada-Newfoundland & Labrador Offshore Petroleum Board, the Canada-Nova Scotia Offshore Petroleum Board, the National Energy Authority of Iceland, the Bureau of Minerals and Petroleum for Greenland (<http://en.nunagis.gl/>), the Norwegian Petroleum Directorate (<http://www.npd.no/>), the Department of Energy and Climate Change for UK licences (<http://og.decc.gov.uk/>), and the Faroese Earth and Energy Directorate (<http://www.jardfeingi.fo/>), respectively. Schematisation of future main Arctic shipping routes is adapted from AMSA (2009). Map projection: equidistant conic.