

Ecological segregation among Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*) in the Northwest Atlantic persists through the nonbreeding season

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Abstract: To study the influence of inter- and intra-specific interactions on patterns of ecological segregation in nonbreeding habitat, we used geolocators to track year-round movements of congeneric and partially sympatric Thick-billed Murres (*Uria lomvia* (L., 1758)) and Common Murres (*Uria aalge* (Pontoppidan, 1763)) from seven Canadian colonies during 2007–2011. Locations from 142 individuals were (i) examined for species- and colony-specific spatiotemporal patterns, (ii) mapped with environmental data, and (iii) used to delineate core wintering areas. Compared with Common Murres, Thick-billed Murres dispersed across a wider range of latitudes and environments, had larger winter ranges, and showed greater variation in seasonal timing of movements. These interspecific differences were consistent at two scales: among colonies spanning a wide latitudinal range and at a sympatric colony. Intraspecifically, nonbreeding ecological segregation was more pronounced among colonies of Thick-billed Murres than of Common Murres: colonies of Thick-billed Murres tended to follow distinct movement patterns and segregate by latitude, whereas colonies of Common Murres segregated very little; moreover, the extent of segregation was more variable among Thick-billed Murres than Common Murres. For Thick-billed Murres, rather than complete divergence of winter ecological niche from Common Murres, we found a “widening” of an overlapping niche. This strategy of increased movement flexibility may enable Thick-billed Murres to mitigate competition both intra- and inter-specifically; we propose this movement strategy may have played a role in species divergence.

Key words: *Uria aalge*, *Uria lomvia*, movement ecology, niche segregation, seabird tracking, wintering areas, seasonal variation.

Résumé : Afin d'étudier l'influence des interactions interspécifiques et intraspécifiques sur les motifs de ségrégation écologique dans les habitats autres que de reproduction, nous avons utilisé des géolocalisateurs pour suivre les déplacements durant toute l'année de guillemots de Brünnich (*Uria lomvia* (L., 1758)) et de guillemots marmettes (*Uria aalge* (Pontoppidan, 1763)) congénères et partiellement sympatriques de sept colonies canadiennes, de 2007 à 2011. Les emplacements de 142 individus ont été (i) examinés pour en déterminer les motifs spatiotemporels propres à chaque espèce et à chaque colonie, (ii) cartographiés avec des données expérimentales et (iii) utilisés pour délimiter les aires d'hivernage principales. Par rapport aux guillemots marmettes, les guillemots de Brünnich se dispersaient sur une plus grande fourchette de latitudes et de milieux et présentaient des aires d'hivernage plus grandes et une plus grande variation du moment des déplacements durant les saisons. Ces différences interspécifiques étaient cohérentes à deux échelles, soit entre différentes colonies couvrant une large fourchette de latitudes et à l'intérieur d'une colonie sympatrique. Au sein de l'espèce, la ségrégation écologique en dehors de la période de reproduction était plus prononcée entre les colonies de guillemots de Brünnich qu'entre celles de guillemots marmettes; les colonies de guillemots de Brünnich tendaient à suivre des motifs de déplacements distincts et à se ségréger selon la latitude, alors que les colonies de guillemots marmettes ne présentaient qu'une très faible ségrégation; en outre, l'ampleur de la ségrégation était plus variable chez les guillemots de Brünnich que chez les guillemots marmettes. Plutôt qu'une divergence complète de la niche écologique hivernale des guillemots de Brünnich par rapport à celle des guillemots marmettes, nous avons observé « l'élargissement » d'une niche chevauchante commune. Cette stratégie de souplesse accrue des déplacements pourrait permettre aux guillemots de Brünnich d'atténuer la concurrence tant intraspécifique qu'interspécifique; nous proposons que cette stratégie de déplacement pourrait avoir joué un rôle dans la divergence des espèces. [Traduit par la Rédaction]

Mots-clés : *Uria aalge*, *Uria lomvia*, écologie des déplacements, ségrégation de niche, localisation d'oiseaux marins, aires d'hivernage, variations saisonnières.

Introduction

When resources are limited, sympatric and competing species are able to coexist through ecological segregation (Lack 1945; Holt 2009). Sympatric species reduce competition through habitat and

dietary partitioning, exhibiting varied patterns of space use, foraging activity, and diet (MacArthur and Levins 1964; Phillips et al. 2009; Masello et al. 2010), all of which are well-documented strategies of niche partitioning at colony sites during the breeding

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season (Wood et al. 2000; Grémillet et al. 2004; Gonzáles-Solís et al. 2007; Wakefield et al. 2013). Following breeding, seabirds are released from central-place foraging constraints and, given the potential for dispersal throughout the marine environment, one might expect a reduction in resource competition that diffuses the pressure for ecological segregation. However, marine resources are patchily distributed, and important wintering areas can concentrate large numbers of nonbreeding seabirds and other top predators (e.g., Grand Banks of Newfoundland: Frederiksen et al. 2011; Hedd et al. 2012; Mosbech et al. 2012; Magnusdottir et al. 2012; Mid-Atlantic Ridge: Walli et al. 2009; Egevang et al. 2010; North Pacific Transition Zone: Block et al. 2011; Benguela Upwelling: Stenhouse et al. 2011), where competition for resources is likely to persist. Here, how inter- and intra-specific interactions may influence ecological segregation in wintering areas (Ratcliffe et al. 2014) is another important piece of the puzzle.

Research on ecological segregation among nonbreeding seabirds has unfolded using two approaches. First, studies dedicated to investigating nonbreeding segregation usually compare winter distributions of sympatric species or neighboring populations. Among the most well-studied have been seabirds of the Southern Atlantic and Indian oceans, where sympatric groups (e.g., petrels, albatrosses, penguins) from Antarctic colonies exhibit species-specific segregation into different water masses of the Antarctic Circumpolar Current, usually targeting different diets (Cherel et al. 2006, 2007; Phillips et al. 2009; Thiebot et al. 2012; Ratcliffe et al. 2014). Winter spatial and diet segregations by sex also occurs in some species (Phillips et al. 2005). Very few studies have compared nonbreeding segregation outside the Antarctic system.

Second, studies have taken a multiple-colony approach to compare winter distributions among colonies of the same species, focusing primarily on intraspecific segregation and the degree of population connectivity on the wintering grounds. These studies generally describe a pattern in which colonies of the same species show considerable convergence on important wintering areas where colony mixing occurs, but with a degree of spatial separation among particular colonies (e.g., Cape Gannets, *Morus capensis* (Lichtenstein, 1823); Jaquemet and McQuaid 2008; Cory's Shearwaters, *Calonectris diomedea* (Scopoli, 1769); González-Solís et al. 2007; Northern Gannets, *Morus bassanus* (L., 1758); Fort et al. 2012; Black-legged Kittiwakes, *Rissa tridactyla* (L., 1758); Frederiksen et al. 2011). The extent to which populations depend upon and partition important wintering areas (Croxall et al. 2005; González-Solís et al. 2007) carries important evolutionary, ecological, and conservation implications. As well, how divergent movement strategies may functionally partition nonbreeding habitat (Friesen et al. 2007), potentially leading to or maintaining genetic differentiation among subpopulations as documented for passerine birds (Helbig 1996; Irwin et al. 2011) and one seabird (Wiley et al. 2012), remains unclear for migratory seabirds.

Despite their differences, these two approaches have broadly overlapping similarities in describing how inter- and intra-specific interactions may shape marine habitat use in the marine environment. Very few studies have combined these two approaches (e.g., Ratcliffe et al. 2014). Integrating an understanding of inter- and intra-specific segregation, across the nonbreeding range of multiple colonies, will be the primary focus of this paper.

Our approach investigates patterns of nonbreeding ecological segregation between sympatric species, at both regional (multiple colony) and local (sympatric colony) scales, through spatial and temporal activity patterns. Our study subjects were the congeneric Thick-billed Murres (*Uria lomvia* (L., 1758)) and Common Murres (*Uria aalge* (Pontoppidan, 1763)). Among the most significant consumers of marine resources in the Northwest Atlantic, these species are closely related, are specialized in underwater swimming by wing propulsion, occupy a similar ecological niche as pursuit-diving piscivores, and share partially overlapping, circumpolar distributions throughout the year (Tuck 1961; Gaston

and Hipfner 2000; Ainley et al. 2002). Because the two species are morphologically and ecologically very similar (Gaston and Jones 1998), competition and pressures for divergence between them is likely intense. Dietary niche partitioning is supported by slight differences in bill morphology (Bédard 1969) reflecting preferences: Thick-billed Murres consume a wide variety of fishes (e.g., Arctic cod (*Boreogadus saida* (Lepechin, 1774)), blennies (suborder Blennioidei) and zooplankton (for which their tongue and palate are better adapted; Bédard 1969), whereas Common Murres consume predominantly shoaling fishes (e.g., capelin (*Mallotus villosus* (Müller, 1776)), sand lance (genus *Ammodytes* L., 1758)) with a small proportion of invertebrates (Gaston and Jones 1998). In the Northwest Atlantic, they have a relatively segregated breeding distribution (Thick-billed Murres concentrating at higher latitudes; see also study colony sizes in Table 1), but sympatry occurs where their ranges overlap. At sympatric colonies, subtle differences in phenology, breeding-site locations, and prey exploitation might decrease interspecific competition (Birkhead and Nettleship 1987a, 1987b; Barrett et al. 1997). Following breeding, both species winter at Low Arctic latitudes of the North Atlantic Ocean (Tuck 1961; Gaston and Hipfner 2000; Ainley et al. 2002). Although Tuck (1961) considered them to segregate partially by thermal preference (with Thick-billed Murres occurring in colder waters and Common Murres occurring in warmer waters), other studies have blurred this categorization, rendering it unclear how winter strategies or preferences of murres are influenced by geography and habitat preference, colony of origin, or the presence of competitors (Gaston et al. 2011, Fort et al. 2012, Linnebjerg et al. 2013). In the Northwest Atlantic, pressure for habitat partitioning may intensify with seasonal arrivals of many other seabirds on the Grand Banks and the Labrador Sea in winter, including murres from populations in Greenland, Iceland, and Svalbard (Tuck 1961; Kampp 1988; Donaldson et al. 1997; Lyngs 2003; Bakken and Mehlum 2005), Black-legged Kittiwakes (Frederiksen et al. 2011), Dovekies (*Alle alle* (L., 1758)) (Fort et al. 2012; Mosbech et al. 2012), and other competitors such as marine mammals and fish. Furthermore, wintering in the Northwest Atlantic, particularly at high latitudes, is energetically challenging for seabirds and requires intense foraging effort (Grémillet et al. 2005; Fort et al. 2009); thus, the location of wintering areas will have strong fitness implications (Fort et al. 2013).

Consequently, we predict that inter- and intra-specific habitat segregation will be maintained during the nonbreeding season. By identifying and comparing winter movements and distribution of Thick-billed Murres and Common Murres, we expect to demonstrate that (i) interspecific segregation occurs, particularly near areas where species originate from a sympatric breeding colony, (ii) segregation occurs primarily through spatiotemporal patterns of movement and distribution, (iii) colonies tend to show distinct wintering strategies, resulting in a degree of intraspecific segregation, and (iv) the resulting winter habitat characteristics vary by species and by colony.

Materials and methods

Study area and device deployments

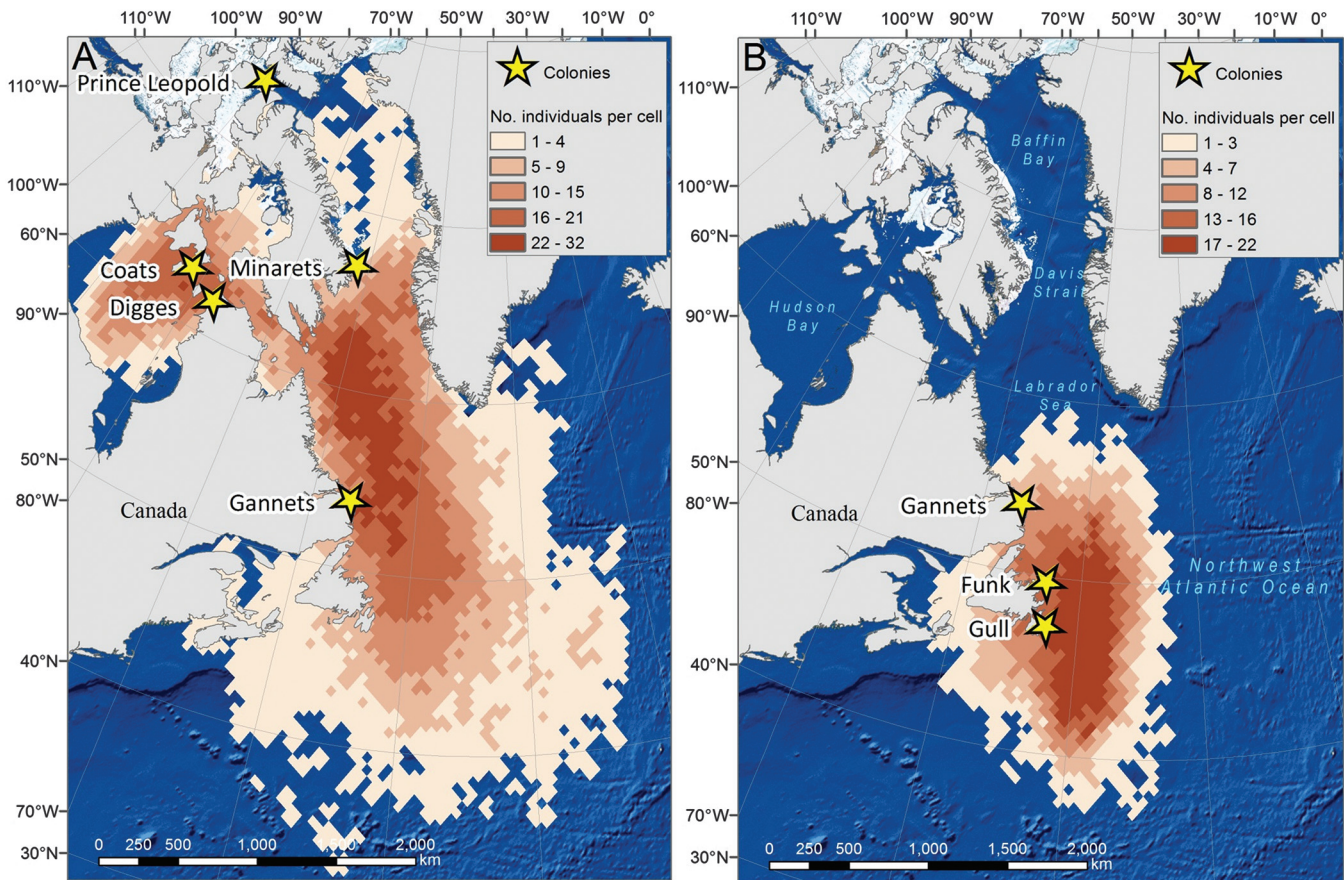
Research took place at seven seabird colonies spanning 47°N–74°N latitudes in Arctic and Eastern Canada during the summers of 2007–2011 (Table 1, Figs. 1A, 1B). These sites support either Thick-billed Murres or Common Murres, except at the Gannet Islands where both species occur (Table 1). Geolocation-immersion loggers (GLS) from British Antarctic Survey (BAS, Cambridge, UK; models Mk5, Mk7, Mk13, Mk15; $n = 266$) or Lotek (St. John's, Newfoundland, Canada; model 2500; $n = 8$) were attached to 282 breeding murres (155 Thick-billed Murres, 127 Common Murres) in 2007–2009 using leg bands (logger, band, and cable ties ≤ 5.4 g, $\leq 0.6\%$ adult body mass). Individuals were chosen by ease of access (near top of colony cliffs in most cases) and based on the presence of an egg or

Table 1. Details of geolocation-immersion loggers (GLS) deployed and retrieved for Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*), as well as tracking data for each study colony and year.

Species	Colony	Position	Colony size (breeding pairs × 2)	GLS		Deployed	Retrieved	Total included	Tracking data			
				Year deployed	Models				Years of data coverage	Unique individuals	Repeat tracks	Total annual tracks
Thick-billed Murre	Prince Leopold	74°02'N, 90°00'W	170 000	2008	BAS Mk5, Mk7, Mk13	21	19	19	2008–2010	19	1	20
				2009	Lotek 2500	5	5					
	Minarets	66°57'N, 61°50'W	260 000	2007	BAS Mk5, Mk7	20	14	14	2007–2008	14	0	14
	Coats	62°53'N, 82°00'W	36 000	2007	BAS Mk5, Mk7	20	18	31	2007–2010	21	8	32
				2008	BAS Mk5, Mk7, Mk13	20	13					
2009				BAS Mk5, Mk7, Mk13	6	3						
Digges	62°32'N, 77°45'W	872 000	2008	BAS Mk5, Mk7	32	10	10	2008–2010	10	3	13	
Gannets	53°56'N, 56°32'W	3 700	2008	BAS Mk5, Mk7, Mk13	14	8	12	2008–2011	11	7	22	
			2009	BAS Mk5, Mk7, Mk13, Mk15	17	11						
Common Murre	Gannets	53°56'N, 56°32'W	62 420	2008	BAS Mk5, Mk7, Mk13	16	12	19	2008–2011	16	7	27
				2009	BAS Mk5, Mk7, Mk13, Mk15	16	9					
	Funk	49°45'N, 53°11'W	825 050	2007	BAS Mk5, Mk7	21	11	19	2007–2011	17	6	31
				2008	BAS Mk5, Mk7, Mk13	25	5					
2009				BAS Mk5, Mk7, Mk13; Lotek 2500	3	3						
Gull	47°16'N, 52°46'W	6 992	2007	BAS Mk5, Mk7	5	0	18	2007–2011	15	7	23	
			2008	BAS Mk5, Mk7, Mk13	30	16						
			2009	BAS Mk5, Mk7, Mk13	11	6						
Overall						282	163	142	2007–2011	123	39	182

Note: Data were retrieved 1–3 years following deployment; in some cases this resulted in a larger number of total annual tracks than unique individuals tracked.

Fig. 1. Study area, colonies, and nonbreeding distribution (September–May) of (A) Thick-billed Murres (*Uria lomvia*) and (B) Common Murres (*Uria aalge*). Data coverage indicates the number of unique individuals per cell (50 km × 50 km grid) but includes all filtered data from geolocation-immersion loggers (GLS) (all months and years pooled). Thus, individuals can be counted in multiple grid cells as they move over the months.



chick. We retrieved 163 (58%) GLS in 2008–2011 and successfully recovered data from 142 (50%; 86 Thick-billed Murres, 56 Common Murres). Most were retrieved after 1 year, but several were carried for 2–4 years, providing repeat tracks for 39 individuals, a total of 182 annual round trips (Table 1), and 108 882 (unfiltered) GLS locations. All populations (except the Minarets) were studied simultaneously during at least 2 years (usually 2008–2010; see Table 1).

Data processing

GLS data were processed following Phillips et al. (2004), using MultiTrace Geolocation software (Jensen Software Systems, Laboe, Germany) and a light threshold processing method (Hill and Braun 2001; Lisovski et al. 2012), which was chosen to minimize data loss and latitudinal discrepancy around the equinox (Lisovski et al. 2012). A light threshold of 1 and a sun angle of -5.5° was used for BAS Mk5, Mk7, and Mk13 (represented at all colonies; Table 1); for BAS Mk15, a light threshold of 10 and a sun angle -2.5° was used (represented at only Gannet Islands). Lotek 2500 devices (Funk, Prince Leopold) employ internal processing algorithms so positional data can be downloaded directly. All positions were processed individually and inspected visually by the same observer (L.M.T.) and clearly erroneous locations were removed (Phillips et al. 2004). Latitudes cannot be accurately assessed during equinox periods (Hill 1994); data affected in this study were from approximately 8 September to 8 October and from approximately 6 March to 5 April. However, equinox data were not deleted a priori because not all GLS were affected equally (perhaps influenced by individual bird behaviour or weather; Lisovski et al. 2012); no apparent patterns in relative error (c.f. Winship et al. 2012) were detected among model type or species. All data during

equinox periods were inspected and reasonable positions retained. In addition, some equinox data (5319 positions, contributing 9% to retained data) were reclaimed using sea-surface temperature matching algorithms (Teo et al. 2004; Fifield et al. 2013; see full description in McFarlane Tranquilla et al. 2013). Data were subsequently smoothed twice (2 day running mean; Phillips et al. 2004). Overall, processing resulted in 54 930 locations (50% of original data), or 27 465 tracking-days (two locations per day). Mean accuracy of GLS location data are approximately 185 km (Phillips et al. 2004) and may vary from 0.5°W to 3.9°W longitudes and from 0.8°N to 3.6°N latitudes (Winship et al. 2012). For these species, which can cover a core home-range area of up to 500 000 km² during the winter alone (McFarlane Tranquilla et al. 2013), this accuracy should be sufficient for tracking broad-scale differences in spatial and temporal habitat-use patterns.

Analyses of spatial and environmental variables

To broaden our understanding of nonbreeding strategies of these species, we investigated segregation at two temporal scales: (1) during the full nonbreeding period (September–May) and (2) for winter only (December–January). This improved our ability to discern spatiotemporal movement patterns and environmental variables throughout the nonbreeding period compared with just the winter period alone. To do this, mean daily latitudes from individual GLS were pooled by colony and mapped against date to determine temporal patterns of distribution (referred to as “profiles”). Similarly, the following environmental variables associated with each GLS location were used to describe habitat variation: (i) bathymetry (1 min grid; chosen because of the spatial resolution of GLS devices; GEBCO

digital atlas version 2, available from <http://www.gebco.net/>), (ii) chlorophyll *a* (CHL; 4 km resolution, measured in milligrams per cubic metre (mg/m³), averaged over 8 days per raster, and from 2007 to 2011; OceanColor database, available from <http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/8Day/4km/chlor/>), (iii) water temperature (obtained directly from GLS, which record temperatures after 20 min of being continuously wet and every 40 min thereafter, and have an accuracy of ± 0.5 °C; Fox 2010), (iv) ice (weekly ice cover charts from the Canadian Ice Service (available from <http://www.ec.gc.ca/glaces-ice/>) for eastern Canadian Arctic, Hudson Bay, east coast of Canada (merged to compile coverage for the study area), in 10ths of coverage, from 2007 to 2011), and (v) night length (or hours of darkness, calculated directly from GLS using time of sunrise and sunset). These variables were chosen to help describe (i) characteristics of nonbreeding marine habitat, (ii) to discern any differences in species- and colony-specific habitat associations across a wide range of nonbreeding habitat, and (iii) to infer environmental conditions, and their implications (c.f. Fort et al. 2009), at core wintering locations. For bathymetry, CHL, and ice, filtered GLS locations were overlaid on environmental maps in ArcMap (Environmental Systems Research Institute, Inc. (ESRI), Redlands, California, USA) and a time series of data (i.e., from 2007 to 2011) was extracted using Marine Geospatial Ecology Tools version 0.8a12 in ArcGIS versions 9.3 and 10 (ESRI). Mean daily water temperatures and night lengths were collected directly from each GLS, pooled by colony, and mapped against date. A separate analysis of environmental variables during winter only (December–January) was also performed. Hours of darkness were extracted directly from GLS only for December when nights are longest and when energetic requirements are highest (c.f. Fort et al. 2009). For each colony, we also described the proximity of distributions to winter sea ice by calculating percent overlap of core winter distributions (see below) with the winter leading ice edge (January only, where ice exceeds 80% (8/10ths); U.S. National Ice Center (NIC), available from <http://www.natice.noaa.gov/products/>). Ice concentrations are resolved at a minimum polygon size of 1000 km² and follow the International Egg Code (available from http://www.natice.noaa.gov/products/egg_code.html) to express area of ice cover (“N_CT”) in tenths, where 0 is ice-free, 1/10ths to 7/10ths rank areas of drift ice in marginal ice zones, and >8/10ths indicate nearly complete ice cover, which is also known as the leading ice edge (Canadian Ice Service, available from <http://www.ec.gc.ca/glaces-ice/>).

In addition to nonbreeding season profiles, we investigated spatial segregation during winter. Core kernel home ranges (50% KHR; Wood et al. 2000; Phillips et al. 2005) in winter (December and January) for each colony were calculated using an equal-area projection with a cell size of 50 km and a search radius of 200 km (Phillips et al. 2004). Colony overlap of winter KHRs was calculated following McFarlane Tranquilla et al. (2013). Furthermore, to determine the degree to which individuals from each colony tended to show similar wintering strategies (thereby resulting in intraspecific segregation), we tested the degree of overlap between individual birds (grouped by colony) using a randomization procedure ($n = 10\,000$ randomizations in R version 2.15.2; R Development Core Team. 2012) in which individual core home ranges were paired at random for each iteration to calculate a mean 50% KHR overlap (c.f. Fifield et al. 2013, Dias et al. 2010). Intercolony distances were measured in ArcMap using Hawth's tools.

Statistical analyses

Ice concentrations were analysed with linear mixed effects (lme) models to account for repeat measurements from individuals. To examine the nonlinear relationship of nonbreeding latitudes (spatial data) and environmental data through time (bathymetry, CHL, water temperature) and between and within species, we used generalized additive mixed models (gamm; Wood, 2012) in R. These models included terms for repeated data from individuals, spatial autocorrelation, and a colony-specific smoothing term (Zuur et al. 2009). Each environmental data set was analyzed separately and

model results were used to depict temporal profiles for each colony. Inclusion of year (tested only when data-collection years for particular colonies overlapped) and sex did not improve the fits of any models (as judged by Akaike's information criterion (AIC) values), so annual data were pooled when graphing temporal profiles. The p values were used to assess significance within groups of fixed effects (e.g., species, colony). Because p values calculated from gamm are approximate (Zuur et al. 2009), we considered p values from ≤ 0.05 to 0.1 to be approaching significance. Model variance, described through standard deviation (SD) and residual of the intercept, were used to help describe differences in variance between species; this is akin to the intraclass coefficient of variation described by Lessells and Boag (1987). The types of environmental data considered here are often collinear, but since they were used only to describe gradual changes and differences in environmental variables among and within species, rather than included together in a habitat-selection model (c.f. Andersen et al. 2013; Ratcliffe et al. 2014), a formal examination of collinearity was not required. In cases when analyses include individually repeated measures, sample sizes are represented as a pair, consisting of total observations and total number of individuals (e.g., $n = 30\,000 \mid 92$).

Results

Nonbreeding segregation by latitude

Latitudinal segregation was observed throughout the nonbreeding season. Thick-billed Murres occupied a much broader distribution than Common Murres (Figs. 1A, 1B) at higher latitudes (gamm, $t = 12.13$, $p \leq 0.001$) and a wider range of latitudes (33°N–77°N; SD (intercept + residuals) = 5.80 + 4.2) than did Common Murres (32°N–58°N; SD (intercept + residuals) = 1.55 + 2.8; Figs. 2A, 2B). Temporally, Thick-billed Murres shifted latitudes throughout the nonbreeding season, whereas Common Murres moved in the fall (until October) and then latitudes were mostly constant until returning to colonies in May (Figs. 2A, 2B).

For sympatric murres from the Gannet Islands, latitudinal variance of winter distribution was greater for nonbreeding Thick-billed Murres (SD (intercept + residuals) = 5.02 + 5.15) than for Common Murres (SD (intercept + residuals) = 0.70 + 3.02), even though the species did not separate to significantly different latitudes (gamm, $t = 0.02$, $p = 0.98$).

Intraspecifically, latitudinal segregation by colony was more obvious among Thick-billed Murres, which segregated into three groups: significant differences in latitude occurred between Coats – Digges – Prince Leopold (PLI) islands, the Minarets Island (gamm; $t = 5.74$, $p < 0.001$), and Gannet Islands (gamm; $t = -12.71$, $p < 0.001$; Fig. 2A). This was accompanied by temporal differences in movement, with some Thick-billed Murres moving southward immediately after the breeding season (August–September; PLI, Minarets), while others remaining near colonies into the fall (October–December; Coats, Digges, Gannets; Fig. 2A). The timing of northward movement toward breeding latitudes also varied widely (January–April) among colonies (Fig. 2A). For Common Murres, latitudinal segregation occurred only for the Gannet Islands, compared with Gull Island (gamm; $t = 2.67$, $p = 0.008$) and Funk Island (gamm; $t = 1.66$, $p = 0.098$; Fig. 2B), and timing of southward movement varied little, from soon after breeding (Gannet Islands; August–September) to early fall (Funk and Gull islands; September–October; Fig. 2b). Common Murres from all three colonies began to return to breeding latitudes in April.

Core winter overlap

Core winter areas (50% KHR) for Thick-billed Murres were in Baffin Bay (western Greenland), Davis Strait, the Labrador Sea, and the Orphan Basin–Grand Bank (Fig. 3A), whereas core winter areas of Common Murres were more restricted to the eastern Grand Bank and the Orphan Basin (Fig. 3A). Interspecific overlap of core colony winter areas was generally low (mean 15%, range 0%–42%; Table 2). Within

Fig. 2. Intraspecific comparison of spatial and temporal ranges of latitudinal movement during the nonbreeding period for (A) five colonies of Thick-billed Murre (*Uria lomvia*) and (B) three colonies of Common Murre (*Uria aalge*). Data reflect mean daily latitude of all samples at each colony after controlling for individual variation (from generalized additive mixed models (gamm)).

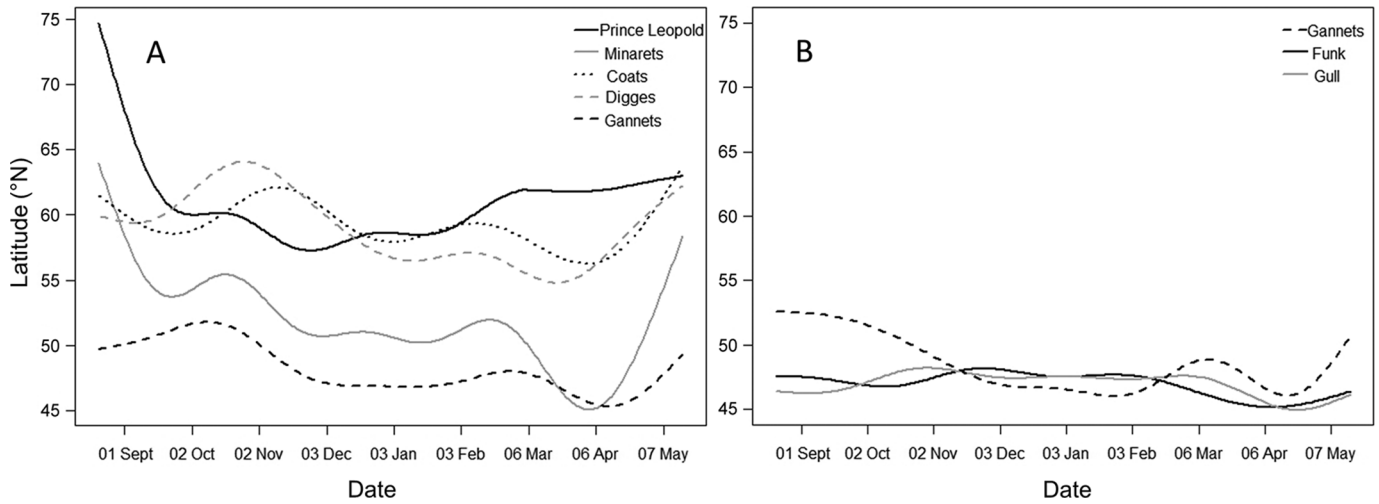
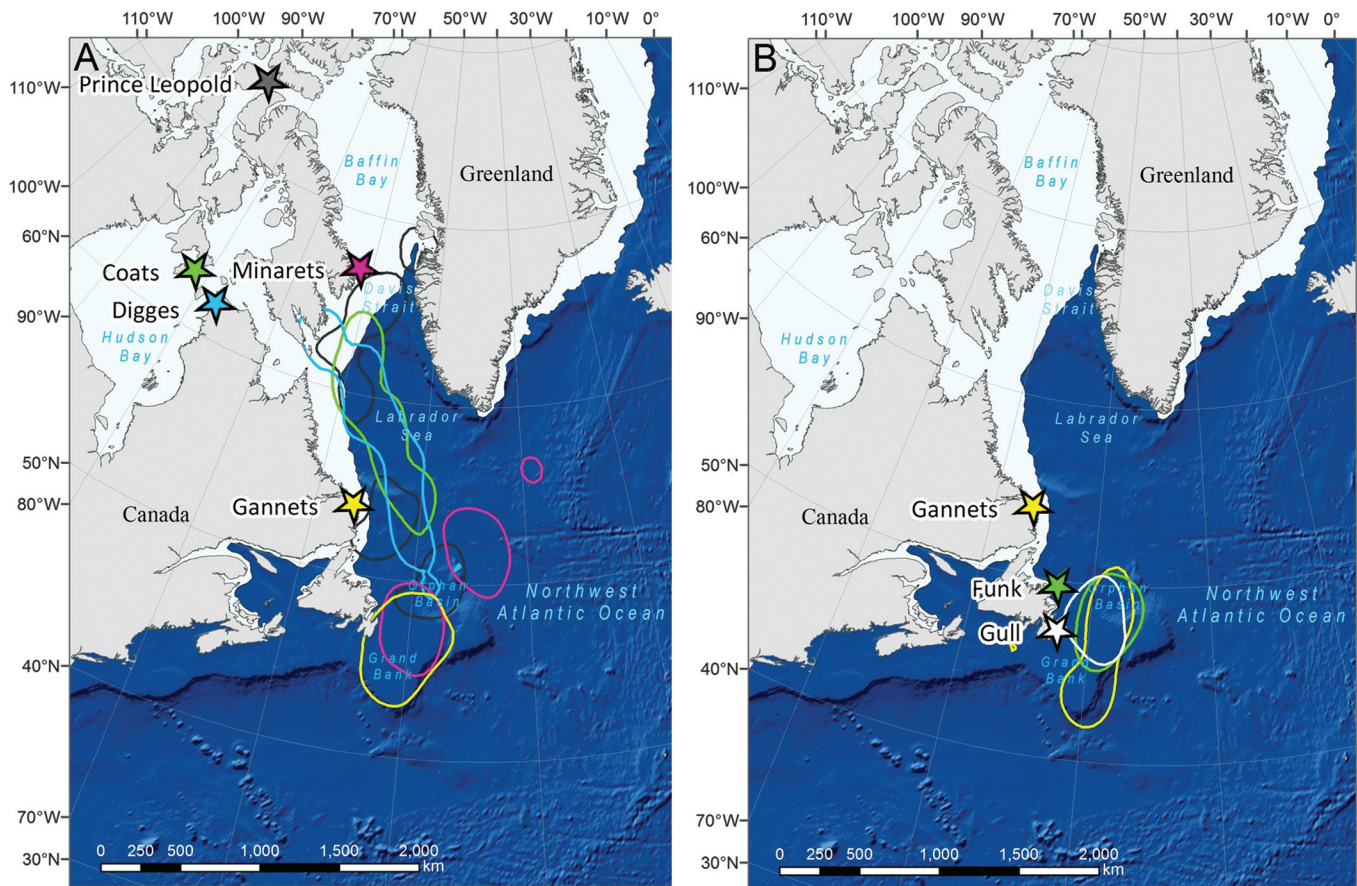


Fig. 3. Intercolony overlap of core winter habitat (50% kernel home ranges (KHR)) among (A) Thick-billed Murres (*Uria lomvia*) and (B) Common Murres (*Uria aalge*) overlaid on the leading ice edge (light blue) in January. Colored stars indicate individual breeding colonies and match the color of the core outline for each colony.



species, overlap of core winter areas of Thick-billed Murre colonies ranged from 0% to 52% (Table 2), whereas overlap was greater and less variable among Common Murres (33%–61%; Table 2, Figs. 3A, 3B). Similarly, overlap of individual core winter areas was less for Thick-billed Murres (mean 23%, range 10%–33%) than for Common Murres (mean 39%, range 36%–44%). As well, individual overlap varied mark-

edly by colony and appeared to be reduced among individuals from northerly colonies (Table 3).

Intercolony distance

There was a significant negative relationship between intercolony overlap in winter and intercolony distance; i.e., colonies

Table 2. Percent overlap of core winter areas (December–January 50% kernel home ranges (KHR)) among pairs of colonies of Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*) (see also Figs. 3A, 3B).

Species	Colonies	No. of GLS	Percent intercolony overlap of core winter areas						
			Prince Leopold	Minarets	Coats	Digges	Gannets (T*)	Gannets (C*)	Funk
Thick-billed Murre	Prince Leopold	19	—	—	—	—	—	—	—
	Minarets	12	19.9	—	—	—	—	—	—
	Coats	32	19.9	0.0	—	—	—	—	—
	Digges	10	21.6	0.4	51.7	—	—	—	—
	Gannets	12	4.5	33.3	0.0	0.0	—	—	—
Mean (±SE) TT percent overlap			15.1±5.5				—		
Common Murre	Gannets	19	9.6	21.9	0.0	1.8	41.8	—	—
	Funk	16	12.3	28.2	0.0	1.9	35.6	33.7	—
	Gull	16	9.2	34.2	0.0	1.8	39.3	36.1	61.8
	Mean (±SE) CC percent overlap			—				43.8±8.9	
Mean (±SE) TC percent overlap			15.8±4.2				—		

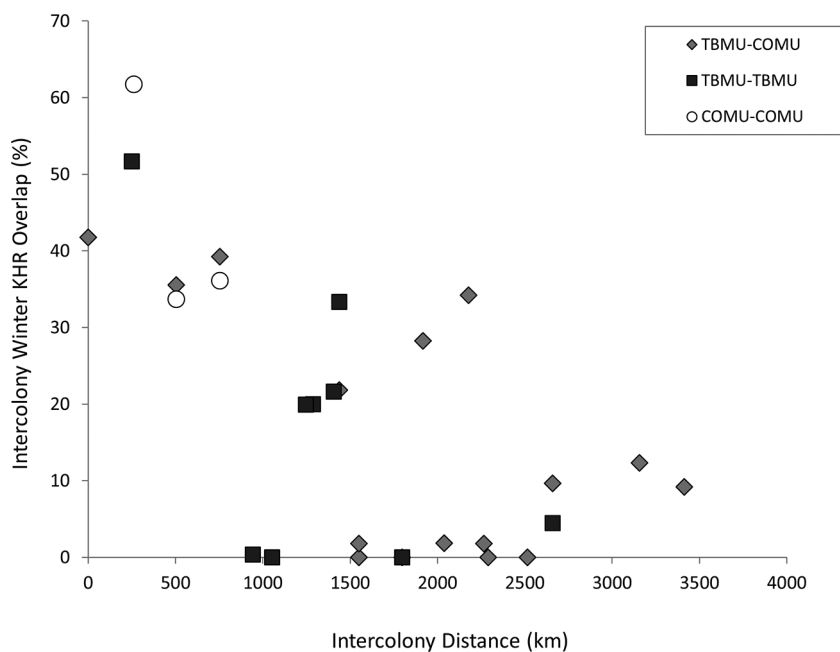
Note: Both interspecific and intraspecific pairwise comparisons are made, indicated by TT (Thick-billed Murre colonies), TC (Thick-billed Murre and Common Murre colonies), and CC (Common Murre colonies). T* and C* indicate Thick-billed Murres and Common Murres, respectively. GLS, geolocation-immersion loggers.

Table 3. Amount (%) of individual 50% kernel home ranges (KHR) overlap within colonies of Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*).

Species	Colony	No. of individuals	Colony latitude	Percent individual KHR overlap (randomized)	
				Mean ± SD	Range
Thick-billed Murre	Prince Leopold	16	74°02'N	10±19	0–90
	Minarets	14	66°57'N	22±27	0–91
	Coats	21	62°53'N	23±22	0–100
	Digges	10	62°32'N	29±23	0–93
	Gannets	11	53°56'N	33±26	0–100
Common Murre	Gannets	14	53°56'N	36±27	0–100
	Funk	17	49°45'N	38±27	0–100
	Gull	13	47°16'N	44±29	0–99

Note: Data are based on a separate randomization (n = 10 000) in which core home ranges were paired at random for each colony.

Fig. 4. Overlap of kernel home ranges (50% KHR) of wintering areas in relation to intercolony distance (km) among and between Thick-billed Murres (*Uria lomvia*) (TBMU) and Common Murres (*Uria aalge*) (COMU).



neither to one another had more similar winter distributions (Fig. 4; general linear model (GLM), $F_{1,26} = 18.4$, $p < 0.001$, $R^2 = 0.5$). However, all colonies did not exhibit this pattern. For example, high core winter overlap occurred between Thick-billed Murres from the southerly Gannet Islands and the northerly Minarets Island (Table 2). This suggests that proximity of colonies is not the only determinant of winter distribution.

Nonbreeding environmental variables

Bathymetry

Thick-billed Murres occurred over significantly deeper water with a wider range of depths (1557 ± 76 m, mean \pm SE) than Common Murres (1217 ± 60 m, mean \pm SE; gamm, $n = 30\ 000$ | 168, $t = -2.01$, $p = 0.045$; Table 4). More variable depths also occurred among Thick-billed Murres from the Gannet Islands where both species occur ($n = 12\ 318$ | 42, $t = -2.01$, $p = 0.05$). Among colonies of Thick-billed Murres, bathymetry varied significantly (Fig. 5A), particularly during December and January (range 950–2360 m; Table 4). Temporally, the change from shallow to deep water (>500 m) occurred at different times among colonies of Thick-billed Murres (i.e., August–September for Prince Leopold, Minarets, Gannet islands vs. November–December for Coats and Digges islands), depending on seasonal movement (Fig. 5A). Most Thick-billed Murres occupied deepest waters in March and April prior to colony return (except for Prince Leopold; Fig. 5A). For colonies of Common Murres, bathymetry varied only during winter when birds from Gull Island occupied shallower waters than those from Gannet and Funk islands (gamm, $t = 2.5$, $p = 0.009$; Table 4, Fig. 5B). Temporally, Common Murres from Funk and Gannet islands had moved to deeper waters by September (Fig. 5B). Common Murres from Funk Island occupied deepest waters during spring.

Chlorophyll a

Thick-billed Murres occupied waters with very low CHL (mg/m³) during winter. Overall, Thick-billed Murres occupied waters with lower CHL than Common Murres (gamm; $t = -4.66$, $p < 0.001$; Figs. 5C, 5D), including at the Gannet Islands where both species occur (gamm, $t = -2.29$, $p = 0.02$). Seasonal variance in CHL was greater for Common Murres (Table 4). Within species, colony differences for Thick-billed Murres were significant between three groups: Coats–Digges–Prince Leopold islands vs. Minarets Island (gamm; $t = 2.17$, $p < 0.001$) vs. Gannet Islands (gamm, $t = 10.21$, $p < 0.03$; Fig. 5C, Table 4). Common Murres from the Gannet Islands wintered in areas with significantly higher CHL than those from Gull and Funk islands (gamm, $t = 3.33$, $p < 0.001$; Fig. 5D, Table 4). Temporally, nonbreeding waters for both species were lowest in CHL during December. CHL profiles were more variable for Thick-billed Murres: very low throughout November–February except for birds from the Gannet Islands and at a maximum during April, May, or September, depending on the colony of origin (Fig. 5C). Among Common Murres, CHL was significantly higher for birds from the Gannet Islands (gamm, $t = 3.3$, $p < 0.001$; Fig. 5D), and temporal patterns were the same for all colonies: lower from September through February, while reaching a maximum in early April.

Water temperatures

Nonbreeding water temperatures (°C) encountered by Thick-billed Murres were significantly colder overall (4.4 ± 0.7 °C) with larger SD than for Common Murres (6.4 ± 0.2 °C; gamm, $t_{[81,22815]} = -5.6$, $p < 0.001$; Table 2, Figs. 5E, 5F). Likewise during winter only, temperatures were colder for Thick-billed Murres (3.3 ± 0.4 °C) than for Common Murres (4.5 ± 0.3 °C; $t_{[80,5219]} = -2.68$, $p = 0.009$). Water temperatures did not vary between the species from the Gannet Islands. Within species, water temperatures were significantly different between all colonies of Thick-billed Murres except for Coats and Digges, whereas there were no significant temperature differences between colonies of Common Murres (Table 4).

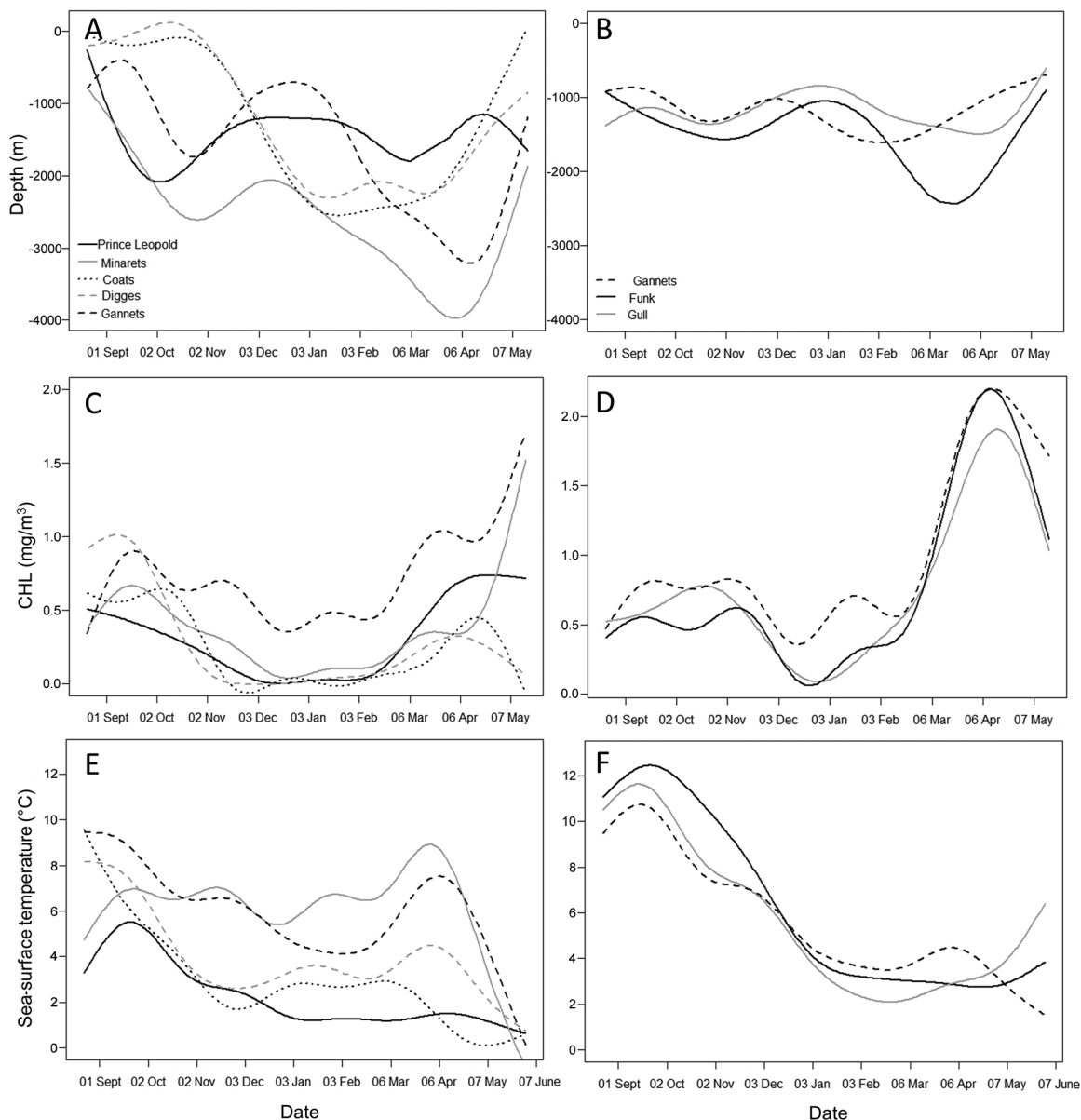
Table 4. Mean values of bathymetry, chlorophyll a (CHL), and water temperature for the overall nonbreeding period (September–April) and winter only (December–January) among species and colonies of Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*).

Species	Data period	Colony	N (observations individuals)	Bathymetry (depth) (m; mean \pm SE)	CHL (mg/m ³ ; mean \pm SE)	Water temperature	
						N (observations individuals)	Mean \pm SE (°C)
Thick-billed Murre	Nonbreeding	Overall	31 337 96	-1557±76 A 664±1410*	0.33±0.07 A 0.25±0.8*	14 621 55	4.4±0.7 A 1.6±2.7*
		SD (intercept+residual)*					
	Winter	Prince Leopold		-1405±295 A	0.02±0.01 A		1.6±0.4 A
		Minarets		-2361±320 B	0.06±0.01 A		6.0±0.4 B
		Coats	9 981 96	-2181±183 B	0.01±0.01 A	3 381 55	2.7±0.5 C
Digges		-2056±329 B	0.02±0.01 A		3.2±0.6 C		
Gannets		-954±284 C	0.41±0.01 B		4.9±0.5 D		
Common Murre	Nonbreeding	Overall	18 700 72	-1217±60 B 455±1282*	0.74±0.08 B 0.34±1.5*	8 194 28	6.2±0.2 A 0.01±3.8*
		SD (intercept+residual)*					
	Winter	Gannets		-1292±124 A	0.5±0.05 A		4.7±0.4 A
Funk		6 871 70	-1108±184 A	0.1±0.01 B	1 922 27	4.7±0.5 AB	
Gull			-812±167 B	0.3±0.04 B		4.2±0.5 AC	

Note: N is the total number of observations (i.e., environmental data linked to spatial location) and individuals for each generalized additive mixed model (gamm). Uppercased letters indicate significance between species overall (boldface and italic types) and within species groups for which statistical tests were run separately.

*Gamm variances, described as the SD of the intercept + residual, are used here to compare the extent of variation between species.

Fig. 5. Year-round (A, B) depth (m), (C, D) chlorophyll *a* (mg/m³), and (E, F) sea-surface temperature (°C) encountered by colonies of Thick-billed Murres (*Uria lomvia*) (left) and Common Murres (*Uria aalge*) (right). Data reflect environmental variables after controlling for individual variation (from generalized additive mixed models (gamm)).



Temporal variation of temperature profiles was also greater among colonies of Thick-billed Murres than Common Murres (Figs. 5E, 5F). Lowest water temperatures for all Thick-billed Murres occurred in May (as they moved back to northern colonies), but the timing of warmest temperatures varied substantially (March–September; Fig. 5E), depending on colony-specific spatial movements. In contrast, all colonies of Common Murres experienced similar changes in water temperature throughout the year, with steady declines until February and maximum temperatures during September (Fig. 5F).

Winter ice cover and night length

Mean (+SE) ice cover (N_CT) was higher and more variable in winter areas of Thick-billed Murres (1.5 + 0.038, interpreted as 15% ice cover) than Common Murres (0.06 + 0.009; lme, $F_{[1,13915]} = 32.35$, $p < 0.0001$; Table 5) and ice also varied significantly by colony (lme, $F_{[6,13915]} = 7.45$, $p < 0.0001$). Although Thick-billed Murres had greater frequency of ice cover >0, most GLS locations for both

species were not associated with ice (Fig. 6). Wintering areas (50% KHR) overlapped the leading ice edge for some Thick-billed Murre colonies (0%–32%), but not Common Murre colonies (Table 5).

Thick-billed Murres occupied winter areas with significantly longer nights (mean 15.9 h of darkness) than did Common Murres (mean 14.5 h; lme, $F_{[2,52]} = 31.9$, $p < 0.0001$) and had significant intercolony variation in night length (ranging from 14.6 to 17.1 h; lme, $F_{[3,28]} = 8.20$, $p = 0.0006$), whereas Common Murres did not (lme, $F_{[2,26]} = 1.11$, $p = 0.35$; Table 5).

Discussion

Ecological segregation

Using a comparative multiple-colony approach, this study demonstrates that ecological segregation among Thick-billed Murres and Common Murres occurred through spatiotemporal movement patterns, which are more variable in Thick-billed Murres. Thick-billed Murres occupied a wider range of latitudes than Com-

Table 5. Ice concentration (based on N_CT, from the International Egg Code, in percent ice cover), percent overlap of core winter ranges (50% kernel home ranges (KHR)) with ice cover (N_CT), and night length (hours of darkness) during winter (December–January) among species and colonies of Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*).

Species	Data period	Colony	Ice cover		KHR		Night length		Hours of darkness (mean ± SE)
			N (observations individuals)	Percent N_CT (variance)	N	Percent overlap	N (observations individuals)		
Thick-billed Murre	Winter	Prince Leopold	23 (15.4)	19	32.6	17.1±0.5 A			
		Minarets	0.4 (0.4)	12	0	na			
		Coats	28 (17.4)	32	14.8	15.9±0.4 B	905 28		
		Digges	21 (14.7)	10	18.2	15.5±0.5 C			
Gannets	1.0 (0.8)	12	0	14.6±0.6 D					
Overall			16 (11.8)	85	13.1	15.9±0.3 A	1773 54		
Common Murre	Winter	Gannets	0.2 (0.2)	19	0	14.6±0.1 A			
		Funk	0.6 (0.5)	16	0	14.5±0.1 A	868 26		
		Gull	1.0 (0.6)	16	0	14.5±0.1 A			
Overall			0.6 (0.4)	51	0	14.5±0.2 B	1719 52		

Note: N is the total number of observations (i.e., environmental data linked to spatial location) and total individuals for each linear mixed effects (lme) model (ice cover) or as the total number of observations (i.e., environmental data linked to spatial location) and individuals for each lme model (night length). Uppercased letters indicate significance between species overall (boldface and italic types) and within species groups for which statistical tests were run separately with respect to night length. na, not available.

mon Murres throughout the nonbreeding period, as well as during winter. This pattern was observed across the broad study area and was also evident among murres from the Gannet Islands where the species breed sympatrically. The pattern also emerges among Thick-billed Murres in Greenland and Svalbard, which show greater latitudinal movement and larger winter distributions compared with sympatric Common Murres from the same colony (Fort et al. 2013; Linnebjerg et al. 2013).

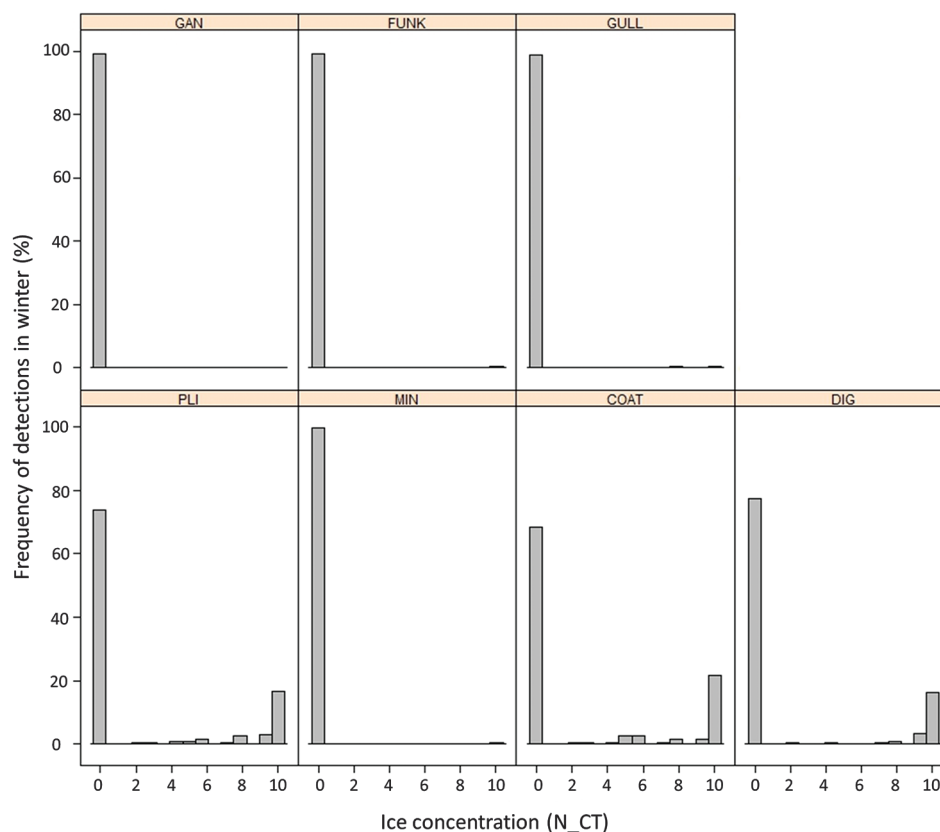
Analysis of GLS-derived latitudinal profiles was useful in describing patterns of temporal variation in colony-specific movement. This approach was slightly different than other studies that map static winter distributions for a colony overall (Fort et al. 2012, 2013; Linnebjerg et al. 2013; Ratcliffe et al. 2014) or that estimate latitude of water masses through isotopic profiling (Cherel et al. 2006; Phillips et al. 2009) in providing a good sense of timing of movement throughout the year for specific colonies. We were able to clearly demonstrate both inter- and intra-specific variations in the timing of movement through the study area (e.g., Figs. 2A, 2B). Two results from this analysis stand out: (1) the substantial range of latitudes used by Thick-billed Murres compared with latitudes used by Common Murres and (2) the fact that although colonies of conspecifics may overlap at a particular latitude (e.g., Thick-billed Murres at Prince Leopold, Coats, Digges; Figs. 3A, 3B), they may not do so at the same time of year and perhaps is reflective of colony-specific differences in migration strategy.

Core winter areas also revealed patterns of inter- and intra-specific segregation. Thick-billed Murres had more varied core winter areas than Common Murres, including in Baffin Bay, Davis Strait, the Labrador Sea, and the Orphan Basin–Grand Bank. In comparison, Common Murre had less variable movement strategies and high spatial overlap among colonies in a relatively restricted winter area on the Grand Bank and Orphan Basin. Less individual overlap among those from northerly colonies (Table 3) suggests that individuals from northerly colonies employ a larger range of strategies. Inter- and intra-specific overlap of core winter areas among colonies of Thick-billed Murres were equally low (15%); in contrast, overlap of core winter areas used by colonies of Common Murres was less between than within species (15% vs. 43%, respectively). Similarly, KHR overlap of individual Thick-billed Murres was lower but more variable by colony (ranging from 10% to 33%) than overlap of individual Common Murres (36%–44%). Further tracking research with devices such as GPS to determine fine-scale segregation of nonbreeding habitat would help discern whether patterns of intraspecific segregation occur among Common Murre colonies where spatiotemporal overlap was greatest.

Environmental variables

The winter conditions influencing murres varied significantly, dependent both on species and colony of origin. Bathymetry, CHL, water temperature, and other oceanographic variables help describe potential differences in foraging habitat and habitat use among marine birds and mammals (Walli et al. 2009; Andersen et al. 2013; Ratcliffe et al. 2014). Similar to latitudinal profiles, we used environmental profiles to describe the variance in winter habitat conditions across a wide range of nonbreeding habitat. Thick-billed Murres encountered a wide variety of environmental conditions in nonbreeding areas throughout the year. In contrast, Common Murres from different colonies encountered similar environmental conditions and appeared to concentrate, and potentially specialize, on a habitat that was only variable due to seasonal fluctuation (e.g., increased CHL in spring) rather than due to intercolony differences in spatial movement. Compared with Common Murres, Thick-billed Murres occupied deeper, colder waters with less CHL. Thick-billed Murres were more likely than Common Murres to encounter ice, although association with ice was not as strong as expected (Gaston 1980), with those from

Fig. 6. Histograms indicating frequency of detections of data from geolocation-immersion loggers (GLS) associated with concentrations of ice (N_{CT} , which range from 0 (no ice) to 10 (maximum ice); see Materials and methods) in winter (December and January) for colonies of Thick-billed Murres (*Uria lomvia*) (Prince Leopold (PLI), Minarets (MIN), Coats (COAT), Digges (DIG), Gannets (GAN)) and Common Murres (*Uria aalge*) (GAN, FUNK, GULL).



the Gannet and Minarets islands remaining well out of range of ice year round. This may partly reflect changing patterns in ice associations over time (Gaston and Robertson 2010). Thick-billed Murres encountered winter temperatures ranging from 2 to 8 °C; yet in spring, Thick-billed Murres from the Gannet and Minarets islands were recorded in warm Gulf stream waters (up to 15 °C) off the Flemish Cap. It would appear that Thick-billed Murres have greater potential for adjusting to a variety of habitats and environments than do Common Murres. This may also reflect differences between the murre species in prey preference, as well as in adjusting to differences in prey migrations and seasonal concentrations of abundant prey. As climate change alters and reduces the distribution and extent of Arctic winter ice cover, at the same time causing seasonal mismatches, shifting isotherms, and associated prey assemblages (Buren et al. 2014), it will be critical to understand tolerance in habitat use and how competitive interactions may be influenced by changes in available winter habitat.

Implications of winter strategy

In addition to moult and migration, seabirds that remain at high latitudes are challenged by increased energetic requirements during the cold months of the North Atlantic winter (Grémillet et al. 2005; Fort et al. 2009). This “energetic bottleneck” coincides with a decrease in available daylight hours during the northern hemisphere winter. Reduction in available daylight is particularly important to Thick-billed Murres, which wintered in areas with longer nights (Table 5). Since murre foraging is reduced and less efficient in the dark (Regular et al. 2010), Thick-billed Murres likely must increase foraging effort to meet energetic requirements during the critical winter period. The location of core winter areas, and the extent to which seabird species and popula-

tions mix at these, are therefore critical to understanding winter survival.

Competition can be a major determinant of the diversity of strategies among individuals within a population (Svanbäck and Bolnick 2007), allowing more room for individual variation and (or) specialization. For Thick-billed Murres, rather than a complete divergence of winter ecological niche from Common Murres, we found a “widening” of an overlapping ecological niche through increased diversity in movement strategy and winter areas. This strategy would mitigate inter- and intra-specific competition. Not only was this pattern of greater variation in Thick-billed Murres found when comparing colonies spanning a wide latitudinal range (i.e., from High to Low Arctic regions), but it was also evident between the species breeding sympatrically at the Gannet Islands. Thick-billed Murres tracked from Bjørnøya, Svalbard, also wintered in a broad area of the North Atlantic, compared with sympatric Common Murres that wintered in a restricted area within 1000 km of breeding colonies (Fort et al. 2013). Similarly, Thick-billed Murres tracked from Kitsissut Avaliit, Greenland, had a larger, more southerly distribution off the coast of Greenland than their Common Murre counterparts (Linnebjerg et al. 2013). Therefore, we suggest that an “increased variation strategy” is one generally adopted by Thick-billed Murres. This functionally decreases migratory connectivity (i.e., how many individuals from breeding colonies migrate to common wintering grounds) both within and among colonies. But why was habitat partitioning indistinct among Common Murres from different colonies, whose core winter overlap was greater than for most Thick-billed Murre colonies, and for which migratory connectivity within and among colonies was high? It may be that

Common Murres in the Northwest Atlantic do not partition habitat from conspecifics at a large scale, perhaps due to relaxed competition where resources are abundant (i.e., the Grand Bank of Newfoundland) or perhaps due to fixed and highly conservative habits restricting migration mobility (e.g., see Fort et al. 2013; Linnebjerg et al. 2013), habitat preference, or diet. Conversely, they may partition at a smaller scale to make up for broadly overlapping habitat. Further tracking using fine-scale GPS devices may uncover local-scale interactions among Common Murres. We did not test for partitioning in three-dimensional space (e.g., dive depth or daily activity patterns), which can effectively partition habitat between competing conspecifics (Hull 2000; Masello et al. 2010; Linnebjerg et al. 2013). Additionally, the role of increased diet partitioning (studied through isotopic analyses) in areas where spatial overlap is high will be helpful in describing smaller scale ecological partitioning. For example, Barger and Kitaysky (2012) documented increased segregation of Thick-billed Murre and Common Murre foraging niches in years of food shortage, when interspecific competition was likely elevated. More detailed research on inter- and intra-specific trophic associations is currently being pursued.

The greater phenotypic and (or) behavioural plasticity of movement strategies among Thick-billed Murres could allow rapid, flexible adjustment (de Jong 1995; Svanbäck and Bolnick 2007; Reed et al. 2009) to seasonal changes in the environment (e.g., ice conditions, shifting isotherms), to the presence of competitors (i.e., other diving alcids) that influence available habitat, and to anthropogenic influences (McFarlane Tranquilla et al. 2013). Indeed, such phenotypic plasticity may have originally played a role in character displacement and divergence (Pfennig and Pfennig 2012) of Thick-billed Murres and Common Murres.

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