Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: Conservation implications

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Morten Frederiksen [a,*], Sébastien Descamps [b], Kjell Einar Erikstad [c,d], Anthony J. Gaston [e], H. Grant Gilchrist [e], David Grémillet [f,g], Kasper L. Johansen [a], Yann Kolbeinsson [h], Jannie F. Linnebjerg [a,1], Mark L. Mallory [i], Laura A. McFarlane Tranquilla [j,2], Flemming R. Merkel [a,k], William A. Montevecchi [j], Anders Mosbech [a], Tone K. Reiertsen [c], Gregory J. Robertson [l], Harald Steen [b], Hallvard Strøm [b], Thorkell L. Thórarinsson [h]

[a] Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
[b] Norwegian Polar Institute, Fram Centre, PB 6606 Langnes, 9296 Tromsø, Norway
[c] Norwegian Institute for Nature Research, Fram Centre, PB 6606 Langnes, 9296 Tromsø, Norway
[d] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science 10 and Technology, 7491 Trondheim, Norway
[e] Environment Canada, National Wildlife Research Centre, Raven Road, Carleton University, Ottawa, Ontario K1A 0H3, Canada
[f] Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, Montpellier, France
[g] Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, 7701 Rondebosch, South Africa
[h] Northeast Iceland Nature Research Centre, Hafnarstett 3, 640 Húsavík, Iceland
[i] Biology Department, Acadia University, 33 Westwood Drive, Wolfville, Nova Scotia, B4P 2R6, Canada
[j] Cognitive and Behavioural Ecology, Department of Psychology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X9, Canada
[k] Greenland Institute of Natural Resources, Postboks 570, 3900 Nuuk, Greenland
[l] Wildlife Research Division, Environment Canada, 6 Bruce Street, Mount Pearl, Newfoundland and Labrador A1N 4T3, Canada

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ABSTRACT

Pelagic seabirds are exposed to an array of potential threats during the non-breeding period, and effective management of these threats on a large scale requires knowledge of which populations winter where. Thick-billed murres (*Uria lomvia*) are emblematic of this conservation challenge, since they breed widely in the circumpolar Arctic, with many declining populations in the Atlantic. Threats facing murres include hunting, oil spills, bycatch and oceanic change influencing prey availability. Previous knowledge of migration pathways was insufficient to estimate the composition of various wintering populations. We collated tracking data (light-based geolocation) of 320 murres from 18 colonies in Canada, Greenland, Iceland, Svalbard and mainland Norway. Data were combined with breeding population counts to estimate the size and composition of wintering populations. The main wintering areas were off Newfoundland and Labrador, off West Greenland, and around Iceland. Winter areas were associated with the interface between High and Low Arctic ocean regimes. There was strong correspondence between wintering area and breeding population status: stable populations breeding in Canada and Northwest Greenland wintered mainly off Canada, whereas declining populations from Svalbard and Iceland wintered mainly off West Greenland and around Iceland. Many populations used distinct post-breeding areas, presumably for moulting; some of these areas were previously unknown. In some populations, there was a clear tendency for females to migrate south earlier than males, which accompany flightless fledglings when they leave the colony. Our study provides a key example of the urgency of coordinated, transoceanic management of vulnerable migratory species such as seabirds.

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1. Introduction

The conservation biology of migratory birds has a long history of achievement, in terms of scientific discoveries and the successful implementation of evidence-based conservation strategies (Newton, 2008). Seabird migration ecology has long lagged behind the investigation of many terrestrial bird groups, but the advent of miniaturized tracking technologies (notably light-based geolocation, Wilson et al., 1992) has recently triggered a major advance in our understanding of seabird migration. This is fortunate since seabirds have become one of the most

threatened groups of vertebrates, with a high proportion of species red-listed or otherwise of conservation concern (Croxall et al., 2012). Indeed, they are exposed to a wide variety of threats, both at their breeding sites (e.g. invasive predators and human disturbance) and at sea (e.g. hunting, bycatch, plastic pollution, and low food availability due to overfishing or climate change). Most of these threats are linked to human activities and highly variable in time and space, so for conservation management agencies to effectively address these issues it is necessary to have an overview of which populations are exposed to which threats and where (e.g. McFarlane Tranquilla et al., 2013).

Outside the breeding season, different breeding populations of migratory seabird species often show great overlap in their spatial distribution and mix extensively (González-Solís et al., 2007; Frederiksen et al., 2012; Fort et al., 2013a). This leads to complications for conservation and natural resource management, because anthropogenic threats in a specific non-breeding area and the associated demographic impacts may affect widely separated breeding populations (cf. Martin et al., 2007). Consequently, considerable research effort has been directed at estimating the composition of non-breeding populations in terms of their breeding origin, or migratory connectivity (Webster et al., 2002; Korner-Nievergelt et al., 2012; Cohen et al., 2014; Guillemain et al., 2014). For pelagic seabirds, such efforts have until recently been hampered by the difficulty of collecting appropriate data. Recoveries of dead ringed birds need careful assessment owing to recovery biases, and morphological or genetic data have proved to be of limited use in resolving the origin of birds found dead in winter (Cadiou et al., 2004). Stable isotopes and trace elements have shown potential for identifying the non-breeding areas of birds captured at the colony, or vice versa (Gómez-Díaz and González-Solís, 2007; Lavers et al., 2013; Militão et al., 2013). However, to date the most reliable method involves the deployment and retrieval of miniature electronic tracking devices (Grémillet et al., 2002), which have allowed researchers to collect data on overwinter distribution of individual seabirds of known breeding origin (Shaffer et al., 2006; Egevang et al., 2010). When such data are obtained from all relevant breeding populations, they allow the composition of wintering populations to be estimated (Frederiksen et al., 2012).

The thick-billed murre or Brünnich's guillemot (*Uria lomvia*, hereafter murre) is emblematic of these scientific and conservation challenges, and we use this species to demonstrate the potential of coordinated, basin-scale tracking studies of migratory seabirds. Murres are numerous and widespread circum-Arctic seabirds (Gaston and Hipfner, 2000), which breed in large colonies on bird cliffs in the Arctic and spend the non-breeding season at sea. Although the species is reported as being of *Least Concern* on the international red list (http://www.iucnredlist.org/), murre populations have declined substantially in recent decades in many parts of the Atlantic Arctic, e.g. in Svalbard (Descamps et al., 2013), mainland Norway (Fauchald et al., 2015), Iceland (Garðarsson et al., in press) and much of Greenland (Merkel et al., 2014). At the same time, breeding populations in Canada and Northwest Greenland have remained stable (Gaston et al., 2012; Merkel et al., 2014). The species is red-listed as *Vulnerable* in Greenland, Iceland and mainland Norway, and as *Near-threatened* in Svalbard (Icelandic Institute of Natural History, 2000; Boertmann, 2007; Kålås et al., 2010). Given the range-wide threats and concerns for the species, an International Murre Conservation Strategy and Action Plan was developed by the Arctic nations (CAFF, 1996).

In the Atlantic sector, current threats potentially affecting murres include hunting, primarily in Greenland and Canada (Gaston and Robertson, 2010; Merkel et al., 2014), chronic oil pollution (Wiese et al., 2004; Robertson et al., 2014), bycatch in gill nets (Hedd et al., 2015), and oceanographic changes leading to decreased food availability (Descamps et al., 2013; Buren et al., 2014). Most threats operate in the non-breeding areas, and for this reason there is a pressing need to understand the distribution of murres outside the breeding season in order to better assess risks and target management efforts. Recoveries

of ringed birds have provided substantial information on these aspects (Bakken et al., 2003; Lyngs, 2003; Gaston et al., 2008), but the value of this information is diminished by a spatial bias in the location of recoveries (on or near shore, mainly through hunting) and a lack of ringing effort in some breeding areas, particularly in recent decades. Since 2007, a large number of breeding adult murres have been equipped with light-based tracking devices (geolocators) in many colonies throughout the Atlantic range. The aim of this study is to assess the potential vulnerability of murre populations in specific non-breeding areas, by collating all existing tracking data for murres in the Atlantic, mapping the distribution of the various breeding populations at different times of the year, and estimating the size and composition of wintering populations in different parts of the range. In addition to providing crucial input to pan-Arctic murre conservation, our results provide a template for future large-scale studies of migratory metapopulations of marine vertebrates.

2. Materials and methods

2.1. Study species and area

The thick-billed murre is a large (ca. 1 kg) diving alcid, which feeds on fish, crustaceans and other invertebrates. Murres are highly specialised for deep diving, with the highest wing loading and the deepest diving ability among flying birds (Gaston, 2004; Elliott et al., 2013). They have an unusual breeding strategy (shared with two close relatives), in which chicks leave the colony accompanied by the male parent when less than half grown and unable to fly (Ydenberg, 1989; Gaston and Jones, 1998). The duration of parental care after leaving the colony is poorly known, probably about 2 months (Burke et al., 2015). Adults are flightless during the primary moult which takes place soon after the breeding season (Birkhead and Taylor, 1977), presumably while males accompany chicks.

The Atlantic breeding area includes Arctic or Sub-Arctic areas in Canada, Greenland, Iceland, Norway (including Jan Mayen and Svalbard) and Russia (Fig. 1). We tracked birds from 18 colonies (5 in Canada, 5 in Greenland, 3 in Iceland, 4 in Svalbard and 1 in mainland Norway), covering all major breeding populations except Jan Mayen and Novaya Zemlya.

2.2. Data collection

Geolocators were deployed on adult breeders during 2007–2013 and retrieved in subsequent years (Appendix A). Devices were of two types: 1) combined geolocators/time-depth recorders from Lotek Wireless (models LTD2400, LAT2500 and LAT2800, mass 3.5–6 g), and 2) stand-alone geolocators from British Antarctic Survey (BAS; models Mk5, Mk7, Mk9, Mk13 and Mk15, mass 1.5–4 g) and Biotrack (models Mk3006 and Mk4083, mass 1.5–2.5 g). All devices were attached to the tarsus, using metal or durable plastic rings. Most of the birds involved in the study were sexed, in all cases using DNA-based methods (Griffiths et al., 1998).

Some of the data presented here have been used before in a national context (Gaston et al., 2011; Montevecchi et al., 2012; Fort et al., 2013b; Linnebjerg et al., 2013; McFarlane Tranquilla et al., 2013; Steen et al., 2013; Frederiksen et al., 2014a; McFarlane Tranquilla et al., 2014). All raw data have however been re-processed for this study using a standardised protocol.

2.3. Data processing

Geolocators collect light intensity data at regular (5 or 10 min) intervals. While BAS/Biotrack loggers store these raw data, Lotek loggers summarise them on board by estimating daily times of sunrise and sunset and, based on these, geographical positions (recent models allow raw light data to be stored for the entire year). Light data from BAS
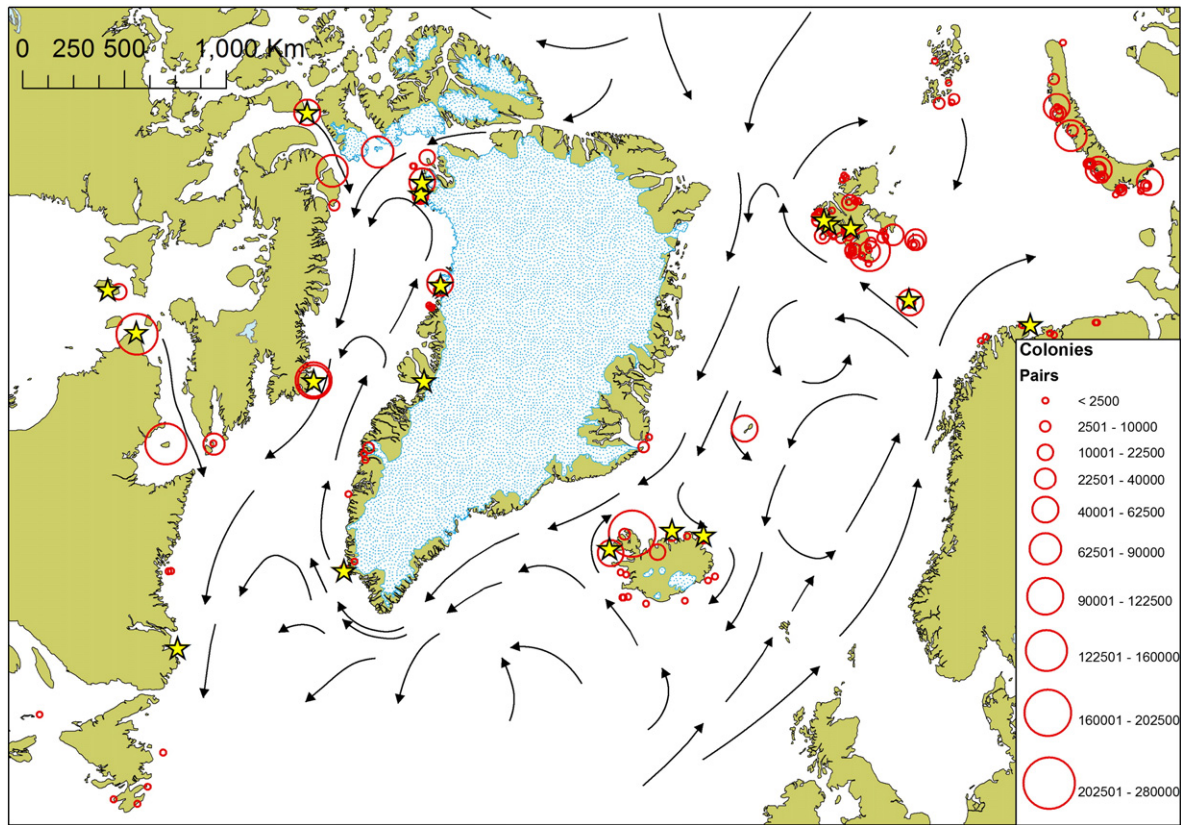
Fig. 1. Map of the North Atlantic, showing the distribution of murre breeding colonies (red circles, scaled by colony size) as well as the locations of study colonies where loggers were deployed (yellow asterisks). Arrows indicate prevailing surface currents. Colony data downloaded from http://www.abds.is/index.php/explore-species/birds/seabirds/murres, accessed 12 Mar 2015. Map projection (all maps): equidistant conic.

and Biotrack loggers were processed in BASTrak v. 18 software (Fox, 2010). We used a minimum dark period of 4 h to minimise the impact of incidental shading, and a threshold light intensity of 10. The optimal sun angle was determined by visual inspection of positions (avoiding erroneous positions on land as far as possible) as −3.5° for BAS loggers and −2.8° for Biotrack loggers. Initially, we used the onboard-calculated positions from Lotek loggers; however, inspection of these positions suggested that they were biased (south in winter, north in summer) relative to positions from BAS loggers deployed in the same colonies (see Appendix B). This apparent bias suggested that the devices were exposed to more light at a given date and latitude than assumed in the onboard algorithm, perhaps because they were originally designed for use on fish rather than birds (S. Walls, pers. comm.). We therefore corrected the positions from Lotek devices by first back-calculating times of sunrise and sunset using the built-in sun angle of −3.44° (S. Walls, pers. comm.), and then re-estimating latitudes assuming a true sun angle of −5° (see Appendix B). These calculations were performed using the R package 'GeoLight' 2.0 (Lisovski and Hahn, 2012).

Further processing in R 3.1.3 (R Core Team, 2015) followed the methods of Frederiksen et al. (2012) based on 3-position smoothing, and calculation of distances between successive positions and from each position to the home colony; data from the breeding season and equinox periods were excluded (15 Sep – 6 Oct and 7 Mar – 4 Apr). Positions were allocated to a set of marine 'areas of interest' (based on Large Marine Ecosystems (Sherman, 2006) and a latitude-longitude grid for offshore areas, see Appendix C) in ArcGIS 10.1 (ESRI, Redlands, CA, USA), with a 100 km buffer so that erroneous positions on land or far outside the known range were ignored. We focused on distribution during the winter period when birds were relatively stationary, here defined as 16 December – 14 February, but also used fall and spring positions to investigate patterns of migrations. Size and composition of the wintering population in each 'area of interest' was estimated as

in Frederiksen et al. (2012), using the most up-to-date estimates of breeding population size (see Appendix D). BAS/Biotrack loggers provide two positions per day, whereas Lotek loggers provide one; the algorithm used to estimate numbers wintering in different areas uses proportions of positions rather than absolute numbers and is therefore not affected by this difference.

3. Results

We retrieved 456 of 671 loggers deployed (68%), although not all of these contained useable data. While most deployments lasted one year, some lasted 2–4 years, and in total the data set contained full or partial information on 440 migration episodes of 320 individuals (Appendix A). Many Lotek devices deployed in Norway (incl. Svalbard) ran out of battery after a few months due to the programming used. A few other loggers also stopped early, and the number of migration episodes represented thus decreased over the season. For the winter period, we had data for only 354 of the initial 440 migration episodes. After removal of breeding and equinox periods, 85,499 positions were available from BAS/Biotrack loggers (two per day), and 31,394 from Lotek loggers (one per day).

After leaving the breeding colonies (typically in August), most individuals remained in the general area for at least several weeks (Fig. 2, see also Appendix E), but some migrated quickly to areas >2000 km from the colony. For the northernmost colonies, positions were unobtainable for the first weeks after colony departure due to constant daylight. At least in the populations in Baffin Bay (both Greenland and Canada), there was a strong tendency that males remained near the colony (<500 km) in August and early September, while most females migrated south immediately after leaving the colony (Fig. 3, see also Appendix E). Some populations concentrated in well-defined areas (presumably moulting) in August and September, e.g. all birds tracked

Fig. 2. Maps showing the monthly median position of each tracked bird. The solid lines in the maps for August, December, January and May indicate approximate latitudes north of which positions are unobtainable at these times of year, due to constant daylight or darkness. The dashed lines in the December panel show the approximate northern and southern limits of the Low Arctic zone, according to Brown (1986). Also shown are the locations of the study colonies (yellow asterisks).

from Spitsbergen colonies occurred in a relatively small area in the Greenland Sea, north of Jan Mayen (Appendix E). Birds from Hudson Bay colonies remained in northern Hudson Bay and adjacent waters until November or early December (Appendix E).

Fig. 3. Monthly distribution of distances between positions and the home colony, exemplified by the colony Kippaku in Baffin Bay, northwest Greenland. Females are shown in red, males in blue. The boxes indicate the first and third quartiles, split by a line indicating the median. The whiskers extend to the most extreme data point which is no >1.5 times the interquartile range away from the box.

Most birds were relatively stationary from November to February. The most important wintering areas were along the Labrador and New-foundland shelves, and in the Davis Strait and Labrador Sea (Fig. 2). Many tracked birds also wintered along the west coast of Greenland (up to approx. 68° N), around Iceland, and in the Barents Sea. Many birds (73%) from the Hornøya colony in mainland Norway wintered so far north (probably in the Barents Sea) that no positions could be obtained during periods in December and January due to constant dark-ness (Fig. 2, see also Appendix E). Males from Baffin Bay colonies tended to winter further north (closer to the colonies) than females (Fig. 3, see also Appendix E).

Positions after the spring equinox period appeared to be of lower quality in many cases, with an apparently very wide dispersal also south of the area shown in Fig. 2. Birds from the more southerly colonies started to move back in April (or possibly earlier in some cases, Fig. 2, see also Appendix E). Most birds from colonies in Baffin Bay did not re-turn to the colony before May, when positions were unobtainable due to constant daylight. Similarly, murres from Svalbard colonies migrated north after the start of constant daylight, in the case of Spitsbergen ap-parently already in April.

We estimate that about 5 million breeding-age murres (83% of the Atlantic population) winter in the western Atlantic, from Newfound-land north to central-west Greenland (Fig. 4a, see also Appendix F), while approximately one million birds (16% of the Atlantic population) are estimated to winter around Iceland. The apparently small winter population in the Barents Sea (37,000) is certainly a considerable under-estimate, as most of the murres breeding in Novaya Zemlya and Franz Josef Land likely winter in this area, and no birds were tracked from these populations. According to our estimates, murres wintering along the Canadian shelf (Newfoundland and Labrador) predominantly origi-nate from Baffin Bay (High-Arctic Canada and northwest Greenland) and Hudson Bay, with Hudson Bay birds on average occurring farthest north (Fig. 4a). On the shelves off west Greenland, birds from
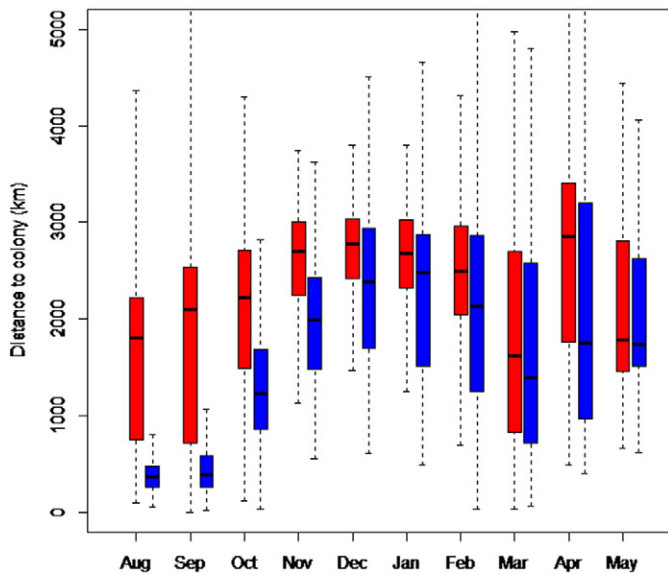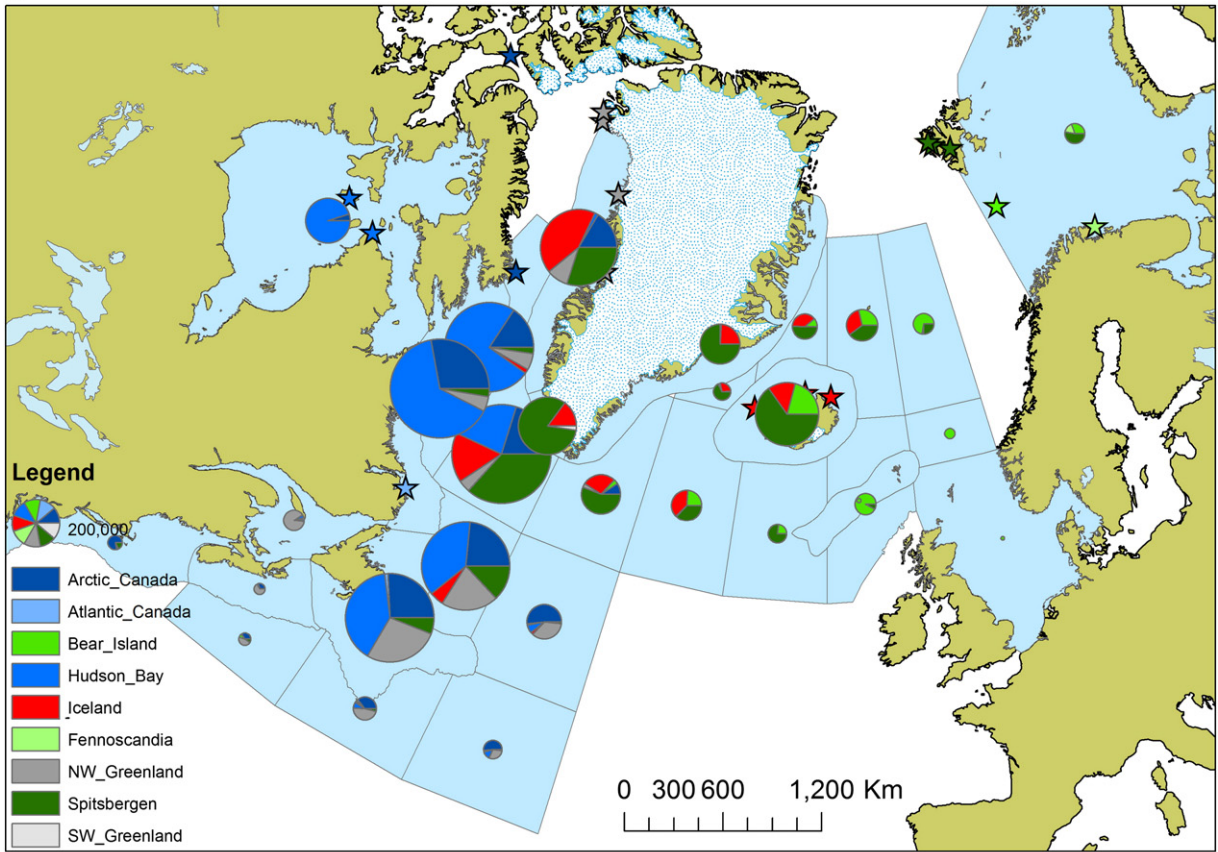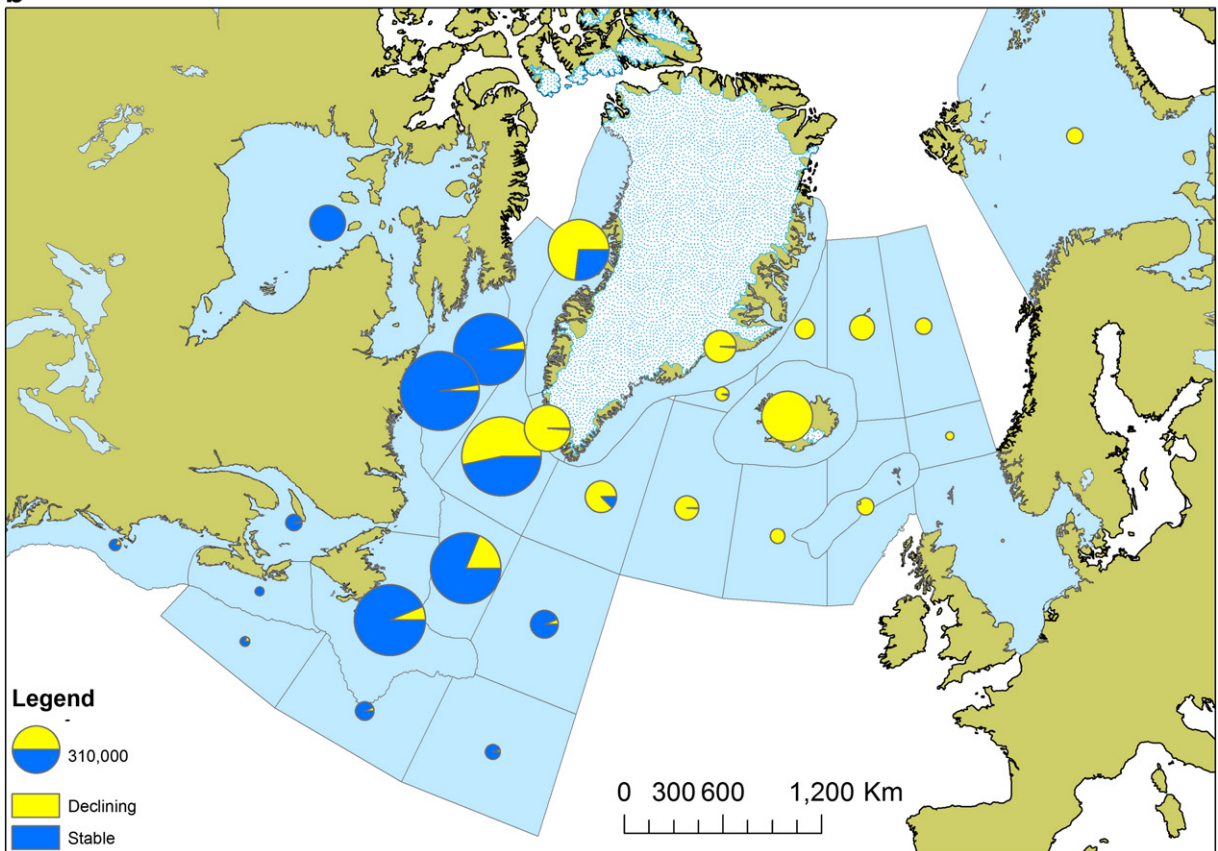
Spitsbergen and Iceland predominate, with some Baffin Bay birds in the more northerly areas. Around Iceland, the majority of birds originate from Spitsbergen, with substantial numbers also from Bjørnøya and local colonies. On the broad scale, our results show a strong association between population status and wintering area (Fig. 4b): populations wintering in Canadian waters are stable, while those wintering off West Greenland and around Iceland are in decline.

4. Discussion

Our results provide an unusually complete description of the non-breeding distribution of a widely distributed seabird on an ocean basin scale. We confirm that thick-billed murres in the Atlantic Ocean winter in and immediately south of the Low-Arctic zone (Fig. 2E). We demonstrate some intriguing and hitherto poorly known patterns, and our results have profound implications for understanding the winter ecology and improving the management of this species in the North Atlantic Ocean. It thus clearly illustrates the potential of efforts to collate and synthesize tracking data across metapopulations of migratory aquatic vertebrates, as a crucial input to international conservation strategies and marine spatial planning.

4.1. Migration and winter distribution

Many murre populations (e.g. those from Spitsbergen, Iceland and Northwest Greenland) appear to follow prevailing surface currents during their autumn migration towards Newfoundland, Labrador and West Greenland (compare Fig. 1 and Appendix E). This is not surprising, given that successfully breeding males accompany flightless chicks during at least the first part of the migration, and that both sexes are flightless for a substantial period during autumn. Murre post-breeding swimming migration has already been documented (Olsson et al., 1999), but details remain poorly known. In other cases, murres remain near colonies until both chicks and adults can fly. For example, Hudson Bay breeders remain near their colonies until late autumn before migrating through the Hudson Strait to the Labrador Shelf, and Bjørnøya birds spend the post-breeding period in the western Barents Sea, later migrating to waters around Iceland (Appendix E). Ringing has demonstrated that some birds from Barents Sea colonies (Bjørnøya, Novaya Zemlya and mainland Norway/Russia) winter off Southwest Greenland as well as Newfoundland (Nikolaeva et al., 1996; Bakken et al., 2003; Lyngs, 2003), implying that much of their migration takes place against prevailing currents. Iceland breeders have to cross a relatively narrow north-easterly current (a branch of the Irminger Current) before reaching the south-westerly East Greenland Current, which leads to the wintering area in southwest Greenland.

In some of our study colonies, there were large differences in migration behaviour of males and females (Fig. 3, Appendix E). Particularly in the population breeding in northern Baffin Bay (4 of our 18 study colonies), many females migrated rapidly to the Newfoundland/Labrador Shelf, while most males remained in Baffin Bay until at least mid-September and subsequently moved gradually south. This difference in behaviour has not been described previously, although satellite tracking from the Ritenbenk colony in West Greenland found different migration routes of males and females during the immediate post-breeding period (Mosbech et al., 2009). In other populations, there was no clear difference in the distribution of sexes during the post-breeding period (e.g. Hudson Bay, Spitsbergen). During mid-winter, the northernmost wintering area off West Greenland (66–68° N) was occupied almost exclusively by males, although the sample size was small. Sex-specific

migration behaviour is common in Procellariiformes (Phillips et al., 2004; Hedd et al., 2014), but to our knowledge has not been documented previously in alcids. However, given the pronounced sexual difference in post-fledging parental care in murres (Burke et al., 2015), it is not surprising that females under some circumstances migrate quickly to distant post-breeding areas to complete moult, whereas successfully breeding males move slowly for several weeks while accompanying flightless chicks.

It was highly surprising to find that a substantial proportion (73%) of murres tracked from Hornøya spent part of the winter so far north that no positions could be obtained due to very low light intensity. Of 26 birds equipped with BAS/BioTrack loggers working through the winter, 19 had periods of 9–58 days where no positions were estimated in November to January. This corresponds to latitudes north of 78° N at the beginning of November, 70° N at winter solstice and 76° N at the end of January. How murres, usually regarded as mainly visual foragers, manage to obtain sufficient food in near-complete darkness is highly intriguing and in need of further study (Regular et al., 2011). Even at lower latitudes, murres regularly dive to depths well over 100 m year-round (Linnebjerg et al., 2013), and at these depths light intensity is likely so low in winter that non-visual foraging also seems necessary.

4.2. Conservation implications

4.2.1. Post-breeding areas

Some populations appeared to use fairly well-defined post-breeding areas. For example, nearly all birds tracked from Spitsbergen colonies used an area in the Greenland Sea north of Jan Mayen in August and September (Appendix E). The limited information from at-sea surveys confirms that many murres occur here at this time of year (Boertmann and Mosbech, 2012), and the area is also important during the post-breeding period for little auks (*Alle alle*) from Spitsbergen and northeast Greenland, which presumably moult here (Mosbech et al., 2012; Fort et al., 2013a). The area is close to the ice edge at this time of year, and presumably highly productive (Perrette et al., 2011); we speculate that Spitsbergen murres initiate moult here and then gradually move south-westward following the prevailing current. The area is partly within the Greenland Exclusive Economic Zone, partly in the Jan Mayen and Svalbard Fisheries Zones, and partly in international waters. There are probably few, if any, important anthropogenic threats to murres in this area at present, but potential future shipping or oil exploration developments in the region will require coordinated management, particularly given the observed decline in the Spitsbergen population (Descamps et al., 2013).

Another quite well-defined post-breeding area occurs in the western Barents Sea, where nearly all birds tracked from Bjørnøya were found in August–September, with Hornøya birds typically found further southeast. Oil exploration activities are expected to increase in the coming years in the Barents Sea, which is also very important for commercial fisheries. Birds tracked from the Hudson Bay colonies remain within the Bay until November or early December (Gaston et al., 2011), presumably reflecting consistently high food availability throughout this period. Shipping in Hudson Bay and Hudson Strait is expected to increase due to the longer ice-free period, and year-round icebreaking has been proposed for future mining developments (Arctic Council, 2009).

4.2.2. Sex-specific distribution

In some study colonies, males and females occurred in different areas, at least at some times of the year (Appendix E). This was most

Fig. 4. (a) Map showing the estimated number of adult murres wintering in each 'area of interest' (see Appendix C). Symbol size indicates the estimated number of birds, and colour shading of each slice indicates the breeding origin (asterisks indicating study colony location are coloured accordingly). Calculations were based on all available positions from the period 16 Dec – 14 Feb in all study years, and the map thus represent an average distribution over this period. The numbers behind the pie charts are listed in Appendix F. (b) This map shows the same data as a), but here the breeding populations have been aggregated into two rough categories, 'stable' (Canada and Northwest Greenland) and 'declining' (all other populations).

apparent in the Baffin Bay population, where nearly all tracked males remained in Baffin Bay throughout August and September, whereas many females quickly migrated south to the Labrador/Newfoundland Shelf (Fig. 3, Appendix E). In addition, males tended to occur further north than females throughout the winter. Spatial separation of males and females greatly increases vulnerability towards additive mortality sources such as hunting (Phillips et al., 2004). This is particularly the case for strictly monogamous species such as murres, where any imbalance in sex ratio in the breeding population leads to reduced breeding output and effective population size (Palestis, 2014; Pichegru and Parsons, 2014). Interestingly, sex ratio differences were seen neither in samples of adult birds killed in the Canadian hunt nor during an oil spill off Newfoundland (Robertson et al., 2006; McFarlane Tranquilla et al., 2010), while Falk and Durinck (1992) found a significant bias towards males in the hunting bag in Central West Greenland. Experience from winter wrecks in Iceland, Greenland and Canada show highly variable sex ratios, with adult females being disproportionately represented in some cases and males in others (Nielsen and Einarsson, 2004; McFarlane Tranquilla et al., 2010; F. Merkel, unpubl. data). These limited observations suggest that differential vulnerabilities of the sexes to mortality sources in the Northwest Atlantic are temporally and spatially variable, and generalizations about sex-specific impacts of hunting, oiling and wrecks should be treated with caution. Nevertheless, hunting management in areas/periods with highly biased sex ratios should consider this increased vulnerability.

4.2.3. Population status and specific threats in the non-breeding areas

On the broad scale, our results show a strong association between population status and wintering area (Fig. 4b): populations wintering in Canadian waters are stable, while those wintering off West Greenland and around Iceland are in decline. The causal links, if any, between threats in the wintering areas and population status are far less obvious, while the management implications are clear.

Breeding-age murres wintering off West Greenland south of approximately 66° N originate mainly from the declining populations in Spitsbergen, Iceland and probably Jan Mayen (Fig. 4a). The small and declining local breeding population also appears to winter mainly in this area, and most likely the rapidly declining East Greenland population does as well. Ring recoveries show that many pre-breeders from Spitsbergen and Bjørnøya also use this area (Lyngs, 2003; Bakken and Mehlum, 2005), and it is highly likely that pre-breeders from Iceland

do the same. The main known anthropogenic threat in this area is hunting, although the numbers reported shot have declined substantially over the last 20 years (Fig. 5). The limited information available suggests that breeding-age birds make up approximately one third of the murre hunting bag in Greenland (Falk and Durinck, 1992; Frich, 1997); with a hunting bag of ~65,000 birds (Fig. 5) this corresponds to 2–3% annual mortality of the ~800,000 breeding-age murres estimated to winter off West Greenland (Appendix F). It is questionable whether even this hunting pressure can be considered sustainable in populations declining at 6% per year (Spitsbergen, Fauchald et al., 2015) or 3.5% per year (Iceland, Garðarsson et al., in press).

Murres wintering around Iceland originate mainly from Spitsbergen, Bjørnøya, as well as from local colonies (Fig. 4a), all populations which are declining (Descamps et al., 2013; Garðarsson et al., in press). There are few known anthropogenic threats for wintering birds in this area; numbers reported shot are low (~5000 birds per year, Fig. 5), and bycatch in fishing gear, which is considered low (Pálsson et al., 2015), mainly occurs during spring (Petersen, 2002). There is a large, but highly variable, fishery for capelin (Mallotus villosus) around Iceland, and the potential effect of this fishery on wintering murre populations is poorly understood.

Atlantic Canada is often regarded as the area with the greatest variety of anthropogenic threats to wintering murres. Numbers of murres reported shot have been high, although they have declined substantially in recent years (Fig. 5). Similarly, the number of birds killed by ship-source chronic oil pollution in Newfoundland waters has declined since the late 1990s (Wilhelm et al., 2009; Robertson et al., 2014). Hydrocarbon extraction off Newfoundland is a new and developing threat to seabirds in the area (McFarlane Tranquilla et al., 2013). At least on a coarse scale, murre populations wintering off Labrador and Newfoundland appear to be stable (Fig. 4). It thus appears that the mortality induced by these various threats is insufficient to cause widespread population declines, although some colonies in Northwest Greenland (known or presumed to winter in this area) do show declines (Merkel et al., 2014). Mortality sources in Atlantic Canada are largely constrained to the southern part of the murre winter range, so populations wintering off Labrador and Baffin Island would not be affected, while those wintering around Newfoundland may be disproportionately affected (McFarlane Tranquilla et al., 2013).

The importance of direct anthropogenic threats in driving population declines of thick-billed murres in the Atlantic thus seems to vary in space and time. In the past, anthropogenic sources have been clearly implicated in driving population trends of both this species and the closely related common murre (Uria aalge) (Evans and Kampp, 1991; Regular et al., 2010). More recently, oceanographic change may also be an important underlying cause of the observed declines. The synchrony in trends among colonies in both Canada and Svalbard suggests that winter conditions are important drivers of murre population change (Gaston, 2003; Smith and Gaston, 2012; Descamps et al., 2013). Year-to-year variation in strength of the Subpolar Gyre (Hátún et al., 2005) affecting conditions in the Irminger and Labrador Seas and around South Greenland has been specifically linked to the decline in Svalbard murres (Descamps et al., 2013). Observed declines in several other seabird species in the North Atlantic have been linked to changes in oceanographic conditions through demographic studies (Frederiksen et al., 2004; Frederiksen et al., 2013), but similar mechanistic studies are lacking for thick-billed murres.

The declining trends in the eastern breeding populations may also be linked to conditions in the breeding areas. However, there is so far no evidence of major problems in the colonies that have been studied. In Svalbard, breeding success has been moderate to high, and although spring conditions have changed markedly (decreasing sea ice extent), this has not been shown to affect e.g. murre breeding propensity (S. Descamps, unpubl. data). Although tick parasitism has been shown to be higher following warm winters, this had no apparent effect on murre body condition or breeding success (Descamps, 2013).
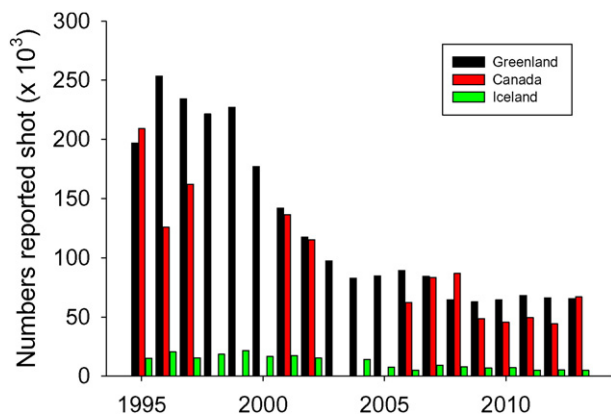

Fig. 5. The reported or estimated hunting bag of murres in Greenland, Canada and Iceland, 1995–2013. Numbers for Greenland and Iceland are based on mandatory reporting by hunters when renewing annual licenses, while numbers for Canada are estimates. Numbers are unavailable for Canada in some years, and for Iceland in 2003. Sources: the Environment Agency of Iceland; the Greenland Ministry of Fisheries, Hunting and Agriculture; National Wildlife Research Centre, Canadian Wildlife Service.

4.3. Limitations of the study

Some breeding areas were not included in this study, due mainly to logistical issues. Most importantly, the large breeding population in Novaya Zemlya (estimated 850,000 pairs, Bakken and Pokrovskaya, 2000) was not represented, although geolocators were deployed there in 2013 and 2014 without success. The limited information from recoveries of ringed birds suggests that part of this population winters in the Barents and White Seas, and another part in southwest Greenland (Nikolaeva et al., 1996). Large numbers of murres winter in the Barents Sea (Fauchald and Erikstad, 2002), and these are almost certainly mainly Novaya Zemlya birds. There is no information on the non-breeding distribution of murres breeding in Franz Josef Land, and only one recovery of a bird ringed in Jan Mayen, from West Greenland (Lyngs, 2003). The location of Jan Mayen in relation to the ice edge and prevailing currents suggests that breeders from this island may have a similar migration pattern to Spitsbergen birds. Limited data from satellite tracking suggests that some murres from the small breeding population in East Greenland winter off Newfoundland (Boertmann and Mosbech, 2012). No information is available for the large population in eastern Hudson Strait (estimated 500,000 pairs, Gaston et al., 2012), and we have here assumed that they behave like breeders from the Hudson Bay colonies.

In this study, we have only tracked the non-breeding distribution of breeding adult murres. Approximately 45% of the population are prebreeders (Mosbech et al., 2009), and attempts at tracking these birds have proved much more difficult, because they can only be marked as chicks before leaving the colony, and the probability of retrieving loggers is very low (S. Descamps and H. Strøm, unpubl. data). Recoveries of dead ringed birds are thus likely to remain the main source of information for these age classes for the foreseeable future, although continued miniaturization of archival and other tags may at some point make tracking of fledged chicks possible (Péron and Grémillet, 2013). Analyses of ring recoveries do not indicate strong age segregation in the wintering areas, although timing of migration likely varies among age classes (Donaldson et al., 1997; Lyngs, 2003).

4.4. Conclusions

Here, we provide the first synthesis of the extensive tracking data collected for thick-billed murres in the North Atlantic Ocean. Our results clearly show that while murres from different breeding populations mix extensively outside the breeding season, there are also times and areas where specific segments of the overall population (breeding populations, or one sex) are more highly concentrated and thus vulnerable. While some of the information presented here confirms existing knowledge, the degree of comprehensiveness and detail represents a large improvement in overall understanding of the distributions of thick-billed murres in the North Atlantic Ocean during the non-breeding period. The trans-Atlantic association of winter murre populations with the interface between High and Low Arctic ocean regimes implicates potential sensitivity to ocean climate change. Management agencies concerned with conservation or the use of living resources should find these results helpful when planning and implementing international management of this declining species.

Improved management at the trans-national scale will require further knowledge. Much relevant information could be extracted from the existing geolocation data, supplemented by new data. For example, an improved understanding of the unusual long-distance swimming migration of murres would be of great interest for both conservation and basic science. Likewise, the sometimes strong spatial separation of males and females warrants further investigation, particularly because it increases the vulnerability of the population to localised sources of mortality. Detailed demographic studies are required for a more mechanistic understanding of population change (Frederiksen et al., 2014b); such studies are available for one small population in Canada (Gaston et al., 1994), for Bjørnøya (Fluhr et al., submitted), and have been initiated in Svalbard and Northwest Greenland, but are still lacking in the other main breeding areas.

Overall, it is clear that migratory connectivity has long been a grey area of seabird ecology and conservation (Newton, 2008). Here, we provide a strong example of how metapopulation-scale tracking allows linking of contrasting regional population trends to the specific migratory strategies of different sub-populations. Our approach, combined with the current wealth of novel information on seabird metapopulation migration reported by similar recent studies (Fort et al., 2012; Frederiksen et al., 2012; Ramos et al., 2013), allows the definition of migratory hotspots and irreplaceable areas, and thus motivates enhanced conservation efforts in international waters (Lascelles et al., 2016).

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