

# Multiple-colony winter habitat use by murrens *Uria* spp. in the Northwest Atlantic Ocean: implications for marine risk assessment

Laura A. McFarlane Tranquilla<sup>1,\*</sup>, William A. Montevecchi<sup>1</sup>, April Hedd<sup>1</sup>,  
David A. Fifield<sup>1</sup>, Chantelle M. Burke<sup>1</sup>, Paul A. Smith<sup>2</sup>, Paul M. Regular<sup>1</sup>,  
Gregory J. Robertson<sup>3</sup>, Anthony J. Gaston<sup>2</sup>, Richard A. Phillips<sup>4</sup>

<sup>1</sup>Cognitive and Behavioural Ecology, Department of Psychology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X9, Canada

<sup>2</sup>Environment Canada, National Wildlife Research Centre, 1125 Colonel By Drive, Raven Road, Carleton University, Ottawa, Ontario K1A 0H3, Canada

<sup>3</sup>Wildlife Research Division, Environment Canada, 6 Bruce Street, Mount Pearl, Newfoundland and Labrador A1N 4T3, Canada

<sup>4</sup>British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

**ABSTRACT:** Limited knowledge of year-round seabird distributions hinders efforts to assess consequences of anthropogenic threats and climate-induced changes in the marine environment. In particular, there is urgent need to understand how populations from different breeding colonies share and partition ocean habitat. Using geolocators, we identified winter habitat use patterns of 115 adult murrens *Uria* spp. from 7 colonies, spanning the eastern Canadian coast from the high Arctic to Newfoundland, during 2007 to 2010. Thick-billed murrens *U. lomvia* dispersed throughout the region (Davis Strait, Labrador Sea, Orphan Basin, Grand Bank) with 0 to 45 % overlap of core wintering areas (50 % kernel home range) among breeding populations. Common murrens *U. aalge* concentrated on the Grand Bank and Orphan Basin, with 50 to 67 % overlap among breeding populations. For both species, most individuals (up to 70 %) wintered offshore, in shelf ( $\leq 500$  m deep) and oceanic zones ( $> 500$  m); fewer than one-third (30 %) of individuals used nearshore zones ( $\leq 50$  km to shore). Tracked common murrens representing  $> 80$  % of the eastern Canadian breeding population converged in winter in areas of high risk from hydrocarbon exploration and extraction activity. In contrast, tracked thick-billed murrens, representing  $\sim 34$  % of the eastern Canadian population, dispersed over a larger area and displayed more variable wintering strategies. Thus population vulnerability to spatially constrained risks may be greater for common than thick-billed murrens. Populations from several colonies of both species converged on the Grand Bank and Orphan Basin, with the implications for each breeding population depending on its particular dispersal pattern. We demonstrate the utility of tracking data for highlighting areas of risk, and improving the targeting of broad-scale marine conservation efforts.

**KEY WORDS:** Ocean habitat · Tracking · Geolocators · North Atlantic · Murrens · Seabirds · Anthropogenic · Risk

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## INTRODUCTION

Seabirds are often used as indicators of anthropogenic and climatic perturbations in the marine

environment. While such perturbations are known to influence breeding performance (Gaston et al. 2005, Barbraud & Weimerskirch 2006, Hipfner 2008), their influence on seabirds during the nonbreeding period

\*Email: lat@alumni.sfu.ca

is more difficult to ascertain due to incomplete knowledge of distributions, particularly of pelagic species in winter. Winter conditions have carry-over effects on breeding performance (Harris & Wanless 1996, Sorensen et al. 2009, Smith & Gaston 2012), and can strongly influence both adult survival and rates of recruitment to breeding populations (Harris & Wanless 1996, Wilson et al. 2001, Frederiksen et al. 2008, Ballerini et al. 2009, Jenouvrier et al. 2009). The impact of spatially explicit habitat perturbations on the wintering grounds depends on the extent to which species and breeding populations converge (Esler 2000, Webster et al. 2002, Phillips et al. 2009). However, for many seabird species, knowledge of winter distribution is insufficient to understand the links between habitat use, habitat perturbations, and population processes (Webster et al. 2002). Knowledge of specific overwintering areas is therefore essential for understanding the impact of environmental perturbations on demography.

International efforts involving the deployment of novel animal-borne tracking technology on a wide range of species are rapidly addressing this winter knowledge gap (González-Solís et al. 2007, Block et al. 2011), but the wintering areas of most northern hemisphere seabirds remain poorly known. In addition, few population studies have compared patterns of habitat use of the same species from multiple breeding colonies (but see Frederiksen et al. 2012) despite their value for assessing relative exposure to habitat perturbations and differing sensitivities to changing environmental conditions (Phillips et al. 2009, Montevecchi et al. 2012).

In the Northwest Atlantic Ocean, the closely related common murre *Uria aalge* and thick-billed murre *U. lomvia* comprise a significant proportion of the winter seabird community, with the eastern Canadian populations totaling ~1.7 million and ~3.9 million birds, respectively (Gaston & Hipfner 2000, Ainley et al. 2002, S. Wilhelm [Environment Canada] unpubl. data). Murres from Canadian colonies are not known to migrate outside the Northwest Atlantic during winter (Gaston et al. 2011, Hedd et al. 2011). Past observations from vessel surveys and band recoveries suggest that wintering murres concentrate in shelf regions (Tuck 1961, Gaston 1980, Donaldson et al. 1997), particularly on Newfoundland's biologically productive Grand Bank (Gaston & Hipfner 2000, Ainley et al. 2002, Burke et al. 2005, Barrett et al. 2006). Although such studies are the only means of assessing historical changes in marine distribution, they are subject to several limitations and sources of bias, for example, band recoveries are

dependent on observer effort and restricted largely to birds washed up dead on coasts or shot, and at-sea survey datasets tend to have gaps in coverage and lack information on colony of origin.

Despite long-term, intense study at breeding colonies in eastern Canada (Tuck 1961, Gaston 1980, Nettleship & Evans 1985, Gaston & Jones 1998), investigations of winter habitat use of *Uria* spp. populations began only recently (Gaston et al. 2011, Hedd et al. 2011). Despite this, much has been inferred about the potential challenges that wintering murres may encounter at sea. In the Northwest Atlantic Ocean, short days, reduced ocean productivity (Myers et al. 1994) and harsh weather during winter induce high energetic costs (Fort et al. 2009), potentially reducing adult survival (Grémillet et al. 2005, Frederiksen et al. 2008, Harris et al. 2010) or leading to stranding or starvation during poor weather (Stenhouse & Montevecchi 1996, McFarlane Tranquilla et al. 2010). Starvation during winter may be the most important cause of natural mortality for Atlantic alcids (Hudson 1985). Climate-induced shifts in marine food web composition or location of key resources (Fleischer et al. 2007, Osterblom et al. 2008) and extreme weather (ACIA 2004) could exacerbate energetic stress during winter. Energetic stress is compounded by a complex range of anthropogenic pressures. In winter, murres are extremely vulnerable to marine oil pollution (Wiese & Robertson 2004, Wiese et al. 2004, Votier et al. 2005, Burke et al. 2012), are hunted for subsistence in nearshore areas throughout the high and low arctic (Elliot 1991, Donaldson et al. 1997, Bakken & Mehlum 2005, Merkel & Barry 2008), and occasionally drown in gill-nets (Benjamins et al. 2008, Stenson et al. 2011). The risks associated with these activities depend on their spatiotemporal overlap with murre distributions.

In the Northwest Atlantic Ocean, productive marine areas such as the Grand Bank are used intensely by humans and numerous seabird populations year-round (Brown 1986, Frederiksen et al. 2012, Hedd et al. 2012). Although both murre species are thought to rely heavily on the Grand Bank in winter (Ainley et al. 2002, Gaston & Hipfner 2000), the importance of this region to wintering populations of murres from eastern Canada, relative to other regions in the Northwest Atlantic Ocean, is not known. The same is true for 3 other marine subregions (Davis Strait, Labrador Shelf, Orphan Basin) where there is intense human activity (AMAP 2010, CNOLPB 2010, Geo-Expro 2010) and potentially high use by wintering seabirds (Merkel et al. 2002, Mosbech et al. 2006, Merkel & Barry 2008). We deployed bird-borne track-

ing devices at 7 widely dispersed sites from high to low arctic regions in eastern Canada (Fig. 1) to: (1) identify important wintering areas used by thick-billed and common murres; (2) evaluate patterns of winter distribution between species and among colonies (breeding populations); (3) evaluate the overlap in habitat use by murres in 4 oceanic subregions with ongoing and increasing human activities; and (4) evaluate potential interactions between wintering birds and these activities.

## MATERIALS AND METHODS

### Study colonies and device attachment

This research was carried out during 2007 to 2010 on thick-billed murres and common murres at 7 seabird colonies in Eastern Canada ranging from 74 to 47°N: Prince Leopold Island in the high Arctic; the Minarets on Baffin Island; Coats Island in Hudson Bay; East Digges Island in Hudson Strait, Nunavut; the Gannet Islands in Labrador; and Funk Island and Witless Bay Islands in Newfoundland (Table 1, Fig. 1; hereinafter the colonies will be referred to using the abbreviated names shown in Fig. 1). British Antarctic Survey (BAS; Mk5/Mk7, 3.6 g; Mk 13, 1.4 g,  $n = 220$ ) or Lotek 2500 (3.6 g,  $n = 17$ ) global

location sensing (GLS) loggers were attached to 237 breeding murres (134 thick-billed and 103 common murres) at colonies during July and August in 2007 to 2009, using leg bands and cable ties (total weight  $\leq 5.4$  g,  $\sim 0.6\%$  adult body mass). All murres equipped with tracking devices were actively breeding (i.e. on eggs or chicks) when captured. Of 237 loggers deployed, 128 (on 87 thick-billed and 41 common murres; 54%) were retrieved at the same sites in following years (Table 1). Most loggers (92%) were collected in the year following deployment; 9 were retrieved 2 yr after deployment, and hence the number of year-round tracks exceeds the number of loggers retrieved (Table 1). Seventeen loggers failed to download. In total, we obtained year-round data from 111 loggers (46% of those deployed; Table 1); including repeated tracks, this provided 115 annual tracks and 75 122 individual GLS locations, or 37 561 tracking-days (2 locations  $d^{-1}$ ). Recent estimates of colony sizes (Gaston et al. 2012; S. Wilhelm [Environment Canada] unpubl. data; Table 1) were used to scale potential presence based on tracking data (see ‘Spatial and statistical analyses’ below) and population estimates were made as described by Gaston (2002) using a combination of aerial photography, ground-truthing, and plot monitoring. The tracked thick-billed murres were from 5 colonies representing about one-third (34%) of the total eastern Canadian population of  $\sim 3.9$  million (Gaston & Hipfner 2000, Wiese et al. 2004). The tracked common murres were from colonies representing  $\sim 82\%$  of the estimated breeding population of common murres in eastern Canada of  $\sim 1.7$  million.

### Data processing

Data from BAS GLS loggers were decompressed using BASTrak software and light data were processed according to Phillips et al. (2004) using MultiTrace Geolocation software (Jensen Software Systems), with the correction factor for day/night movement set to 0.7, an angle of elevation of  $-5.5$ , and light threshold of 1. This angle of elevation provided the best overall representation of locations in the study area according to a set of 3 complementary approaches to evaluate the data: (1) assessing the distribution of logger positions during stationary

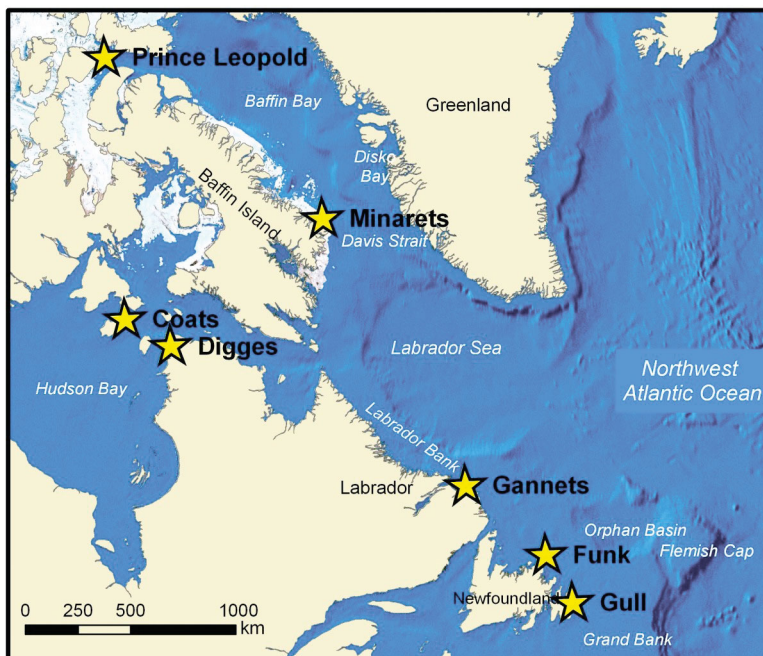


Fig. 1. The Northwest Atlantic Ocean Study Area and (★) breeding colonies where global location sensor (GLS) loggers were deployed on thick-billed and common murres

Table 1. Tracking of winter habitat use by thick-billed murre and common murre from colonies in eastern Canada: details of sites, species tracked, years when global location sensor (GLS) loggers were deployed, and numbers of loggers deployed and retrieved. Colony sizes are shown as the number of breeding pairs  $\times$  2. Loggers deployed were British Antarctic Survey Mk5/Mk7 (BAS) or Lotek 2500 geolocation-immersion loggers. The number of loggers successfully downloaded is less than the number retrieved in cases where GLS logger failure prevented data retrieval. In some cases the number of annual tracks is higher than original number downloaded because loggers held  $\geq 2$  yr of data. See Fig. 1 for location of colonies

Site	Species tracked	Location	Colony size	Year deployed	No. and type of loggers deployed	No. of loggers retrieved each year	Total no. of loggers successfully downloaded	Total no. of annual tracks recorded
Prince Leopold	Thick-billed	74°02'N, 90°00'W	172000 <sup>a</sup>	2008 2009	24 (BAS) 5 (Lotek)	16 5	18	18
Minarets	Thick-billed	66°57'N, 61°50'W	260000 <sup>a</sup>	2007	20 (BAS)	14	14	14
Coats	Thick-billed	62°53'N, 82°00'W	36000 <sup>b</sup>	2007 2008	20 (BAS) 20 (BAS)	18 16	29	30
Digges	Thick-billed	62°32'N, 77°45'W	872000 <sup>a</sup>	2008	31 (BAS)	10	10	10
Gannets	Thick-billed	53°56'N, 56°32'W	3700 <sup>c</sup>	2008	14 (BAS)	8	5	5
Gannets	Common	53°56'N, 56°32'W	62420 <sup>c</sup>	2008	16 (BAS)	12	8	8
Funk	Common	49°45'N, 53°11'W	825048 <sup>c</sup>	2007 2008 2009	20 (BAS) 20 (BAS) 12 (Lotek)	10 0 3	13	13
Witless Bay	Common	47°16'N, 52°46'W	500000 <sup>c</sup>	2007 2008	5 (BAS) 30 (BAS)	5 16	16	17
Total			2731168		237	128	111	115

<sup>a</sup>2011, A.J. Gaston unpubl. data; <sup>b</sup>2010, Gaston & Robertson (2010); <sup>c</sup>2011, S. Wilhelm [Environment Canada] unpubl. data

ground-truthing at the southernmost colony (Witless Bay; Fig. 1); (2) assessing travel past obvious topographic features (e.g. through Hudson Strait); and (3) plotting latitudinal variance against date for all processing parameters, and choosing the parameter that minimized loss of data around the equinox (Lisovski et al. 2012). Selection of processing parameters by examining predicted locations during the breeding season (cf. Frederiksen et al. 2012) was not appropriate because the shading of devices during colony attendance by murre resulted in poor quality light curves and hence large location error. For this reason, most of the breeding season data was discarded. However, incidentally, in years when mammalian predators at 2 colonies caused nesting failure in early incubation (Burke et al. 2011), device shading was less likely to occur even though birds were still present in surrounding waters, and GLS locations based on the angle of elevation used for all data ( $-5.5$ ) were within 200 km of colonies (L.A.M.T. unpubl. data).

The same processing parameters were applied to data from all BAS devices, irrespective of year or latitude of origin. Data from multiple years from the same colonies, and in some cases the same individuals, show a high degree of consistency in core areas and individual distances traveled (L.A.M.T. unpubl.

data). For the purposes of this study, years were pooled. Lotek 2500 devices employ internal processing algorithms and positional data are downloaded directly. For both BAS and Lotek devices, clearly erroneous locations resulting from light level interference that represented unrealistic movements ( $>500$  km  $d^{-1}$ ) or were outside the likely species' range were removed (Phillips et al. 2004).

We explored the use of sea-surface temperature (SST) matching to improve geolocation accuracy (Teo et al. 2004). This algorithm (implemented in Matlab version 7.10 R2010a) uses the longitude and the water temperatures recorded in real time by the logger to estimate the best latitude by matching with satellite SST images. We used NOAA Modis A nighttime SST averaged over 8 d at a 4 km resolution (MODIS A NSST 8d-4k). However, due to inconsistent latitudinal stratification in SST gradients in the Labrador Sea, latitudes estimated by the SST-matching algorithm produced extremely variable results, suggesting improbable movements back-and-forth over hundreds of kilometres north or south between successive locations. As such, temperature-based latitude estimates for the murre contributed very little new information (8% of total detections; L.A.M.T. unpubl. data) and was much less reliable than light-based latitudes (see also Lam et al. 2010).

In the analysis presented here, we defined winter as November to February, avoiding problems associated with latitude estimation around the equinoxes (Hill & Braun 2001, Teo et al. 2004). In our study area, the periods most affected by these problems were September to early October and late February to March, during which time latitudes with consistent southerly or northerly bias were excluded (see review in Lisovski et al. 2012). The resulting data were smoothed twice (2-d running average), retaining the original fixes at the start and end of any periods where data were missing (Phillips et al. 2004).

### Spatial and statistical analyses

Bird locations were mapped in ArcMap 9.3 (ESRI 2009). Kernel home range (KHR) analyses were performed on data from the winter period using the Kernel Density Tool from the ArcMap Spatial Analyst Toolbox, in a North Pole Lambert azimuthal equal-area projection, with a cell size of 50 km and search radius of 200 km. Percent volume contours, which isolate areas corresponding to various increments in the probability density function (Gibin et al. 2007) were created using Hawth's Tools (version 3.27). The 50% density KHR contours were considered to represent the core areas used during the winter. Winter 2007/08 is referred to as winter 2008; 2008/09 is 2009 etc. Maps of bathymetry were obtained online from the GEBCO Digital Atlas (GEBCO One Minute Grid, version 2, www.gebco.net).

KHR provided a convenient means of summarizing areas of greatest use for each colony over the winter period. For this analysis, individuals were pooled by colony (sub-population). To calculate wintering range overlap, 50% KHRs of colonies were overlaid and the ArcMap Intersect tool was used to calculate the pairwise area of overlap ( $A_O$ ) in km<sup>2</sup>. Percent overlap between colonies A and B was calculated as:

$$\text{Winter Range Overlap} = A_O / (\text{Area}_A + \text{Area}_B - A_O) \quad (1)$$

**Proportional Use.** For more detailed spatial analysis, KHRs were assessed separately for each bird, allowing evaluation of variation among individuals from each colony. To calculate Proportional Use, we determined presence of all individual murre KHRs, proportional to the total tracked from their respective colony, within 3 marine zones of the Northwest Atlantic, defined as nearshore ( $\leq 50$  km from the coast), shelf ( $< 500$  m deep, excluding waters  $< 50$  km from shore) and oceanic ( $> 500$  m deep) (Fig. 2). The 3 marine zones were chosen based on bathymetry

and biological relevance. For example, seabirds are hunted within 50 km from shore (Merkel & Barry 2008), and often associate with bathymetric features such as the continental slope or shelf (Brown 1986, Kenyon et al. 2009). In a second exercise, we determined the overlap of individual murre KHRs with the 3 marine zones in 4 subregions (Davis Strait Area, Labrador Shelf, Orphan Basin, Grand Bank; Fig. 2), selected on the basis of known concentrations of anthropogenic activity to illustrate the intensity of anthropogenic activity in those subregions, absence (–) or presence (low +; medium ++; high +++) was scored purely in relative terms and ascertained by means of literature review (references in Table 2). Subregion boundaries were hand drawn (in ArcMap) to approximate conventional characterizations according to bathymetry and basement topography (Chian et al. 2001, Skaarup et al. 2006). For each bird, presence was determined in a binary manner depending on whether the KHR did (1) or did not (0) intersect the oceanic zones within each region (see example, Fig. 2). Locations on land (which reflect geolocation error) were included in the nearshore category. Individual presence in oceanic zones was standardized relative to number of zones used by that individual, such that values for occurrence for each individual summed to 1:

$$\text{Occurrence in Zone } (O_{ij}) = (P_{ij}) / \sum N_j \quad (2)$$

where  $P_{ij}$  is the presence (binary, i.e. 0 or 1) of an individual bird from Colony  $i$  in Zone  $j$ , divided by  $\sum N_j$ , the sum of occurrences of the individual in all zones. Thus, if a bird was present in all 3 zones (nearshore, shelf, oceanic), it would have an occurrence of 0.33 in each. Note this does not equate to time spent in each zone, nor to the area of KHRs overlapping in each zone. This approach was used for all birds within the general Northwest Atlantic Study Area. As a separate exercise, the same approach was to standardize individual presence of birds from each colony wintering in particular zones and subregions ( $O_{ik}$ ).

To determine the proportion of birds from each colony wintering in particular zones/subregions, individual Occurrence in Zone was averaged, to calculate the Proportional Use of Zone  $j$  and Subregion  $k$  by each colony:

$$\text{Proportional Use of Zone } j (P_{iz}) = \text{avg.}(O_{ij}) \quad (3)$$

$$\text{Proportional Use of Subregion } k (P_{ik}) = \text{avg.}(O_{ik}) \quad (4)$$

To determine  $P_{iz}$  and  $P_{ik}$  for each species overall,  $O_{ij}$  and  $O_{ik}$  were averaged across colonies. KHRs for some individuals did not intersect with any of the

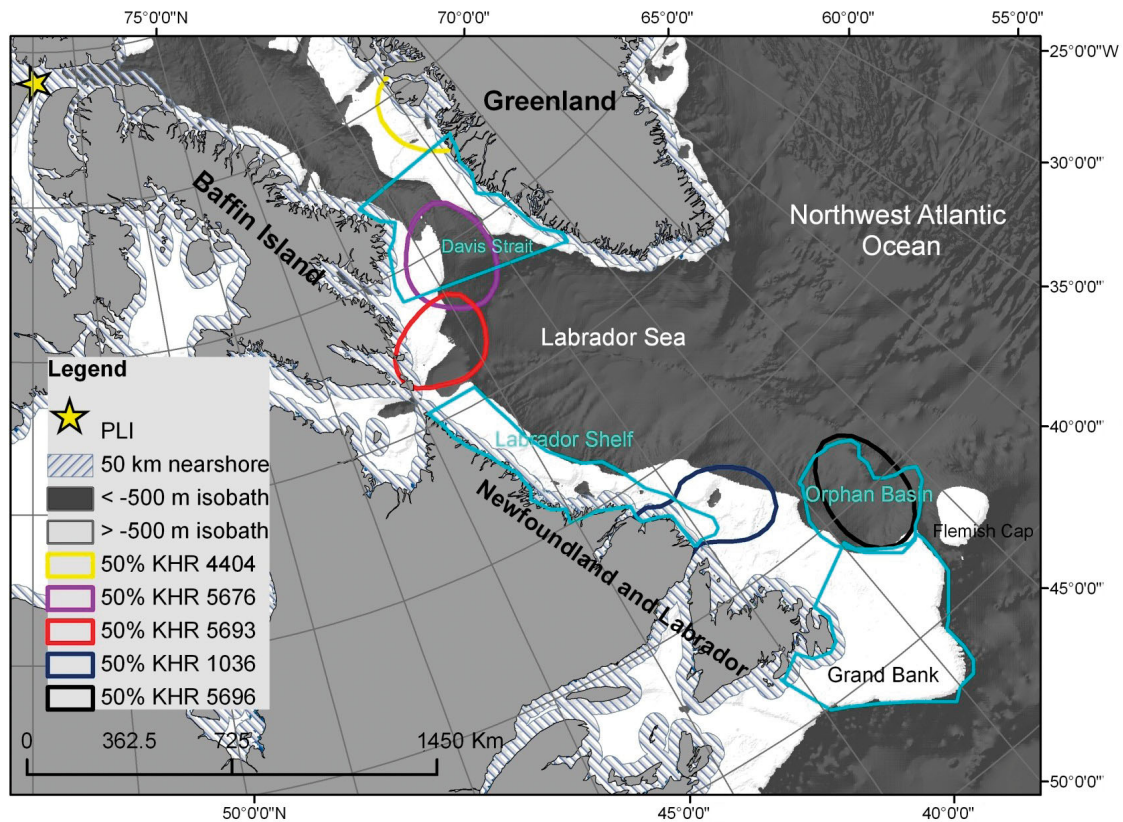


Fig. 2. Location of marine zones in the Northwest Atlantic Study Area: nearshore ( $\leq 50$  km), shelf ( $\leq 500$  m deep, excluding waters  $\leq 50$  km from shore) and oceanic ( $> 500$  m deep). Location of subregions (Davis Strait Area, Labrador Shelf, Orphan Basin, Grand Bank) within the study area affected by human activity. Examples of core (50%) wintering kernel home ranges (KHR) of 5 individual thick-billed murres (BAS loggers 4404, 5676, 5693, 1036, 5696) from the colony on Prince Leopold Island (PLI)

identified subregions, and these were pooled into 'Other'.

**Potential Presence.** To estimate the number of birds from each colony present in a particular marine zone/subregion, we calculated Potential Presence by scaling Proportional Use (i.e.  $P_{iz}$  and  $P_{ik}$ ) to colony size (Table 1) by simple multiplication. We assumed that the behavior of our sample of tracked birds was representative of all birds at the colony. However our estimates did not consider the presence of birds in each zone or region from other breeding colonies where devices were not deployed.

## RESULTS

### Wintering areas and Proportional Use

#### Thick-billed murres

Core wintering areas stretched over  $27^\circ$  of latitude from waters off West Greenland ( $\sim 70^\circ$  N), south to

the Scotian Shelf ( $\sim 43^\circ$  N). Birds from Arctic colonies (representing  $> 95\%$  of the Canadian breeding population) were found mainly north of  $45^\circ$  N. Proportional Use was spread across the 3 marine zones but was highest in the oceanic zone (58%) compared to offshore shelf (27%) and nearshore (15%) zones (Table 3). Among colonies Proportional Use of the oceanic zone was high for birds from Minarets, Coats, and Digges; whereas birds from Prince Leopold (and to a lesser extent, Gannets) exhibited high Proportional Use of nearshore zones (Table 3, Fig. 5).

Colony-specific core wintering areas (pooled individuals and years) showed considerable variation by colony (Fig. 3). For Prince Leopold ( $n = 18$ , winters 2009 and 2010), multiple centers were found in the Davis Strait area, west of Greenland (Hellefiske Banke/Disko Bay), the northern Labrador Sea, along the Labrador Bank in the southern Labrador Sea, and over the Orphan Basin (Fig. 3A). For the Minarets ( $n = 14$ , winter 2008), 2 centers were identified over the eastern Grand Bank and the northern

Table 2. Presence/absence (+/–) of anthropogenic threats affecting the NW Atlantic Study Area overall and within particular subregions during winter (see Fig. 2). Relative presence is based on a literature review of anthropogenic activities in subregions (Bakken & Falk 1998, Wiese et al. 2001, 2004, Merkel et al. 2002, Bakken & Mehlum 2005, Mosbech et al. 2006, Benjamins et al. 2008, Merkel & Barry 2008, Wilhelm et al. 2009, AMAP 2010, C-NLOPB 2010, Carstens 2010, Stenson et al. 2011). The table provides a relative estimate of anthropogenic impact, indicating that some areas (Grand Bank, Orphan Basin) are more impacted than others. Marine zones were defined as near-shore ( $\leq 50$  km from the coast), shelf ( $\leq 500$  m deep, excluding waters  $\leq 50$  km from shore) and oceanic ( $> 500$  m deep). na: the marine zone is not present in the area (e.g. the Grand Bank has no oceanic zone)

Area	Type of threat	Marine zone		
		Nearshore	Shelf	Oceanic
NW Atlantic Study Area	Hunting	+	–	–
	Gillnet/fishing gear	+	+	–
	Oil production/exploration	–	+	+
	Shipping/chronic oiling	+	++	++
Davis Strait	Hunting	+	–	–
	Gillnet/fishing gear	–	–	–
	Oil production/exploration	+	+	+
	Shipping/chronic oiling	–	–	–
Labrador Shelf	Hunting	+	–	na
	Gillnet/fishing gear	+	–	na
	Oil production/exploration	–	+	na
	Shipping/chronic oiling	–	–	na
Orphan Basin	Hunting	na	–	–
	Gillnet/fishing gear	na	–	–
	Oil production/exploration	na	+	+
	Shipping/chronic oiling	na	++	++
Grand Bank	Hunting	++	–	na
	Gillnet/fishing gear	+	+	na
	Oil production/exploration	–	++	na
	Shipping/chronic oiling	++	+++	na

Table 3. Proportional Use by tracked thick-billed murres and common murres, as determined by proportion of individual 50% kernel home ranges (KHRs) per colony that intersected with nearshore, shelf, and oceanic marine zones in the Northwest Atlantic Study Area (Fig. 2). Numbers in bold indicate zones of highest use per colony. See also Fig. 5 for colony-specific details

Colony	No. of annual tracks recorded	Marine zone		
		Nearshore	Shelf	Oceanic
<b>Thick-billed murre</b>				
Prince Leopold	18	0.31	<b>0.39</b>	0.31
Minarets	14	0.06	0.24	<b>0.70</b>
Coats	30	0.08	0.18	<b>0.74</b>
Digges	10	0.13	0.33	<b>0.53</b>
Gannets	5	0.17	0.37	<b>0.47</b>
Total	115	0.15	0.27	<b>0.58</b>
<b>Common murre</b>				
Gannets	8	0.24	0.36	<b>0.40</b>
Funk	13	0.04	<b>0.65</b>	0.31
Witless Bay	17	0.11	<b>0.52</b>	0.37
Total	38	0.11	<b>0.53</b>	0.36

Orphan Basin/southern Labrador Sea (Fig. 3B). For Coats ( $n = 30$ , winters 2008, 2009 and 2010), multiple centers were located in Hudson Bay (representing habitat use until December), and in the northern and central/south Labrador Sea, where birds resided in January and February (Fig. 3C). Similarly for Digges ( $n = 10$ , winters 2009 and 2010) there were multiple centers, first in Hudson Bay prior to winter migration (up to late November or early December), and then in the northern/central Labrador Sea and over the Orphan Basin (in December to February) (Fig. 3D). For Gannets ( $n = 5$ , winter 2009), multiple centers were found inshore near coastal Newfoundland, over the eastern Grand Bank, the northern Orphan Basin/south Labrador Sea, and the Scotian Shelf (Fig. 3E).

Analysis of colony-specific Proportional Use of inshore, shelf, and oceanic zones, within subregions, showed that individuals from Prince Leopold were distributed widely throughout the study area and used all identified subregions (Fig. 5), with the highest Proportional Use in the shelf zone (Table 3). Individuals from the Minarets, Coats, Digges, and Gannets used slightly fewer subregions, with the highest Proportional Use in the oceanic zone (Table 3), particularly in the Orphan Basin (Fig. 5).

#### Common murres

Core wintering areas spanned  $10^\circ$  of latitude over  $\sim 43$  to  $53^\circ$  N and were much more restricted than those of thick-billed murres (Fig. 4). Differences among colonies were more apparent in the patterns of habitat use (inshore versus offshore) than in the regions visited (L. A. McFarlane Tranquilla unpubl. data). Proportional Use was highest in the shelf (53%), followed by oceanic (36%) and nearshore (11%) zones (Table 3). Among colonies, the highest Proportional Use of the shelf and nearshore zones was by birds from Funk and Gannets, respectively (Table 3, Fig. 5).

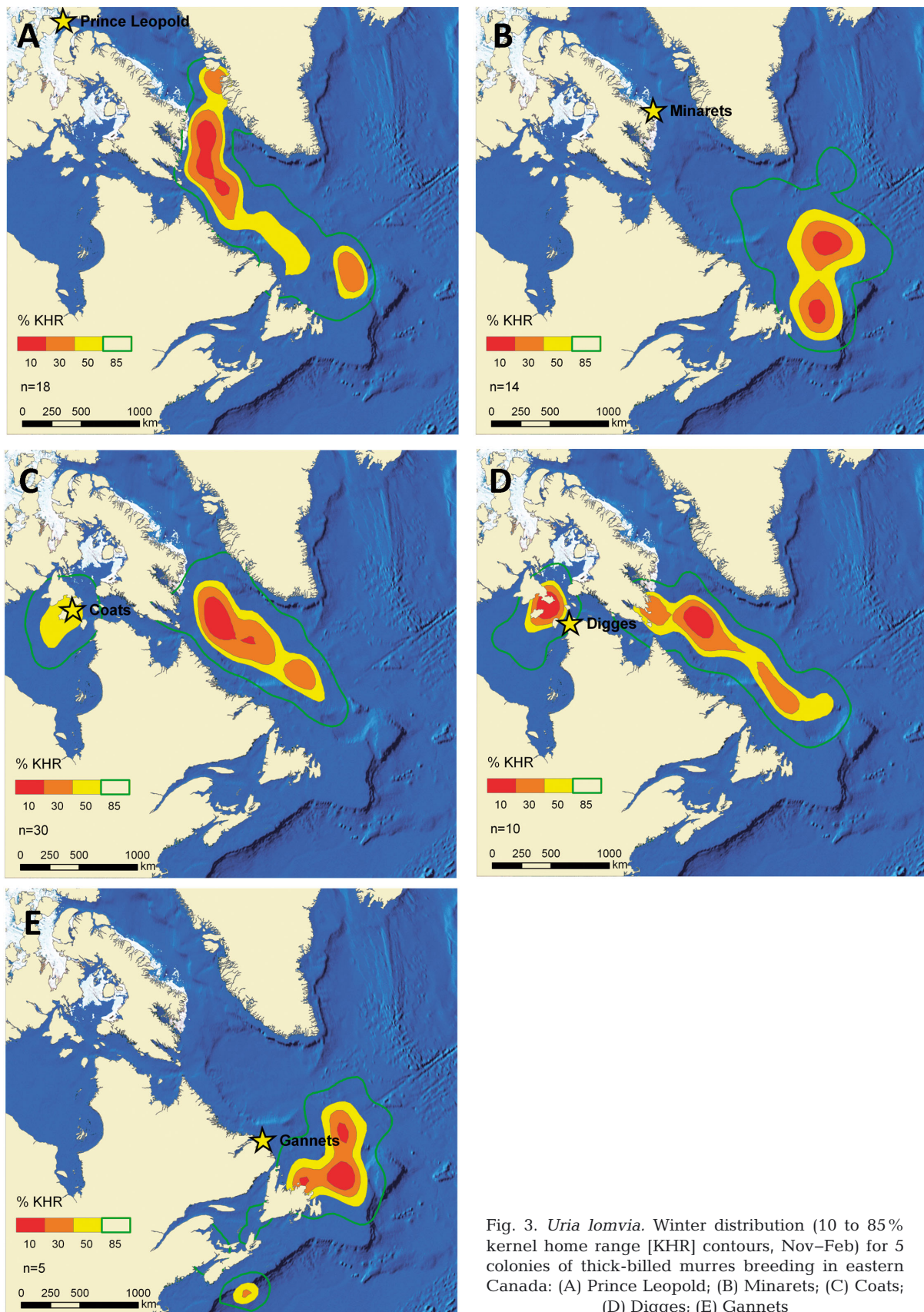


Fig. 3. *Uria lomvia*. Winter distribution (10 to 85% kernel home range [KHR] contours, Nov–Feb) for 5 colonies of thick-billed murres breeding in eastern Canada: (A) Prince Leopold; (B) Minarets; (C) Coats; (D) Digges; (E) Gannets



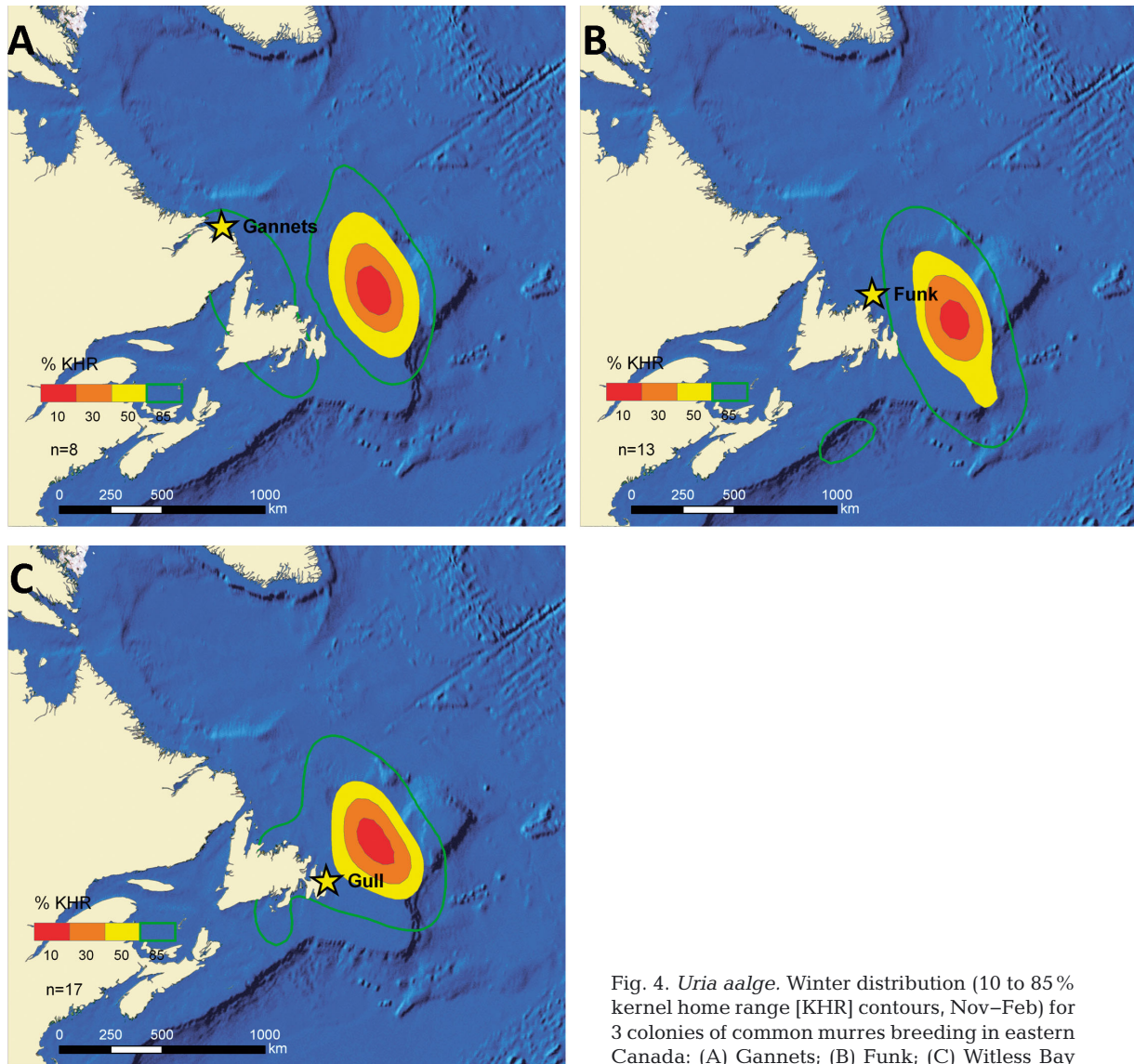


Fig. 4. *Uria aalge*. Winter distribution (10 to 85% kernel home range [KHR] contours, Nov–Feb) for 3 colonies of common murres breeding in eastern Canada: (A) Gannets; (B) Funk; (C) Witless Bay

Colony-specific core wintering areas (pooled individuals and years) for each colony were as follows: For Gannets ( $n = 8$ , winter 2009), core habitat was centered over the northeastern Grand Bank/Orphan Basin (Fig. 4A). For Funk ( $n = 13$ , winter 2008 and 2010), the core area was mainly over the eastern Grand Bank/southern Orphan Basin (Fig. 4B). For Witless Bay ( $n = 17$ , winter 2009 and 2010), the core area had a single center on the northeastern Grand Bank/Orphan Basin (Fig. 4C).

Analysis of colony-specific Proportional Use of inshore, shelf, and oceanic zones, within subregions, showed roughly equal Proportional Use of shelf and oceanic zones by murres from Gannets, and that birds from this colony used the most subregions

(Fig. 5). For both Funk and Witless Bay, the highest Proportional Use was in the shelf zone, particularly on the Grand Bank (Table 3, Fig. 5).

### Range Overlap

The Winter Range Overlap between colonies is shown in Table 4. Average core winter range (50% KHR) for thick-billed murres ( $550\,892 \pm 41\,895 \text{ km}^2$ , mean  $\pm$  SE) was significantly larger than that of common murres ( $202\,107 \pm 11\,414 \text{ km}^2$ ; ANOVA,  $F_{1,6} = 38.14$ ,  $p < 0.001$ ; see Table 4). Core use areas of thick-billed murre colonies overlapped by an average of 17%, ranging from 0.2% (Coats and Gannets) to

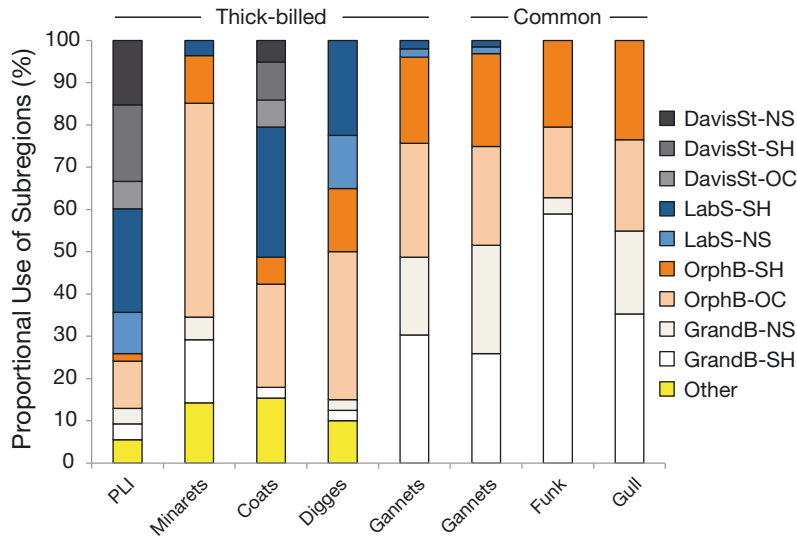


Fig. 5. *Uria lomvia* and *U. aalge*. Proportional Use (per colony) of thick-billed murre and common murre in 3 marine zones (NS: nearshore; SH: shelf; OC: oceanic) in 4 subregions of the study area (Davis Strait, Labrador Shelf, Orphan Basin, Grand Bank) in winter. 'Other' indicates that the birds were tracked to areas outside the 4 subregions. PLI: Prince Leopold Island

47% (Coats and Digges). Core use areas of the 3 tracked common murre colonies overlapped by an average of 60% (49 to 67% for each colony pair; Table 4). Total area of kernel home range was independent of sample size (linear regression,  $F_{1,6} = 0.0002$ ,  $p = 0.9$ ) and breeding population size at each colony (linear regression,  $F_{1,6} = 0.35$ ,  $p = 0.6$ ). Given the high degree of consistency among years in core use areas used by birds from each colony, and by the same individuals, it was considered acceptable to

calculate overlaps in range even where data were not available in every year.

**Composition of subregions**

The composition of the birds within each subregion was based on the Proportional Use of Subregions ( $P_{ik}$ ), scaled to colony size (Fig. 6). In Davis Strait, all 3 zones (nearshore, shelf, oceanic) were occupied solely by thick-billed murre from Prince Leopold and Coats. On the Labrador Shelf, the nearshore zone was occupied by thick-billed murre from Prince Leopold and Digges (Figs. 5 & 6A); and by common murre from Gannets (Figs. 5 & 6B). Birds from these 3 colonies also used the Labrador Shelf, as did thick-billed murre from Coats and Minarets. In the Orphan Basin, all

colonies of both species were represented in both the shelf and oceanic zones, with murre from Gannets in the smallest proportion (Fig. 6). All colonies and species were present to some extent on the Grand Bank (least abundant were thick-billed murre from Coats; Fig. 6). Among tracked thick-billed murre, those from Gannets made highest proportional use of the Grand Bank (Table 3, Fig. 5); however, after scaling to colony size, the nearshore zone of the Grand Bank was used most heavily by thick-billed murre

Table 4. Area of Core Winter Range (50% kernel home range) of thick-billed murre and common murre and percent overlap of core range between birds from different colonies

Species	Colony	Core Winter Range (km <sup>2</sup> )	Winter Range Overlap (%)			
			Prince Leopold	Minarets	Coats	Digges
Thick-billed murre	Prince Leopold	648 454	–	–	–	–
	Minarets	493 389	9.9	–	–	–
	Coats	578 859	23.3	1.0	–	–
	Digges	614 814	23.3	6.5	46.6	–
	Gannets	418 943	10.1	46.1	0.2	6.7
Average		550 892 ± 41 895 SE		$\bar{x} = 17.4\% \pm 1.7\text{ SE}$		
Common murre	Gannets	224 803	–	–		
	Funk	192 879	49.4	–		
	Witless Bay	188 640	67.9	64.1		
	Average		202 107 ± 11 414 SE	$\bar{x} = 60.5\% \pm 3.3\text{ SE}$		

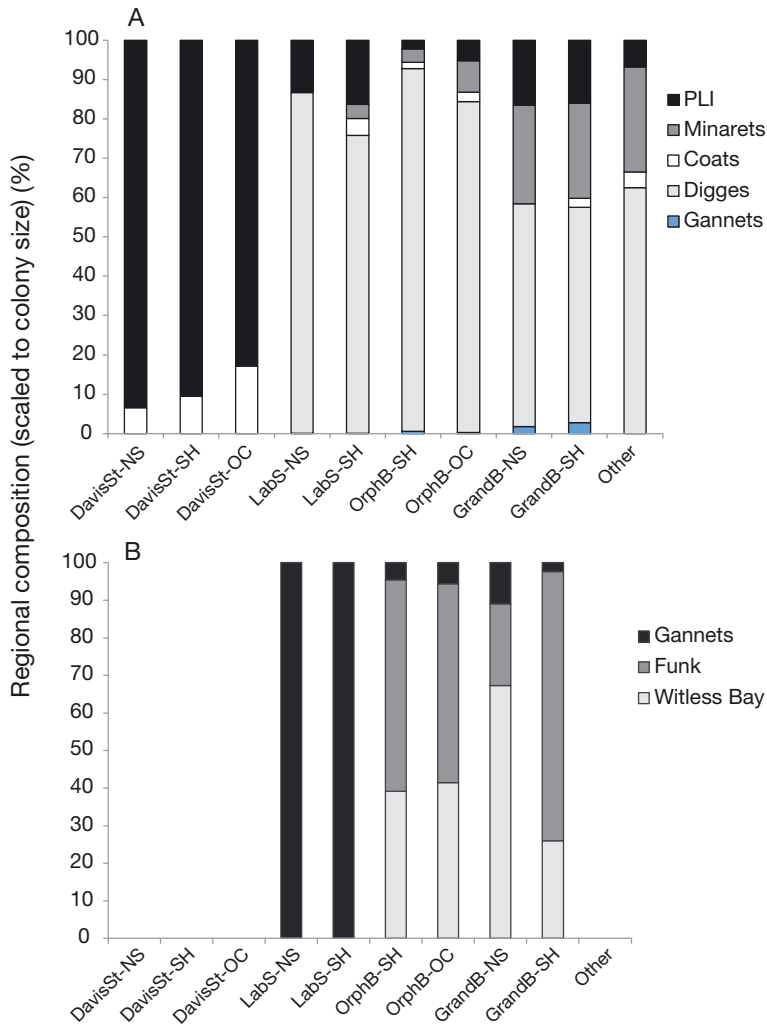


Fig. 6. *Uria lomvia* and *U. aalge*. Composition of subregions (%) by populations from different colonies of (A) thick-billed murres and (B) common murres, based on the Proportional Use of the subregions scaled to colony size. Only populations from the study colonies are included (i.e. other murre populations potentially using these areas are not considered). NS: nearshore; SH: shelf; OC: oceanic. NS: nearshore; SH: shelf; OC: oceanic. PLI: Prince Leopold Island

from Digges, the Minarets, and Prince Leopold (see below; Figs. 6 & 7). The shelf zone of the Grand Bank was dominated by common murres from Funk (Table 3; Figs. 6 & 7).

### Potential Presence

As explained above, we used Proportional Use of Zones ( $P_{iz}$ ) per colony, scaled to colony size and summed by species, to determine the number of common murres and thick-billed murres from tracked colonies that could potentially be present in each zone/sub-region of the study area throughout

the winter. Thick-billed murres were most numerous in the oceanic zone of the Orphan Basin and common murres most numerous on the shelf of the Grand Bank; thick-billed murres were least numerous in the nearshore zone of the Grand Bank and throughout Davis Strait and common murre were least numerous in the nearshore zone of the Grand Bank (Fig. 7). From the colonies from which we tracked birds, up to 363 000 thick-billed murres are potentially present in the Orphan Basin in winter (driven in large part by the huge colony at Digges); and over 680 000 common murres are potentially present on the Grand Bank (shelf) during winter (driven by the large colony at Funk; see Figs. 5 & 6). Combining species from the 7 tracked colonies, up to 903 300 murres are potentially present on the Grand Bank, and up to 1 065 400 in the Orphan Basin throughout the winter.

## DISCUSSION

### Species comparison

We report the first comparative study of winter distributions of adult thick-billed and common murres from multiple breeding colonies using geolocation. Thick-billed murres had larger winter ranges than common murres, with considerable spatial variation in core habitats, and low overlap among colonies. Common murre core winter habitat was mostly restricted to the Grand Bank and areas immediately adjacent, with high overlap among colonies.

Previous study suggested that, within and between murre species, the extent of migration from breeding to wintering areas is likely a response to developing ice conditions at high latitudes (Tuck 1961). Our results suggest that seasonal ice cover is not the only determinant of variation in migration strategies; we found greater individual variability in movements of thick-billed murres than common murres. This pattern held across all study colonies, and also in the comparison of birds tracked from Gannets, where the 2 species breed sympatrically.

The extent to which individuals show plasticity in migratory strategy will likely determine colony- and species-specific vulnerabilities to anthropogenic

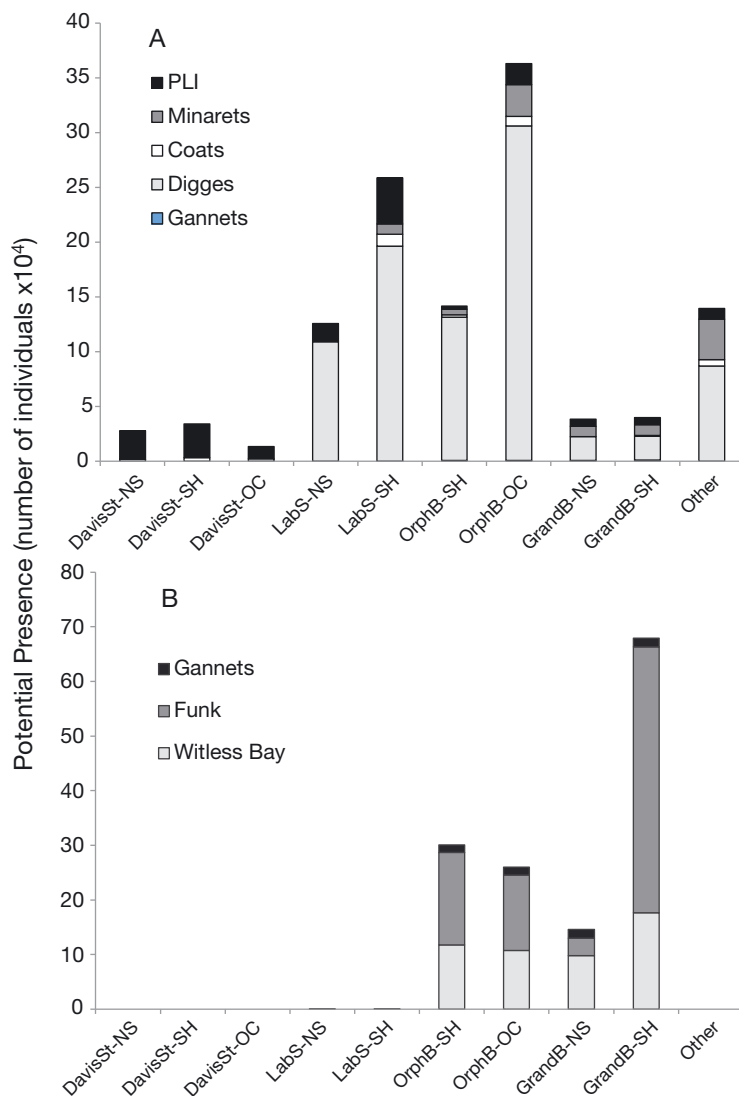


Fig. 7. *Uria lomvia* and *U. aalge*. Potential Presence in winter of (A) thick-billed murres and (B) common murres in the 3 marine zones (NS: nearshore; SH: shelf; OC: oceanic) of the 4 subregions in the study area (Davis Strait, Labrador Shelf, Orphan Basin, Grand Bank). Only populations from the study colonies are included (i.e. other murre populations potentially using these areas are not considered). PLI: Prince Leopold Island

threats or rapid environmental change (Phillips et al. 2009, Dias et al. 2010, Quillfeldt et al. 2010). Given their wider range of winter habitat and greater spatial variation among colonies, thick-billed murres have the potential to encounter a greater diversity of threats (in all marine zones/subregions) but also to experience a dilution of specific, spatially constrained risk to the population overall. Variable migratory strategies (Dias et al. 2010, Quillfeldt et al. 2010) or habitat preferences leading to heterogeneous marine distributions could partially insulate a population from any threats restricted to one region

(Phillips et al. 2009). The colonies from which we tracked thick-billed murres represent ~35% of the eastern Canadian population; other breeding populations may show similarly variable movement strategies, further diluting risk. By contrast, common murres might encounter a narrower suite of threats but the population in eastern Canada as a whole may be more susceptible to threats in particular areas (e.g. Grand Bank, Orphan Basin). The impact of risk encounter in light of narrow habitat use and invariant movement strategy seems particularly significant considering that the colonies from which we tracked common murres represent 85% of the eastern Canadian population. When birds from different colonies share wintering grounds in which foraging conditions deteriorate or other threats increase, resulting declines in population size are likely to be widespread (Esler 2000, Gaston 2003, Frederiksen et al. 2012). The relative influences of movement strategies, foraging conditions and winter energy budgets on ecology and survival in these congeners warrant further study.

### Wintering areas

During the winter, thick-billed murres dispersed widely throughout the study area, from Davis Strait, throughout the south and central Labrador Sea, to the Grand Bank. Thick-billed murres from the Arctic colonies where >95% of the Canadian population breeds, were found mainly north of 45°N, making little use of the Scotian Shelf, Gulf of St. Lawrence, or the southern Grand Bank, and showed highest Proportional Use of oceanic waters. Proportional Use of nearshore areas was higher only for particular colonies at Gannets (coastal areas of Newfoundland and Labrador) and Prince Leopold (coastal areas of West Greenland in the Davis Strait area). These findings contrast with a previous findings that thick-billed murres were mostly confined to nearshore and continental shelf waters (Gaston & Hipfner 2000), but this was largely based on band recoveries of pre-breeding birds from Arctic colonies that were hunted in coastal Newfoundland (Gaston 1980, Donaldson et al. 1997); the winter distributions of breeding-age murres likely differ substantially

from those of pre-breeders (Donaldson et al. 1997, McFarlane Tranquilla et al. 2010). We tracked very few breeding-aged thick-billed murres from the Arctic colonies to coastal Newfoundland and Labrador, an observation that accords with recent banding recoveries (Gaston & Robertson 2010).

Common murres migrated shorter distances than thick-billed murres, with no appreciable southward movement. Winter distributions were also more localized, with birds typically remaining offshore over the Grand Bank and Orphan Basin, with periods spent in nearshore habitat by some individuals from all colonies (see also Hedd et al. 2011). Common murres showed highest Proportional Use of shelf zones; common murres from Gannets were more common in nearshore waters than those from other colonies. Contrary to Gaston & Jones (1998), adult common murres from this study were not replaced on the Grand Bank in winter by adult thick-billed murres, nor did any breeding-aged common murres winter south of the Scotian Shelf.

Differences between our observations and results of previous studies could reflect recent changes in murre winter distributions or in the spatial segregation of age classes. Harris et al. (2010) used banding records to corroborate apparent changes in winter distributions of tracked Atlantic puffins *Fratercula arctica*, demonstrating that a combination of tracking and banding studies can help elucidate temporal aspects of environmental change. For thick-billed murres from Coats, band recoveries from Newfoundland hunters fluctuate with winter ice conditions (Gaston & Robertson 2010), indicating that the position of the ice front influences murre distributions. Thick-billed murres commonly associate with cold water masses and ice edges (Gaston & Jones 1998). Those from Coats and Digges exit Hudson Bay only as freeze-up occurs and their movement to the Labrador shelf is apparently determined by ice conditions in Hudson Bay (Gaston et al. 2011). On the other hand, birds from Prince Leopold and Minarets move south well in advance of freeze-up (L. A. McFarlane Tranquilla unpubl. data). Hence their wintering distributions are not merely a response to ice conditions, but a pre-determined migration. Similarly, common murres associate with cold water and forage primarily on cold water prey (capelin *Mallotus villosus*). Coincident with climate change, spatial shifts of marine thermoclines can alter predator and prey distributions, as species strive to remain in their preferred thermal environment (Montevecchi & Myers 1997, Hijmans & Graham 2006, Grémillet & Boulinier 2009, Nye et al. 2009, Quillfeldt et al. 2010).

With reduction in the southward extent of winter ice cover (Johnston et al. 2005) and warming of surface waters in the Northwest Atlantic (Spielhagen et al. 2011), some murres may have shifted their winter distributions northwards, to remain within preferred water masses and maintain spatial associations with ice and prey.

### Implications for risk assessments and management priorities

For both species, adult murres may be less exposed to nearshore risks such as hunting and chronic oiling from shipping traffic (Donaldson et al. 1997, Merkel & Barry 2008, Wilhelm et al. 2009) than previously thought, with disproportionate effects on breeding populations with high nearshore presence (Fig. 5). In addition, given the spatial contraction of the Newfoundland gillnet fishery in winter (Benjamins et al. 2008, Stenson et al. 2011) and the distribution of both murre species on the northern edges of the Grand Bank, bycatch is not expected to be a major source of adult winter mortality. In contrast, risks encountered in shelf and offshore areas are likely to be more significant for birds from our study colonies. In shelf areas of Newfoundland, Labrador and Greenland, seismic testing, hydrocarbon exploration, and offshore petroleum production are burgeoning ventures (AMAP 2010), with the potential to release oil and chemicals in the ocean (Wiese et al. 2001, Wilhelm et al. 2007, Burke et al. 2012). In particular, the Grand Bank and Orphan Basin emerge as areas of concern where anthropogenic activities overlap with sizeable breeding populations of murres (this study; see also Hedd et al. 2011) and other species (kittiwakes *Rissa tridactyla*, Frederiksen et al. 2012; sooty shearwaters *Puffinus griseus*, Hedd et al. 2012; dovekies *Alle alle*, Mosbech et al. 2012). With climate-induced reduction of annual ice cover, there is increasing pressure to extract submarine hydrocarbon resources in arctic waters (AMAP 2010). The resulting substantial increase in offshore vessel activity would be a potentially major and chronic source of disturbance and oil mortality for seabirds (Wiese & Robertson 2004).

The potential for encountering anthropogenic threats at particular wintering sites will vary according to both the number and spatial concentration of risks (e.g. Table 2), and the number and variety of birds using the area (Table 3, Figs. 5 & 6). If anthropogenic risk affects ages, sexes, and breeding populations indiscriminately (Robertson et al. 2006), then the potential for encountering risk depends entirely

on spatiotemporal overlap of seabird habitat with anthropogenic threats. Differences in spatial distribution according to age, sex (Donaldson et al. 1997, González-Solís et al. 2007, Phillips et al. 2009, Gaston & Robertson 2010), colony (this study; Donaldson et al. 1997, Frederiksen et al. 2012) or breeding performance (Bogdanova et al. 2011) will determine the demographic influence of risks. Overall impact of exposure will also depend on the size of the breeding population congregating in risk-prone areas during winter. The concept of uneven distribution of risk has been introduced for murres using band recoveries (with the winter murre hunt having a larger impact on particular murre colonies; Gaston 1980, Elliot 1991, Donaldson et al. 1997). Bird-borne tracking technology allows an assessment over larger spatial and temporal scales (Montevecchi et al. 2012).

The estimated numbers of murres potentially present in each marine zone (nearshore, shelf, oceanic) and subregion (Davis Strait, Lab Shelf, Orphan Basin, Grand Bank) depends on the assumption that murres from each colony behave similarly to those we tracked, and must therefore be treated with caution. Notably, a large proportion of murres wintering in the Northwest Atlantic likely originate from other untracked colonies in eastern Canada (e.g. common murre colonies in Labrador, thick-billed murre colonies in Hudson Strait and the High Arctic), Greenland and, to a lesser extent, northern Europe (Tuck 1961, Kampp 1983, Donaldson et al. 1997, Gaston 2002). It is, however, undeniable that areas such as the Grand Bank and Orphan Basin are used heavily by murres, both in terms of the sheer number of individuals and in the number of breeding populations represented (all 7 colonies studied; Fig. 6). Observations from pelagic seabird surveys confirm that murres have been, and currently are abundant in these areas during winter (Tuck 1961, Brown 1986, Fifield et al. 2009). These are also the areas with the highest incidence of anthropogenic perturbations (Table 2). We suggest that monitoring and mitigation of potential risk encounter on the Grand Bank and in the Orphan Basin should be a critical focus for conservation and management in the Northwest Atlantic, not just for murres, but for many other avian, mammalian, and fish species inhabiting this area. Integration of multiple tracking studies to target conspecific seabirds throughout their range would further identify key colonies and candidate marine areas on which to focus conservation efforts (González-Solís et al. 2007, Block et al. 2011, Croxall et al. 2012, Frederiksen et al. 2012, Montevecchi et al. 2012). Furthermore, public access to spatially-explicit maps of mar-

ine anthropogenic activity will facilitate quantitative and robust risk assessments in the future.

Understanding the extent and importance of marine areas to local, regional, or international populations of marine animals should be a first priority for comprehensive conservation planning (Croxall et al. 2012). Using tracking technology, we demonstrate that murres from different colonies vary in their winter habitat use and potential exposure to anthropogenic threats. Thus, not only is it important to understand the spatial extent and potential lethal impact of risks from an environmental perspective, but it is absolutely critical to understand *what* is at risk—which species, populations, colonies—and how this might change through time. The integration of tracking data from multiple studies and across international boundaries has great potential to identify important areas common to many marine species in our internationally-shared marine environment.

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