ECOLOGICAL SEGREGATION OF MURRES (*URIA LOMVIA, URIA AALGE*) DURING THE NONBREEDING SEASON IN THE NORTHWEST ATLANTIC OCEAN

by

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ABSTRACT

When resources are limited and similar species co-occur, ecological segregation is likely to occur year-round, through spatial, temporal, behavioural and/or dietary segregation. This study investigates year-round ecological segregation between partially sympatric, congeneric Thick-billed Murres *(Uria lomvia*) and Common Murres (*Uria aalge*). In the Northwest Atlantic, the species exhibit a latitudinal divergence in breeding distributions. However, both winter in Low Arctic regions, where the potential for spatial overlap is greater than during the breeding period. Given the inaccessibility of murres at sea, the inter- and intra-specific interactions of murres wintering in the Northwest Atlantic have not been previously studied.

Using tracking devices and isotopic analyses, this study integrates spatial and temporal movements during the nonbreeding period, relative overlap of winter habitat, and trophic positions during the nonbreeding period. Thick-billed and Common Murres remained partially segregated throughout the year, with some overlap among particular colony groups. Thick-billed Murres moved over a broad range of latitudes throughout the year, had varied core wintering locations, encountered variable environmental conditions, made variable seasonal movements, and had broad trophic positioning. In comparison, Common Murres concentrated and converged on more narrow wintering areas, where colonies had high spatial overlap, encountered similar environmental conditions with consistent temporal patterns, and occupied similar trophic positions. Habitat segregation occurred mostly spatially; but where spatial overlap was greater, inter-specific dietary segregation increased. Most individual murres (both species) exhibited consistent wintering strategies across 2-3 years, with a few individuals shifting habitats between years. Variation in winter movement patterns stemmed more from between-individual variation (particularly among Thick-billed Murres) than from annual changes within individuals.

Ecological segregation is expressed through more varied movement, habitat use, and diets of Thick-billed Murres, resulting in a wider ecological niche that is related both to the range of available habitat and prey, and to inter-specific competitive interactions with Common Murres. Relative connectivity among species and colonies at wintering sites also has implications for overall population vulnerability to spatially-discrete risks or wintering conditions, which will be greater for the relatively concentrated Common Murres than for more dispersed Thick-billed Murres.

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CHAPTER 1 - INTRODUCTION AND OVERVIEW

1.1 ECOLOGICAL SEGREGATION

A central tenet of evolutionary theory is that competition for finite resources promotes ecological segregation (Diamond 1978, Svanbäck and Bolnick 2007, Pfennig and Pfennig 2012). Species are distributed in proportion to the abundance of resources critical to their survival (MacArthur and Levins 1964). Where species overlap and compete for resources, ecological diversification occurs (Svanbäck and Bolnick 2007, Reifova et al. 2011), often through character displacement and niche separation (Diamond 1978, Reifova et al. 2011). Species may segregate ecologically through diversity in range and distribution, body size, morphology, physiology, and behaviour (MacArthur and Levins 1964, Bédard 1969, Masello et al. 2010, Navarro et al. 2013). Over time, selection for divergent characteristics can facilitate reproductive isolation and speciation.

Among sympatric species with similar morphology and habitat preferences, inter- and intra-specific competition is reduced by niche partitioning (Grémillet et al. 2004, Bailleul et al. 2005, Forero et al. 2005, Cherel et al. 2007, Pfennig et al. 2007, Holt 2009, Phillips et al. 2009). Such partitioning can occur in multiple dimensions, but usually along the three main axes of space, time, and diet (Holt 2009, Thiebot et al. 2012, Navarro et al. 2013). Although species are adapted to particular niches, this does not completely preclude competition for dynamic resources. Between particular species, the degree to which ecological partitioning is necessary can change with prey availability or seasonal food requirements (Breed et al. 2006), and can be adjusted through flexible behaviours (Pfennig et al. 2007, Barger and Kitaysky 2011), that can diversify (Svanbäck and Bolnick 2007) or specialize (Bolnick et al. 2002) resource use among competitors. Where geographic ranges overlap, ecological partitioning among sympatric populations can be more obvious than among allopatric populations of the same species (Diamond 1978, Reifova et al. 2011), demonstrating phenotypic plasticity in responses to competition. Niche variation within and between populations can therefore be

supported by genetic, phenotypic, and behavioural changes (Svanbäck and Bolnick 2007, Agashe and Bolnick 2010).

1.2 SEGREGATION IN THE MARINE ENVIRONMENT

In the marine environment, patterns of ecological segregation provide insight into the processes connecting marine animals with each other and with their habitat. Yet, owing to the dynamic nature of marine ecosystems, patterns of habitat use among marine animals are complex. Broad-scale patterns in the ocean are determined by fluid dynamics, creating patterns of patchiness and aggregation (Levin 1994). Heterogeneity in oceanographic features thus determines the distribution of resources, which in turn, determine the distribution of marine predators such as seabirds and marine mammals. However, not all species or populations respond similarly to dynamic oceanographic features (Kitaysky and Golubova 2000, Hyrenbach et al. 2002). Where particular oceanographic features aggregate prey, foraging guilds of oceanic seabirds (e.g. surface feeders, plunge-divers, pursuit-divers) segregate in the marine environment to exploit the distinct prey assemblages to which they are adapted. Within seabird foraging guilds, resource competition drives further habitat segregation and specialization for specific prey niches (Bédard 1969, Gaston and Jones 1998). Species may segregate ecologically by differences in size, morphology and/or behaviour (e.g. in spatial or temporal foraging patterns; MacArthur and Levins 1964, Bédard 1969, Bailleul et al. 2005). Among congeneric species highly similar in distribution, morphology and diet, spatial and temporal habitat partitioning becomes the expected strategy (Masello et al. 2010). Spatial arrangements of seabirds and prey are also complicated by factors operating at hierarchical scales (Huettmann and Diamond 2006), from large-scale oceanic and global weather processes, to local-scale ecological interactions such as enhancement, competition and predation (Fauchauld and Tveraa 2006, González -Solis and Shaffer 2009). Seabirds locate food at sea through processes operating at different

scales, from large-scale spatial memory of predictable resources, to small-scale local enhancement cues from multispecies aggregations that enhance the visibility of subsurface prey (Hunt 1990, Weimerskirch 2007, Fauchauld 2009). In local enhancement, predators take cues from each other to better locate subsurface food patches at sea (Hunt 1990, Davoren et al. 2003, Grunbaum and Veit 2003), and to facilitate prey capture (eg. when surface-feeding seabirds gain access to fish driven into upper water column by subsurface predators; Hunt 1990, Davoren et al. 2010). Multispecies aggregations are common (Hunt 1990), yet their benefits are offset by the density-dependent instability of the spatial interactions between predator and prey, and by disruptive or interference competition between predators at smaller scales (Davoren et al. 2003, Gremillet et al. 2008, Fauchauld 2009). Both of these can cause a spatial mismatch in the distributions of predators and prey, despite prey being abundant in particular areas (Hunt 1990, Gremillet et al. 2008, Fauchauld et al. 2009). Resoundingly, scale is a critical variable in defining and detecting interactions between seabirds, their prey, and their competitors (Hunt 1990, Huettmann and Diamond 2006, Fauchauld et al. 2009). Furthermore, physiological and behavioural mechanisms, migration strategies, and demographic patterns within populations (e.g., colony, age, or sex) can structure patterns of habitat use (Esler 2000, Hyrenbach et al. 2002, Webster et al. 2002, Breed et al. 2006, González-Solis et al. 2007) and movement and foraging strategies can be varied and flexible (Oedekoven et al. 2001, Phillips et al. 2005, Regular et al. 2008). Thus it becomes difficult to generalize when discussing ecological relationships between and within species. Study of congeneric, sympatric species allows insight into ecological segregation in the marine environment, while minimizing any complications associated with differences of habitat, lineage and foraging guild.

1.3 SEABIRD SPATIAL ECOLOGY

The spatial ecology of marine animals has been under scrutiny recently due to the persistent increase of threats to marine ecosystems worldwide (Halpern et al. 2007), particularly industrial fishing (Furness 2003, Pauly et al. 2005), marine oil pollution (Montevecchi et al. 2012) and climate change (Edwards and Richardson 2004, Cheung et al. 2010). As sentinels of the marine environment (Davoren and Montevecchi 2003, Iverson et al. 2007), seabird marine habitat associations can be critically informative of biological and physical information, including climate-driven oceanic processes and changes in food web assemblages (Hunt et al. 1990, Ainley et al. 1996, Montevecchi and Myers 1997, Hyrenbach and Veit 2003, Montevecchi 2007, Gaston et al. 2010). Understanding how marine communities use and interact with their environment is needed to predict, respond to, and to mitigate marine ecosystem changes (Jenouvrier et al. 2009).

The depth of information to be gleaned from patterns of seabird marine habitat use, combined with the complexity of how marine animals interact with their dynamic environment, has driven an explosion of research on seabird spatial ecology in recent years (González-Solís and Shaffer 2009, Tremblay et al. 2009), facilitated by rapid advances in tracking technology (Burger and Shaffer 2008, Wilson and Vandenabeele 2012) and chemical (isotope) analyses (Cherel et al. 2006, 2007, Phillips et al. 2009). Previous assessments of seabird habitat use have involved at-sea surveys and band returns, which are limited by observer encounter rate, and can only describe coarse-scale populations/habitat associations. In contrast, the year-round tracking of individuals allows greater insight into processes governing animal movement (Phillips et al. 2006, Shaffer et al. 2006, Kubetzki et al. 2009), individual decisions (Oppel et al. 2009), and how year-round movement strategies influence individual fitness and survival (Daunt et al. 2006, Frederiksen et al. 2008, González-Solis and Shaffer 2009, Fort et al. 2013). In particular, studying individuals identifies migration routes and location

of wintering grounds, which may vary substantially among and between individuals. Migratory connectivity (i.e. the extent to which individuals from the same breeding area or population migrate to the same nonbreeding area; Esler 2000) has implications for demographic independence of subpopulations, as segregation on wintering grounds may support genetic structure among subpopulations (Webster et al. 2002, Friesen et al. 2007). As well, the extent to which sub-populations mix in wintering areas influences population sensitivity to environmental conditions (Frederiksen et al. 2011), particularly when carry-over effects from one season can impact performance in the next (Marra et al. 1998, Webster et al. 2002, Sorensen et al. 2009, Harrison et al. 2011). Hence, the degree of segregation of breeding populations on wintering grounds is critical for understanding community- and population-level responses to ecological and environmental processes (Esler 2000, González-Solis et al. 2007, Frederiksen et al. 2011), and for developing comprehensive conservation and management approaches.

1.4 LIFE AT SEA DURING THE NONBREEDING PERIOD

Seabirds are extremely well-studied while at land-based breeding colonies. In contrast, studies of birds at sea have been much more challenging and patterns of habitat use and ecological segregation during the nonbreeding period are not well understood. At the colony, habitat partitioning has been well documented when breeding seabirds are central-place foragers, competing for resources within the colony's foraging range (Ashmole 1963, Monteiro et al. 1996, Masello et al. 2010). 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. Yet marine resources are patchily distributed, and ocean hotspots 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). In these areas, competition for resources is likely to persist; but is complicated by scale- and density-dependent relationships between predators, competitors, and prey (Hunt 1990, Davoren et al. 2003, Fauchauld 2009, Drew et al. 2013). How inter- and intra-specific interactions might also shape the marine distribution of species and populations from particular colonies is not well understood.

Research on ecological segregation for 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 Antarctic seabirds of the Southern Atlantic and Indian Oceans, where sympatric Procellariiforms (albatrosses, petrels) and penguins (King Penguin *Aptenodytes patagonicus*, Rockhopper Penguin *Eudyptes chrysocome filholi* and Macaroni Penguin *E. chrysolophus*) from Antarctic colonies exhibit species-specific nonbreeding strategies by segregating into different water masses of the Antarctic Circumpolar Current, and targeting different diets (Cherel et al. 2006, 2007, Phillips et al. 2009, Thiebot et al. 2012). Winter spatial and diet segregation by sex also occurs in some species (Phillips et al. 2005, Jaeger et al. 2009). Very few studies have compared nonbreeding segregation outside the Antarctic system.

Second, studies have taken a multi-colony approach to compare winter distributions among colonies of the same species, focusing primarily on intra-specific 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. For example, Cape Gannets (*Morus capensis*) from two neighboring colonies showed foraging segregation in both breeding and nonbreeding periods (Jaquemet et al. 2008). Cory's Shearwaters (*Calonectris diomedea*) from three breeding colonies showed preference for three major wintering sites but also substantial mixing (González-Solis et al. 2007). Northern

Gannets (*Sula bassana*) from five European breeding colonies had distinct wintering strategies, with convergence of some colonies on particular wintering areas and some mixing and overlaps among colonies (Fort et al. 2012a). Frederiksen et al. (2011) comprehensively described wintering areas of kittiwakes (*Rissa tridactyla*) from 19 colonies in the North Atlantic with a similar result: some distinct wintering strategies between colonies with broad convergence on a few important wintering areas. The extent to which populations depend upon and partition important wintering areas (Croxall et al. 2005, González -Solis et al. 2007) also carries important evolutionary, ecological and conservation implications. 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 research approaches have broadly overlapping similarities in describing how inter- and intra-specific interactions may shape marine habitat use in the marine environment. Yet to my knowledge, no studies have combined these two approaches. Integrating an understanding of inter- and intra-specific segregation, across the nonbreeding range of multiple colonies, will be the primary focus of this thesis.

1.5 STUDY SPECES: THE MURRES (URIA)

Ecological segregation among nonbreeding seabirds in Northwest Atlantic has been poorly studied to date. Among the most significant consumers of marine resources in this region are the abundant populations of Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*). These species are closely-related, occupy a similar ecological niche as pursuit-diving piscivores, and likely share overwintering habitat to some degree (Gaston and Hipfner 2000, Ainley et al. 2002), making them excellent

candidates for a study of ecological segregation (Bédard 1969).

Thick-billed Murres and Common Murres (Figure 1.1) are auks, a family that is confined to the northern hemisphere. They are specialized in underwater swimming by wing-propulsion and exploit subsurface ecological niches which are relatively free from competition from other avian groups (Tuck 1961, Bédard 1969, Gaston and Jones 1998). These circumstances have allowed considerable adaptive radiation within the auk family, particularly in the traits of body size and bill morphology, likely in response to inter- and intra-specific competition for food (Bédard 1969). Thick-billed and Common Murres share partially overlapping, circumpolar distributions throughout the year (Tuck 1961, Irons et al. 2008; Figure 1.2). Because the two species are primarily deep-diving piscivores, and are morphologically and ecologically very similar, 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, blennies) and zooplankton (for which their tongue and palate are better adapted; Bédard 1969), whereas Common Murres consume predominantly shoaling fishes (e.g. capelin, sandlance) with a small proportion of invertebrates (Gaston and Jones 1998). How overall diet patterns are influenced by competitive interactions (Birkhead and

Figure 1.1. Thick-billed and Common Murres breeding sympatrically on the Gannet Islands, Labrador.

Nettleship 1987a,b,c, Barrett et al. 1997, Barger and Kitaysky 2011), and how this may change with season (Elliot et al. 1990, Moody and Hobson 2007), requires further investigation.

Thick-billed Murres breed at high latitudes completely within the Arctic and cold water regions, north to 82^{o}N latitude and bounded to the south by the 5^{o}C isotherm (Tuck 1961, Nettleship and Birkhead 1985, CAFF 2004; Figure 1.3). In comparison, Common Murres breed in mid- to low Arctic areas, north to 76^{o}N, with 75% of the world population breeding in low Arctic and cold water regions (Nettleship and Birkhead 1985, CAFF 2004), bounded to the south by the 15^{o}C-20^{o}C isotherms (Tuck 1961, Nettleship

Figure 1.2. Distribution and size of Thick-billed and Common Murre colonies in the circumpolar countries. *From Irons et al. 2008*

and Evans 1985). Generally, Thick-billed Murres are considered the "cold-water"species and Common Murres the "warm-water" equivalent (Tuck 1961). Distribution of breeding colonies overlaps extensively in the North Pacific, but is more segregated in the North Atlantic, between the Barents Sea and the Northeast Atlantic, and in the Canadian Arctic vs. the Northwest Atlantic (Figure 1.3). At colonies where the species breed sympatrically, inter-specific competition for food and breeding sites is expected to be high, and mitigated by varied strategies of breeding phenology, diurnal activity,

foraging, and prey selection (Bédard 1969, Birkhead and Nettleship 1987 a,b,c). Yet in some cases, ecological segregation at sympatric colonies is not evident (Barrett et al. 1997, Gaston and Jones 1998, Bryant and Jones 1999). This does not mean that competition and segregation does not occur, but rather that ecological segregation is complex, often occurring over multiple dimensions (e.g. in 3-dimensional space, including dive depth and temporal activity patterns; Masello et al. 2010) and potentially dependent on local resource abundance (Barger and Kitaysky 2011).

1.5.1 Murre Winter Ecology

While relatively well-studied during breeding, patterns of ecological segregation among *Uria* during the winter is not known. How *Uria* may segregate in patterns of movement, spatial distribution, and trophic position during the nonbreeding period, when many of the populations of Thick-billed and Common Murres may be more aggregated, is the primary focus of this thesis.

Current knowledge of *Uria* migratory movement and winter distribution has been gleaned from decades of banding recoveries (particularly from hunting), mortality events and at-sea surveys (Tuck 1961, Gaston 1980, Nettleship and Birkhead 1985, Kampp 1988, Elliot et al. 1990, Donaldson et al. 1997, Ainley et al. 2002, Gaston and Hipfner 2000, Lyngs 2003, Bakken and Mehlum 2005, Gaston and Robertson 2010, Reynolds et al. 2011). Thick-billed Murres from eastern Canada, western Greenland, Svalbard and Iceland overwinter in the Labrador Sea, concentrating off eastern Newfoundland (Kampp et al. 1988, Gaston and Jones 1998, Lyngs 2003), and in smaller numbers south to Georges Bank (Gaston and Hipfner 2000). Some Canadian Thick-billed Murres also winter in coastal areas of SW Greenland (Tuck 1961, Lyngs 2003). To some extent, Thick-billed Murres segregate in winter areas according to colony, age and sex

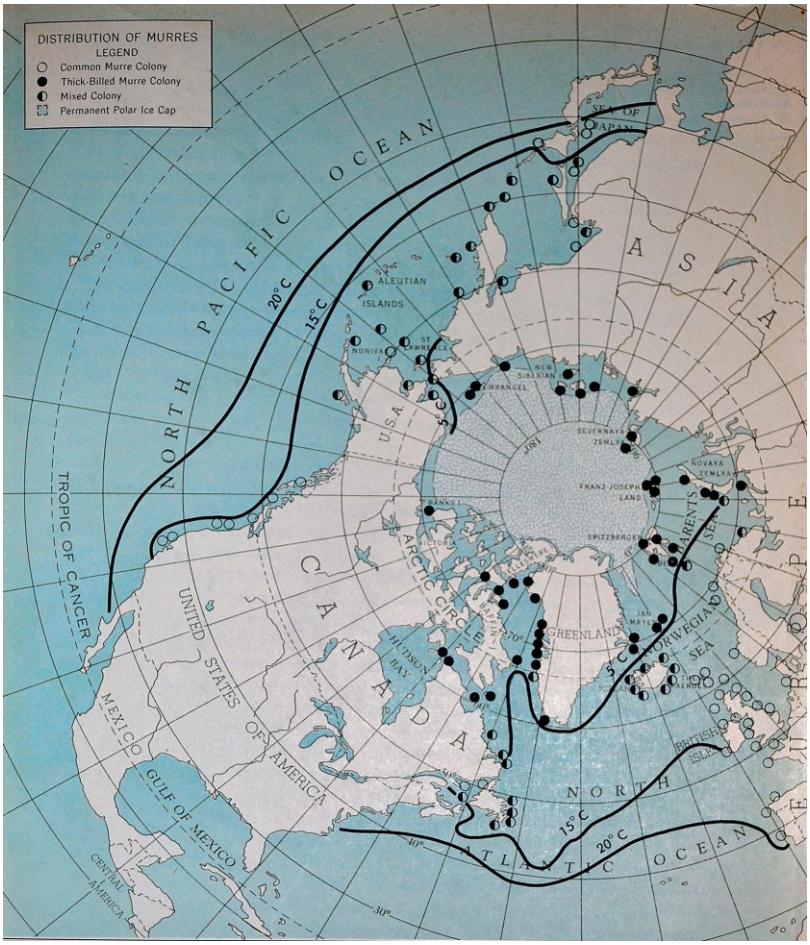

Figure 1.3. Breeding distribution of murres in relation to August surface isotherms. *Figure 5 from Tuck 1961*

(Tuck 1961, Gaston 1980, Kampp 1988, Donaldson et al. 1997, Lyngs 2003, Bakken and Mehlum 2005), though how these factors influence patterns of segregation are not well known. Post-breeding migration between August – October (depending on location; Brown 1985) is poorly described. Year-round ranges in the north are occupied in winter only as ice conditions permit, and seaward limits of distributions are speculative (Gaston and Hipfner 2000, Gaston and Robertson 2010). Long-term trends in the retraction of Arctic sea ice cover (Bates et al. 2008) might reduce the necessity for long distance migration in winter and may have recently influenced winter distribution of Thick-billed

Murres such that fewer are killed in the coastal Newfoundland murre hunt (Gaston and Robertson 2010). In comparison, Common Murres from the Northwest Atlantic winter offshore (on the Grand Banks), south to the Scotian Shelf and Georges Bank (Gaston and Jones 1998). Common Murres from other populations are not known to migrate to Canadian waters (Tuck 1961, Lyngs 2003). Common Murres disperse from breeding colonies from August – September (Tuck 1961, Ainley et al. 2002). Similar to Thick-billed Murres, spatial use of wintering areas by Common Murres may be partly structured by colony and age (Reynolds et al. 2011), but there is no research comparing winter distribution patterns within and among Common Murre populations. Both species rely heavily on the Grand Banks as a moulting area (Huettmann and Diamond 2000, Gaston and Hipfner 2000). Colony-specific details on migration and winter habitat are recently known for just a few populations (Gaston et al. 2011, Hedd et al. 2011).

Given that both species overwinter in frigid low Arctic regions in the Northwest Atlantic, bounded to the north by developing ice conditions and to the south by warmer waters of the Gulf Stream, the potential for inter-specific spatial overlap and the pressure for niche divergence during winter may be greater than during the breeding period. Adding pressure, overwintering in the harsh conditions of the Northwest Atlantic is energetically demanding, requiring increased foraging effort (Fort et al. 2009). As well, many other seabirds converge 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), kittiwakes (Fredericksen et al. 2011), Dovekies (Mosbech et al. 2012, Fort et al. 2012b).

Though migratory connectivity among breeding colonies of the murres is not well documented, it is a key factor influencing their evolutionary ecology. Shared wintering areas could facilitate the inter-mixing of murre populations; indeed, Atlantic breeding populations are not genetically distinct and likely have moderate levels of genetic exchange (Birt-Friesen et al. 1992). The population impact of conditions encountered on the wintering grounds depends on the extent to which species and

subpopulations converge (Esler 2000, Webster et al. 2002, Phillips et al. 2009), yet current knowledge of murre winter distribution is insufficient to understand links between habitat use and environmental conditions (Webster et al. 2002). Patterns of movement and distribution during the nonbreeding period are thus essential for interpreting the importance of wintering areas and the biological response to threats and challenges that murres encounter in the marine environment (Suryan et al. 2006, Croxall et al. 2012). The extent of connectivity between breeding and wintering areas, for multiple colonies of Thick-billed and Common Murres, will be explored in this thesis.

1.6 RESEARCH APPROACH AND THESIS OBJECTIVES

To determine patterns of ecological segregation in the congeneric *Uria*, the objective of this thesis is to engage three aspects of the ecological niche: time, space, and diet (cf. Theibot et al. 2012). I apply bird-borne tracking technology and stable isotopic analyses to better understand the winter relationships of these two very similar congeneric species. I expect that competitive and environmental pressures during winter sustain continued pressures for niche separation. By identifying and comparing winter movements and distribution, I expect to identify (1) niche separation though patterns of space, time, and/or diet; (2) patterns of migratory connectivity between and within colonies; and (3) increased competition and niche partitioning in areas with greater inter-specific spatial overlap.

To do this, spatio-temporal distribution patterns are compared between and within species, colonies, and individuals, using bird-borne tracking devices (geolocation loggers; Phillips et al. 2004) to follow the year-round movements of free-ranging birds. Additionally, analyses of stable isotopes in murre blood and feathers (Hobson and Clarke 1993, Cherel et al. 2000) provide insight into the trophic (dietary) associations of the species through the year. The strength of this approach is in the improved insights afforded by integrating spatial, temporal, and dietary information, at different levels of

species and population organization across multiple years, and in both allopatric and sympatric parts of their range, to help interpret patterns of ecological segregation. This research will be used to inform the following hypotheses: that 1) species differ in wintering strategy; 2) intra-specific segregation occurs to some degree, with colonies showing distinct wintering strategies; 3) inter-specific segregation in wintering areas is most pronounced among sympatrically-breeding species and 4) individual movement and wintering strategies is consistent across years.

1.6.1 Study Area

Through collaborative research (see section 1.8), this study samples and tracks Thick-billed and Common Murres from colonies spanning 28^{o}N latitude from low to high Arctic regions in eastern Canada Thick-billed Murres were tracked from five colonies: Prince Leopold Island (74°02'N, 90°00'W, 2008-10) in the Canadian High Arctic; the Minarets on Baffin Island (66°57'N 61°50' W, 2007-08); Coats Island (62°53'N, 82°00'W, 2007-10) and East Digges Island 62°32'N, 77°45'W, 2008-10) in Hudson Bay, Nunavut; and Gannets Islands, Labrador (53°56'N, 56°32'W, 2008-11). Common Murres were studied at three colonies spanning ~6^{o} of latitude: Gannet Islands, Labrador (2008-11), where they overlap in breeding distribution with Thick-billed Murres; Funk Island (49˚45'N, 53˚11'W, 2007-11) and Gull Island (47°16'N, 52°46'W, 2007-2011) in Newfoundland (Figure 1.4).

The broad distribution of breeding colonies means that murres tracked in the nonbreeding (winter) period intersect with several marine regions, including Baffin Bay and Davis Strait; Hudson Bay and Hudson Strait; Labrador Sea, Labrador Shelf and Newfoundland Shelf; the Orphan Basin, Flemish Cap, and Grand Banks of Newfoundland. These regions in the Northwest Atlantic are characterized by southward flow of cold, low-salinity waters of the Labrador Current from the north, and the northward flow of warm, high-salinity Gulf Stream waters from the south. The

confluence of the two currents near the Grand Banks of Newfoundland creates highly productive marine conditions for foraging marine predators.

1.7 THESIS GOAL AND ORGANIZATION

The goal of this thesis is to investigate ecological segregation between congeneric murre (*Uria* spp.) from eastern Canadian colonies, during the nonbreeding period. Inter- and intra-specific comparisons are used to assess mechanisms that support ecological segregation and niche divergence. Research will inform the following five themes in a step-wise fashion:

1) *Patterns of ecological segregation* - Chapter 2 takes a large-scale approach, examining year-round patterns of distribution and habitat, inter- and intra-specific overlap of core winter habitat, and degree of segregation between species and among colonies;

2) S*easonal movement strategies* - Chapter 3 subsets year-round distribution patterns to examine seasonal variation in patterns of habitat use, by species and colony, and includes details of timing and distance of nonbreeding movements;

3) *Individual repeatability* - Chapter 4 examines how successive annual movements of individual murres, can help explain variation in winter distribution; and how migratory mechanisms could shape ecological segregation;

4) S*patial and trophic associations* – Chapter 5 focuses on the interaction of spatial habitat use with trophic connections, particularly with reference to trophic segregation in areas of species overlap, and to seasonal trophic shifts;

5) *Implications for risk assessment* – Chapter 6 synthesizes the implications of murre winter spatial ecology, migratory connectivity, and ecological segregation in light of anthropogenic risk.

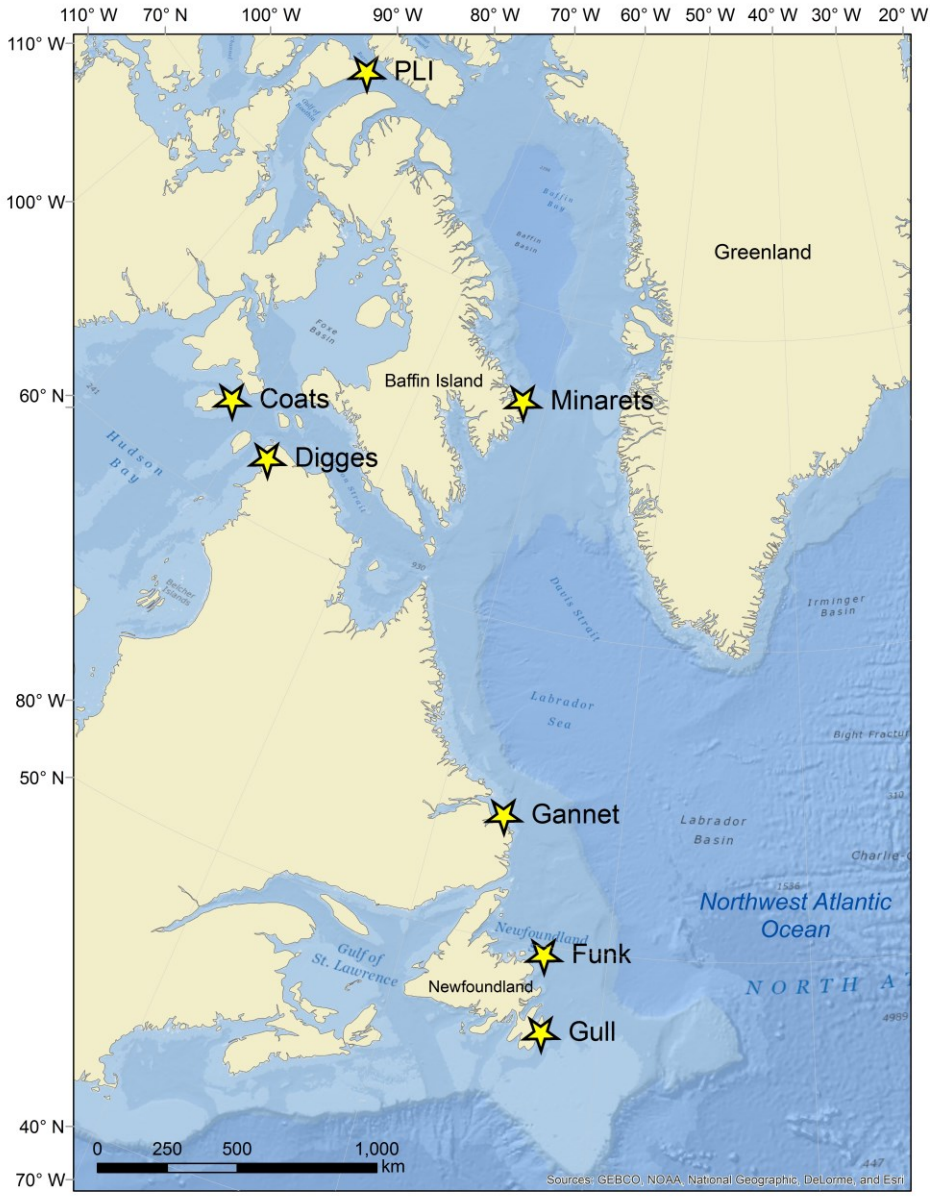

Figure 1.4. Northwest Atlantic study area and seven breeding colonies where Thick-billed Murres (Prince Leopold (PLI), Minarets, Coats, Digges, Gannet islands) and Common Murres (Gannet, Funk, Gull islands) were studied.

This thesis is organized in manuscript form: the introduction and conclusion chapters bound five manuscripts (Chapters 2-6), one of which has been published in a peer-reviewed journal (Chapter 6), with the remaining chapters in preparation. Each chapter begins with a point-form summary of main research findings. Because each manuscript is a self-contained unit destined for peer-review (required by MUN to appear as they will be published), there is some inevitable repetition in methods and literature cited sections, for which I extend my apologies to the reader. Repetition of methods which are similar across chapters is reduced by referring to Chapter 6 which has been published (Marine Ecology Progress Series 472:287-303). Formatting of tables and figures is consistent throughout the thesis. As required by Memorial University, Chapter 6 is presented as in its published form, with the exception that the abstract is formatted as a point-form summary to match other chapters.

1.8 CO-AUTHORSHIP STATEMENT

This thesis represents work from a five-year PhD project in the Cognitive and Behavioural Ecology Programme at Memorial University of Newfoundland. With support from the International Polar Year Program (2007-2008), this collaborative project was initiated by two principal co-investigators, William A. Montevecchi and Anthony J. Gaston, with partners at Environment Canada/Canadian Wildlife Service (Gregory J. Robertson, Grant Gilchrist) and the British Antarctic Survey (Richard A. Phillips). Funding, research proposals, and selection of field sites originated with these investigators and set the project in motion. Subsequent research questions specific to this thesis were developed through interaction of the author (LMT) with the thesis supervisor (WAM) and the thesis committee (April Hedd, Greg Robertson, Rodolphe Devillers). Additional contributions were made as follows:

i) design and identification of the research proposal:

WAM, AJG, GJR, AH, LMT

ii) practical aspects of the research:

Field data (GLS deployments and retrievals, blood and tissue samples) at seven colonies was championed by a host of field biologists (see also Acknowledgements), represented by AJG, WAM, AH, LMT, as well as Chantelle Burke, Kyle Elliot, Dave Fifield, Mark Mallory, Paul Regular, and Paul Smith. Field coordination was facilitated by LMT, Christine Eberle Dave Fifield, Grant Gilchrist, Greg Robertson, Regina Wells, and Sabina Wilhelm. GLS tracking data was downloaded and processed primarily by LMT (colonies at Prince Leopold, Minarets, Coats, Digges, Gannets, Funk, and Gull Islands), with help from A. Hedd (at Funk Island) and P. Smith (at the Minarets). Extensive technical advice for processing GLS data was provided by D. Fifield and R.A. Phillips. Environmental data collection and SST corrections performed by LMT (see methods sections) were possible through the support and programming knowledge of D. Fifield. Preparation of tissue samples for isotopic analyses was done by LMT, with assistance from MUN undergraduate students Dianna Brooks and Andrew Murphy.

iii) data analyses:

LMT performed all statistical analyses, with support, advice, and technical expertise from D. Fifield, G. Robertson, P. Regular, A. Hedd, R. Devillers and A. Buren.

iv) manuscript preparation:

LMT is the principal author of all chapters of this thesis, interpreted statistical results, wrote all text, and prepared all tables and figures (with help for some figures from P. Regular). Three photographs displayed in the thesis were taken by LMT. Thesis chapters were greatly improved by comments and revisions provided by W.A. Montevecchi, G.J. Robertson, A. Hedd, R. Devillers, P. Regular, D. Fifield, C. Burke, A.J. Gaston, R.A. Philips, and T. Diamond.

Coauthors above may apply to one or more chapters of this thesis and are identified as co-authors or contributors therein.

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CHAPTER 2 – ECOLOGICAL SEGREGATION AMONG CONGENERIC THICK-BILLED AND COMMON MURRES IN THE NORTHWEST ATLANTIC THROUGH THE NONBREEDING PERIOD

CHAPTER 2 – ECOLOGICAL SEGREGATION AMONG CONGENERIC THICK-BILLED AND COMMON MURRES IN THE NORTHWEST ATLANTIC THROUGH THE NONBREEDING PERIOD

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2.1. SUMMARY

1. Among seabirds, ecological segregation and habitat partitioning have been well documented at breeding colonies; but are not well understood during the nonbreeding period seabirds disperse from colonies. Yet, how overwintering seabirds move, compete and segregate in wintering areas is critical to understanding population processes.

2. This study demonstrates that ecological segregation between congeneric and partially-sympatric Thick-billed and Common Murres occurs during the nonbreeding period. The species exhibited spatial and temporal separation, providing a degree of segregation at both inter- and intra-specific scales.

3. Movements and distribution of Thick-billed Murres were more variable than those of Common Murres, and were characterized by a wider range of latitudes and environments, larger home ranges, and greater differences in seasonal timing of movements. These inter-specific differences were consistent at two scales: 1) among colonies spanning a wide latitudinal range, and 2) at a sympatric colony at the Gannet Islands. Thick-billed Murres from different colonies tended to follow similar movement patterns and segregate by latitude, while Common Murre colonies segregated very little. Colonies farther apart tended to overlap less, and segregation was greater and more variable among Thick-billed than Common Murres.

4. We hypothesize that owing to their greater phenotypic and behavioural flexibility in nonbreeding movements and habitat selection, Thick-billed Murres mitigate both inter- and intra-specific competition through widening of the ecological niche that overlaps with Common Murres.

2.2. INTRODUCTION

When resources are limited, sympatric and competing species are able to co-exist through ecological segregation (Lack 1945, Holt 2009). Sympatric species typically reduce inter- and intra-specific competition through dietary and habitat partitioning, often through varied patterns of space use, foraging activity and diet composition (MacArthur and Levins 1964, Phillips et al. 2009, Masello et al. 2010). The degree to which ecological partitioning is necessary between particular species can change with availability of food resources, and can be adjusted through flexible behavioural responses among competitors (Barger and Kitaysky 2011, Svanbäck and Bolnick 2007). As well, where geographic ranges overlap, ecological partitioning between sympatric populations can be more marked than in allopatric populations of the same species (Reifova et al. 2011). Thus ecological segregation can be viewed as a dynamic process where both phenotypic and behavioural plasticity play important roles in modifying the diversity of strategies employed for accessing resources, thereby reducing competitive interactions (Svanbäck and Bolnick 2005, Pfennig and Pfennig 2012).

Among seabirds, habitat partitioning during the breeding season is well documented. Seabirds at breeding colonies are central-place foragers dependent on the nearby waters for food that fluctuates seasonally and can be depleted under high predation pressure (Ashmole 1963, Monteiro et al. 1996). Differences in spatial distribution, prey choice, foraging behaviour, or diurnal activity schedules, can help mitigate intra-and inter-specific predation pressures and competition for resources (Wood et al. 2000, Grémillet et al. 2004, Gonzales-Solis 2007, Paredes et al. 2008, Masello et al. 2010), with potential for behavioural adjustment according to local or annual prey conditions (Burke et al. 2009, Barger and Kitaysky 2011). Following breeding, seabirds are released from the constraints of central-place foraging from nesting sites. Given the potential for dispersal throughout the marine environment, one might expect competition for resources to be reduced during nonbreeding. There is,

however, a growing understanding that marine hotspots concentrate large numbers of seabirds and other marine predators during nonbreeding periods (e.g. Benguela Upwelling: Stenhouse et al. 2011; Grand Banks of Newfoundland: Frederiksen et al. 2011, Hedd et al. 2012, Mosbech et al. 2012; Mid-Atlantic Ridge area: Walli et al. 2009, Egevang et al. 2010, Hedd et al. 2012; North Pacific Transition Zone: Block et al. 2011; northwest coastal Africa: Camphuysen and van der Meer 2005; Fort et al. 2012), where competition for resources is likely to persist. As well, particular patterns of migration, movement and dispersal of nonbreeding seabirds to wintering areas determine (Lack 1968, Phillips et al. 2005) and/or depend upon (Wakefield et al. 2011) the degree of competition occurring at wintering grounds. Buoyed by the combination of animal tracking and isotopic analyses, recent research suggests that habitat partitioning among closely-related species and subpopulations continues into the nonbreeding period (Cherel et al. 2006, 2007, Phillips et al. 2009, Ramos et al. 2009, Thiebot et al. 2012), and could act as a genetic barrier maintaining population structure (Friesen et al. 2007). Thus, the degree to which seabird populations depend upon, and partition, important winter hotspots and other wintering areas (Croxall et al. 2005, Gonzales-Solis et al. 2007) carries important evolutionary, ecological and conservation implications. The degree to which inter- and intra-specific competition influence habitat partitioning during the nonbreeding period has only recently become a tangible research subject, with the advent of miniaturized tracking technology (Gonzales-Solis et al. 2007, Frederiksen et al. 2011, Thiebot et al. 2012).

This paper investigates patterns of ecological segregation during the nonbreeding period in the Canadian murres (*Uria*), through patterns of space and time (cf. Thiebot et al. 2012). The congeneric murres share partially overlapping, circumpolar distributions throughout the year (Tuck 1961). *Uria* are primarily deep-diving fish-eaters, sharing similar ecology and morphology, but with slight differences in bill structure reflecting dietary preferences (Bédard 1969): Common Murres (*U. aalge*) mostly eat shoaling fishes (capelin, cod, herring, sandlance) and Thick-billed Murres (*U.*

lomvia) consume a wider variety of shoaling fish and invertebrates (Gaston and Jones 1998). The species maintain relatively segregated breeding habitat, with Thick-billed Murres concentrating at higher latitudes than Common Murres. Where breeding distributions overlap, subtle differences in phenology, breeding site locations, and prey delivered to nestlings may decrease competition (Birkhead and Nettleship 1986 a, b, c, Barrett et al. 1997). Following breeding, both species from Canadian colonies likely overwinter at Low Arctic latitudes of the North Atlantic Ocean (Tuck 1961, Ainley et al. 2002, Gaston and Hipfner 2000, Gaston and Jones 1998). Here, partial segregation has been observed according to thermal preferences, with Thick-billed Murres staying in colder waters (~5°C isotherm) and Common Murres spreading southward to the 15^{o}C February isotherm (Tuck 1961), but how these patterns might be influenced by geographic location or colony of origin has not been well described. Wintering in the harsh Northwest Atlantic is energetically demanding for seabirds, requiring intense foraging effort (Grémillet et al. 2005, Fort et al. 2009). Furthermore, murres from Greenland, Iceland, and Svalbard (Tuck 1961, Kampp 1988, Lyngs 2003, Bakken and Mehlum 2005, Fort et al. 2013), along with dovekies (*Alle alle;* Mosbech et al. 2012) and kittiwakes (*Rissa trydactyla*; Fredericksen et al. 2011) also wintering in the NW Atlantic. The resulting pressure for habitat partitioning could be intense, but the degree to which ecological segregation occurs is unknown.

To investigate inter- and intra-specific ecological segregation in *Uria* species, year-round tracking data were collected from miniaturized tracking devices (geolocation-immersion sensors or GLS; Phillips et al. 2004) on Thick-billed and Common Murres from seven colonies spanning the eastern Canadian High and Low Arctic. Segregation was investigated at three levels of ecological organization: between (1) congeneric species, (2) colonies within species, and (3) individuals in each subpopulation (cf. Thiebot et al. 2012). Study objectives were to describe and compare: 1) patterns of spatio-temporal habitat use during the nonbreeding period; 2) associated patterns in habitat characteristics; and 3) distribution and overlap of core winter areas. It was

expected that ecological groups (species, colonies) minimize competition by varying spatial and temporal patterns of nonbreeding habitat use.

2.3. METHODS

Study area and species- This research was carried out at seven seabird colonies in Arctic and Eastern Canada from 2007-2011 (see Table 2.1 for specific colony years): Prince Leopold Island in the Canadian High Arctic; the Minarets on Baffin Island; Coats Island and East Digges Island in Hudson Bay, Nunavut; Gannet Islands, Labrador; and Funk Island and Gull Island in Newfoundland (Table 2.1, Figure 2.1). These breeding colonies support either Thick-billed Murres or Common Murres, except at the Gannet Islands where both species breed (Table 2.1).

Device deployments – Small geolocation-immersion loggers (GLS, or geolocators) from British Antarctic Survey (BAS, Cambridge, UK; models Mk5, Mk7, Mk13, Mk15; n = 266) or Lotek (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, < 0.6% adult body mass). We retrieved 163 (58%) in 2008-2011, and recovered data from 142 geolocators (50%; 86 Thick-bills, 56 Common). Most were retrieved after one year, but 42 of them were carried for 2-4 years, providing repeat tracks for 42 individuals, 182 annual round-trips (Table 1), for a total of 108,882 (unfiltered) GLS locations. All populations (save the Minarets) were studied simultaneously during at least two years (usually 2008-2010; see Table 1).

Table 2.1. Details of geolocators deployed and retrieved, and tracking data for each study colony and year. 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.

					Geolocators				Tracking data		
Species	Colony	Position	Colony size (breeding pairs x 2)	Year Deployed	Deployed	Retrieved	Total Included	Years of data coverage	Unique individuals	Repeat Tracks	Total annual tracks
Thick-billed Murre	Prince Leopold	74°02'N 90°00'W	170,000[a]	2008	21	19					
				2009	5	5	19	2008-10	19	1	20
	Minarets	66°57'N 61°50' W	260,000[a]	2007	20	14	14	2007-08	14	0	14
	Coats	62°53'N 82°00' W	36,000[b]	2007	20	18					
				2008	20	13					
				2009	6	3	31	2007-10	21	10	32
	Digges	62°32'N 77°45' W	872,000[a]	2008	32	10	10	2008-10	10	3	13
	Gannets	53°56'N 56°32'W	3,700[c]	2008	14	8					
				2009	17	11	12	2008-11	11	8	22
Common Murre	Gannets	53°56'N 56°32'W	62,420[c]	2008	16	12					
				2009	16	9	19	2008-11	16	8	27
	Funk	49˚45'N 53˚11'W	825,048[c]	2007	21	11					
				2008	25	5					
				2009	3	3	19	2007-11	17	6	31
	Gull	47°16'N 52°46'W	6,992[c]	2007	5	0					
				2008	30	16					
				2009	11	6	18	2007-11	15	6	23
Overall					*282*	*163*	*143*	*2007-2011*	*124*	*42*	*182*

[a]2011, A.J. Gaston [Environment Canada] unpublished data; [b]2010, Gaston and Robertson; [c]2011, S. Wilhelm [Environment Canada] unpublished data

Data processing – Geolocator data were processed following Phillips et al. (2004) using MultiTrace Geolocation software (Jensen Software Systems) and a light threshold method (Hill and Braun 2001, Lisovski et al. 2012). This required adjustment of processing parameters for each GLS model, to find specific thresholds that minimize data loss and latitudinal discrepancy around the equinox (Lisovski et al. 2012). BAS Mk 5, 7, and 13 required a light threshold of 1 and sun angle of elevation of –5.5^{o}; comparable results for BAS Mk 15 were achieved with a light threshold of 10 and a sun angle of elevation -2.5^{o}. These parameters provided the best overall representation of locations in the study area (see McFarlane Tranquilla et al. 2013). Lotek 2500 devices employ internal processing algorithms so positional data can be downloaded directly. Positions from each bird were processed and visually inspected by the same observer (LMT) and clearly erroneous locations, representing unrealistic movements (> 500 km/day) or outside the likely species' range, were removed (Phillips et al. 2004, McFarlane Tranquilla et al. 2013). Latitudes cannot be accurately assessed during equinox periods (Hill 1994), and data affected in this study were from ~8 September – 8 October, and ~6 March – 5 April. However, equinox data were not deleted a priori because not all geolocators were affected equally (perhaps influenced by bird behaviour or weather; Lisovski et al. 2012). All data during equinox periods were inspected and reasonable positions, within a 500-km radius of the last known accurate position, were retained. In addition, some equinox data (5319 positions, contributing 9% to retained data) was reclaimed using a sea surface temperature (SST) matching algorithm (Teo et al. 2004), used during equinox periods only (September-October, February – April; see McFarlane Tranquilla et al. 2013 for full details). This process worked only when the SST matching algorithm contributed reasonable data in areas where thermal stratification was evident (e.g. the Grand Bank and Scotian Shelf). All data were smoothed twice (2-day running average), retaining the original fixes at the start and end of periods where data were missing (Phillips et al. 2004) or replaced with SST-corrected data. Overall, processing resulted in 54,930 locations (50% of original raw data), or 27,465 tracking-

days (2 locations per day). Mean accuracy of GLS location data are between 100-200 km (Phillips et al. 2004, Teo et al. 2004).

Analyses of spatial and habitat characteristics – Segregation was investigated during the nonbreeding period (September – May), and for winter only (December-January), by assessing spatio-temporal movement patterns and associated environmental features. To do this, average daily latitudes from geolocators were pooled by colony and mapped against date to determine temporal patterns of distribution (referred to as "profiles"). Latitudes (rather than longitudes) were chosen as they better represent the geographical structure of the study area (especially the Labrador Sea). Similarly, environmental features (bathymetry[6], chlorophyll_a[7] (CHL), ice[8], water temperature[9], and night length[10]) associated with each location were used to describe habitat variation. For bathymetry, CHL, and ice, filtered GLS locations were overlaid on environmental maps (rasters or shapefiles) in ArcMap and a time series of data (i.e. 2007-2011) were extracted using Marine Geospatial Ecology Tools (version 0.8a12) in ESRI ArcGIS (versions 9.3 and 10). Rather than using a static average of environmental data extracted to kernel density contours (cf. Thiebot et al. 2012), this automated extraction of a time series of points (across 2007-2001) enabled assessment of the dynamic changes in year-round environmental features (i.e. profiles) as birds moved through the annual cycle. Average daily water temperatures and night lengths were

[6] GEBCO digital atlas ver. 2, www.gebco.net, 1-min grid; chosen due to spatial resolution of GLS devices

[7] OceanColor Database, http://oceandata.sci.gsfc.nasa.gov/ MODISA/Mapped/8Day/4km/chlor/; 4-km resolution, mg/m^3, averaged over 8 days per raster, 2007-2011

[8] Canadian Ice Service , http://www.ec.gc.ca/glaces-ice/, weekly ice cover charts for eastern Canadian Arctic, Hudson Bay, east coast of Canada (merged to compile coverage for the study area), in 10ths of coverage, 2007-2011

[9] directly from geolocators, 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)

[10] hours of darkness, calculated directly from geolocators using time of sunrise and sunset

compiled directly from geolocators, pooled by colony, and mapped against date. Figures depicting the profiles begin at the end of one breeding season (August) and continue to the start of another (May/June); thus winter is depicted in the center portion of figures. Environmental features during winter (December-January) were defined separately. Hours of darkness were extracted only for December when nights are longest, and when energetic requirements are highest (cf. Fort et al. 2009). We also calculated percent overlap of winter home ranges (see below) with the winter leading ice edge (NOAA[11], January only, where ice exceeds 80% (8/10ths), to describe the proximity of colonies to winter sea ice. Ice concentrations are resolved at a minimum polygon size of 1000 km^2 and follow the international Egg Code to express area of ice cover ("N_CT") in tenths, where 0 is ice-free, 1-7/10^{ths} rank areas of drift ice in marginal ice zones, and >8/10^{ths} indicate nearly complete ice cover, also known as the leading ice edge[3].

In addition to non-breeding season profiles, we investigated spatial segregation during winter. Core kernel home ranges (50% KHR) has been used effectively to estimate main foraging areas of sympatric species (Wood et al. 2000, Phillips et al. 2005). Core KHR 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 (mimicking geolocator accuracy; Phillips et al. 2004, Teo et al. 2004). Colony overlap of winter KHRs was calculated following McFarlane Tranquilla et al. (2013). The degree of overlap of individual birds within each colony was determined using a randomization procedure (n = 10,000 randomizations in R version 2.15.2) to calculate mean 50% KHR overlap (cf. Fifield 2011). Inter-colony distances were measured in ArcMap.

Statistical analyses - Ice concentrations were analysed with linear mixed effects models (lme) to account for repeat measurements from individuals. To examine the non-linear

[11] http://www.natice.noaa.gov/products/

relationship of nonbreeding latitudes (spatial data) and environmental data (bathymetry, CHL, temperature) through time, between and within species, we used generalized additive models (gamm; Wood 2012) in R. These models accounted for repeated data from individuals, spatial autocorrelation, and included a colony-specific smoothing term (Zuur et al. 2009). Latitudes and each environmental dataset were 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 AIC values) so annual data was pooled when graphing temporal profiles. P-values were used to assess significance within groups of fixed effects (e.g. species, colony). Because p-values calculated from gamm models are approximate (Zuur et al. 2009), we considered those from $\leq$ 0.05-0.1 to be approaching significance. Model variance, described through standard deviation (stdev) of the intercept (ie. random effect; birdid) and the residual were used to help describe differences in variance between species. The types of environmental data considered are often collinear, but given that they were used to describe differences in environmental features among and within species, and not included together in a habitat selection model (cf. Anderson et al. 2013), a formal examination of collinearity was not required. In cases when analyses include individually-repeated measures, sample sizes are represented as a pair, of total observations and total number of individuals (e.g. n = 30,000|92).

2.4. RESULTS

2.4.1 Nonbreeding segregation by latitude

Between the species, Thick-billed Murres occupied a much broader distribution, and strong latitudinal segregation was observed throughout the nonbreeding season (Figure 2.1). Thick-billed Murres generally occupied higher latitudes (gamm, t =12.13, p < 0.001), and a wider range of latitudes (38-69°N; stdev (intercept + residuals) = 5.80 +

4.2) than Common Murres (35-56°N; stdev (intercept + residuals) = 1.55 + 2.8; Figure 2.2). Temporally, Thick-billed Murres shifted latitudes throughout the nonbreeding season, whereas Common Murres moved in fall (until October) and then latitudes were mostly constant until returning to colonies in May (Figure 2.2 a, b).

At the Gannet Islands alone where both species occur, latitudinal variance was greater for nonbreeding Thick-billed Murres (stdev (intercept + residuals) = 5.02 + 5.15) than for Common Murres (stdev (intercept + residuals) = 0.70+ 3.02), although here the species did not separate to significantly different latitudes (gamm, t = 0.02, p = 0.98).

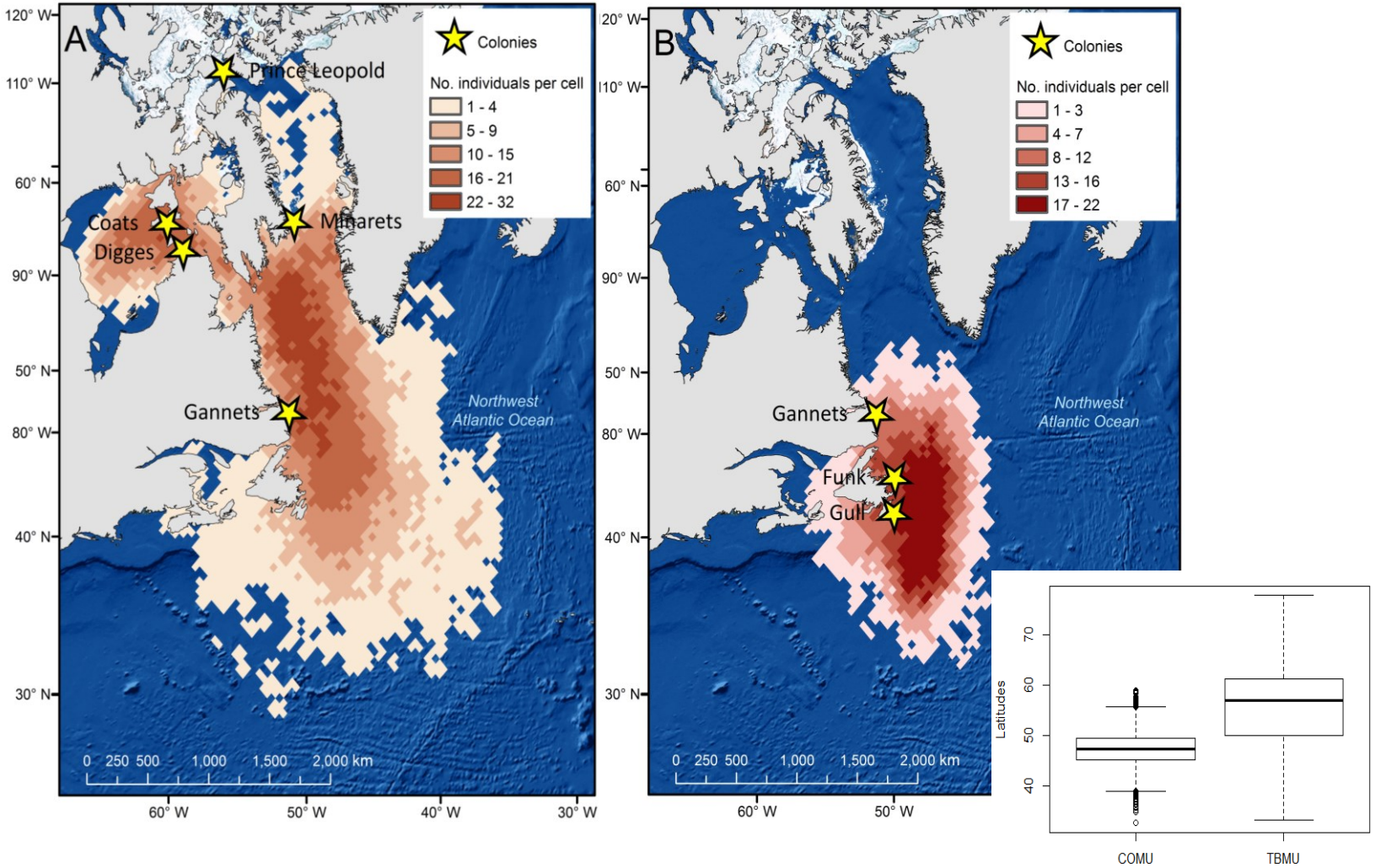

Figure 2.1. Study area, colonies and nonbreeding distribution (Sept – May; number of unique individuals per cell (50 x 50 km) of data coverage; filtered geolocator data, all years pooled) of (A) Thick-billed Murres (TBMU) and (B) Common Murres (COMU). Inset compares latitudinal range between species (boxplots indicate lower (25%) and upper (75%) quantiles and whiskers indicate min and max values).

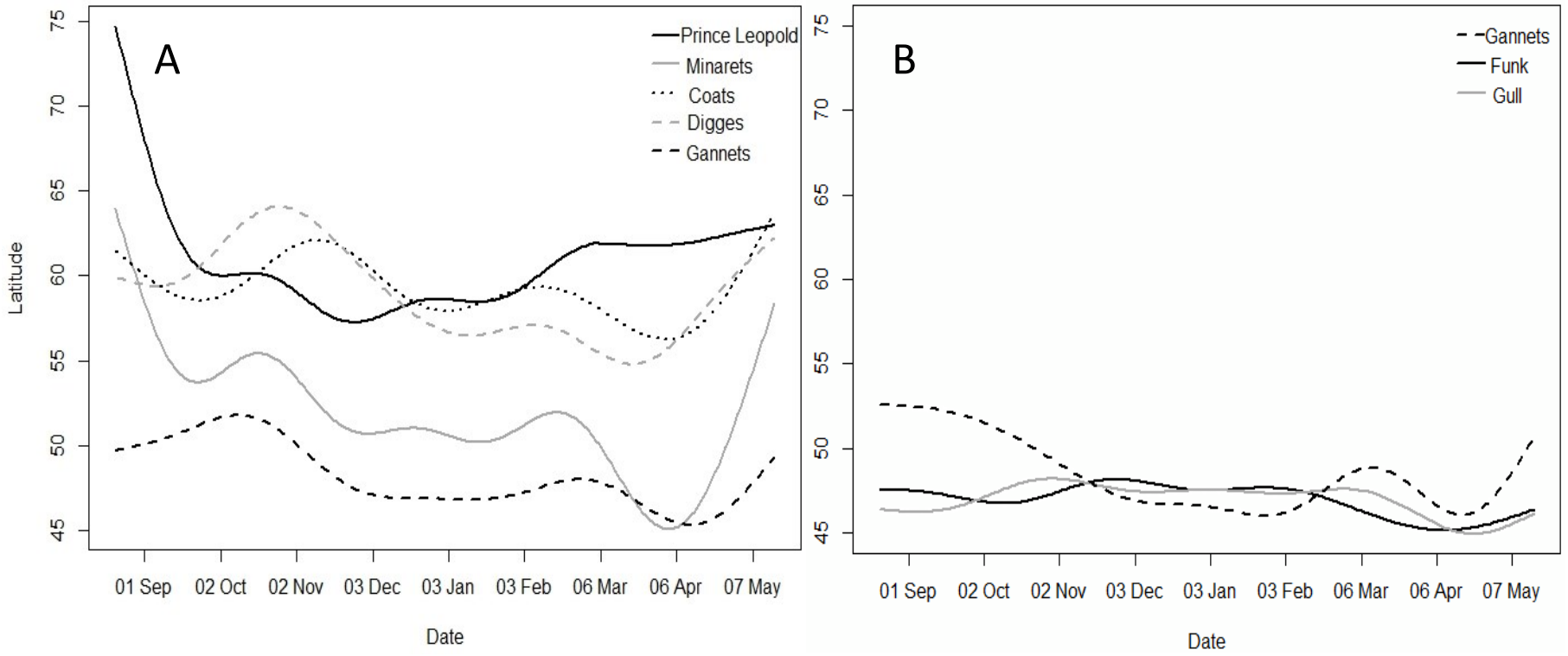

Figure 2.2. Intra-specific comparison of spatial and temporal range of movement during the nonbreeding period for Thick-billed Murre and Common Murre through latitudinal profiles for (A) five colonies of Thick-billed Murre and (B) three colonies of Common Murre. Curves reflect latitudes after controlling for individual variation (from gamm models).

Intra-specifically, 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, the Minarets (gamm; $t = 5.74$, $p < 0.001$) and Gannet islands (gamm; $t = -12.71$, $p < 0.001$; Figure 2.2a). This was accompanied by temporal differences in movement, in which some Thick-billed Murres moved southward immediately after the breeding season (August-September, PLI, Minarets), while others remained near colonies into the fall (October-December, Coats, Digges, Gannets; Figure 2.2a). The timing of northward movement toward breeding latitudes also varied widely (January – April) depending on colony (Figure 2.2a). Among Common Murres, latitudinal segregation occurred only for the Gannet Islands, compared to Gull (gamm; $t = 2.67$, $p = 0.008$) and Funk islands (gamm; $t = 1.66$, $p = 0.098$; Figure 2.2b). Common Murres from the Gannet Islands moved southward soon after breeding (August -September), whereas those from Funk and Gull islands moved only slightly southward or northward (respectively) in September-October (Figure 2.2b). Common Murres from all three colonies returned to breeding latitudes in April.

2.4.2 Nonbreeding habitat - environmental characteristics

Bathymetry -Thick-billed Murres occurred over deeper water with a wider range of depths (1557 m $\pm$ 76 se; Table 2.2) than did Common Murres (1217 m $\pm$ 60 se; gamm, $n = 30{,}000|168$, $t = -2.01$, $p = 0.045$; Table 2.2). This pattern of more variable depths was also evident among birds from the Gannet Islands where both species occur ($n = 12{,}318|42$, $t = -2.01$, $p = 0.05$). Among Thick-billed Murres colonies, bathymetry varied significantly (Figure 2.3a), particularly during December and January (range 950-2350m, Table 2.2). Temporally, the change from shallow to deep water occurred at different rates among colonies of Thick-billed Murres, depending on seasonal movement; for example, those from Prince Leopold, Minarets, and Gannet islands moved into deep water (>500m) by August/September, whereas those from Coats and Digges islands

remained in shallower waters (in Hudson Bay) until late November/December before moving offshore (Figure 2.3a). Most Thick-billed Murres occupied deepest waters in march and April prior to colony return (except for Prince Leopold; Figure 2.3a). Among Common Murre colonies, 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 2.2, Figure 2.3b). Temporally, Common Murres from Funk and Gannet islands appeared to move to deeper waters by September, but those from Gull Island remained in shallower (shelf) waters year-round (Figure 2.3b). Common Murres from Funk occupied deepest waters during spring.

Chlorophyll_a – Most strikingly, Thick-billed Murres occupied waters with very low CHL during winter. Overall, CHL was lower in the nonbreeding period for Thick-billed than for Common Murres (gamm; $t = -4.66$, $p < 0.00$; Figure 2.3), including for the comparison for Gannet Island where both species occur (gamm, $t = -2.29$, $p = 0.02$). Seasonal variance in CHL was greater for Common Murres (Table 2.2). Within species, colony differences for Thick-billed Murres were significant between three groups: Coats/ Digges/Prince Leopold vs. Minarets (gamm; $t = 2.17$, $p < 0.001$) vs. Gannet Islands (gamm; $t = 10.21$, $p < 0.03$; Figure 2.3c, Table 2.2). Common Murres from the Gannet Islands had significantly higher CHL than those from Gull and Funk Islands (gamm, $t = 3.33$, $p < 0.001$; Table 2.2), during the nonbreeding period overall and also during winter. Temporally, nonbreeding wters for both species were lowest in CHL during December. Profiles were more variable for Thick-billed Murres: CHL in nonbreeding areas remained very low throughout November – February except for areas used by Gannet Islands birds; and timing of maximum CHL depended on colony of origin and associated movement patterns (April for Minarets and Gannet Islands; June for Coats Island); September for Digges Islands; Figure 2.3c). Among Common Murres, CHL was significantly higher for Gannet Islands birds (gamm, $t = 3.3$, $p < 0.001$; Figure 2.3d), and

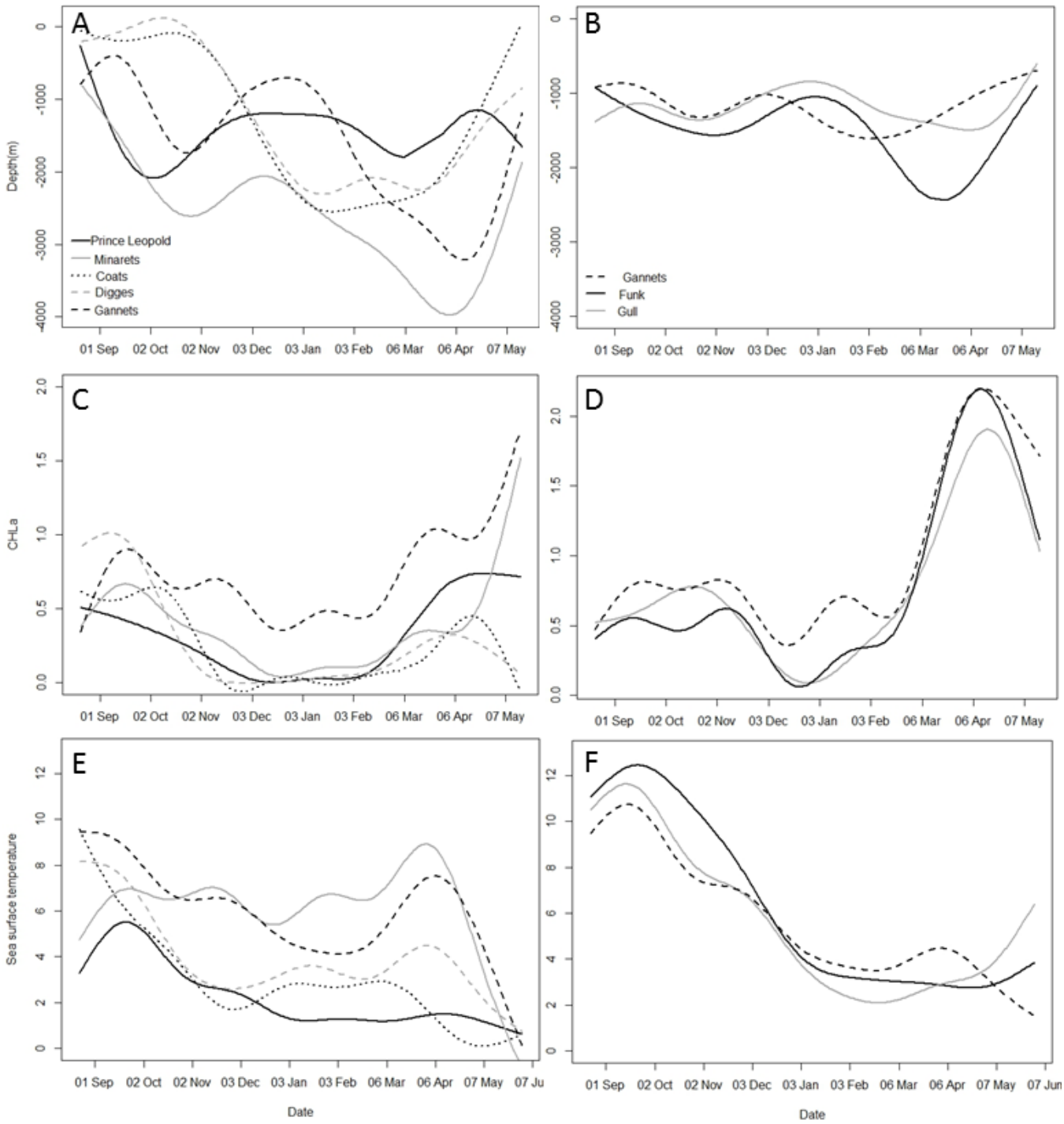

Figure 2.3. Year-round (A, B) depth (m), (C, D) chlorophyll_a (mg/m^3), and (E, F) sea surface temperature (°C) encountered by colonies of Thick-billed Murres (left) and Common Murres (right). Curves reflect environmental features after controlling for individual variation (from gamm models).

temporal patterns were the same for all colonies: low from June through February, reaching a maximum in April.

Water temperatures - Nonbreeding water temperatures (°C) for Thick-billed Murres were significantly colder (4.4 $\pm$ 0.7) with larger standard deviation than for Common Murres (6.4 $\pm$ 0.2; gamm, $t_{22815,81} = -5.6$, $p < 0.001$; Table 2.2, Figure 2.3). During winter months, temperatures were colder for Thick-billed Murres (3.3 $\pm$ 0.4 se) than for Common Murres (4.5 $\pm$ 0.3 se; $t_{5219,80} = -2.68$, $p = 0.009$). Temperatures did not vary among species from the Gannet Islands. Within species, temperatures were significantly different among Thick-billed Murre from all colonies except Coats and Digges, whereas there were no significant differences among winter temperatures for Common Murres from different colonies (Table 2.2). Temporal variation of temperature profiles was also greater among Thick-billed than Common Murre colonies (Figure 2.3 c,d). 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 April-July), depending on colony-specific spatial movements (i.e. Thick-billed Murres from Coats, Digges and Prince Leopold encountered warmest waters during the breeding season (June/July) but those from the Gannets and Minarets were in warmest waters during spring (April/early May; Figure 2.3e)). In contrast, all colonies of Common Murre experienced similar changes in temperature throughout the year, with steady declines until February, and maximum temperatures in the breeding season (Figure 2.3f).

Table 2.2. Mean values of bathymetry, chlorophyll_a (CHL) and sea-surface temperature (SST) for the overall nonbreeding period (September – April) and winter only (December-January) among species and colonies of murres. N are depicted as total observations (i.e. datapoints) and total individual birds for each model (gamm). Where letters (in italics) differ between two groups, the differences are significant; statistical tests within species were run separately. * indicate gamm model variances, described as the stdev (standard deviation) of intercept + residual, used here to help compare the extent of variation between species.

			Bathymetry & Chlorophyll_a					Temperature		
Species	Data Period	Colony	N observations |individuals	depth (m) ± se		CHL (mg/ml^3) ± se		N observations |individuals	SST (^{o}C) ± se	
Thick-billed Murre	Nonbreeding	Overall	31337|96	**-1557 ± 76**	***A***	**0.33 ± 0.07**	***A***	14621|55	**4.4 ± 0.7**	***A***
		*stdev (intercept + residual)**		*664 + 1410**		*0.25 + 0.8**			*1.6 + 2.7**	
	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	9981|96	-2181 ± 183	*B*	0.01 ± 0.01	*A*	3381|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	18700|72	**-1217 ± 60**	***B***	**0.74 ± 0.08**	***B***	8194|28	***6.2 ± 0.2***	***A***
		*stdev (intercept + residual)**		*455 + 1282**		*0.34 + 1.5**			*0.01 + 3.8**	
	Winter	Gannets		-1292 ± 124	*A*	0.5 ± 0.05	*A*		4.7 ± 0.4	*A*
		Funk	6871|70	-1108 ± 184	*A*	0.1 ± 0.01	*B*	1922|27	4.7 ± 0.5	*AB*
		Gull		-812 ± 167	*B*	0.3 ± 0.04	*B*		4.2 ± 0.5	*AC*

.

Winter ice cover and night length– Average ice cover (N_CT) was higher and more variable in winter areas of Thick-billed Murres (1.5 + 3.4 SD; interpreted as 15% ice cover) than Common Murres (0.06 + 0.7 SD; lme, $F_{1,13915}$= 32.35, $p < 0.0001$; Table 2.3), and ice cover 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 (Figure 2.4). Wintering areas (50% KHR) overlapped the leading ice edge for some Thick-billed Murre colonies (0-32 %), but not for Common Murre colonies (Table 2.3).

Thick-billed Murres occupied areas with significantly longer nights (15.9 h of darkness) than did Common Murres (14.5 h; lme, $F_{2,52}$= 31.9 $p < 0.0001$), and had significant inter-colony variation in night length (lme, $F_{3,28}$= 8.20, $p = 0.0006$). Night length was similar for all colonies of Common Murre (lme, $F_{2,26}$= 1.11, $p = 0.35$; Table 2.3, Figure 2.5).

Table 2.3. Mean ice concentration (N_CT; where 1 is 10% and 10 is 100%), percent overlap of core winter ranges (50% KHR) with ice cover (N_CT), and mean of hours of darkness (night length) during winter (December-January) among species and colonies of murres. N are depicted as total observations and individuals for each model (lme) (mean night length), or as total individuals (ice cover). Letters (in italics) indicate significant differences in night length between groups).

			Ice Cover				Mean night length		
Species	Data Period	Colony	N observations |individuals	N_CT (variance)	N (KHR)	% KHR-Ice Overlap	N observations |individuals	Hours of darkness ± se	
Thick-billed Murre	Winter	Prince Leopold		2.3 (15.4)	19	32.6	905|28	17.1 ± 0.5	*A*
		Minarets		0.04 (0.4)	12	0		n/a	
		Coats	7919|96	2.8 (17.4)	32	14.8		15.9 ± 0.4	*B*
		Digges		2.1 (14.7)	10	18.2		15.5 ± 0.5	*C*
		Gannets		0.1 (0.8)	12	0		14.6 ± 0.6	*D*
		Overall		1.6 (11.8)	85	13.1	1773|54	**15.9 ± 0.3**	***A***
Common Murre	Winter	Gannets		0.02 (0.2)	19	0	868|26	14.6 ± 0.1	*A*
		Funk	6148|70	0.06 (0.5)	16	0		14.5 ± 0.1	*A*
		Gull		0.10 (0.6)	16	0		14.5 ± 0.1	*A*
		Overall		0.06 (0.4)	51	0	1719|52	**14.5 ± 0.2**	***B***

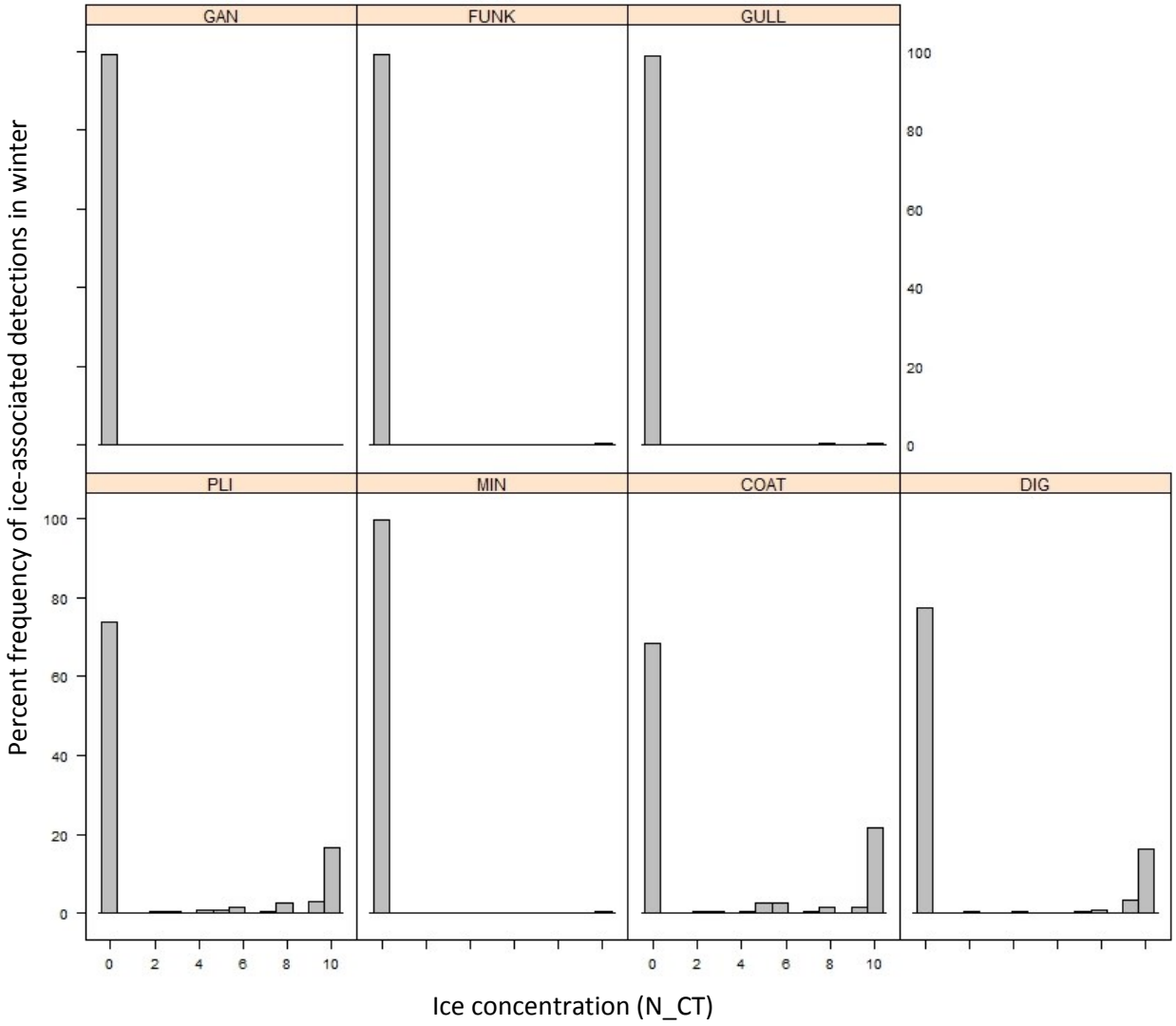

Figure 2.4. Histograms indicating frequency of detections of GLS data associated with concentrations of ice (N_CT, which range from 0 [no ice] to 10 [maximum ice]; see methods) in winter (December, January) for colonies of Thick-billed Murres (Prince Leopold, Minarets, Coats, Digges, Gannets) and Common Murres (Gannets, Funk, Gull).

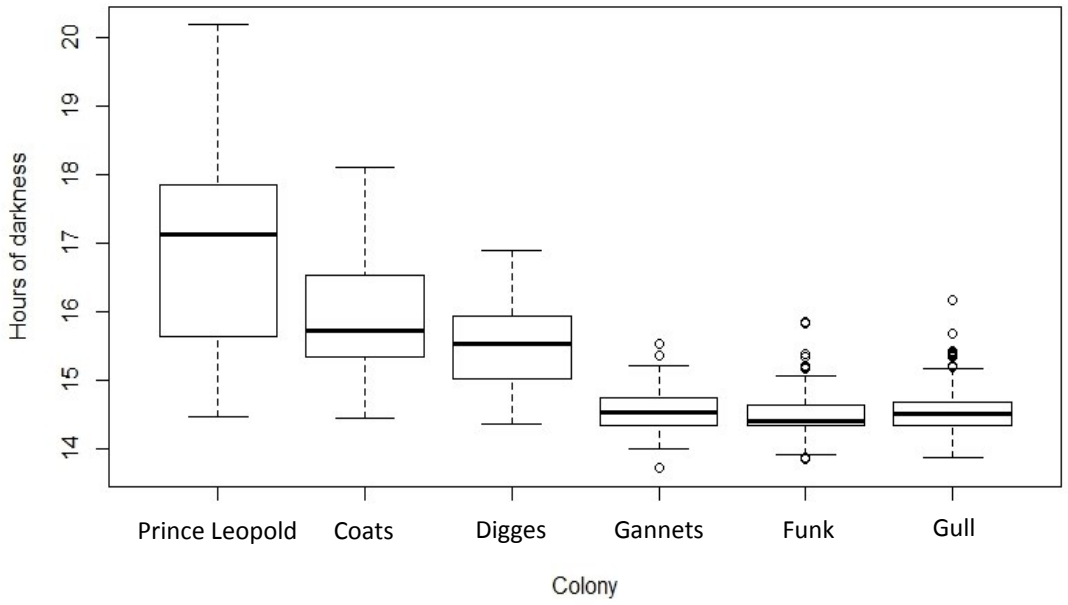

Figure 2.5. Daily hours of darkness (night length) for colonies of Thick-billed Murres (Prince Leopold, Coats, Digges, Gannets) and Common Murres (Gannets, Funk, Gull) in winter (December only; see methods). Boxplots indicate lower (25%) and upper (75%) quantiles, whiskers indicate minimum and maximum values, and points indicate outliers.

2.4.3 Core winter overlap

Core winter areas and 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 Banks (Figure 2.6), whereas core witner areas of all Common Murre colonies were more restricted to the eastern Grand Bank and over the Orphan Basin. Between the species, overlap of core winter areas was generally low (15%, range 0 - 42 %) except for Thick-billed Murres from the Gannet Islands with most Common Murre colonies (Table 2.4). Within species, overlap of core winter areas of Thick-billed Murre colonies ranged from 0 – 52 % (Table 2.4), and was greater and less variable among Common Murres (33 – 61%; Table 2.4, Figure 2.6). Similarly, overlap of individual core winter areas was less for Thick-billed Murres (average 23%, range 10-33%) than for Common Murres (average 39%, range 36-44%) and was strongly dependent on colony (Table 2.5).

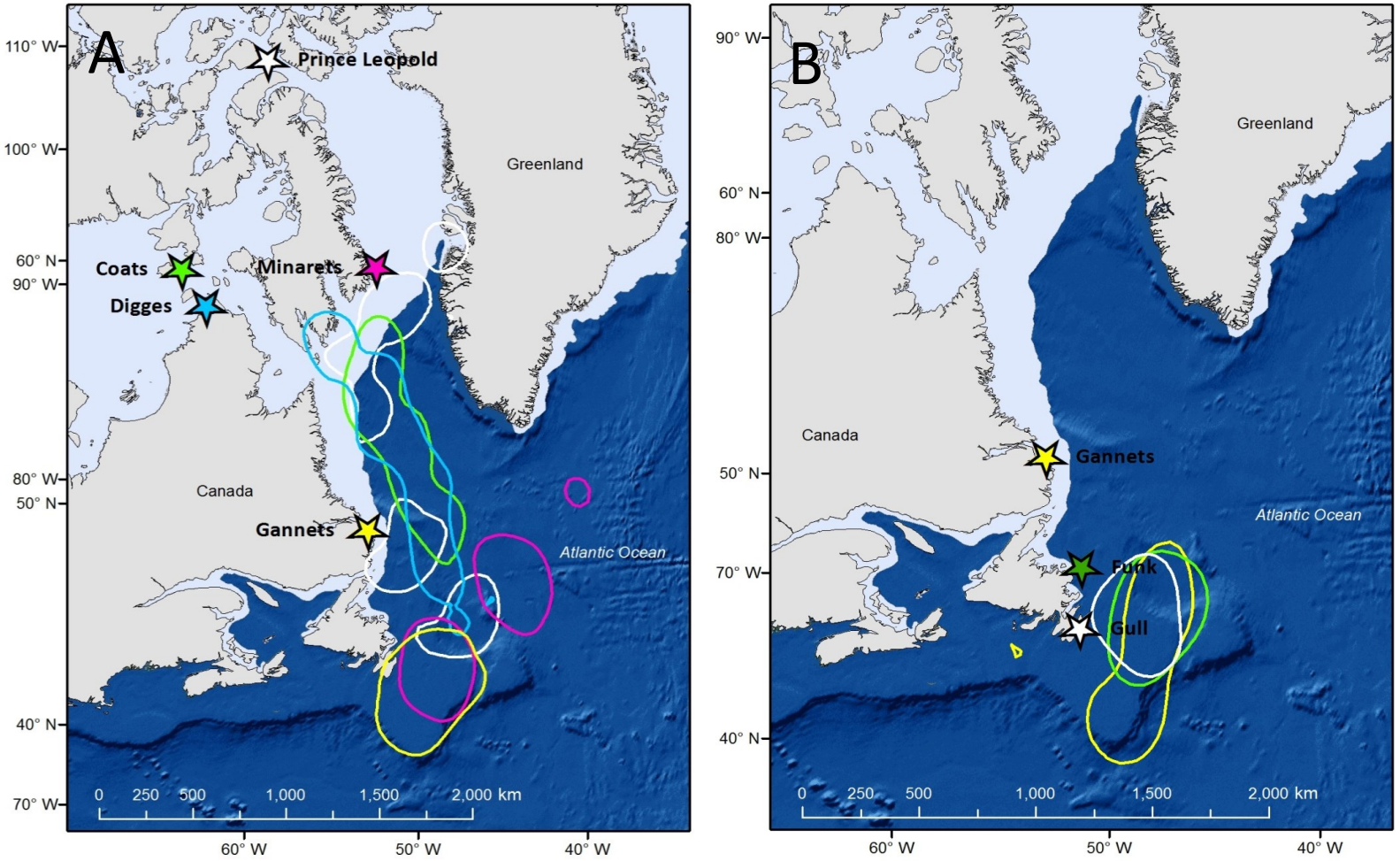

Figure 2.6. Inter-colony overlap of core winter habitat (50% KHR) among A) Thick-billed Murres and B) Common Murres, overlaid on the leading ice edge (light blue) in January. Colored stars indicate individual breeding colonies and match the color of the core outline for each colony.

Table 2.4. Percent overlap of core winter areas (Dec-Jan 50% KHR) among pairs of Thick-billed Murre and Common Murre colonies (see also Figure 2.2). Both inter-specific and intra-specific pairwise comparisons are made, indicated by TT (Thick-billed Murre colonies), TC (Thick-billed/Common Murre colonies) and CC (Common Murre colonies). T* and C* indicate Thick-billed and Common Murres, respectively.

Species	Colonies	N Geolocators	Inter-colony Overlap of Core Winter Areas (%)						
			Prince Leopold	Minarets	Coats	Digges	Gannets (T*)	Gannets (C*)	Gull
Thick-billed Murre	Prince Leopold	19	-	-	-	-	-	-	-
	Minarets	12	19.9	-	-	-	-	-	-
	Coat	32	19.9	0.0	-	-	-	-	-
	Digges	10	21.6	0.4	51.7	-	-	-	-
	Gannets	12	4.5	33.3	0.0	0.0	-	-	-
	Average TT Overlap		*15.1% ± 5.5 s.e.*					-	
Common Murre	Gannets	19	9.6	21.9	0.0	1.8	41.8	-	-
	Gull	16	9.2	34.2	0.0	1.8	39.3	36.1	-
	Funk	16	12.3	28.2	0.0	1.9	35.6	33.7	61.8
	Average CC Overlap		-					*43.8% ± 8.9 s.e.*	
	Average TC Overlap		*15.8% ± 4.2 s.e.*					-	

Table 2.5. Amount (%) of individual 50% KHR overlap within colonies. Data are based on a separate randomization (n = 10,000) of individual overlaps for each colony.

Species	Colony (individuals)	% Individual KHR overlap (randomized) Mean (SD), Range
Thick-billed Murre	Prince Leopold (16)	10 (19) 0-90
	Minarets (14)	22 (27), 0-91
	Coats (21)	23 (22), 0-100
	Digges (10)	29 (23), 0-93
	Gannets (11)	33 (26), 0-100
Common Murre	Gannets (14)	36 (27), 0-100
	Funk (17)	38 (27), 0-100
	Gull (13)	44 (29), 0-99

Inter-colony distance: There was a negative relationship between colony level overlap in winter KHR and inter-colony distance, such that colonies closer to each other tended to have more similar winter distributions (Figure 2.7; glm, $R^2 = 50.1\%$; $F_{1,26} = 18.4$, $p < 0.00$). However, all colonies did not fit this pattern; for example, high overlap of core winter areas occurred between Thick-billed Murres from the southerly Gannet Islands and the northerly Minarets and Prince Leopold islands (Table 2.4).

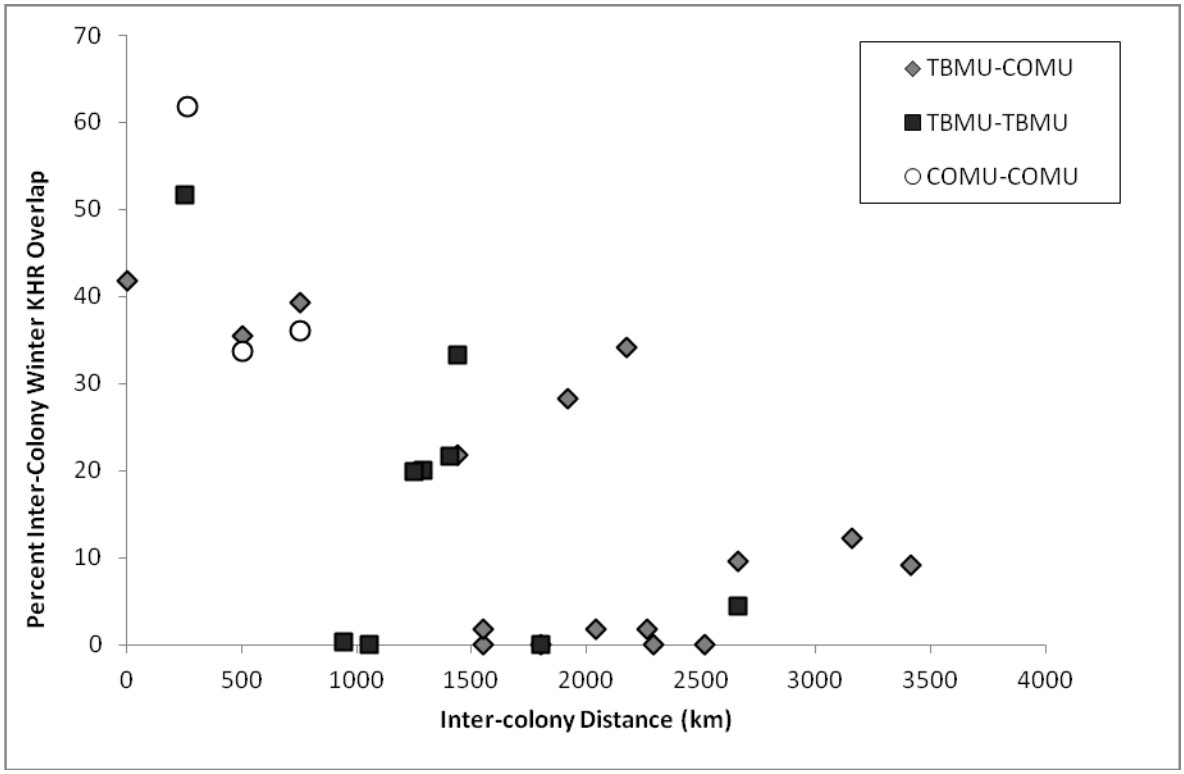

Figure 2.7. Overlap of kernel home ranges (50% KHR) of wintering areas in relation to inter-colony distance (km) among and between Thick-billed Murres (TBMU) and Common Murres (COMU).

2.5. DISCUSSION

Using a multiple-colony approach, this study demonstrates segregation between congeneric Thick-billed and Common Murres throughout the nonbreeding period. As pursuit-diving, sympatric, and congeneric species, Thick-billed and Common Murres occupy a very similar ecological niche. Because competition influences patterns of space and resource use (Svanbäck and Bolnick 2007, Wakefield et al. 2009, 2011), partitioning among ecological groups was expected. Other studies have also shown that habitat partitioning among closely-related species continues into the nonbreeding period (Cherel et al. 2006, 2007, Phillips et al. 2009, Ramos et al. 2009, Linnebjerg 2012, Thiebot et al. 2012), but most of these patterns have been investigated from sympatric colonies. We expand this approach and were able to document intra-specific segregation during the nonbreeding season, among several colonies of murre spanning a wide latitudinal range. Due to this segregation, the winter conditiiosn influencing murres varied substantially, according both to species and colony.

2.5.1 Ecological segregation

Ecological segregation among Common and Thick-billed Murres seems to occur through spatio-temporal movement patterns, which are more variable in Thick-billed Murres. Thick-billed Murres occupied a wider range of latitudes than Common Murres, throughout the non-breeding period as well as during winter. Not only was this pattern observed across the broad study area, but it was also evident among murres from the Gannet Islands where the species breed sympatrically. A similar pattern of greater latitudinal movementand larger winter distributions among Thick-billed Murres has recently been demonstrated by Linnebjerg et al. (2012) and Fort et al. (2013) who studied the two species from sympatric colonies in Greenland and Svalbard (respectively).

Latitudinal segregation is not often assessed directly through geolocation studies, but rather is assessed by estimating latitudes and/or water masses through isotopic analyses (cf. Cherel et al. 2006, Philips et al. 2009). We found that mapping latitudinal profiles was very useful in describing colony-specific patterns throughout the year, in terms of both spatial and temporal movements. Similarly, profiles depicting environmental features effectively illustrated how the environments differed among colonies and through the annual movement cycle of murres.

2.5.2 Environmental features

Bathymetry, CHL and sea surface temperature are often used to describe potential differences in foraging habitat and habitat selection among seabirds and marine mammals (Anderson et al. 2013). For example, sea-surface temperature and CHL can help describe areas of primary productivity (Marra 2002). Similarly, bathymetric (e.g. continental slopes, shelves), oceanographic (e.g. areas of upwelling, vertical stratification) and hydrographic (e.g. fronts and eddies) features aggregate prey and attract marine predators such as whales, seabirds and tuna (Pierotti 1988, Jahncke et al. 2005, Bost et al. 2009, Walli et al. 2009). Thick-billed Murres encountered a wide variety of these environmental conditions in nonbreeding areas, through a more variable distribution coupled with natural seasonal fluctuations. Compared to Common Murres, Thick-billed Murres occupied waters that were deeper, colder, and with less CHL. In comparison, Common Murres from different colonies encountered similar environmental conditions that depended more on seasonal fluctuation (e.g. increased CHL in spring) than on spatial movement. Thick-billed Murres were also more likely than Common Murres to encounter ice, although ice associations were not as strong as expected for Thick-billed Murres (Gaston 1980) and may reflect changing patterns in ice associations over time (Gaston and Robertson 2010), or reduced ice cover in our study years. Our study showed extensive variation in the environmental features of

nonbreeding habitats among Thick-billed Murre colonies, but not among Common Murres. This may indicate a greater potential for flexible behavioural adjustment to different habitats or environments among Thick-billed Murres.

Consideration of how their marine distribution is influenced by environmental determinants has been common for these two species. Thick-billed Murres and Common Murres are, respectively, considered "cold-water" and "warm-water" tolerant ecological counterparts, their seasonal distributions generally tracking the summer and winter position of the 5^{o}C and 15^{o}C isotherms (Tuck 1961, Gaston and Jones 1998) and at least partially responsive to ice cover. While we can confirm that Thick-billed Murres generally remained in colder waters than Common Murres year-round, temperatures recorded by GLS loggers on free-ranging Thick-billed and Common Murres suggest a more complex picture. Thick-billed Murres encountered winter temperatures ranging from 2-8 degrees; yet in spring, Thick-billed Murres from the Gannet and Minarets Islands were recorded in warm Gulf stream waters (up to 15^{o}C) off the Flemish Cap (see also Chapter 3). Similarly, association with the leading ice edge was not obvious; birds from Coats, Digges, and Prince Leopold did partially intersect with ice in winter but those from the Gannet and Minarets Islands remained well out of range of ice year-round.

2.5.3 Core winter overlap

Core home range overlap also illustrated patterns of inter- and intra-specific segregation during the winter. Thick-billed Murres had more varied core winter areas than Common Murres, including in Baffin Bay (western Greenland), Davis Strait, the Labrador Sea, and the Orphan Basin/Grand Bank (McFarlane Tranquilla et al. 2013), partially dependent on colony of origin. Individuals from particular colonies tended to aggregate in similar winter areas, but with some distributional variation among individuals (McFarlane Tranquilla unpubl. data), and less individual overlap among those from northerly

colonies (Tble 2.4). This suggests that prior knowledge of important winter foraging areas (Guilford et al. 2011, Wakefield et al. 2011) along with colony-specific cultural effects (Grémillet et al. 2004) may combine to determine movement strategies for populations of Thick-billed Murres. This may also be true for Common Murres, but in comparison, their less variable movement strategies caused a high spatial overlap among colonies in a relatively restricted winter area on the Grand Bank and Orphan Basin.

For adult Thick-billed and Common Murres, inter-specific competition during winter appears to be minimized by low spatial and temporal overlap. Overlap of core winter areas for Thick-billed Murre colonies was equally low (15%) for inter- and intra-specific comparisons; in contrast, for Common Murres colonies, overlap of core winter areas was less between species than within species (15% vs. 43%; respectively). Despite higher inter-specific overlap with Common Murres from nearby colonies, Thick-billed Murres tended to roam more widely (see also Chapter 3). This suggests that movement patterns can be adjusted where greater overlap occurs. Similarly, KHR overlap of individual Thick billed Murres was lower but more variable by colony (ranging from 10-33%) than was overlap of individual Common Murres (36-44%). Although colony overlap was high for Common Murres, the detailed inspection of latitudinal and habitat profiles during winter may suggest a small degree difference in timing of habitat use (depth, temperature) between colonies, particularly between the colonies that overlapped the most (61% between Funk and Gull island colonies). Also, although colonies converge at a large scale to a similar wintering site, there may be less overlap between individuals at a small scale. Further tracking study with devices such as GPS to determine fine-scale segregation of nonbreeding habitat would help discern patterns of intra-specific segregation among proximate Common Murre colonies.

2.5.4 Implications of winter strategy

Among seabirds, the nonbreeding period encompasses post-breeding, wintering, and pre-breeding phases of the annual cycle and usually includes two feather moults and a migration of some scale (long- or short-distance). In addition to moult and migration, seabirds must also meet energetic requirements for survival on wintering grounds, which at high latitudes can be a challenge (Grémillet et al. 2005, Fort et al. 2009). In the Northwest Atlantic, Fort et al. (2009) found energetic requirements to be greatest in November and December, and influenced by geographic location (e.g. higher latitudes incurred higher energy expenditure). This "energetic bottleneck" coincides with a decrease in the available hours of daylight during the northern hemisphere's winter equinox. Reduction in available daylight is of particular importance to Thick-billed Murres, which wintered in areas with longer nights (Table 2.4); and 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 in the Northwest Atlantic (Fort et al. 2009). The location of core winter areas, and the extent to which seabird species and populations mix there, are therefore critical to understanding overwinter survival.

For Thick-billed Murres, rather than a complete divergence of winter ecological niche from Common Murres, we found instead a *widening* of an overlapping ecological niche. This strategy would mitigate both inter- and intra-specific competition, which can be a major determinant of the diversity of strategies among individuals within populations (Svanbäck and Bolnick 2007), allowing more room for individual variation/specialization. Not only was this pattern of greater variation in Thick-bills found when comparing colonies spanning a wide latitudinal range (i.e. at study colonies from High to Low Arctic regions) but it was also evident between the species breeding sympatrically at the Gannet Islands. Fort et al. (2013) also found that Thick-billed Murres tracked from Bjørnøya, Svalbard, wintered in a broad area of the North Atlantic, compared to sympatric Common Murres which wintered in a restricted area within

1000 km of the breeding colony. 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 is habitat partitioning indistinct among Common Murres from different colonies, whose core winter overlap was greater than that for most Thick-billed Murre colonies, and for which migratory connectivity within and among colonies is high? It may be that Common Murres in the NW Atlantic do not partition habitat from conspecifics at a large scale, perhaps due to relaxed competition where resources are abundant (i.e. Grand Bank of Newfoundland), or due to fixed and highly conservative habits restricting mobility, habitat preference and diet. Conversely, they may partition at a smaller scale to make up for broadly overlapping habitat, as well as broadly overlapping diet associations (LMT, unpublished data; see Chapter 5). Further tracking using GPS devices may uncover local-scale interactions among Common Murres. We did not test for partitioning in 3-dimensional space (e.g., dive depth, or daily activity patterns), which can effectively partition habitat between competing conspecific seabirds (Hull 2000, Masello et al. 2010, Linnebjerg 2012). Additionally, the role of increased diet partitioning in areas where spatial overlap is high will be helpful in describing smaller-scale ecological partitioning. For example, Barger and Kitaysky (2011) documented increased segregation of Thick-billed and Common Murre foraging niches in years of food shortage, when inter-specific competition was likely elevated. More detailed research on inter- and intra-specific trophic associations is currently being pursued (see Chapter 5).

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 environment (e.g. ice conditions, shifting isotherms), the presence of competitors that influence available habitat, and to anthropogenic influences (McFarlane Tranquilla et al. 2012). Indeed,

such phenotypic plasticity may have originally played a role in character displacement and divergence (Pfennig and Pfennig 2012) of Thick-billed and Common Murre species.

Particular to the Northwest Atlantic, the intersection of the Labrador Current and the Gulf Stream contracts the 15^{o}C February isotherm to a narrow band running along the edge of the Grand Bank. Thus thermal habitat preference of the available winter range may constrict and concentrate Common Murres in the NW Atlantic. At the same time, seasonal ice cover reduces the amount of Thick-billed habitat available in the north, restricting the available winter habitat toward the Grand Bank in late winter. These conditions could combine to further increase inter- and intra-specific competition in the NW Atlantic where the species overlap at the southern edge of their distribution. As climate change alters and reduces the distribution and extent of Arctic winter ice cover, at the same time causing shifting isotherms and associated prey assemblages, it is critical to understand flexibility in habitat use and how competitive interactions may be influenced by changes in available winter habitat. This will be particularly important in the case of Common Murres, which show a high degree of inter-colony connectivity on the wintering grounds.

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CHAPTER 3 – CONTRASTING MOVEMENT STRATEGIES OF NONBREEDING THICK-BILLED AND COMMON MURRES

CHAPTER 3 - CONTRASTING MOVEMENT STRATEGIES OF NONBREEDING THICK-BILLED AND COMMON MURRES

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3.1 SUMMARY

1. Among seabirds, patterns of migration and seasonal movement will determine the extent of flexibility in response to the dynamic marine environment, and are critical to identifying important nonbreeding habitat areas to identify conservation concerns. We tracked multiple colonies of Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*) to gain insight into both inter- and intra-specific differences in 1) patterns of migration and 2) changes in seasonal spatial distribution within the nonbreeding period (fall-winter-spring).

2. Colony arrivals and departures were more synchronous at higher latitudes, and birds from higher-latitude colonies travelled farther to wintering sites. However, colony latitude did not influence the date of colony departures/arrivals, which were remarkably similar despite the wide latitudinal range. Most birds made directed movements to staging/wintering areas in the Labrador Sea within 8-26 days of colony departure, excepting Thick-billed Murres from Coats and Digges which staged in Hudson Bay for ca. 100 days prior to migration to the Labrador Sea.

3. Compared to Common Murres, individual Thick-billed Murres travelled 3.6 times farther to winter centroids (~560 km vs. 2,030 km, respectively), and had home ranges ~2 times larger. Consequently, Thick-billed Murre colony winter home ranges (i.e. individuals pooled) were 2-4 times larger than for Common Murres. Furthermore, Thick-billed Murres showed strong seasonal shifts in core distribution from fall to winter and particularly in spring, when birds were most widely dispersed. For Common Murres, seasonal shifts in core distributions were not dramatic.

5. Patterns of distribution varied more strongly in relation to species, colony, and season than to anticipated geographical influences. Building a picture through individual, colony, and seasonal movement patterns, Thick-billed Murres employ a greater diversity of movement strategies than do Common Murres. This has implications for relative sensitivity of each species to changes and disturbances that may affect various components of nonbreeding habitat.

3.2 INTRODUCTION

To cope with seasonal fluctuations in food abundance, many species migrate to and from productive breeding and wintering areas. Migration strategies among seabirds vary from rapid and directional, to drifting or dispersive movements (Newton 2008). The range of migration strategies is easily conceptualized across species groups; for example, shearwaters and terns make dramatic trans-equatorial migrations, whereas cormorants and shags are more dispersive (Nelson 1979). However, when studied between closely-related species and within species, patterns of migration can offer insight into the extent of phenotypic and/or behavioural variation contributing to the flexible use of space (Shaffer et al. 2006, Oppel et al. 2009, Kubetzki et al. 2009, Dias et al. 2010, Guilford et al. 2011).

Recently, a proliferation of tracking research has provided substantial insight into migration and winter habitat use among pelagic seabirds (González-Solís and Shaffer 2009, Block et al. 2011, Wilson and Vandenabeele 2012). This research has shown that particular seabird species dispersing from breeding colonies may travel along similar routes to shared wintering areas (Hedd et al. 2012), may take different routes to shared areas (Egevang et al. 2010) or that they may winter in entirely different areas (González-Solís et al. 2007, Kubetzki et al. 2009, Bogdanova et al. 2011, Fifield 2011, Magnusdottir et al. 2012). Similarly, movement strategies among multiple

colonies can be variable (Frederiksen et al. 2011, Fort et al. 2012). Differences in movement strategy depend on a suite of influences, ranging from weather conditions, to physical distribution of marine foraging areas, to mechanisms structuring habitat use by age, sex, colony and individual. Clearly, knowledge of migration strategies, migration corridors and wintering areas will be critical to understanding population dynamics (Esler 2000, Webster et al. 2002, Reynolds et al. 2011) and conservation needs of pelagic seabirds (Fredericksen et al. 2011, Fort et al. 2012).

Despite recent growth in the field, seasonal movements of pelagic species have been best described for species that traverse great expanses of ocean to occupy highly productive areas in "endless summer" conditions (cf. Shaffer et al. 2006). Many pelagic seabirds, however, remain year-round in areas that experience intense seasonal fluctuations in marine productivity, such as the Northwest Atlantic (Barrett et al. 2006, Campbell and O'Reilly 1988).

Here, I investigate inter- and intra-specific migration patterns for two such seabirds: the closely-related Thick-billed Murre (*Uria lomvia*) and Common Murre (*U. aalge*). Seasonal movements in the two species vary from short to longer-distance migration. Thick-billed Murres breeding at high latitudes are thought to move farther to winter within ice-free lower latitudes (Gaston and Hipfner 2000), whereas Common Murres' breeding and overwintering areas are closer together (Ainley et al. 2002). Migration can be more directional (cf. Newton 2008) among Thick-billed Murres, particularly for those breeding at high latitudes (Tuck 1961, Kampp 1988). Among Common Murres, migration is considered more dispersive, but is complex and less well understood (Tuck 1961, Gaston and Jones 1998). As for many species breeding at higher latitudes, timing of breeding within the seasonally productive window is critical, and often is more synchronous than at lower latitudes. Although it is reasonable to expect that migration patterns occur in response to spatial and temporal variation in seasonal ice cover (Tuck 1961, Gaston and Robertson 2010, Gaston and Hipfner 2000), environmental determinants of migration may be only part of the story. Other factors

such as competition (Wakefield et al. 2012), phenotypic variability, individual movement decisions (Oppel et al. 2009, Guilford et al. 2011) and "cultural differences" associated with colony of origin (Grémillet et al. 2004) in which individuals from a particular colony exhibit similar wintering tactics (Phillips et al. 2009, Thiebot et al. 2012), may also contribute to movement strategies.

Until recently, details of migration and wintering areas for eastern Canadian murres have been gleaned from decades of banding and analyzing recovery distributions (Gaston 1980, Donaldson et al. 1997, Lyngs 2003). This information incompletely describes migratory timing, patterns of movement through time, and winter areas of occupancy that might be seasonally inaccessible to observers. Building on research describing winter habitat among several murre colonies (Gaston et al. 2011, Hedd et al. 2011; Chapter 2), we further explore geographic patterns of migration and seasonal areas of occupancy for Thick-billed and Common Murres from seven colonies from High to Low Arctic regions in eastern Canada. Importantly, our comparison included colonies in both allopatric and sympatric parts of the species' breeding ranges.

If murres migrate partly in response to environmental and/or geographic constraints, then we would expect those breeding at higher latitudes to 1) depart and arrive at colonies more synchronously, 2) migrate earlier and farther to suitable wintering areas, 3) shift southward as the winter progresses and inclement conditions develop at high latitudes, and as a result, 4) have larger year-round home ranges. Furthermore, we expect 5) birds within species, and to some extent within colonies, will display similar patterns of migration and seasonal movement.

3.3 METHODS

Study area and species - This research was carried out at seven eastern Canadian seabird colonies: Prince Leopold Island in the Canadian High Arctic (74°02' N, 90°00'W,

2008-10); the Minarets (66°57’ N, 61°50’ W, 2007-08) on Baffin Island; Coats Island (62°53’ N, 82°00’ W, 2007-10) and East Digges Island (62°32’ N, 77°45’ W, 2008-10) in Hudson Bay, Nunavut; Gannet Islands, Labrador (53°56’ N, 56°32’W, 2008-11); Funk Island (49˚45'N, 53˚11'W, 2007-11) and Gull Island (47°16’N, 52°46’W, 2007-2011) in Newfoundland (Figure 3.1). These colonies support Thick-billed Murres *or* Common Murres, except at the Gannet Islands where they nest sympatrically. All murres equipped with tracking devices were actively breeding (i.e. on eggs or chicks) when captured.

Deployments – As described in Chapter 2, five geolocator models (British Antarctic Survey (BAS) Models Mk5, Mk7, Mk13, and Mk 15, n = 266; or Lotek 2500, n = 16) that record light, temperature, and salt water immersion were attached to murres in July or August using leg bands (logger, band and cable ties < 1% adult body mass). Geolocators were deployed on 282 breeding Thick-billed Murres (155) and Common Murres (127) in 2007-2009, retrieved from 163 birds (58%) in 2008-2011, with reliable data from 143 devices (52%; 87 Thick-billed, 56 Common). Most loggers were collected in the year following deployment; however several were left on for >1 year (maximum 3 years), providing repeat tracks for 42 individuals and a total of 182 annual round-trips.

Geologger processing – Following the methods described in McFarlane Tranquilla et al. (2013), light data from BAS geolocators was processed using MultiTrace Geolocation software (Jensen Software Systems) according to Phillips et al. (2004). Processing was done using a “light threshold” method (described in Hill and Braun 2001, Lisovski et al. 2012) to minimize loss of data and latitudinal discrepancy before and after the equinox (Lisovski et al. 2012). Equinox periods were not deleted *a priori* because equinox errors were highly variable depending on the individual logger, likely reflecting differences in device, weather, or bird behaviour (see Lisovski et al. 2012); thus, all data during equinox periods were inspected and reasonable positions were retained. As well,

during equinox periods only, sea-surface temperatures (SST) were used to improve geolocation accuracy (Teo et al. 2004) on a case-by-case basis when the SST matching algorithm contributed reasonable data in areas where latitudinal thermal stratification was evident (e.g. the Grand Banks of Newfoundland and Scotian Shelf; see McFarlane Tranquilla et al 2013, and Chapter 2 for a full discussion). The resulting SST-corrected positions (only 9% of retained geolocator data) were added to fall (September-October) and spring (February-April) periods. For both BAS and Lotek devices, clearly erroneous locations resulting from light level interference that represented unrealistic movements (> 500 km/day) or were outside the likely species' range were removed (Phillips et al. 2004). Positional data were smoothed twice (2-day running average), retaining the original fixes at the start and end of any periods where data were missing (Phillips et al. 2004) or replaced with SST-corrected data. Mean accuracy of GLS location data are assumed to be ~ 186 $\pm$ 114 km, as determined by Phillips et al. (2004).

Colony attendance and timing of migrations – BAS geolocators record wet/dry activity every 3 seconds to provide total wet activity in 10-minute intervals (Fox 2010). The subsequent pattern of wet/dry activity can help determine when breeding murres stop regularly attending the colony, and when they first arrive in spring. To reduce the possibility that observed dry periods were due to extended periods of flight, only dry periods > 6 hours in the appropriate season were presumed to indicate birds were attending colony sites. In the absence of activity data, individual locations were plotted in GIS and colony departures and arrivals were presumed when birds entered a 200-km buffered circle (simulating geolocator location error; Phillips et al. 2004) around the colony. Due to limited memory capacity (Mk7 devices) and some mid-year device failures, there are fewer details for spring (i.e. colony arrivals) than for fall and winter periods. As well, equinox influences sometimes made exact fall departure timing unclear.

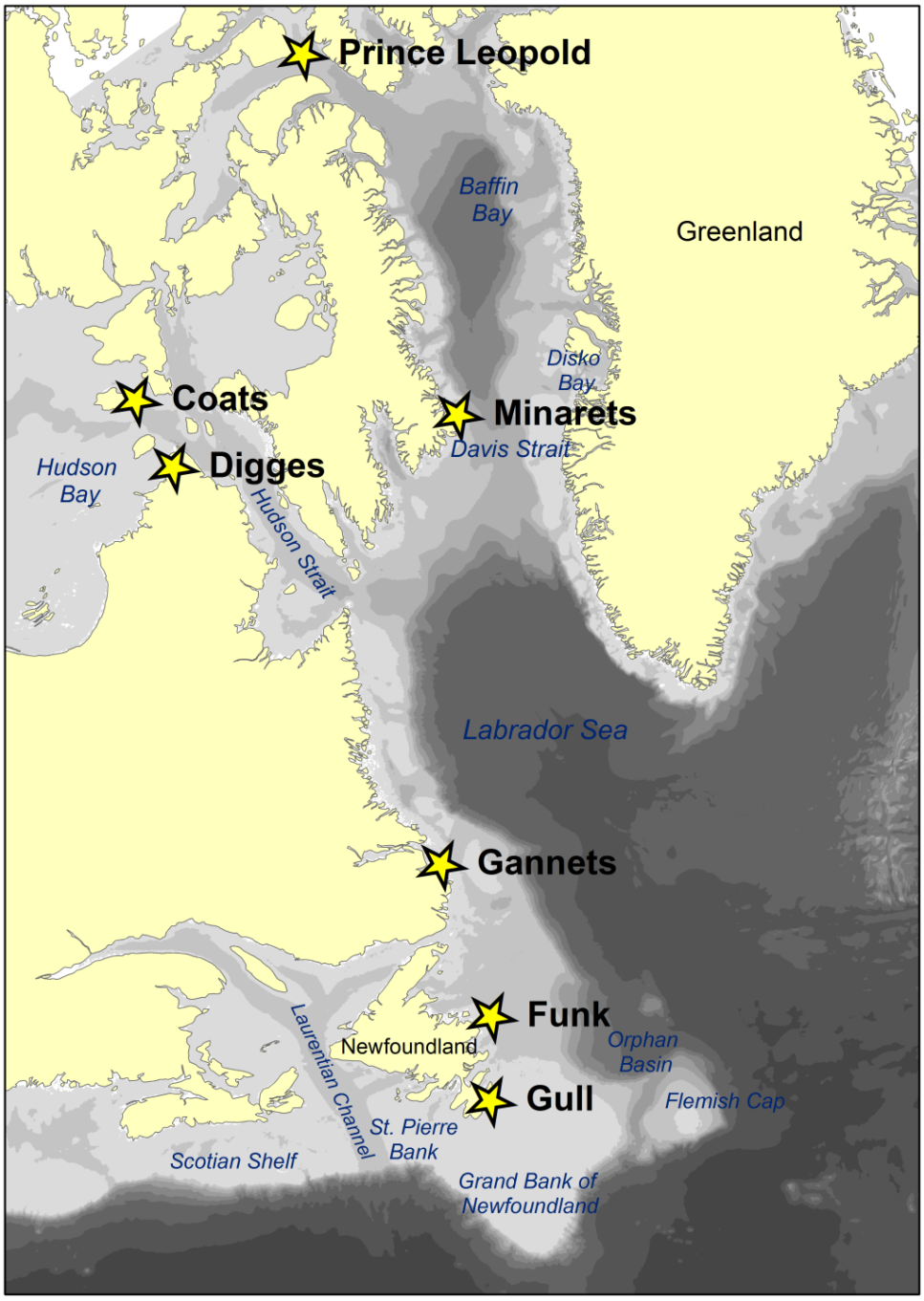

Figure 3.1. Study area and colonies of Thick-billed Murres (Prince Leopold, Minarets, Coats, Digges, Gannets) and Common Murres (Gannets, Funk, Gull). Place names are referenced in the text.

Describing migration timing was difficult due to the indeterminate endpoint for many murres; while some travelled rapidly to particular locations, others shifted throughout the nonbreeding period, hence we divided the analysis into 4 sections by season (fall, early winter, late winter, and spring; see below). Further complicating analyses, fall migration patterns differed substantially between colonies, particularly for birds from Coats and Digges Island, for which what might be termed "fall migration" actually occurred during early winter. Given these complications, the "fall migration" was defined for all colonies as "post-breeding migration", and its endpoint was defined as the date when individual birds first stopped in a potential marine wintering area (such in the Labrador Sea, or more generally the NW Atlantic) for more than 10 days within a radius of 200km. Similarly, definite start and end times for most pre-breeding migrations were not possible to define for most individuals, excepting murres from the Minarets and Gannet Islands who exhibited a clear spring staging area (see results). Year-round GLS tracks for all birds were mapped in ArcMap and scrutinized on an individual basis by the same observer (LMT) to make these determinations.

Mammalian predators were present at two colonies, the Gannet Islands (2010; polar bear) and Funk Island (2009, 2010; arctic fox), causing colony-wide disturbance and failed breeding (Burke et al. 2011; this study). As a result, colony departure (determined from wet-dry activity) in both Common and Thick-billed Murres from the Gannet Islands was 10-13 days earlier in 2010 than in 2008/2009 (Thick-billed Murres, ANOVA $F_{2,19}$=2.59, p=0.01; Common Murre, ANOVA $F_{2,23}$ = 9.31, p=0.001), although several birds remained in the colony vicinity on the water (LMT unpublished data). Subsequent analyses of departure and migration timing therefore exclude 2010 Gannet Island data. Surprisingly, colony departure among Common Murres from Funk Island did not vary by year ($F_{2,33}$=0.04, p=0.99; suggesting continued colony attendance even if breeding attempts had failed), so all Funk data was retained in data analyses. As well, for murres which remained near the Gannet Islands colony but did not shade the

geologger (i.e. not incubating eggs), we had a unique opportunity to calculate the mean distance from the colony in summer; this was done as a separate analysis.

Kernel home range (KHR) and distance analyses – Positional data were used to create 50% and 95% KHRs for each individual (single track per year). Individual KHRs were created in R (version 2.15.2) using the "adehabitat" package with LSCV smoothing. In addition, positional data for individuals were pooled by colony, to create 50% and 95% KHRS for each colony during four seasons in the non-breeding period: fall, immediately post-departure from the colony (late August – September), early winter (November-December), late winter (January-February) and spring (March-April). The winter months were split this way because murres from Coats and Digges Islands did not move out of Hudson Bay until early-mid December. KHRs for each season were evaluated using the Kernel Density Tool in the ArcMap Spatial Analyst Toolbox (ArcMap 9.3, ESRI 2009) with a cell size of 50 km and a search radius of 200 km (Phillips et al. 2004), and using Lambert Azimuthal Equal-Area Projection. 50% kernel contours (50% KHR) were considered to be the "core" home range for each colony (Wood et al. 2000, Phillips et al. 2005) and were drawn in ArcMap 9.3 with Hawth's Tools (version 3.27).

Distances from the colony to monthly centroids for each individual in all nonbreeding months (September – May) were calculated using the Spatial Statistics Toolbox in ArcMap 9.3. Distances for individuals were averaged by month, to describe mean distance year-round, for each colony. To describe distance to wintering areas, we used only the mean monthly centroid at the start of the late winter period (January centroid). This helped resolve the discrepancies in timing of the post-breeding migration among colonies.

Statistical analyses - General linear models (glm) in R (version 2.15.2) were used to make colony-level comparisons, e.g. timing of colony arrivals and departures and size of KHRs, in relation to latitude (and including species or season where appropriate). Relative synchrony of departures and arrivals was assessed with glm, by regressing the

variance of mean dates for each colony against latitude. Although colony attendance did not vary significantly by year, annual variances were different, thus analysis of synchrony included each year separately rather than pooling variance across years. Linear mixed-effects models (lme), with individual as a random factor, were used for analyses which included data from individuals (e.g. for individual distances and KHR sizes). Eighty-five percent (85%) KHR colony ranges were used to investigate the effect of latitude on home range size. All dates in tables are presented as mean $\pm$ SD days.

3.4 RESULTS

3.4.1 Colony departures

Birds at higher latitudes had more synchronous colony departures (glm, $F_{1,17} = 4.98$, $p = 0.04$, $R^2 = 0.23$; Figure 3.2). However, date of colony departure was not influenced by latitude. Thick-billed Murres departed colonies only 4 days later (23 August) than Common Murres (19 August; glm, $F_{1,154} = 7.36$, $p = 0.007$; see Table 3.1). At the Gannet Islands where they breed sympatrically, departure dates of Thick-billed and Common murres were the same (glm, $F_{1,46} = 0.17$, $p = 0.681$).

Among Thick-billed murre colonies (see Table 3.1), departure dates showed no relationship to latitude (glm, $F_{1,96} = 0.003$, $p = 0.09$), year (glm; $F_{2,60} = 0.75$, $p = 0.48$), colony ($F_{4,60} = 1.75$, $p = 0.15$) or sex ($F_{1,60} = 1.68$, $p = 0.20$). Among Common Murre colonies, departure dates varied only by colony (glm, $F_{2,44} = 33.6$, $p \leq 0.001$; wherein Gull Island murres left the colony 8-13 days earlier) and sex ($F_{1,44} = 15.23$, $p \leq 0.00$; wherein males (17 August, n = 18) left the colony ~3 days earlier than females (20 August, n = 34)).

3.4.2 Colony arrivals

There was not a significant trend for greater synchrony of colony arrivals at higher latitudes (glm, $F_{1,14}$=0.28, p = 0.61, R^2=0.02). Date of colony arrival was weakly influenced by latitude (glm, $F_{1,125}$=5.74, p = 0.02, R^2=0. 04; Figure 3.2), and was not related to species, year, or sex (p > 0.5 in all cases), but slight variation by colony occurred: among Thick-billed Murres, colony arrivals were ~ 10 days later for birds returning to Prince Leopold and Gannet Islands. Among Common Murres, birds arrived 10-13 days earlier at Funk Island than at Gull or Gannet Islands (Table 3.1).

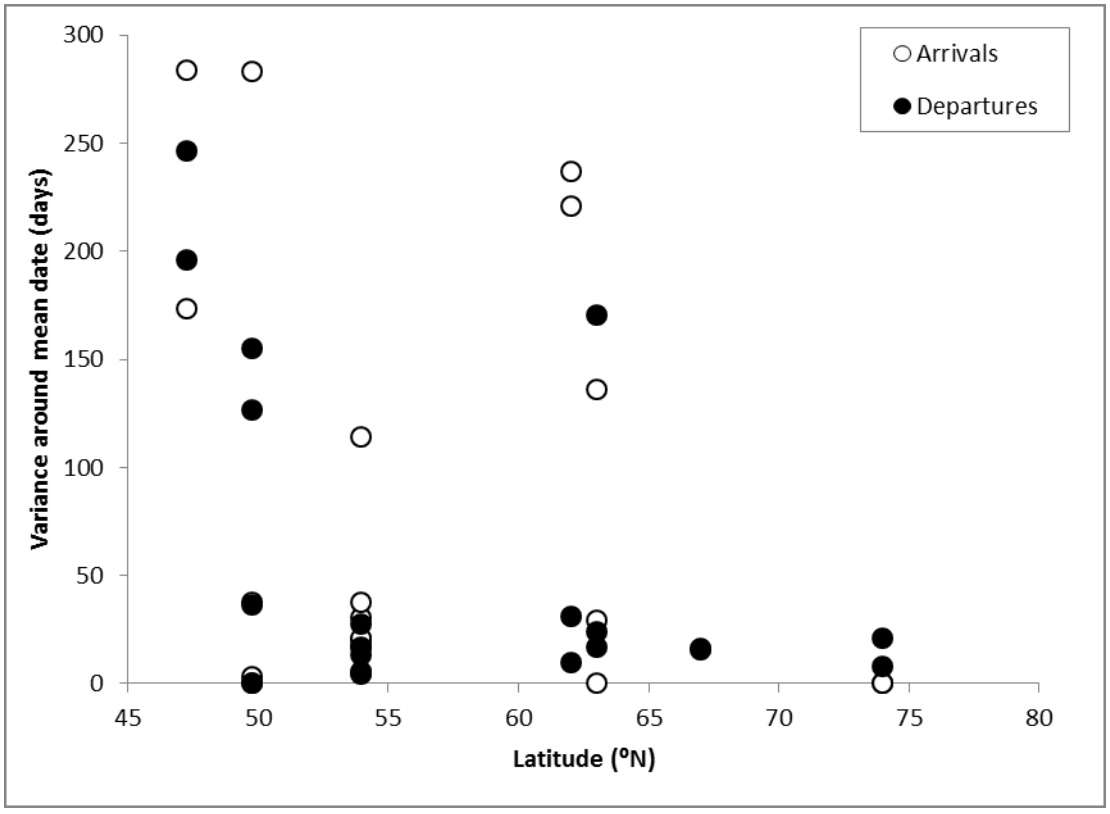

Figure 3.2. Synchrony of colony arrivals and departures, as determined by variance around mean date by latitude. Multiple points at each latitude (i.e. colony position) indicate multiple years at each colony.

Table 3.1. Details of migration timing for colonies of Thick-billed and Common Murres. Mean dates (+ SD days) are estimated from individually tracked birds (N) and pooled by colony of origin. Note (*) includes fall staging in Hudson Bay; see Figure 3.4. Note also colony arrivals and departures may not always contain the same N, due to discrepancy in activity data that make colony attendance unclear in some cases.

			Colony Departures (Fall)		Arrival in Labrador Sea/ NW Atlantic	Duration to Labrador Sea/ NW Atlantic	Colony Arrivals (Spring)	
Species	Colony	Latitude (^{o}N)	N	Mean Date	Mean Date	Days	N	Mean Date
Thick-billed Murre	Prince Leopold	74	19	24-Aug ± 4	12-Sep ± 22	19 ± 21	2	13-May ± 6
	Minarets	67	14	23-Aug ± 4	2-Sep ± 4	8 ± 3	11	4-May ± 4
	Coats	63	32	21-Aug ± 6	1-Dec ± 14	101 ± 16*	22	5-May ± 7
	Digges	62	13	25-Aug ± 4	4-Dec ± 15	101 ± 15*	11	4-May ± 14
	Gannets	54	14	26-Aug ± 14	14-Sep ± 20	26 ± 19	20	15-May ± 7
	Overall		*92*	*23-Aug ± 5*	*23 Oct ± 44**	*60 ± 44**	*66*	*8-May ± 7*
Common Murre	Gannets	54	18	26-Aug ± 4	12-Sep ± 26	23 ± 24	21	13-May ± 8
	Funk	50	26	21-Aug ± 9	30-Aug ± 12	9 ± 8	24	3-May ± 11
	Gull	47	21	13-Aug ± 15	7-Sep ± 17	16 ± 9	16	16-May ± 14
	Overall		*65*	*19-Aug ± 12*	*5 Sep + 18*	*15 ± 16*	61	*11-May ± 11*

3.4.3 Migration

Post-breeding – Thick-billed Murres from Coats and Digges Island spent the fall in Hudson Bay and arrived in the Labrador Sea much later (1 December $\pm$ 14 SD days and 4 December $\pm$ 15 SD days, respectively) than the other colonies (Table 3.1) This equates to staging in Hudson Bay for 101 $\pm$ 16 SD and 102 $\pm$ 15 SD days (respectively). For the other 3 Thick-billed Murre colonies, timing of first arrivals in the Labrador Sea was remarkably similar (Table 3.1). Excluding Coats and Digges Island, arrival in the Labrador Sea did was not related to latitude ($F_{1,92}$ = 1.17, p = 0.281) and did not differ between Thick-billed (10 September $\pm$ 19 SD) and Common Murres (5 September $\pm$ 18 SD; $F_{1,92}$=2.4, p = 0.124; Table 3.1), nor was it related to latitude of colony.

Pre-breeding - A few individuals from all colonies made direct return movements from discrete spring areas but small sample sizes preclude colony-specific analyses. Only Thick-billed Murres from the Minarets showed a clear, discernible movement from offshore spring areas, covering ca. 3000 km (see also Figure 3.4) back to breeding colonies in 9 $\pm$ 4 SD days.

3.4.4 Distances travelled

Winter centroids – Distance travelled to winter centroids was positively related to colony latitude (lm, $F_{1,165}$ = 225.9, p < 0.001, R^2=0.82; Figure 3.3). Distance was also significantly influenced by species and colony. Individual Thick-billed Murres (n = 97) travelled 3.6 times farther than Common Murres (n = 69) from colonies to winter centroids (2027 $\pm$ 966 km (range 443-4038) and 558 $\pm$ 324 km (range 99-1296) respectively; lme, $F_{1,164}$=147.3, p < 0.001; Table 3.2). At the Gannet Islands, mean distance to winter centroid did not vary significantly by species (lme, $F_{1,42}$=0.001, p = 0.98); however, unlike Common Murres, Thick-billed Murres continued to disperse

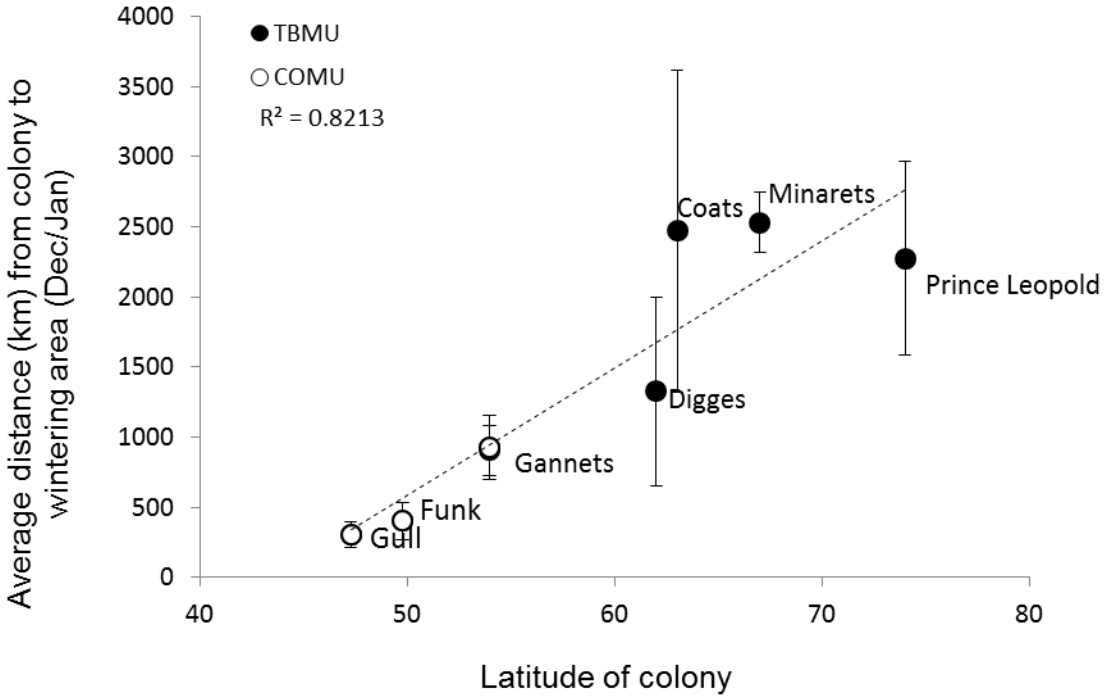

Figure 3.3. Mean distance (SD) travelled by murres to wintering areas (mean center, Jan) is positively related to latitude of colony of origin, both within and between species. Data are averaged across individuals and years (2007-2011) for each colony.

Table 3.2. Seasonal Kernel Home Range (KHR) areas (km^2), distance travelled (km) to winter mean center, and range of nonbreeding distances (September-April) travelled, for individuals (N) pooled by colony and across years for Thick-billed and Common Murres.

			85% KHR	50% KHR				Distances Travelled	
Species	Colony	N	All YR	Fall	Early Winter	Late Winter	Spring	Winter centroid (km ± SD)	Range (min-max) (km)
Thick-billed Murre	Prince Leopold	19	1,825,340	351,982	530,421	567,040	233,835	2233 ± 703	202-4423
	Minarets	12	2,223,050	325,590	365,756	492,388	631,936	2582 ± 208	1192-3554
	Coats	32	1,840,550	139,984	496,059	386,983	667,985	2602 ± 1067	99-5463
	Digges	10	2,083,500	169,116	471,652	450,923	562,655	1542 ± 587	99-2924
	Gannets	12	1,771,690	304,305	258,368	437,544	786,368	949 ± 162	35-1799
		Overall	*1,979,698*	*234,749*	*397,959*	*441,960*	*662,236*	*2,027 ± 966*	*35-4423*
Common Murre	Gannets	19	989,637	214,074	267,816	300,375	194,673	948 ± 226	35-1296
	Funk	16	672,725	167,026	192,421	236,802	178,824	409 ± 136	37-661
	Gull	16	674,740	255,826	178,599	185,126	144,573	304 ± 100	46-304
		Overall	*673,733*	*211,426*	*185,510*	*210,964*	*161,699*	*558 ± 324*	*35-1296*

throughout winter, until a maximum in spring (Table 3.2, compare Figure 3.4a and b). Considering species separately, distances to winter centroids varied significantly by colony for both Thick-billed (glm, $F_{4,92}$=20.7, $p < 0.001$) and Common Murres (glm, $F_{2,66}$=99.2, $p < 0.001$; see Table 3.2).

Year-round monthly centroids– Figure 3.4 illustrates considerable variation in the distance and seasonal timing of movement between species, and among colonies. The maximal distance of migration away from colonies in Thick-billed Murres (1799 - 5463 km) was 4.2 times farther than for Common Murres (304-1296 km; Table 3.2). In both species, distances varied significantly by colony (lme, $F_{4,69}$ = 16.9, $p < 0.001$ in Thick-billed Murres; lme, $F_{2,42}$= 65.1, $p < 0.001$ in Common Murres). As well, intra-specific variation of distances was greater in Thick-billed (lme output, std.dev. of the random effect (birdid) = 624 km) than in Common Murres (lme output, std.dev. of the random effect (birdid)= 38.5 km). Timing of movement also varied among colonies. For example, most Thick-billed Murres from Prince Leopold moved quickly from their colony in fall and were farthest away by October; Thick-billed Murres from Coats and Digges did not move progressively farther from colonies until a clear migration between November and December (Figure 3.4a), and were farthest from colonies by January; and Thick-billed Murres from the Minarets and Gannets Islands were farthest from their colonies in April (Figure 3.4a). In contrast, Common Murres (especially from Funk & Gull) stayed near colonies year-round; only birds from the Gannet Islands showed an obvious peak distance during April (Figure 3.4b).

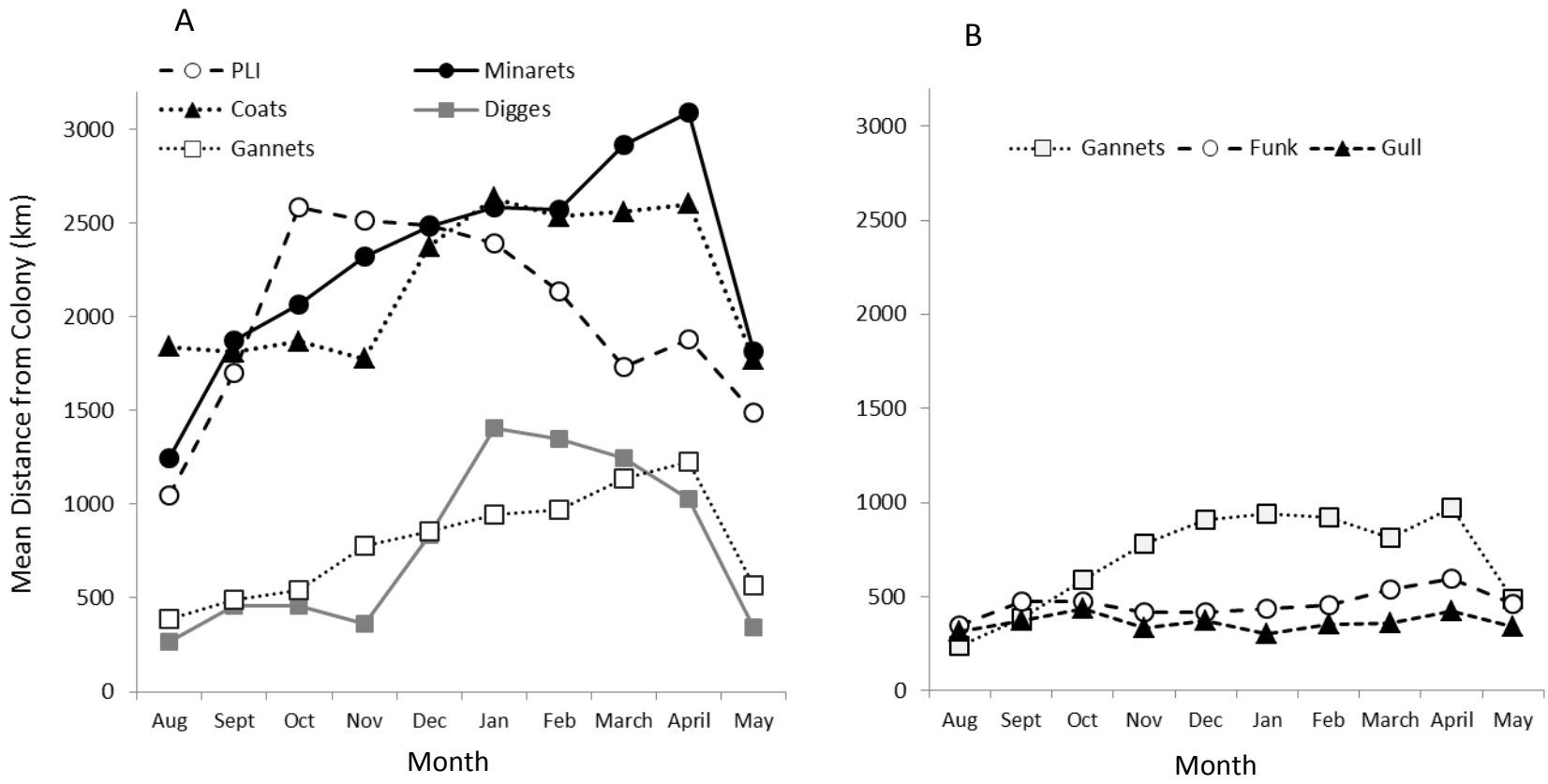

Figure 3.4. Mean monthly distance (km) travelled from the colony (individuals pooled) shows substantial variation in timing of maximum distance among (A) five colonies of Thick-billed Murres; but less so among (B) three colonies of Common Murres.

3.4.5 Home range size

Size of KHRs varied substantially by species and season, as presented in Table 3.2. Overall, range size (85% KHR, all year) for murres was not dependent on latitude (glm, $t_{2,5}$= 0.78, p = 0.46) but rather, was driven most strongly by species differences in range size (glm, $t_{2,5}$ = 4.17, p = 0.009), and by season (see below).

Home range size was substantially larger for Thick-billed Murres, at both the individual and the colony levels. Kernel home ranges (both 95% and 50%) of individual Thick-billed Murres (1,210,615 km^2 $\pm$ 633,869 SD and 256,221 km^2 $\pm$ 122,859 SD, respectively) were ~ 2 times larger than that of individual Common Murres (666,690 km^2 $\pm$ 260,628 SD, and 158,606 km^2 + 66,084 SD, respectively; lme, $F_{1,70}$=23.27, p < 0.001), with significant variation by colony ($F_{6,70}$=3.3, p = 0.006). At the Gannet Islands, where the species breed sympatrically and overwinter at similar latitudes, individual Thick-billed Murres (258,593 km^2 $\pm$ 93,361 SD) also had significantly larger home ranges than Common Murres (175,965 km^2 $\pm$ 73,129 SD; lme, $t_{1,25}$ = 2.8, p = 0.02).

At the colony level, kernel home ranges of Thick-billed Murres colonies were 2-4 times larger than Common Murres (glm, $F_{1,6}$ = 79.7, p < 0.001) in all seasons of the year (Table 3.2). The seasonal difference between the species was most notable during spring (March-April) when Thick-billed Murres (except for those from Prince Leopold; Figure 3.5) were more dispersed than Common Murres (Figures 3.6, Table 3.2).

3.4.6 Seasonal distributions

Fall– Immediately after colony departure, core use areas for Thick-billed Murres were variable, reflecting a diversity of colony-based strategies. At some colonies (Prince Leopold, Minarets), individual birds adopted one of two strategies: some individuals moved slowly away from colonies (through Baffin Bay, Figure 3.5a; or in the upper Labrador Sea, Figure 3.5b) while others made a more rapid migration southward. This pattern did not obviously correspond to sex (i.e. it was not simply slowly-migrating males with fledglings vs. rapidly-migrating females). In contrast, the fall strategy for

birds from Coats and Digges was to remain in Hudson Bay (Figure 3.5c,d). At the Gannet Islands, birds began moving in fall to the Strait of Belle Isle/Newfoundland Bank (Figure 3.5e). For Common Murres, core use areas in fall varied slightly among colonies, reflecting fall movement to the Strait of Belle Isle/Newfoundland Bank and on the eastern Grand Banks of Newfoundland (Figure 3.6).

Early and Late Winter–For Thick-billed Murres, winter strategies were variable, but colonies tended to converge on a particular strategy: murres from Prince Leopold Island dispersed widely in early winter, staying mostly in the mid- to upper-Labrador Sea, then began to move back toward the Davis Strait by late winter (Figure 3.5a). Murres from Coats and Digges stayed in Hudson Bay until December, but then dispersed widely throughout the Labrador Sea and beyond in late winter, particularly those from Coats (Figure 3.5c), one of which migrated to the Scotian Shelf (LMT unpubl. data), and some from Digges which reached the Orphan Basin/Grand Banks of Newfoundland (Figure 3.5d). Murres from Minarets and Gannets also dispersed more widely from early to late winter (Figure 3.5b,e), and stayed closer to the Orphan Basin/Grand Banks. For most colonies, core areas in late winter begin to splinter, reflecting increased differences in distributions of individual birds (Figure 3.5a,b,c,e).

Common Murres from all colonies remained centered on the eastern Grand Banks and Orphan Basin throughout winter. Slight variation was seen for some birds from Funk Island which moved southwest to shelf waters near the Laurentian Channel/southern St. Pierre Bank (Figure 3.6b).

Spring– Three main spring strategies were seen among Thick-billed Murres: murres from Prince Leopold appeared to stage in Davis Strait off western Greenland, having already moved there in late winter (Figure 3.5a); murres from Coats and Digges began movement northward and into Hudson Strait (Figure 3.5c,d); and for murres from the

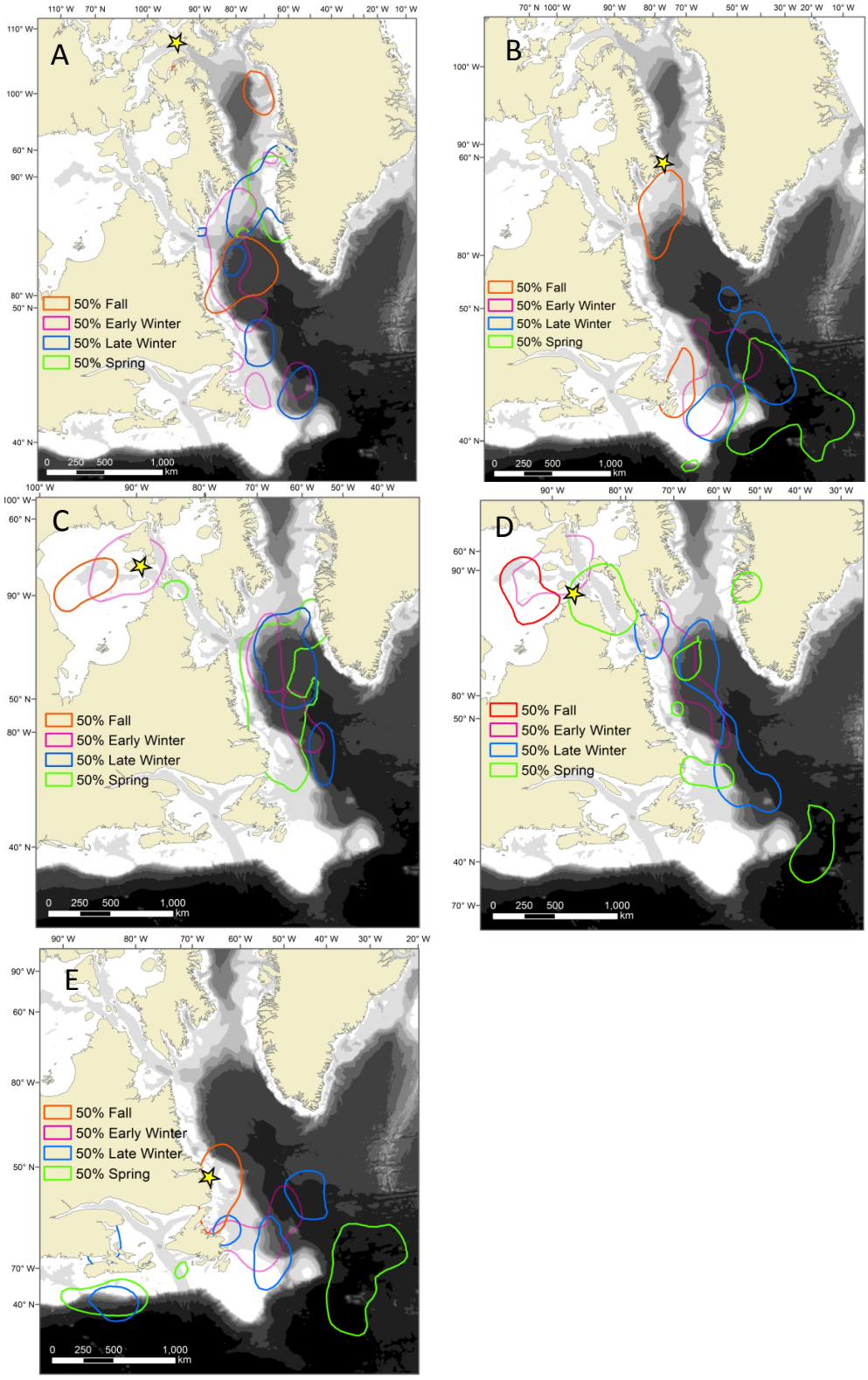

Figure 3.5. Seasonal variation (fall, early winter, late winter, spring) in core use areas (50% KHR) of Thick-billed Murres at 5 colonies (indicated by a yellow star): (A) Prince Leopold (B) Minarets (C) Coats (D) Digges (E) Gannet Islands.

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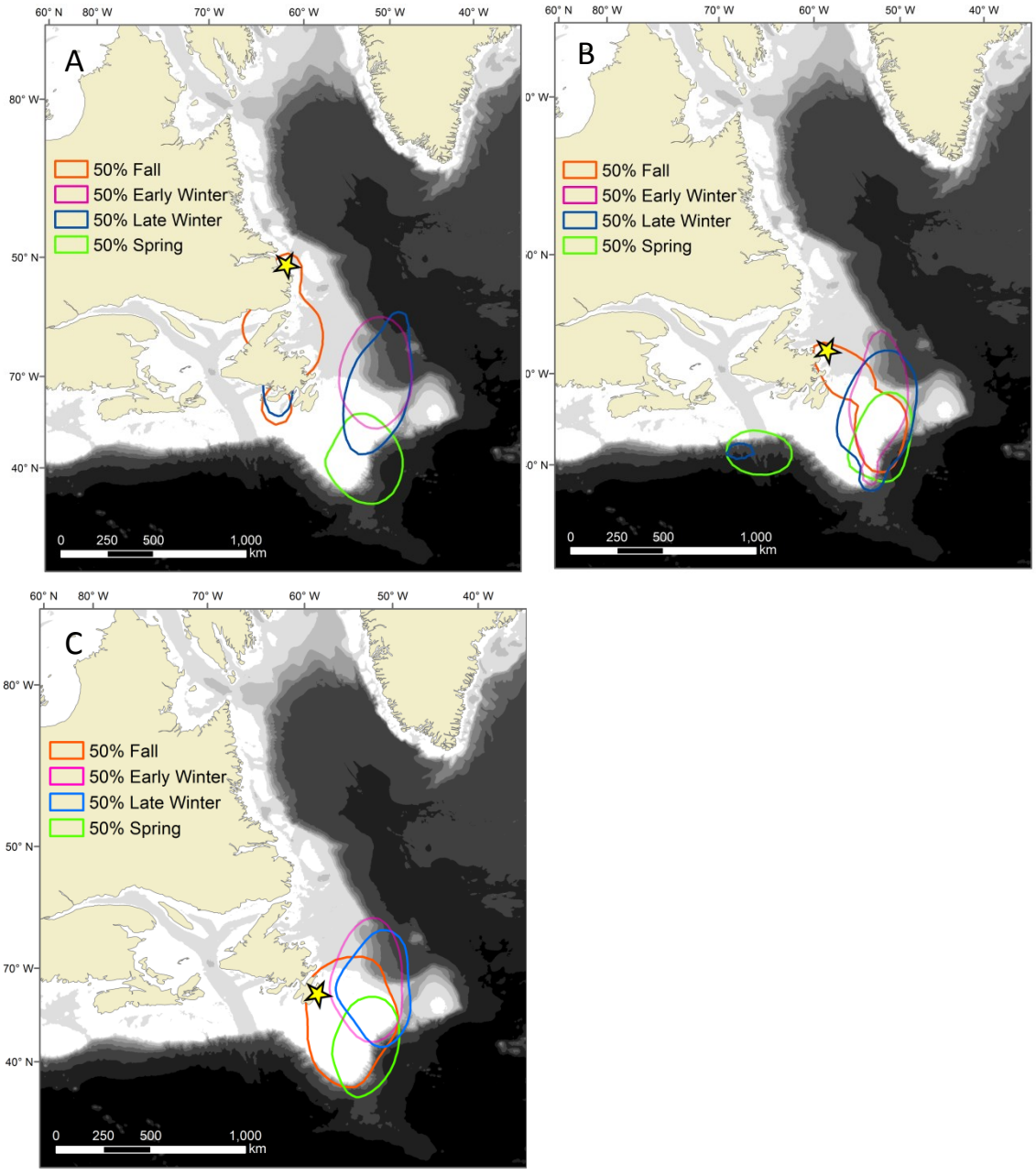

Figure 3.6. Seasonal variation (fall, early winter, late winter, spring) in core use areas (50% KHR) of Common Murres at 3 colonies (indicated by a yellow star): (A) Gannet (B) Funk (C) Gull Islands.

Minarets and Gannets, there was a widening of the their core area, as most birds shifted into pelagic waters west of the Mid-Atlantic Ridge with some using the Scotian Shelf (Figure 3.5b,e; see also Table 2). Thick-billed Murres (Gannets, n = 5/11, all 5 of which repeated use across 2-3 years ; Minarets; n = 7/14) using the core area west of the Mid-Atlantic Ridge (~34-53°N, 28-43°W) staged there for 50 + 7(SD) days before beginning spring migration toward breeding colonies.

Common Murres from all colonies concentrated on the northeastern Grand Banks in spring (Figure 3.6), with continued use of the shelf waters near the Laurentian Channel/southern St. Pierre Bank for some murres from Funk Island.

3.5 DISCUSSION

Details of migration and seasonal movements between closely-related species, particularly those that do not make dramatic seasonal movements, are not often reported. Here we compared seven colonies of Thick-billed and Common Murre to illustrate differences in seasonal movement strategies between species and for multiple colonies (Frederiksen et al 2011, Fort et al. 2012). Broad patterns of migration and seasonal movements tended to be shared by species and colony groupings, a finding supported by a growing body of research on other species (Phillips et al. 2009, Frederiksen et al. 2011, Thiebot et al. 2012).

3.5.1 Colony departures and arrivals

Murres at higher latitudes had slightly more synchronous colony departures but not arrivals. However, the date of colony departure was remarkably similar for species and colonies, and was unrelated to latitude. By the end of August, birds from all colonies had stopped attending colony sites, as determined by activity data of geolocators and confirmed by subsequent movement away from colonies (Figure 3.4; see also Chapter 2

and Gaston et al. 2011). This suggests that the regulation of colony attendance, and the timing of subsequent departure, are not limited to geographical variance in environmental constraints, and likely incorporate biological (i.e. breeding and chick-rearing) constraints. Timing of colony departures and arrivals can also depend on breeding outcome in many species (e.g. Bogdanova et al. 2011); in this study, we assumed successful nesting in all birds (all tagged birds had eggs or chicks), however, a paucity of breeding outcome data for murres precludes this analysis.

3.5.2 Migration and distances travelled

Although murres were distributed widely throughout the study area, they did not disperse gradually or randomly (also recently supported by Fort et al. (2013) for Thick-billed Murres tracked from Svalbard). Post-breeding Thick-billed Murres moved to their first staging areas (usually in the Labrador sea) within 8-26 days of leaving breeding colonies, except for those from Coats and Digges, which stayed in Hudson Bay for ~ 100 days before migrating to the Labrador Sea. Common Murres also made direct, shorter-distance movements following breeding, within 9-23 days of leaving breeding colonies. Pre-breeding migrations were mostly not discernible, except for Thick-billed Murres from the Minarets which travelled ~3000 km from spring staging areas to the colony in ~9 days.

Generally, murres from higher latitudes travelled farther to wintering grounds. This is in contrast to a recent study by Fort et al. (2012), in which northern colonies of Northern Gannets (*Morus bassanus*) occupied the northernmost wintering grounds. Yet distance travelled was also highly dependent on species and colony. Thick-billed Murres travelled on average 2030 km to winter centroids, and individuals reached maximal values of 1799-5400 km from colonies during the nonbreeding season. In comparison, Common Murres travelled on average 560 km to winter centroids, and individuals reached maximal values of 300-1300 km from colonies during the nonbreeding season.

3.5.3 Size and seasonal distribution of kernel home ranges

For both species, core home range sizes were reduced during the winter months. Only for Thick-billed Murres did core habitat increase during spring (March-April). For Thick-billed Murres, seasonal shifts in core distributions indicated migratory movements of birds from breeding colonies, most notably, 1) southward movement of birds out of Baffin Bay and a shift toward the Grand Banks/Orphan Basin from fall to winter; 2) movement out of Hudson Bay (Coats and Digges Islands) from early to late winter; and 3) widest dispersal in spring, with a shift to the Mid-Atlantic Ridge (murres from the Minarets and Gannet Islands colonies) and some occurrence on the Scotian Shelf. For Common Murres, seasonal shifts in core distributions were not dramatic, but do indicate migratory movements of birds away from the colony to fall centers in the Strait of Belle Isle/Newfoundland Basin and eastern Grand Banks, the Orphan Basin and St. Pierre Bank in early and late winter, and the northeastern Grand Banks in spring.

Although wintering areas were partially discrete among Thick-billed Murre colonies, colony ranges (85% KHR) for both species were independent of colony latitude. This suggests that dispersal distance from the colony did not change consistently as the season progressed (Table 3.2, Figure 3.4). Rather, distance travelled, size of kernel home range, and variance of both, were more strongly linked to colony-specific seasonal movement patterns/strategies. For example, home range area for Prince Leopold Island was largest in early winter and contracted in spring. For these birds, the area off Southwest Greenland used in spring (and for some individuals, used year-round; LMT unpubl.data), including Hellefiske Banke and Disko Bay, is an important marine area used year-round by both species of murre, Dovekie (*Alle alle*) and King Eiders (*Somateria spectabilis*; Boertmann et al. 2004, Mosbech et al. 2006, Linnebjerg 2012). For Thick-billed Murres from Coats and Digges, core spring habitat was larger than in winter, because it included individuals spread among three locations: those already staging in Hudson Strait, those beginning to move back toward colonies at high latitudes *and* those still in wintering areas. Finally, for murres from the Minarets and Gannet Islands, home-ranges were largest in spring compared to winter when individuals moved farthest from

colonies, many of them to deep pelagic waters near the Mid-Atlantic Ridge. Why Thick-billed Murres from the Minarets made definitive and directional movements to this offshore area, despite nesting near to the year-round hotspot in Southwest Greenland, remains to be seen. However, inter-specific competition with Thick-billed Murres from Prince Leopold (this study) and other Greenland colonies (Linnebjerg 2012) offers a plausible explanation.

3.5.4 Implications of seasonal movement patterns

These patterns reflect two differing strategies of seasonal distribution in spring: first, birds from three of the higher-arctic colonies (Coats/Digges/Prince Leopold) were staging or on their way back to high latitudes by spring. These colonies are located within ice-locked landmasses of Hudson Bay and Baffin Bay. Murres are known to time their return to colonies to spring ice break-up (Gaston et al. 2009), which presumably requires close attention to environmental cues (McNamara et al. 2011), and may account for the early return to northern latitudes. As for other arctic-breeders, the careful timing of return to colony sites is likely critical to breeding success in a short arctic summer (Weber et al. 1998). Furthermore, they may be relying on the "capital breeding" strategy of building up the reserves necessary for egg-production in productive staging areas on their way to breeding colonies (Klaassen et al. 2006, Jacobs et al. 2009). Second, Thick-billed Murres from Minarets/Gannets move farthest and distribute most widely in spring, and many individuals occupied an area between the Grand Banks and the Mid-Atlantic Ridge, recently described as a productive marine hotspot attracting a diverse array of over 30 pelagic seabird species year-round (Boertmann 2011, Wakefield 2011). The advantages of foraging in a persistently productive hotspot just prior to the breeding season may outweigh the need to be close to breeding colonies as soon as seasonal conditions allow. Besides, birds from the Gannets and Minarets are able to return quickly to colony sites when necessary.

Common Murre colonies were consistently centered on the eastern Grand Banks in spring, underlining the seasonal importance of this area to pre-breeders about to

return to colonies. Like the area west of the Mid-Atlantic Ridge (Boertmann 2011, Wakefield 2011), the Grand Banks is another seasonally productive marine area that attracts a host of seabirds year-round (Barrett et al. 2006, Hedd et al. 2012). Here, seasonal fluctuations in food availability appear not dramatic enough to necessitate movement from nearby Common Murre colonies to other winter sites.

The main difference in wintering strategy between Thick-billed and Common Murres was the degree of intra-specific variation. Thick-billed Murres showed a surprising amount of variation in area use, both between colonies and seasonally, whereas patterns of movement among Common Murre colonies were very similar, with little seasonal variation. This broad conclusion is supported at the Gannet Islands (this study) and at Bjørnøya, Svalbard (Fort et al. 2013) where both species breed sympatrically. At the Gannet Islands, although Thick-billed and Common Murres were equally near low-latitude wintering grounds, Thick-billed Murres ranged more widely, with greater seasonal and individual variation in distribution. As alluded to by Linnebjerg (2012) for other alcids, differences in patterns of seasonal movement may be evidence of past divergence of migratory and overwintering strategies among the species. As documented for several passerine birds (Helbig 1996, Irwin et al. 2011), one can speculate that divergent strategies of seasonal movement may have functionally partitioned nonbreeding habitat, potentially leading to or maintaining genetic differentiation between the migratory Thick-billed Murres, and the more resident Common Murres.

During the nonbreeding season, seabird mortality can be high (Frederiksen et al. 2008, Reynolds et al. 2011), particularly in the North Atlantic Ocean where reduced ocean productivity (Myers et al. 1994), short days, and harsh weather induce high energetic costs (Grémillet et al. 2005, Fort et al. 2009) leading to starvation (Hudson 1985, McFarlane Tranquilla et al. 2010); or which may have detrimental carry-over effects for the breeding season (Sorensen et al. 2009) even when adult survival is high (e.g. for Common Murres in Witless Bay; Robertson et al. 2006). Environmental conditions and food availability on wintering grounds are therefore critical, but can vary

spatially and temporally within and between years. It seems reasonable that these conditions could favour development of phenotypic variation and/or behavioural flexibility in responding to environmental cues (Grémillet et al. 2005, Oppel et al. 2009). The ability of murres to overcome wintering challenges may vary depending on species and wintering location. Thick-billed Murres' more variable use of nonbreeding habitat may buffer the species against environmental stochasticity; however, Common Murres may employ other strategies to survive the winter, such as trading off high travel costs of migration against increased foraging effort (Fort et al. 2013). Tracking studies will continue to provide insight into the extent of phenotypic variation in migration movements and in the use of space within and between populations (Shaffer et al. 2006, Kubetzki et al. 2009, Dias et al. 2010, Guilford et al. 2012). Linking seasonal changes in distribution to trophic connections (see Chapter 5) will provide further insight into the ability of species and populations to respond and adapt to changing climate conditions and conservation risks at overwintering sites.

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CHAPTER 4 – INDIVIDUAL WINTER MOVEMENT STRATEGIES IN TWO SPECIES OF MURRE (*URIA*) IN THE NORTHWEST ATLANTIC

CHAPTER 4 - INDIVIDUAL WINTER MOVEMENT STRATEGIES IN TWO SPECIES OF MURRE (*URIA*) IN THE NORTHWEST ATLANTIC

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4.1 SUMMARY

1) Individual wintering strategies and patterns of winter site fidelity in successive years are highly variable among seabird species. Yet, an understanding of consistency in timing of movements and the degree of site fidelity is essential for assessing how seabird populations might be influenced by, and respond to, changing conditions on wintering grounds.

2) To explore annual variation in migratory movements and wintering areas, we applied bird-borne geolocators on Thick-billed Murres (*Uria lomvia,* n=19) and Common Murres (*U. aalge,* n = 20) from five colonies in the Northwest Atlantic for 2-4 consecutive years.

3) Inter-specific differences were striking: Thick-billed Murres ranged widely and exhibited highly variable wintering strategies, whereas most Common Murres wintered relatively near their colonies, with individual variation represented more by the relative use of inshore vs. offshore habitat.

4) Within individuals, some aspects of the overwintering strategy were more repeatable than others: colony arrival and departure dates were more consistent by individual Common than Thick-billed Murres, while distances travelled to wintering area and the sizes of home ranges (95% utilization distributions) were repeatable for both species.

5) Over the 3-4 year timescale of our study, individuals employed either fixed or flexible wintering strategies; although most birds showed high winter site fidelity, some shifted core ranges after 2 or 3 years. We hypothesize that these long-lived birds use spatial memory, garnered from years of experience at sea, to inform and adjust annual movement strategies.

4.2 INTRODUCTION

Many seabirds migrate seasonally to wintering areas, where foraging and environmental conditions, affected by natural and anthropogenic processes, can influence their populations dynamics (Croxall et al. 2005, Phillips et al. 2009). These influences can be direct, through mortality, or indirect, through carry-over effects of winter body condition to subsequent reproduction (Sorensen et al. 2009, Harrison et al. 2011). Individual migratory strategies appear to vary considerably among species. For example, most birds from the same breeding population may migrate to the same region (Phillips et al. 2005, Hedd et al. 2012), or portions of the population may migrate to different regions (Kopp et al. 2011, Fort et al. 2012). Similarly, during successive years individuals may take one or several different routes to reach these areas (Kubetzki et al. 2009, Egevang et al. 2010, Guilford et al. 2011, Stenhouse et al. 2011). Variation in individual movement strategies or winter distribution can be linked to colony of origin, sex, age, experience, or breeding status (Phillips et al. 2009, Bogdanova et al. 2011, Fort et al. 2012, Fifield et al. 2013). Thus, information on individual movement strategies, both within and among years, can highlight the relative consistency in use of migratory corridors and in discrete wintering grounds which may need conservation attention (Croxall et al. 2005, Gonzales-Solis et al. 2007).

Among the few studies of seabirds that tracked the same birds repeatedly, some species showed high wintering-site fidelity (Croxall et al. 2005, Phillips et al. 2005, Fifield et al. 2013, Guilford et al. 2011), whereas in others, individuals shifted wintering locations between years (Oppel et al. 2009, Dias et al. 2010, Quillfeldt et al. 2010). Furthermore, the degree of flexibility in destination, travel times, timing of departure to and arrival at wintering sites can vary by species and is dependent on particular environmental or energetic constraints (Conklin et al. 2012). The extent of individual flexibility in wintering strategies provides valuable insight into selection pressures within

and between populations (Shaffer et al. 2006, Kubetzki et al. 2009, Oppel et al. 2009, Conklin et al. 2012). Individual behavioural flexibility will influence the capacity of populations to cope with rapid climatic and habitat changes (Reed et al. 2009, Dias et al. 2010).

The aim of this study was to assess individual consistency in wintering strategy in two closely related species, Thick-billed Murre (*Uria lomvia*) and Common Murre (*U. aalge*). Both species are abundant in the northern hemisphere and exhibit contrasting migratory strategies: Thick-billed Murres migrate long distances from high-latitude breeding sites to lower-latitude wintering areas, whereas Common Murres make much shorter-distance migrations (Hedd et al. 2011, Fort et al. 2013, McFarlane Tranquilla et al. 2013). Adult survival, breeding success, and population size have been linked to winter conditions in both species (Harris and Wanless 1996, Gaston 2002, Smith and Gaston 2012), underlining the intense selection pressures and consequences of behavioural decisions during the nonbreeding period. Our objective was to determine the degree of consistency in migration strategies by individuals in successive years by determining if they 1) arrive or depart colonies on similar dates, 2) travel the same distances, and 3) winter in the same areas; and 4) we investigated whether these patterns differed between species. We discuss implications of varying degrees of repeatability in particular components of the overwintering strategy and their relationships with migratory connectivity.

4.3 METHODS

Study Area – As part of a larger study (McFarlane Tranquilla et al. 2013), Thick-billed and Common Murres were captured at six breeding colonies spanning 47- 74^{o}N latitude in eastern Canada (Figure 4.1), during the summers of 2007-2011. These colonies support Thick-billed Murres or Common Murres, except at the Gannet Islands where the species

breed sympatrically (Table 4.1). At each colony, birds (confirmed breeders by the presence of eggs or chicks) were captured from breeding cliffs and a small geolocation-immersion logger (GLS; British Antarctic Survey (BAS) Models Mk 5, Mk 7, Mk 13, Mk 15; $\leq$ 3.5 g) was attached to the leg using a band and cable ties (including logger $\leq$ 5.4 g, $\leq$ 0.6% body mass). The logger was replaced in birds that were recaptured in the following year in order to track the same individual repeatedly; some elusive individuals were retrieved 2-4 years after the device was attached. These delayed retrievals resulted in 42 individuals with tracks for more than one year, for a total of 90 annual tracks (Table 4.1).

Data processing - GLS data were processed, filtered, and smoothed twice to determine year-round spatial distribution (refer to McFarlane Tranquilla et al. 2013 for a full description). Year-round tracks were assessed individually to describe general winter movement. To determine the timing of the start and end of annual migration, colony arrival and departure dates were estimated using immersion (wet/dry) data. The loggers test for saltwater immersion every 3 sec and log either the total number of positive tests at 10-minute intervals, or every change of state from wet to dry and *vice* versa exceeding > 6 sec). The subsequent pattern of wet/dry activity was particularly helpful in defining colony attendance, especially colony departure dates in late summer (when light data from the GLS device is affected by approach of the vernal equinox; Lisovski et al. 2012), and for detailing colony attendance at high latitudes when light data is adversely affected by very long daylengths (i.e one cannot calculate the timing of sunset when there is no sunset; Hill and Braun 2001). To reduce the possibility that observed dry periods were due to extended periods of flight (i.e. during migration to or from colonies), only those lasting > 6 h at the appropriate time of year were presumed to indicate birds attending colonies. In the absence of immersion data (in some cases, GLS devices recorded light but not immersion because the relevant memory sector was full, or there was partial device failure), individual locations were mapped in a GIS and

colony departures and arrivals were presumed to reflect dates of final exit or initial entry of the area within a 185-km radius of the colony (similar to the mean geolocation error; Phillips et al. 2004). Due to erroneous positions generated by light shading at the colony, this approach was less precise so it was used only when wet/dry activity data was absent. Comparisons of arrival and departure dates in consecutive years were standardized according to the mean dates (± SD), for each colony in each year. We were thus discerning whether individual birds were relatively early or late. Colony departure information on the Gannet Islands was excluded for 2010, when a polar bear *Ursus maritimus* was present; but was included for Funk Island in 2009 and 2010, when an arctic fox *Vulpes lagopus* was present at Funk Island (Burke et al. 2011), as colony attendance timing there was not detectably affected (LMT unpubl. data). As well, despite differences in life history, colony arrival and departure times did not differ detectably between male and female Thick-billed Murres, and differed by only 3 days in Common Murres (LMT unpubl.data). Sex was therefore not included as an explanatory variable in individual colony attendance patterns in this analysis.

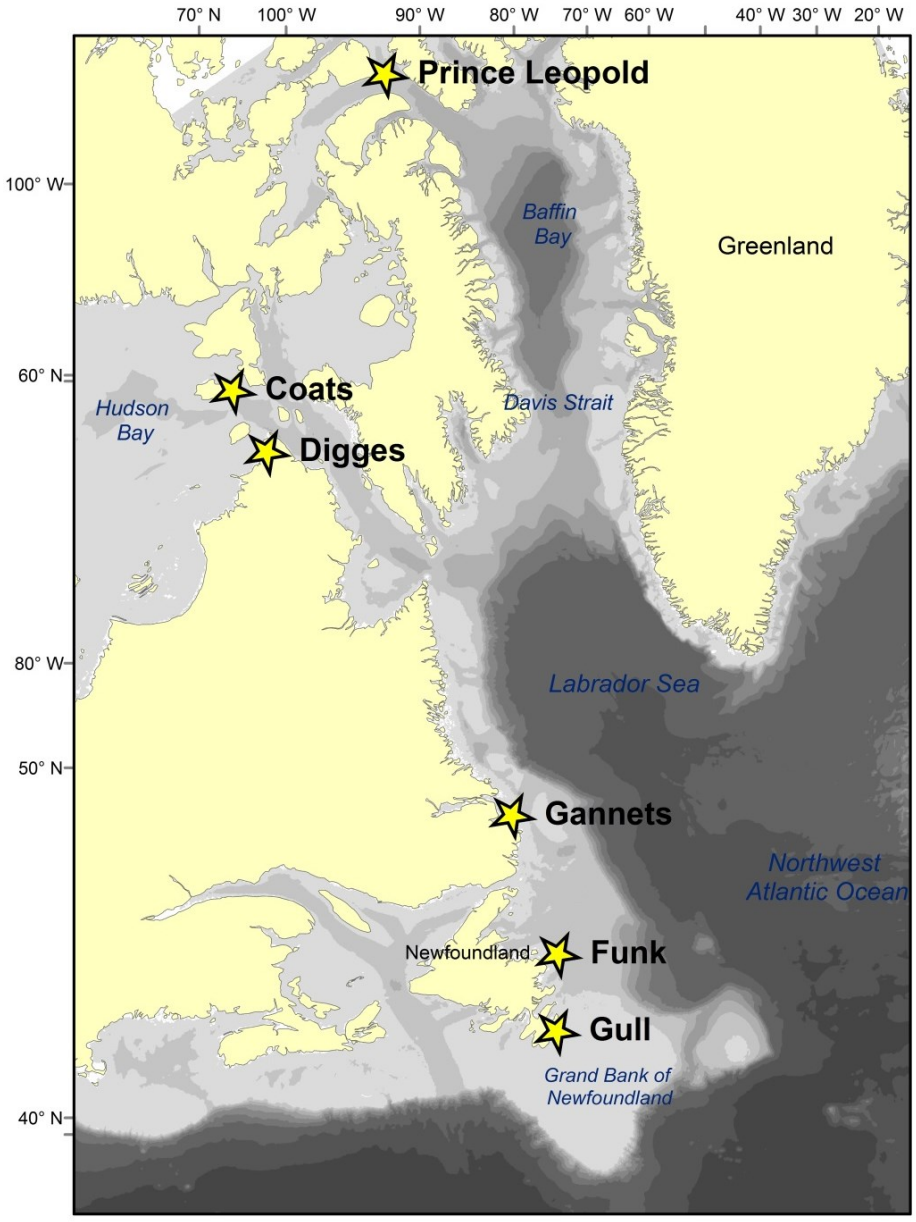

Figure 4.1. Study area and colonies of repeat-tracked Thick-billed Murres (Prince Leopold, Coats, Digges, Gannets) and Common Murres (Gannets, Funk, Gull).

Table 4.1. Details of collection of GLS tracking devices among repeat-tracked individuals of Thick-billed and Common Murres at each study colony. Data were retrieved 1, 2, or 3 years following deployment.

Species	Colony	Latitude, Longitude	Years Data Collected	Repeat Individuals	Number of Annual Tracks
Thick-billed Murre	Prince Leopold	74°02'N , 90°00'W	2008-10	1	2
	Coats	62°53'N, 82°00' W	2007-10	10	17
	Digges	62°32'N, 77°45' W	2008-10	3	6
	Gannets	53°56'N, 56°32'W	2008-11	8	18
Common Murre	Gannets	53°56'N, 56°32'W	2008-11	7	16
	Funk	49˚45'N, 53˚11'W	2007-11	6	18
	Gull	47°16'N, 52°46'W	2007-11	7	14
Overall			*2007-2011*	*42*	90

Spatial calculations - To facilitate comparisons of winter areas, data were restricted to January (mid-winter) when all birds had reached wintering grounds and GLS positions were maximally dense, indicating that birds remained resident in the same area. Centroids of the locations of each bird in January each year were calculated using ESRI ArcMap 10.1 (Spatial Statistics Toolbox). Great-circle distances from the colony of origin to each centroid were calculated using ArcMap. Wintering areas for each individual in each year were considered to be those within the 50% and 95% utilization distributions or kernel contours (KHR), calculated from the GLS point data in January and using LSCV smoothing, in the "adehabitatHR" (Calenge 2006) package in R (version 2.15.2; R Core Development Team 2012). The 50% and 95% KHR are referred to below as the core and home ranges, respectively. All means are presented ± SD.

KHR Overlap – The use of KHR highlighted areas of concentrated use for each individual in January. Birds were considered to have shifted distribution from one year to the next when core ranges (50% KHR) did not overlap.

The yearly overlap in winter range A_o (for 50% and 95% KHRs separately) was calculated as the area of KHR in year j that overlapped the area in year $j + 1$. This was done by merging yearly KHRs for each individual to calculate the total area of both years (A_{tot}) in km^2. Yearly KHR area in each individual year (A_j) was then subtracted from the total area (A_{tot}) to determine the Area of Overlap (A_O):

[1] $A_O = ((A_j + A_{j+1}) - A_{tot})$,

recognizing that in some cases, $A_o = 0$ (i.e. the area did not overlap). For each year (e.g. year 1 on year 2, and year 2 on year 1), Percent Habitat Overlap (P) was calculated for each year (j), as:

[2] $P_j = A_o/A_j$

Repeatability statistics- Individual repeatability in consecutive years was calculated for five aspects of wintering strategy: 1) timing of colony departure and

arrival to determine start and endpoints of migration; 2) distance travelled between colony and winter (January) centroids; 3) the size (km^2) of individual core (50% KHR) and home ranges (95% KHR); 4) distance between annual centroids; and 5) percent overlap of kernel core and home ranges. Repeatability of these aspects was measured using three approaches: first, using linear mixed-effect models (lme; with individual and colony set as a random factor, and using conditional R^2 values; Nakagawa and Schielzeth 2012) to assess relationships of variables between successive years. Second, using an intra-class correlation coefficient (Lessells and Boag 2012) to quantify among-groups variance (s^2_A) and within-individual variance (s^2) components, where repeatability (r) is calculated as:

[3] $r = s^2_A / (s^2 + s^2_A)$

High r scores indicate consistent behaviour, since the greatest variance occurs among, not within, individuals (Lessells and Boag 2012). Third, inter-centroid distances and KHR overlaps were compared to randomized distributions (n=10,000 randomizations) using Kolmogorov-Smirnov (KS) tests and also comparing the median of distributions. Randomized distributions of centroids and KHR overlaps were created using a larger dataset of tracked individuals (n=112; see McFarlane Tranquilla et al. 2013), many of which were tracked only once. Because of inherent differences between them, the species were considered separately for each analysis.

4.4 RESULTS

Forty-two individuals (22 Thick-billed Murres, 20 Common Murres) were tracked for 2-4 consecutive years, providing a total of 90 annual tracks (Table 4.1; Appendix 1). Detailed examples of consistent monthly movements in consecutive winters for six individual Thick-billed Murres are provided in Figure 4.2. Some inter-annual variation in monthly positions occurred (eg. Figure 4.2, Digges 20118) but overall, wintering patterns

were very similar across years. Quantitative assessment of travel timing, distances, KHR sizes, and regional fidelity are presented as follows:

4.4.1 Timing of migration

Relative departure dates of individuals (standardized to annual means for each colony) were not correlated between consecutive years in either species (Thick-billed Murres, lme, $F_{1,5}$=1.98, p = 0.22, R^2=0.23; Common Murres, lme, $F_{1,11}$ = 3.7, p = 0.08, R^2 = 0.24; Figure 4.3a). Similarly, the repeatability (*r*) of standardized departure dates was low for Thick-billed Murres (*r* = 0) and high only for Common Murres from Gannet and Funk Islands (*r* = 0.56, 0.82, respectively, Table 4.2; full details on individual migration timing in Appendix 1). Overall, consecutive departure dates differed on average by 6.7 ± 5.3 days (range 2-27 days) in Thick-billed Murres and by 5.7 ± 4.6 days (range 0-16 days) in Common Murres.

Standardized arrival dates in consecutive years (year one vs. year two) were not correlated in Thick-billed Murres (lme, $F_{1,15}$=0.07, p = 0.93, R^2 =0.001), or Common Murres (lme, $F_{1,11}$=4.3, p = 0.06, R^2=0.25; Figure 4.3) - i.e. there was no strong consistency in whether individuals arrived at colonies early or late in consecutive years. However, compared to departure dates, relative arrival dates of individuals were generally more repeatable, but still lower for Thick-billed Murres (*r* = 0 – 0.18) than for Common Murres (*r* = 0.34 – 0.41; Table 4.2). Arrival dates between consecutive years differed on average by 11.5 ± 8.1 days (range 2-35 days) in individual Thick-billed Murres, and by 12.6 ± 9.3 days (range 1-32) in individual Common Murres.

Table 4.2. Repeatability (r), measured through intra-class correlation coefficients, among wintering parameters of Thick-billed and Common Murres (calculated separately for each colony). High scores of r indicate consistent individual behaviour. N indicates number of repeat measurements (may include multiple per individual).

	Repeatability (r)					
Wintering Parameter	N	Thick-billed Murre		N	Common Murre	
Colony departure date (standardized)	17	Coats	0.00	6	Gannets	0.56
	6	Digges	0.00	18	Funk	0.82
	10	Gannets	0.00	10	Gull	0.00
Colony arrival date (standardized)	12	Coats	0.18	16	Gannets	0.35
	4	Digges	0.00	16	Funk	0.41
	14	Gannets	0.04	8	Gull	0.34
Distance to winter centroid (km)	18	Coats	0.40	18	Gannets	0.32
	6	Digges	0.46	22	Funk	0.29
	20	Gannets	0.00	14	Gull	0.61
Size of 50% KHR (km^2)	16	Coats	0.19	20	Gannets	0.00
	6	Digges	0.29	26	Funk	0.07
	18	Gannets	0.54	14	Gull	0.19

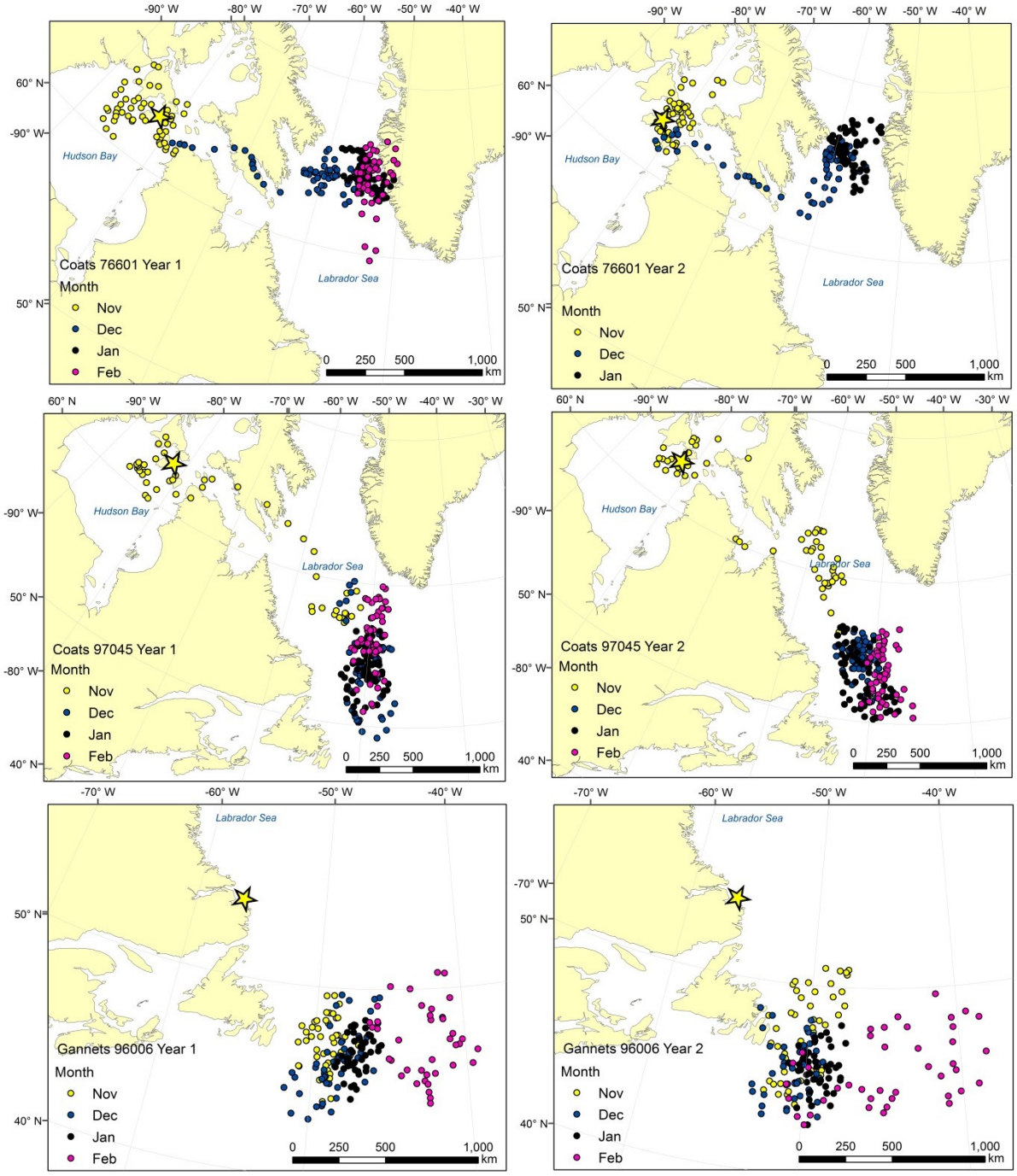

Figure 4.2. Examples of repeated winter tracks among 3 Thick-billed Murres from Coats and the Gannet Islands. Numbers (e.g. 76601) denote individual bird ID. Note GLS records stopped in January for Coats 76601 in Year 2.

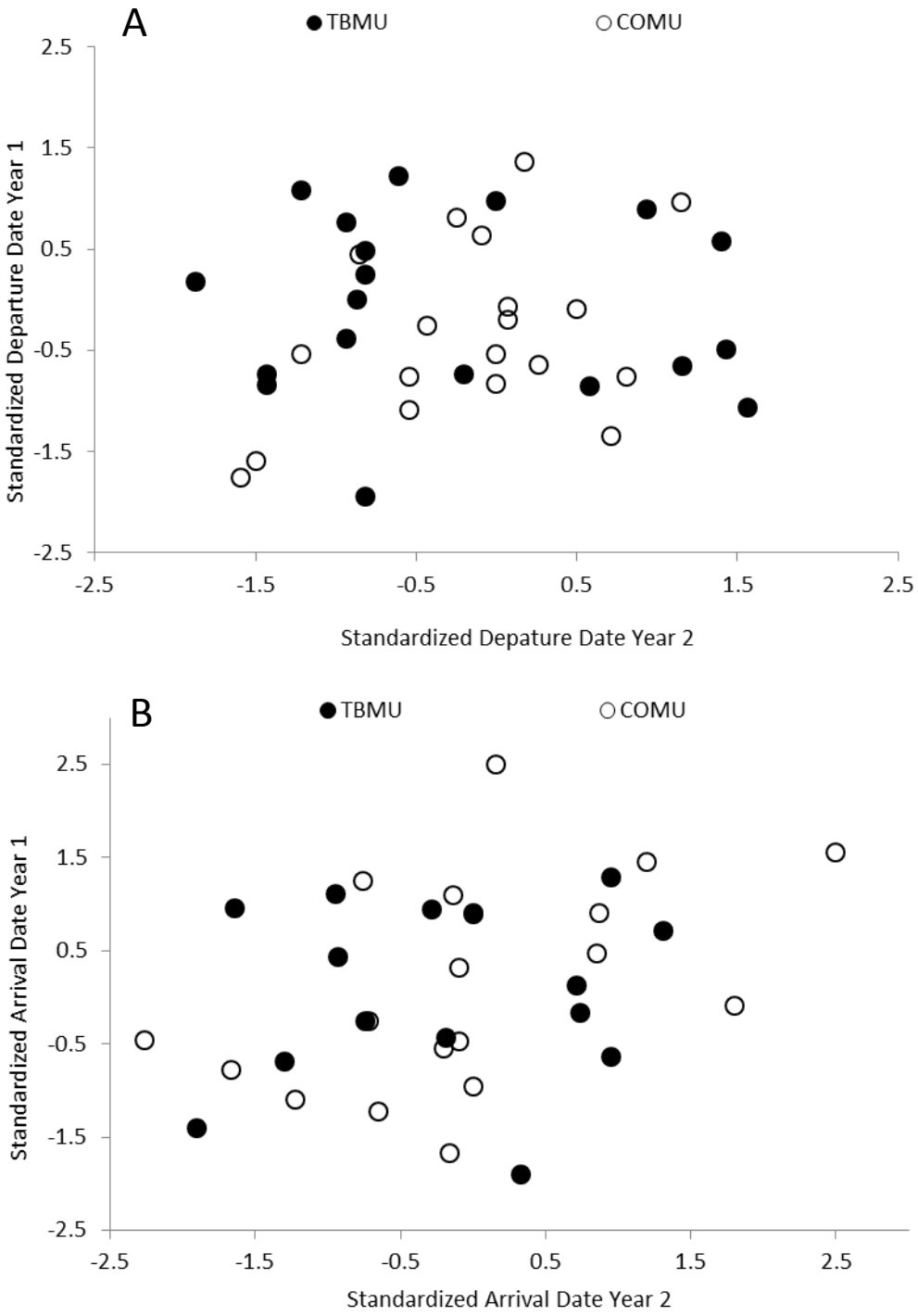

Figure 4.3. Consistency between repeated (A) colony departures and (B) colony arrivals in consecutive years, for Thick-billed Murres (TBMU) and Common Murres (COMU). Dates are standardized to colony means, indicating whether early (or late) birds were more likely to do the same in successive years.

4.4.2. Winter centroids

Travel distances - Distances travelled to consecutive winter centroids were highly correlated, in both Thick-billed Murres (lme, $F_{1,16} = 3.44$, $p < 0.003$, $R_c^2=0.66$; Figure 4.4, 4.6a) and Common Murres (lme, $F_{1,24} =8.96$, $p < 0.006$, $R_c^2=0.78$; Figure 4.5, 4.6b). Similarly, distances travelled to consecutive winter centroids were moderately to highly repeatable (depending on colony) for both Thick-billed Murres (r = 0.0 - 0.46) and Common Murres (r = 0.32 – 0.61; Table 4.2). Six Thick-billed Murres (particularly from Coats and Digges islands) travelled shorter distances in the second winter (Figure 4.6a); yet a change in distance travelled (points outlined in red) did not always indicate a shift in distribution (i.e. no 50% KHR overlap) between years.

Inter-centroid distance - The median distance between consecutive winter centroids was small, differing by 239 km (range 22-1212 km) for Thick-billed Murres 169 km (range 43 – 631 km) for Common Murres. Furthermore, in Thick-billed Murres, the median distance between consecutive winter centroids was significantly lower for birds tracked in consecutive years (239.1 km) than the distance between random pairs of centroids (897.6 km; KS test, D=0.66, $p < 0.0001$). Similarly in Common Murres, the median distance between consecutive winter centroids was significantly lower for birds tracked repeatedly (169.8 km) than randomly-paired centroids (333.2 km; KS test, D=0.51, $p < 0.0001$).

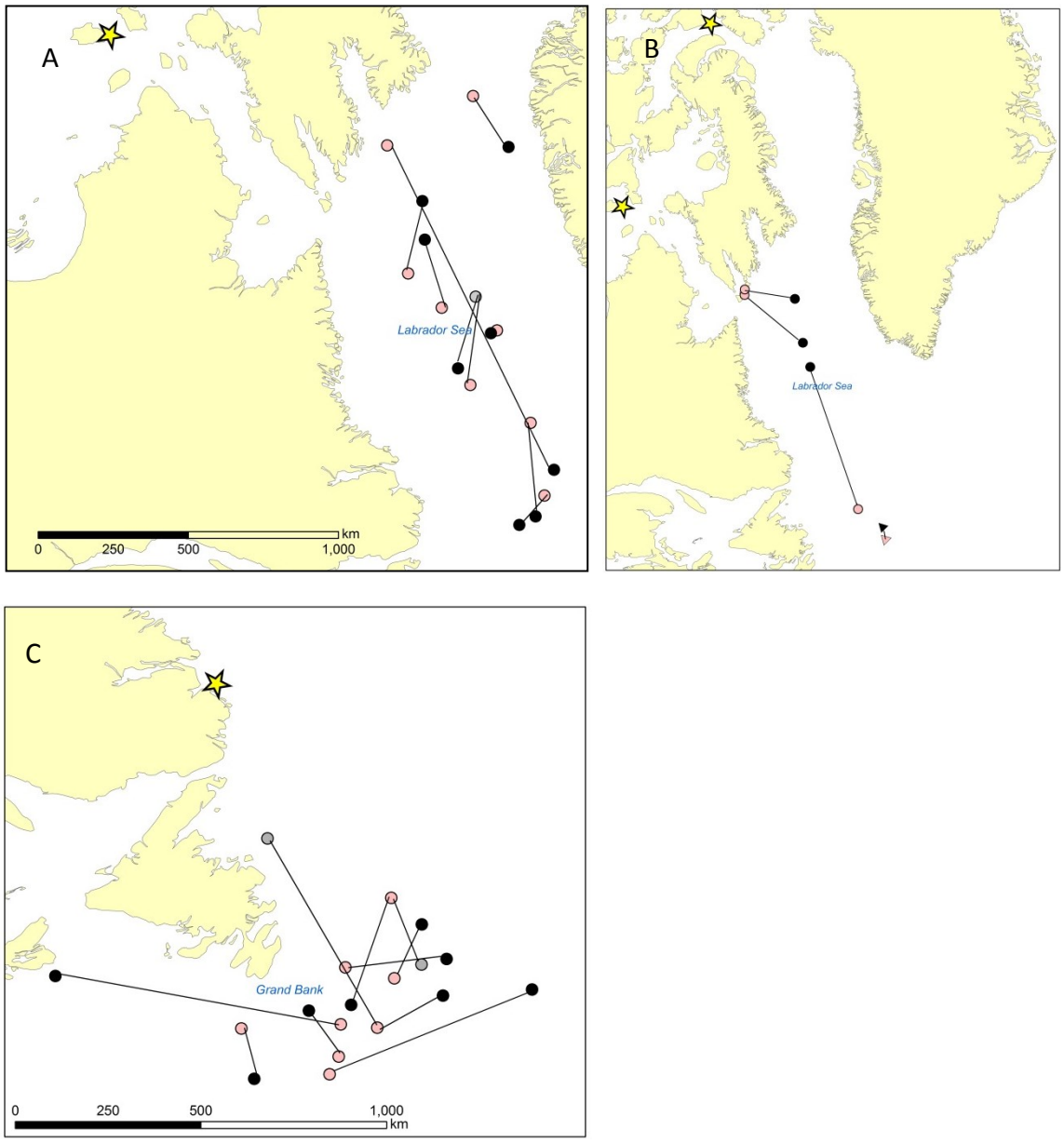

Figure 4.4. January centroids in consecutive years for individual Thick-billed Murres at (A) Coats, (B) Digges (circles) and Prince Leopold (stars), and (C) Gannet Islands, grouped by colony of origin and colored pink (year 1), black (year 2), or grey (year 3) for consecutive years. Lines connect two or three centroids for each individual. Stars indicate colony of origin.

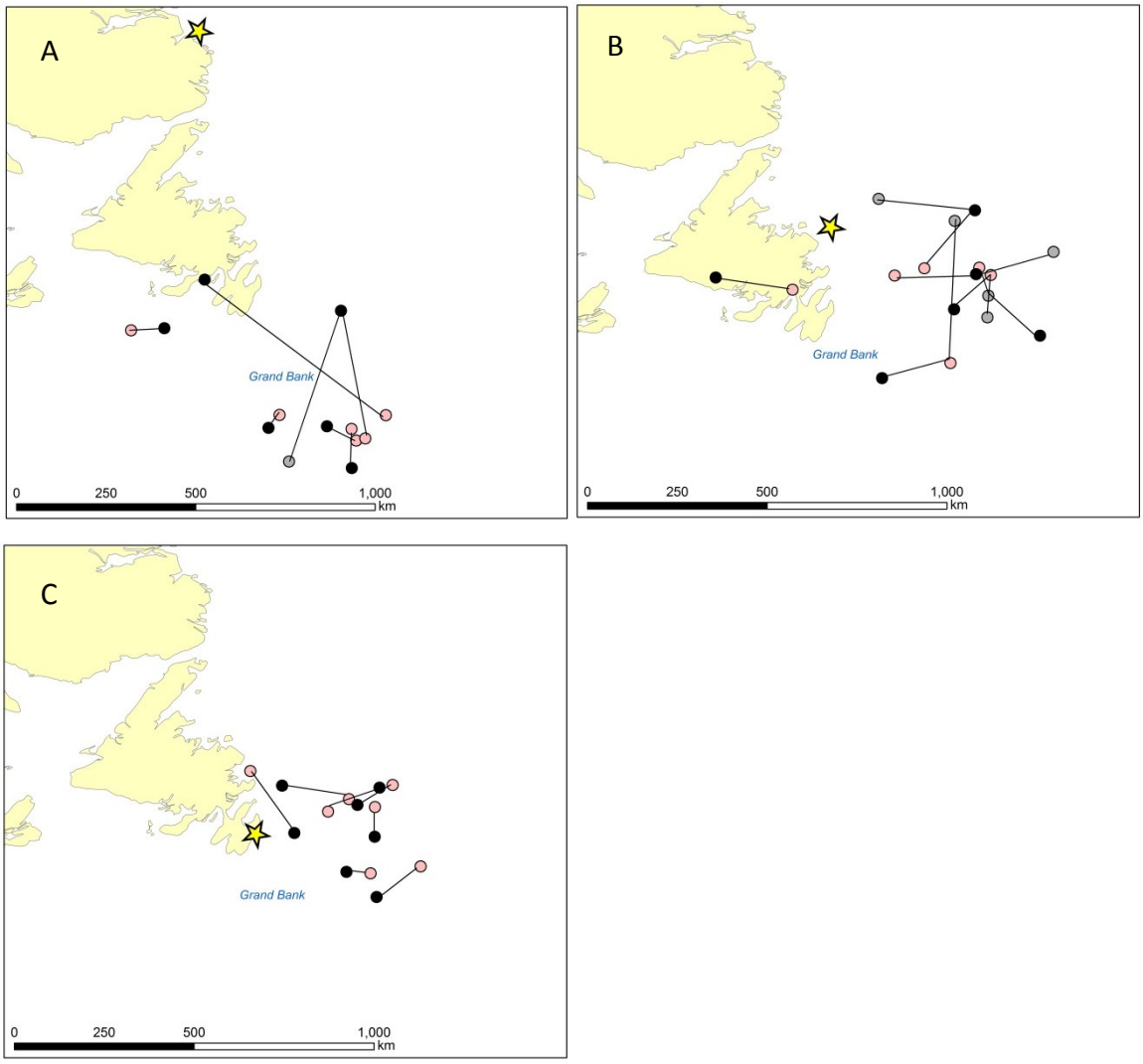

Figure 4.5. January centroids in consecutive years for individual Common Murres, at (A) Gannets, (B) Funk and (C) Gull Islands, grouped by colony of origin and colored pink (year 1), black (year 2), or grey (year 3) for consecutive years. Lines connect two or three centroids for each individual and stars indicate colony of origin. Note some very nearshore GLS observations sometimes (incorrectly) appear to be on land. These points are included only to indicate "nearshore" GLS detections and do not indicate inland detections.

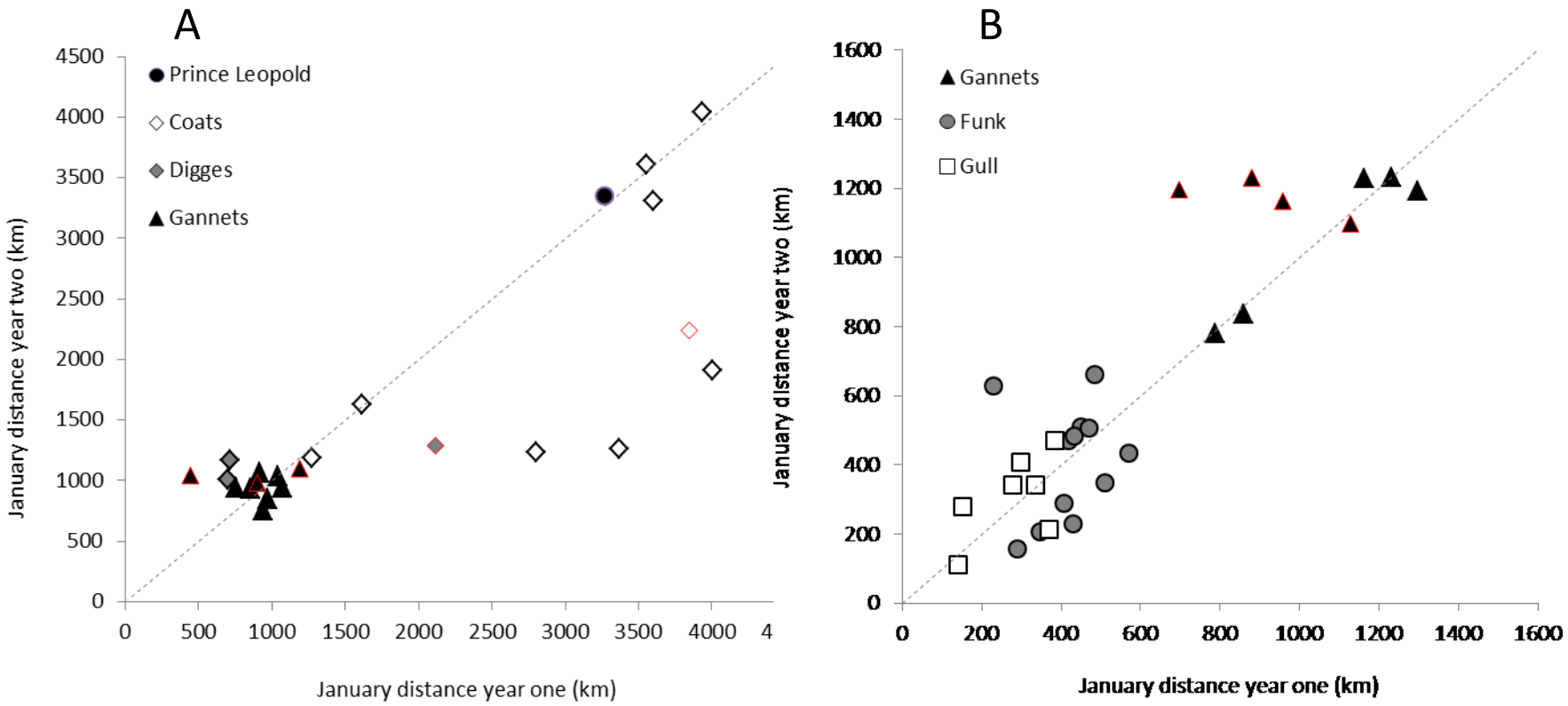

Figure 4.6. Relationship of distance travelled (km) to the January centroid in consecutive years (year one vs. year two), for (A) Thick-billed Murres and (B) Common Murres. Dotted line represents the hypothetical 1:1 relationship if distances are the same in successive years. Markers outlined in red indicate birds that switched regions across years.

4.3.3 Winter distributions

Range sizes– The size of core ranges was not strongly correlated between consecutive years, in either Thick-billed Murres (lme, $F_{1,16} = 3.98$, p =0.06, R^2=0.17; Figure 4.7; see also Appendix 2) or Common Murres (lme, $F_{1,24} = 0.07$, p = 0.93, R^2=0.02; Figure 4.7), and variance appeared to be higher for individuals with larger home ranges (Figure 4.7). Repeatability (*r)* in the size of core ranges (50% KHR) was relatively higher for Thick-billed Murres (*r* = 0.19 – 0.54) than for Common Murres (*r* = 0 – 0.19; Appendix 2).

Spatial distribution – Although the majority of individuals maintained the same migration strategies (see also Figure 4.2), others shifted wintering locations between years (Figures 4.8, 4.9). For example, individual Thick-billed Murres from Coats Island showed consistent annual use of either the northern Labrador Sea and Davis Strait, or the mid-Labrador Sea, or the southern Labrador Sea (winters 2008, 2009, 2010); whereas individual Thick-billed Murres from Digges Island shifted core areas (winters 2009, 2010; Figure 4.8). The small sample size at Digges (n=3) cannot be used to suggest a colony-specific bias in the propensity of individuals to show site fidelity, but rather to illustrate flexibility in core winter areas in some individuals. Among Common Murres, individuals generally followed consistent strategies of using either nearshore or offshore habitat in consecutive years (Figure 4.9). In both species, some individuals exhibited high regional fidelity in the first two years but shifted distribution in the third (e.g. Gannet Islands, Figure 4.8, blue KHRs and Figure 4.9, yellow KHRs).

Wintering range overlaps – The extent of overlap of consecutive KHRs was extremely variable, ranging from 0-64% (home range) and 0-37% (core) in Thick-billed Murres, and 0-95% (home range) and 0-58% (core) in Common Murres. The extent of home range overlap was significantly lower in Thick-billed Murres (lme, $F_{1,31}$=4.31, p = 0.05) and also varied significantly by colony ($F_{4,31}$=2.79, p = 0.05; but only at Digges Island, $t_{1,31} = -2.6$, p

= 0.02) and year ($F_{3,45}$ = 3.5, p = 0.02). Core range overlap did not vary significantly by species ($F_{1,44}$ = 3.06, p = 0.09), colony ($F_{4,30}$ = 1.23, p = 0.32) or year ($F_{3,44}$ = 2.01, p = 0.12). Extent of overlap was not related to KHR size (linear regression, $F_{1,35}$=0.13, p = 0.72).

Despite the observed variability in relative overlap of KHRs between years, the median overlap of both home and core ranges for each species was significantly different from the randomized distributions (Table 4.3). For Thick-billed Murres, this overlap was greatest for consecutive home ranges (ca. 50% overlap of 95% KHR; Table 4.3) compared to randomized distributions (0% overlap; KS tests, D = 0.63, p = 0.0001 for both year 1 on year 2 and year 2 on year 1). Consecutive core ranges (50% KHR) overlapped much less (ca. 18%; Table 4.3), and only slightly more than that expected by chance (16%; KS tests, D = 0.47, p = 0.001 for both years).

Similarly, for Common Murres, consecutive home ranges (95% KHR) overlapped more (ca. 68%; Table 4.3), compared to randomized home ranges (ca. 32%; KS test, D = 0.52, p < 0.0001 year 1 on year 2; KS test D = 0.53, p< 0.0001, year 2 on year 1). Overlap of consecutive core ranges (ca. 36%; Table 4.3), was not significantly greater than expected by chance (ca. 33%; KS tests, D = 0.11, p = 0.96 in both cases; Table 4.3).

Table 4.3. Average percent overlap of consecutive January home ranges (95% and 50% KHR) of repeat-tracked Thick-billed and Common Murres, compared to a randomized distribution of overlap between individuals.

Species	Group	% Annual Overlap ± SD (median)			
		95% KHR year 1 on 2	95% KHR year 2 on 1	50% KHR year 1 on 2	50% KHR year 2 on 1
Thick-billed Murre	Within-individual	50 ± 28 (47)	49± 32 (48)	18 ± 21 (16)	18 ± 18 (16)
	Randomized	17 ± 31 (0)	na	16 ± 31 (0)	na
Common Murre	Within-individual	68 ± 28 (68)	67 ± 27 (68)	36 + 31 (29)	37 + 42 (27)
	Randomized	32 ± 29 (27)	na	33 ± 30 (29)	na

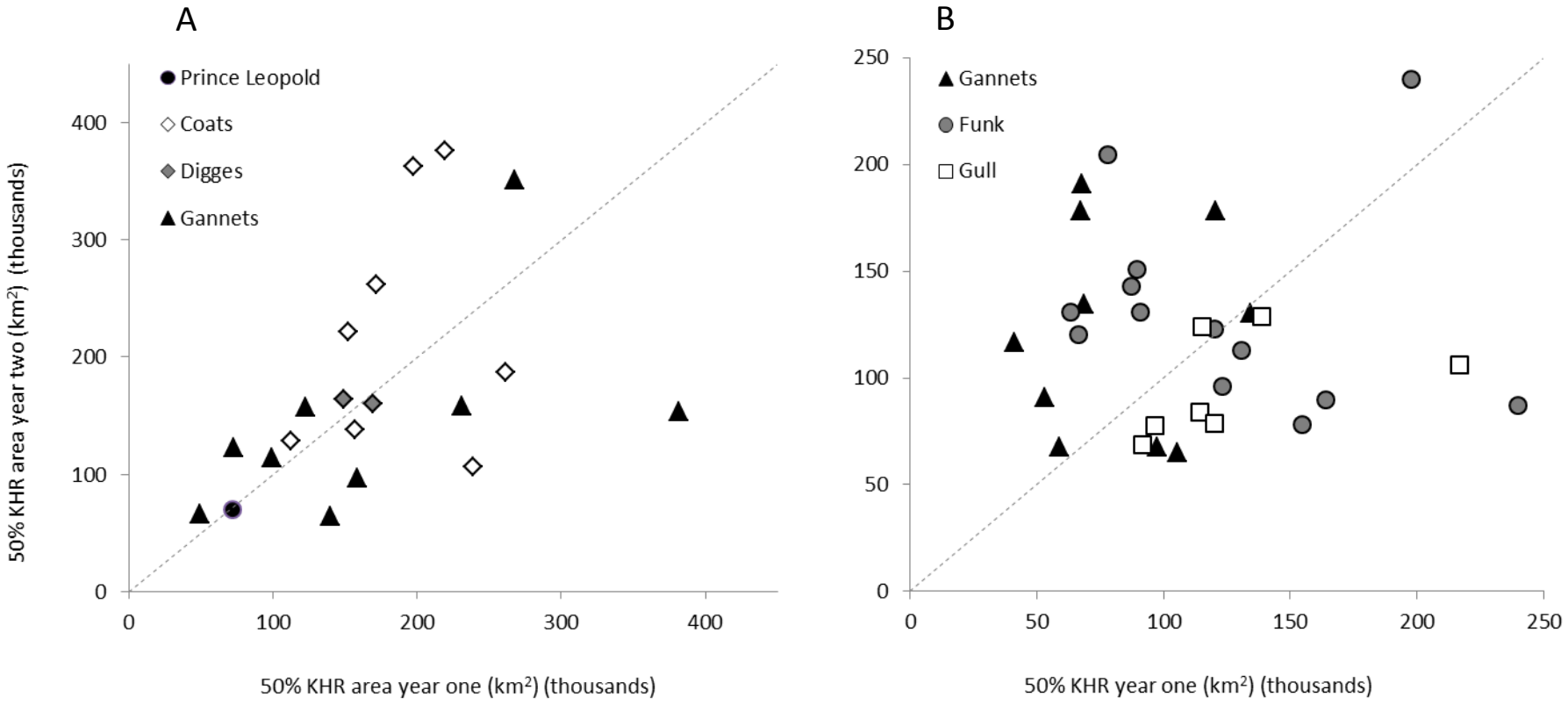

Figure 4.7. Relationship of 50% KHR core range sizes (km^2, in thousands) in consecutive years (year one vs. year two), for (A) Thick-billed Murres and (B) Common Murres. Dotted line represents the hypothetical 1:1 relationship if core sizes are the same in successive years

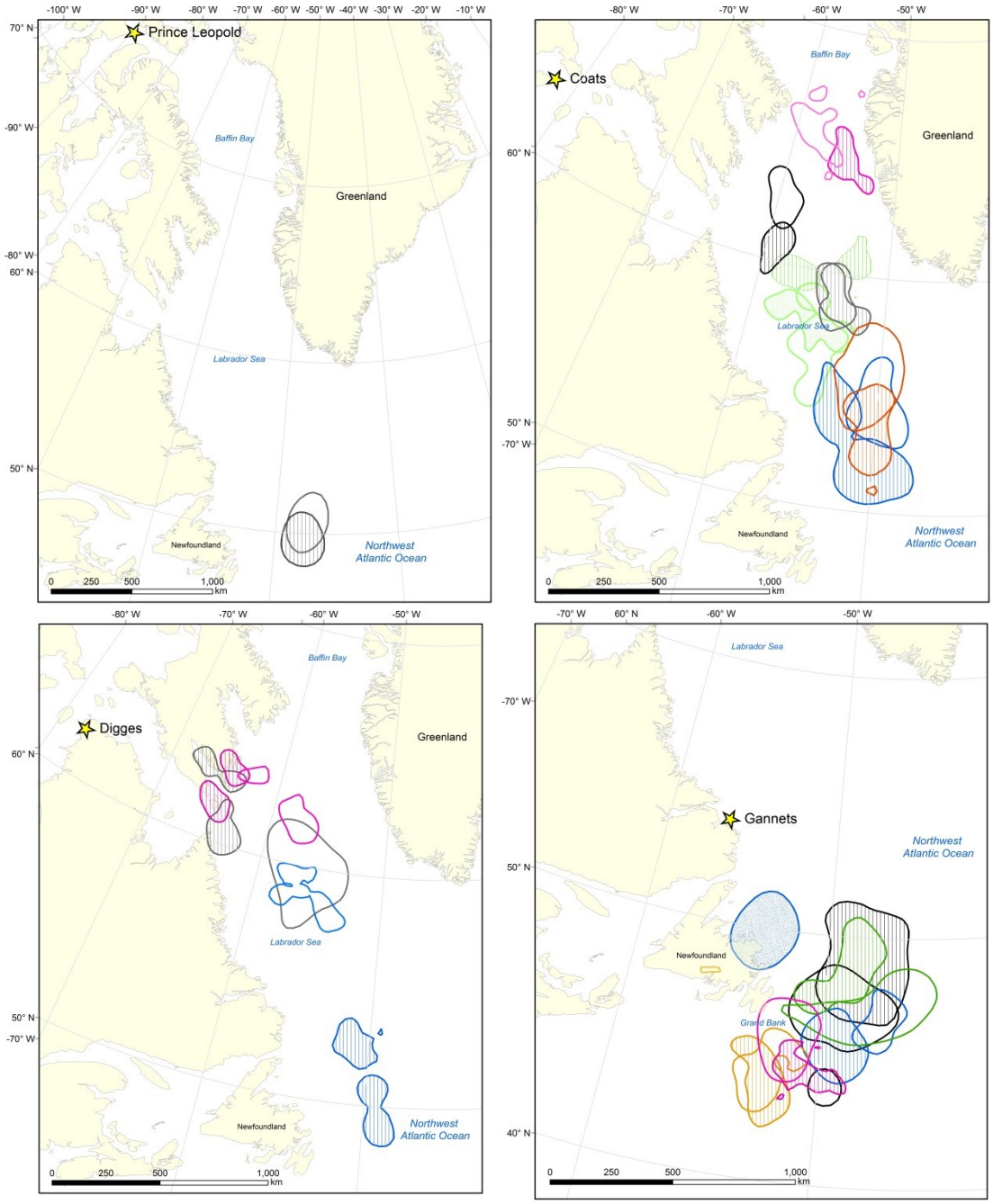

Figure 4.8. Examples of core winter areas (50% KHR) of individual Thick-billed Murres from four different colonies (Prince Leopold, Coats, Digges, Gannet Islands), tracked across consecutive years in the Labrador Sea and Northwest Atlantic Ocean. Colors note repeated observations for the same individual, with open (year 1) cross-hatching (year 2) or stippling (year 3) to identify difference between years. To facilitate interpretation, only a selection of repeat tracks is shown in areas of high kernel overlap.

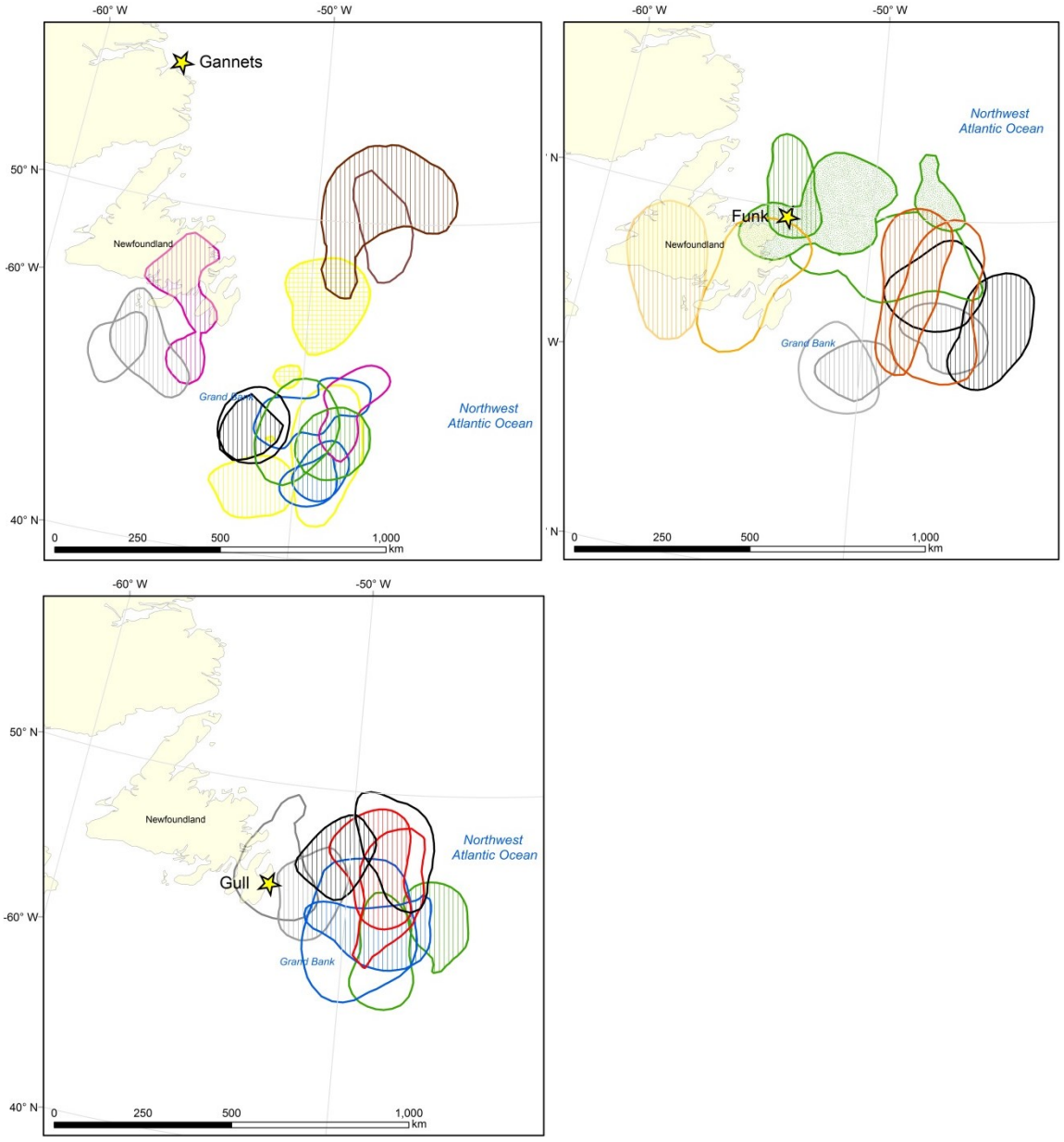

Figure 4.9. Examples of core winter areas (50% KHR) of individual Common Murres from three different colonies (Gannet, Funk, Gull Islands), tracked across consecutive years in the Labrador Sea and Northwest Atlantic Ocean. Colors note repeated observations for the same individual, with open (year 1), cross-hatching (year 2), or stippling (year 3) to identify difference between years. To facilitate interpretation, only a selection of repeat tracks is shown in areas of high kernel overlap.

4.5 DISCUSSION

This study documents a high degree of inter-annual consistency of overwintering strategies in many, but not all, individual Thick-billed and Common Murres; and a high degree of repeatability among some, but not all, characteristics of nonbreeding movements. Individual murres travelled similar distances from colonies, made repeated movements to particular wintering areas, and had similarly-sized core winter areas in consecutive winters. Yet variability, both among and within individuals, and also between stages of the nonbreeding period (Conklin et al. 2012), can potentially illustrate a capacity for flexibility in both species.

4.5.1 Colony attendance

The timing of departure and arrival at the colony were remarkably consistent for some individuals (arriving and departing on the same day each year), but not for others (up to ~ 30 days difference between years). As a result, the relative departure dates for individuals in successive years were not correlated (though there was a slight positive trend in Common Murres). Similarly, relative arrival dates at the colony each year were not consistent for individual murres. This was unexpected, given that timing of breeding among experienced murres tends to be consistent (de Forest and Gaston 1996). However, in other species, timing of colony departures can be related to breeding success (Phillips et al. 2005, Bogdanova et al. 2011, Fifield et al. 2013) and timing of arrivals can be influenced by energetic investments that carry over from the previous breeding attempt (Catry et al. 2013), thus repeatability in consecutive years could depend partly on individual breeding outcome. As well, given that timing of arrival and breeding is strongly linked to environmental conditions in these in these and many other seabird species (Birkhead and Nettleship 1982, Wanless and Harris 1988, de Forest and Gaston 1996), variable local environmental conditions, particularly spring ice

conditions near Thick-billed Murre colonies, are likely responsible for low repeatability in individual arrival times across years (Fifield et al. 2013, Pulido 2007). Although all tracked murres were confirmed breeders at the time of device deployment, final breeding outcomes were not confirmed, and could not be used to account for individual consistency in arrivals or departures. As well, since colony attendance was mostly determined using GLS immersion data (dependent on having a dry logger for >6 hours; see methods), birds staging at sea (wet logger) in the vicinity of the colony would not be noted as attending. Any variability in the duration of staging at sea, either pre- or post-breeding, could influence the observed repeatability of attendance dates.

Studies on other long-distance migrants (Black-Browed Albatrosses *Thalassarche melanophris* (Phillips et al. 2009), Northern Gannets *Sula bassana* (Fifield et al. 2013), Bar-tailed Godwits *Limosa lapponica baueri* (Conklin et al. 2012)) also suggest that timing is not necessarily repeatable for all components of the migration cycle (last visit to land, out-migration, periods at stopover and wintering sites, return migration etc.). That is, repeatability in timing is of intrinsic importance for some events but not others, likely determined by a combination of genetic and environmental influences (Pulido 2007, Fifield et al. 2013). These could include environmental cues, annual conditions at staging or stopover sites, and physiological constraints, particular to the ecology of each species. Indeed, ongoing consideration of murre movement strategies outside the winter period has revealed colony differences in migration timing and spring stopover sites among Thick-billed Murres (LMT, unpubl.data). Further study will provide insight into the degree of individual flexibility at different stages (Conklin et al. 2012) in the migration cycle of murres.

4.5.2 Wintering site fidelity

Compared to other measures of repeatability, distance travelled to winter sites was less variable within individuals (i.e. higher repeatability (*r*) values denote a decrease in

within-individual variance, s^2, compared to among-individual variance, s^2_A). This is unsurprising given that many individuals followed the same movement strategies in consecutive years, showing both site fidelity to particular wintering areas (Figures 4.2, 4.8, 4.9) and remarkable similarity in the centroids of distribution in January (which in many cases were closer than the average GLS error of ~ 185 km (Phillips et al. 2004). Notable examples are the Thick-billed Murre from Prince Leopold Island which twice travelled ~ 3200 km to a wintering site in the southern Labrador Sea (Figures 4.4, 4.8); two Thick-billed Murres from Coats Island which left Hudson Bay at similar times each year to travel to the northern Labrador Sea and Davis Strait region in two years, or to travel to the mid- and southern Labrador Sea in two years (Figures 4.4, 4.8); and Common Murres from the Gannet Islands travelling to the southeast Grand Banks in two years (Figures 4.5, 4.9).

Regional site fidelity is common among seabirds, particularly long-distance migrants such as Gray-headed Albatrosses *Thalassarche chrystostoma* [1], Black-browed Albatrosses (Phillips et al. 2005), Northern Gannets (Fifield et al. 2013), and South Polar Skuas *Stercorarius maccormicki* (Kopp et al. 2011). We recorded a diversity of individual wintering strategies among and within species (particularly Thick-billed Murres), but varying degrees of site fidelity, with most individuals repeating and some switching winter sites between years. Dias et al. (2010) demonstrated that even given remarkable flexibility in wintering sites between years, individual Cory's Shearwaters (*Calonectris diomedea*) tended to choose the same areas more often than expected by chance. To date, there have been few studies of nonbreeding site fidelity that extend to more than two years, limiting the potential interpretation of repeatability. Catry et al. (1999) noted a decrease in repeatability of laying date after five years in Great Skuas (*Stercorarius skua*), hypothesizing low repeatability (and high plasticity) of many traits by seabirds in response to the dynamic nature of the marine environment. However, a time series of 5-8 years of data on stable isotope ratios measured in whiskers of fur seals *Arctocephalus gazella* and *A. tropicalis* suggested a high degree of individual consistency

in the use of particular water masses across years (Kernaleguen et al. 2012). As described by Conklin et al. (2012), the degree of repeatability may vary depending on the trait. The capacity among seabird species for a combination of fidelity and flexibility, in which individuals may choose from a range of alternative strategies (Guilford et al. 2011, Dias et al. 2010), deserves further, longer term attention.

At the level of the breeding colony, overall winter distribution patterns of murres do not seem to differ significantly between years (McFarlane Tranquilla et al. 2013), suggesting cultural (cf. Grémillet et al. 2004) or geographic determinants of migratory movements. Similarly, Phillips et al. (2005) recorded the consistent use of large-scale wintering regions in a pooled sample of Black-browed Albatrosses tracked in one or two years, and Frederiksen et al. (2011) noted similar winter distributions of Black-legged Kittiwakes (*Rissa tridactyla*) when data existed for two years. Yet in tracking studies, annual consistency of observed wintering patterns of particular populations may partly depend on how many repeat-tracked individuals are included. Knowing both the range of alternative strategies used by individuals, and the propensity of individuals to repeat particular strategies, will provide insight into the long-term persistence of important wintering areas for particular colonies.

4.5.3 KHR size and overlap

Overlap of individual KHRs was higher than expected by chance, yet similar to the distance travelled, the degree of range overlap (95% KHR) between years was extremely variable among individuals, ranging from 0-64% in Thick-billed Murres, and from 0-95% Common Murres, even when individuals occupied the same wintering region. These degrees of overlap were similar to that found in Northern Gannets (Fifield et al. 2013), and it may be that fidelity is much greater at the regional scale than in terms of core habitat (Croxall et al. 2005, Phillips et al. 2009, Conklin et al. 2012). As well, the amount of range overlap in January, but not core overlap, of individuals varied by colony and

year. This suggests that regional or environmental effects that vary across years can influence overall home range positioning but does not significantly influence core habitat locations for most individuals.

Interestingly, the overlap of consecutive individual Common Murre core winter ranges (50% KHR) did not differ from chance. This may be due partly to the limited geographical extent of suitable habitat in particular areas, such as on the Grand Bank (Figures 4.8, 4.9), resulting in increased between-individual overlap and potentially, increased competition. However, between years, although overall winter ranges remain the same, the time when birds occupy particular portions of their winter range may vary (e.g. inshore in December in one year, inshore in January in another). Thus, slightly different degrees of overlap may have been observed if other periods were chosen, due to variation in temporal patterns of winter movement.

4.5.4 Implications for fitness

Phenotypic plasticity, in which a diverse range of behaviours or strategies are employed by different individuals in a population, is expected to improve the capacity of the populations to adapt to environmental changes (Webster et al. 2002, Reed et al. 2010). In the current study, variation in winter movement patterns stemmed more from between-individual variation (phenotypic plasticity) than from annual changes in individual decisions (behavioural plasticity). This was particularly true among Thick-billed Murres, which showed great among-individual variation in spatial use of winter habitat (Table 4.2, Figure 4.8); among-individual variation in winter ranges among Common Murres was less striking (Table 4.2, Figure 4.9). Individual Common Murres tended to aggregate on the Grand Banks, where among-individual variation in movement may be bounded by limits of the species' thermal preference (5-15^{o}C isotherm (Tuck 1961)). In concert with increased phenotypic plasticity, Thick-billed Murres display weaker migratory connectivity; that is, the extent to which individuals of

a population summer and winter in the same places (Esler 2000). This diversity of individual wintering areas has implications for demographic independence among their respective populations, i.e. anthropogenic and other environmental factors influencing birds at particular wintering sites will not affect all Thick-billed Murre populations equally (McFarlane Tranquilla et al. 2013). This in turn should influence management and conservation strategies (Esler 2000, Webster et al. 2002). In contrast, Common Murres, with individuals from all three colonies overwintering in a similar location, show much lower plasticity, stronger migratory consistency (both within and between colonies), and will be more susceptible to localized disturbances in winter. Multiple-colony tracking of seabird populations will continue to be critical in identifying population-level threats on wintering grounds (Webster 2002, Phillips et al. 2009, Frederiksen et al. 2011, Fort et al. 2013).

Behavioural plasticity that enables individuals to shift strategies or explore multiple locations in response to variable environmental conditions, likely improves individual fitness (Webster et al. 2002, Dias et al. 2010, Quillfeldt et al. 2010), particularly by developing spatial memory (Roshier et al. 2008, Oppel et al. 2009). Young birds that disperse further will have knowledge of more alternative wintering sites (Baker 1980, Dias et al. 2010). While many individuals exhibited consistent wintering strategies, some showed flexible use of different areas between years. Like other cognitively complex species, we suggest that these long-lived birds (potentially reaching 25+ years of age (Gaston and Hipfner 2000, Ainley et al 2002) may use their spatial memory (Regular et al. 2013) garnered from years of experience, to inform and adjust annual movement tactics (Dias et al 2010). Guilford et al. (2011) proposed an "exploration-refinement hypothesis" for Atlantic Puffins *Fratercula arctica*, suggesting that their migration strategy is developed through a series of exploratory movements and individual learning. Whether or not annual movement adjustments occur in response to resource availability (Roshier et al. 2008) or environmental conditions (Oppel et al 2009, Reed et al. 2010) requires further investigation. The advantages of

plasticity strongly depend on the reliability of cues that seabirds use to make decisions in a stochastic ocean environment.

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CHAPTER 5 – YEAR-ROUND ISOTOPIC SEGREGATION AND SEASONAL CHANGES IN TROPHIC NICHE OF THICK-BILLED MURRES AND COMMON MURRES

CHAPTER 5 - YEAR-ROUND ISOTOPIC SEGREGATION AND SEASONAL CHANGES IN TROPHIC NICHE OF THICK-BILLED MURRES AND COMMON MURRES

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5.1 SUMMARY

1) Seabird communities partition resources through patterns of habitat use, spatial separation and diet. Yet it is unclear how patterns of trophic segregation may vary in concert with changes in the spatial patterns of species and colony members across the annual cycle; for spatial considerations will determine necessity for competitively-mediated trophic shifts.

2) Combining tracking and stable isotope analyses, we describe spatial and trophic connections of congeneric Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*) to investigate 1) inter- and intra-specific patterns of habitat use, 2) geographic patterns in isotopic signatures, 3) seasonal trophic shifts (between tissues) and 4) areas of increased spatial overlap where competition may influence trophic shifts.

3) Thick-billed Murres consistently had a wider isotopic niche width (both $\delta^{15}N$ and $\delta^{13}C$) and sometimes a lower trophic position ($\delta^{15}N$) than Common Murres, indicating more generalist foraging strategy year-round. This pattern was most pronounced at a colony where the species breed sympatrically and show high spatial overlap year-round; elsewhere, it varied according to spatial location and seasonal timing. Notably, Thick-billed Murres fed on higher trophic prey in locations where Common Murres did not occur; and in places where the species overlap, Thick-billed Murres took substantially lower trophic level prey than elsewhere in their distribution. Intra-specific spatial overlap appeared less influential in driving trophic differences.

4) Seasonal shifts from the breeding to the nonbreeding season involved movement to more pelagic (i.e. depleted carbon) environments ($\delta^{13}C$), a widening of trophic niche width, and a lowering of trophic position ($\delta^{15}N$). However, seasonal trophic shifts did

not occur in parallel for the two species; the lowest ($\delta^{15}N$) and broadest trophic niche occurred during *pre-breeding* (late winter/spring) for Thick-billed Murres but during *post-breeding* (fall) for Common Murres, carrying strong implications for relative vulnerability of the species to energetic challenges at different times of year.

6) We propose that for the *Uria* species, ecological segregation is expressed through more varied movement and habitat use of Thick-billed Murres, resulting in a wider ecological niche that is related both to the range of available habitat and prey, and to inter-specific competitive interactions with Common Murres.

5.2 INTRODUCTION

In seabird communities, marine resources are partitioned through differences in habitat use and foraging strategy, including differences in prey selection. In turn, patterns of resource use help define the ecological niche occupied by particular seabird species or populations. Ecological niche partitioning is well-demonstrated near seabird colonies where competition for limited food resources causes segregation in time, space, foraging behaviour, and target prey (Ridoux 1994, Masello et al. 2010). However, when released from the spatial restriction of breeding colonies, seabird community structure often changes substantially, and it is unclear whether the resulting demands on available resources necessitate competitive ecological partitioning. For many seabirds, habitat partitioning among closely-related species and subpopulations continues into the nonbreeding period (Gonzáles-Solís et al. 2007, Phillips et al. 2009, Ramos et al. 2009, Thiebot et al. 2012), and trophic shifts between breeding and nonbreeding periods are common (Cherel et al. 2006, 2007, 2008; Gladbach et al. 2007, Jaeger et al. 2010). Yet, owing to seasonal movement patterns, changes in food availability and nutritional requirements, and geographic heterogeneity of the marine isotopic landscape (Cherel et al. 2008), the size and position of the ecological niche occupied by a particular seabird group likely changes throughout the year.

Seabird populations are shaped by the conditions encountered at wintering areas as well as breeding sites. These conditions include climate, ocean productivity and anthropogenic disturbance (Grémillet et al. 2005, Sandvik et al. 2005, Fredericksen et al. 2008, Fort et al. 2009, Montevecchi et al. 2012), foraging conditions and food quality (Sorenson et al. 2008, Osterblom et al 2008), and presumably also competitive interactions (cf. Grémillet et al. 2004, Thiebot et al. 2012). Seabird species and colonies can show distinct heterogeneity in wintering movement and foraging strategies (Cherel et al. 2006, Reed et al. 2009, Oppel et al. 2009, Fort et al. 2013), yet to what degree

heterogeneity is shaped by competitive interactions in the winter environment remains extremely unclear for most seabirds.

This is where research on ecological segregation using seabird tracking and dietary analyses has been invaluable in revealing inter- and intra-specific interactions in the nonbreeding season. Tracking studies have revealed nonbreeding spatial and temporal segregation in the wintering strategies of colonies and sympatric species, especially in the southern Atlantic and Indian Oceans (Phillips et al. 2005, 2009, Gonzales-Solis et al. 2007, Thiebot et al. 2012), but with some study at northern latitudes (Frederiksen et al. 2011, Fort et al. 2013). Similarly, stable isotopes have been used to describe variation in diets and putative habitat of sympatric competitors, to illustrate resource partitioning between species, colonies, sexes and age classes (Hebert et al. 1999, Forero et al. 2005, Cherel et al. 2006, 2007, Phillips et al. 2009, Jaeger et al. 2010, Thiebot et al. 2012). Importantly, stable isotopes provide insight into seabird foraging ecology during the nonbreeding period (Cherel et al. 2000), when most seabirds are offshore and difficult to observe. Because most seabirds molt during the nonbreeding season, isotopic signatures of diets are integrated and fixed in feathers at the time of growth (Hobson and Clark 1993, Cherel et al. 2007). The carbon ratio ($^{13}C/^{12}C$, $\delta^{13}C$) can help discern benthic (inshore, more positive $\delta^{13}C$) from pelagic (offshore, more negative $\delta^{13}C$) dietary origins (Hobson et al. 1994) and can determine foraging locations when seabirds use different water masses (Quillfeldt et al. 2005, Cherel et al. 2007, Phillips et al. 2009), at least in areas where marine isoscapes are well-defined (Cherel et al. 2008). The nitrogen ratio ($^{15}N/^{14}N$, δ15N) indicates relative trophic enrichment of consumers in relation to their food. Stable isotopes can thus identify shifting trophic connections and movement patterns across the annual cycle (Cherel et al. 2007, Phillips et al. 2009), potentially offering insight into seasonal changes in habitat quality. Recent approaches (Bearhop et al. 2004, Layman et al. 2007, Jaeger et al. 2010, Jackson et al. 2011) have furthered the traditional comparison of isotopic means by quantifying isotopic variance between and within species. This approach effectively

describes niche width (Bearhop et al. 2004) and can illustrate relative levels of dietary specialization in seabird communities (cf. Layman et al. 2007, Jaeger et al. 2010, Jackson et al. 2011), which is of particular interest to studies of ecological segregation.

Very few studies have benefitted from the combination of tracking and isotopic approaches (cf. Phillips et al. 2009, Gonzáles-Solís et al. 2011). Tracking studies can clearly describe wintering areas but lack information on diet associations, thereby missing a critical component of niche segregation (Holt 2009, Thiebot et al. 2012); while the use of winter diets alone to infer foraging strategies can be complicated by unknown nonbreeding movements of consumers across large spatial scales (Bond and Jones 2009, Phillips et al. 2009) with regional and seasonal variation in isotopic composition (Rau et al. 1990, 1992, Bearhop et al. 2004, Pomerlau et al. 2012). Therefore, integrating knowledge of spatial and trophic connections of marine animals is critical for improved biological interpretation (Bond and Jones 2009, Phillips et al. 2009) of ecological segregation.

Ecological segregation among nonbreeding seabirds in Northwest Atlantic has been poorly studied to date. Among the most significant consumers of marine resources in this region are the abundant populations of Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*). These species are the most closely-related alcids, have overlapping distributions, often breed sympatrically, and occupy a similar ecological niche (Gaston and Hipfner 2000, Ainley et al. 2002), making them excellent candidates for a study of ecological segregation (Bédard 1969). Traditional diet analyses show Thick-billed Murres consume a variety of forage fish and zooplankton (cod, capelin, sandlance, euphausiids, amphipods, copepods; Gaston and Jones 1998, Elliot et al. 1990), whereas Common Murres specialize more on forage fish (capelin, sandlance; Davoren and Montevecchi 2003, Gaston and Jones 1998). Much study has determined that ecological segregation between and within the species occurs through divergent space use, timing of breeding, and dietary associations (Tuck 1961, Bédard 1969), yet this has been described almost exclusively during the breeding season (Birkhead and

Nettleship 1987a,b, Barrett et al. 1997), and comparisons between colonies are rarely made (but see Provencher et al. *in press*). Outside the breeding season, diet composition of both murres may (Tuck 1961, Elliot et al. 1990, Moody and Hobson 2007) or may not shift to different trophic levels (Lilliendahl 2009, Moody and Hobson 2007). Few studies have compared Thick-billed and Common Murre winter diets in shared winter areas (Moody and Hobson 2007) and in previous winter studies, colony origins and seasonal movement patterns have been unknown. How inter- and intra-specific competitive interactions of these species may shape winter habitat use has been heretofore poorly described (but see Linnebjerg 2012, Fort et al. 2013), and knowledge of wintering movements and trophic interactions has not been integrated.

Combining tracking and isotopic data, we investigate spatial and trophic connections of multiple colonies of Thick-billed and Common Murre in eastern Canada. Our objectives were to (1) use tracking data to investigate inter- and intra-specific patterns of spatial habitat use, (2) describe geographic patterns in isotopes by linking tracking data to isotopic signatures during known feather growth periods (3) determine whether seasonal trophic shifts occur and how they may differ between species, and (4) identify areas of increased spatial overlap where competition may influence trophic shifts.

5.3 METHODS

Study area and device attachment- Research was carried out at six Canadian seabird colonies from 2007-2011: Prince Leopold Island in the Canadian High Arctic (74°02'N, 90°00'W, 2008-10); Coats Island (62°53'N, 82°00'W, 2007-10) and East Digges Island (62°32'N, 77°45'W, 2008-10) in Hudson Bay, Nunavut; Gannet Islands, Labrador (53°56'N, 56°32'W, 2008-11); Funk Island (49˚45'N, 53˚11'W, 2007-11) and Gull Island (47°16'N, 52°46'W, 2007-2011) in Newfoundland (Figure 5.1). These colonies support

Thick-billed Murres or Common Murres, except at the Gannet Islands where the species breed sympatrically. As part of a tracking study (see McFarlane Tranquilla et al. 2013), geolocators (British Antarctic Survey) were attached to 282 murres (155 Thick-billed Murres, 127 Common Murres) in 2007-2009. Of these, 163 (58%) were retrieved in 2008-2011, with reliable data from 143 geolocators (52%; 87 Thick-bills, 56 Common). All murres equipped with tracking devices were captured in July/August and were actively breeding (i.e. on eggs or chicks) when captured. Geolocator (GLS) point data were processed as detailed in McFarlane Tranquilla et al. (2013). Filtered, twice-smoothed point data are presented in Figure 5.1, for the post-breeding (fall; late August – September) and pre-breeding (late winter/spring; March-April) periods.

Tissue sampling and feather molt timing - Tissue samples were taken at breeding colonies, from tracked birds at the time of geolocator retrievals, and from control birds confirmed to be breeding nearby. Three tissue types were sampled, providing isotopic signals at different stages of the annual cycle for each individual: 1) whole blood, with an isotopic turnover of ~12-15 days (Hobson and Clark 1993) provided a breeding isotopic signal (n = 261; 110 Thick-billed Murre, 151 Common Murre) at all colonies except Digges Island, 2) flight feathers (secondary coverts; n = 326; 165 Thick-billed Murre, 161 Common Murre) that provided a post-breeding (fall) isotopic signal (Pyle 2009) for all colonies, and 3) alternate plumage (breast feathers; n = 317; 166 Thick-billed Murre, 151 Common Murre) provided a pre-breeding isotopic signal (Pyle 2009, P Pyle pers. comm, GJR pers. obs.) for all colonies (see also details below).

Stable isotope preparation – Following Cherel et al. (2007), feather samples (tip section only) were rinsed in 2:1 chloroform:methanol to remove surface contaminants and whole blood was dried, ground, and lipid-extracted. Samples were analyzed at the Stable Isotope Facility, University of California Davis, USA. Results are presented in standardized delta notation (δ) in parts per thousand (‰) relative to PeeDee Belemnite

($\delta^{13}C$) and air ($\delta^{15}N$). Replicate measurements of internal laboratory standards indicated measurement errors (standard deviations) of 0.11‰ and 0.21‰ for ^{13}C and ^{15}N, respectively. To facilitate more direct seasonal comparison, isotopic signatures of the three tissues (alternate and breast feathers and blood) were converted to putative dietary values using fractionation factors. Following Becker et al.'s (2007) study on capelin-fed murres, two diet-feather fractionation values were used to convert feather isotopic values to putative dietary values: 3.6‰ ($\delta^{15}N$) and 2.5‰ ($\delta^{13}C$) for alternate (breast) feathers; and 3.7‰ ($\delta^{15}N$) and 1.9‰ ($\delta^{13}C$) for primary feathers (note that despite these differences in fractionation value, they influence only the magnitude, but not the direction of seasonal shifts). Following Cherel et al. (2005), the average diet-blood fractionation used was 2.63 ‰ ($\delta^{15}N$) and 0.37 ‰ ($\delta^{13}C$) (averaged for three piscivorous seabirds). All fractionation factors were subtracted from raw isotopic values prior to analysis.

Stable isotopes and spatial patterns – To investigate the potential relationship of spatial location with isotopic signatures, we used Spatial Join in ArcMap to integrate all tracking data with isotopic data according to time: individual-specific GLS point locations during post-breeding (i.e. fall, late August-September; see Figure 5.1) were matched a single value for its flight feathers; and during pre-breeding (i.e. spring, March-April) were matched a single value for its alternate feathers. Murre flight feather moult takes ~25 days (Thompson et al. 1998), and although alternate moult is not well studied in murres, it is generally agreed that alternate feathers grow more slowly (Widelitz et al. 2003) and that this moult period would be longer than primary moult (Pyle 2009). It thus seemed reasonable to estimate a 2-month window for each season to represent the potential time and space over which feather isotopic signatures were integrated. Using neighborhood statistics (Spatial Analyst) we created an output value (mean) for each cell (identified in 180-km^2 rectangular neighborhoods, mimicking GLS-location error; see Phillips et al. 2004) that contained point data (ESRI 2012), to describe isotopic

characteristics of individuals occupying similar space. This approach assumes that birds sharing space also share access to similar prey, and that integrating multiple isotopic signatures would reveal geographic patterns. Distance to coast and bathymetry were extracted for fall and spring GLS datapoints to investigate potential trends in isotopic signatures based on geography, using general linear models (glm).

Overlap of stable isotopes and kernel home ranges - To help understand potential competitive interactions, isotopic values were compared to inter-colony distance and spatial overlap of Common and Thick-billed Murre core spring areas (kernel home ranges [KHR], following methods in chapter 3). Following Barger and Kitaysky (2011, supplementary material), a bivariate plot of mean nitrogen and carbon values (alternate feathers only) was used to calculate pairwise inter-colony isotopic distance (Euclidean) between all colonies. Isotopic distance was plotted against inter-colony distance (km) and inter-colony % KHR overlap for each pairwise colony comparison. Similarly, to help understand the relationship between spatial/geographic habitat and trophic niche, kernel home range area (spring only, when spatial overlap is greater among colonies) was compared with trophic niche metrics (alternate feathers only, to match putative spring timing).

Isotopic niche calculations - To compare trophic niche widths between and within species, we calculated Layman et al.'s (2007; see also Bearhop et al. 2004) metrics, a recently-developed approach that uses stable isotope ratio variance to compute a convex hull area in bivariate space representative of trophic niche space and the extent of trophic diversity (NR, δ^{15}N range; CR, δ^{13}C range; TA, total area of convex hull; CD, mean distance to centroid; MNND, mean nearest neighbor distance; SDNND, standard deviation of nearest neighbor distance). These measurements were compared within and between species. As Layman et al.'s method may suffer from sample size discrepancy, standardized ellipse areas (SEA) were calculated as a second measure of

niche width. This approach resolves sample size concerns by creating Bayesian standardized ellipses through posterior draws on isotopic data, to represent niche space (Jackson et al. 2011, Lavoie et al. 2012). Calculations were performed using the SIAR package of R 2.12.2 (R Development Core Team, 2012). Differences in isotopic variance and niche width were tested using ANOVA.

Statistics – In order to deal with repeated measures of individuals and heterogeneity (unequal variance) among species, seasons, and tissues, a linear mixed effects (lme) approach was used. Two separate global models (i.e. containing all potential explanatory variables) were built, one for nitrogen and one for carbon, specifying unique variance terms (varIdent in R, version 2.15.2; see also Zuur et al. 2009) for species, tissue type, colony, and year. Nonsignificant variables were dropped in a backwards-selection process using AIC to rank consecutive models (Zuur et al. 2009). However, nearly all explanatory variables and several interaction terms were significant determinants of nitrogen and carbon, making results very difficult to interpret holistically. Therefore, once significant terms were identified (using lme and accounting for repeated measures and heterogeneity), we subset the global lme into reduced lme models to investigate and discern specifically where differences occurred between groups. This involved repeating the lme exercise separately for species and colonies (still accounting for heterogeneity in variance), to discern where specific differences occurred between groups. 95% confidence limits (using "effects" package in R) were examined to determine within-group differences (e.g. between tissue types). Results incorporate all relevant variables but focus on 1) seasonal shifts and 2) inter-specific and 3) intra-specific differences. Statistics were done using R 2.12.2 (R Development Core Team, 2012).

5.4 RESULTS

Spatial distribution of Thick-billed and Common Murres during times in the nonbreeding season when feather moult occurs (fall flight feather moult, August-September; spring breast feather moult, March – April) is presented in Figure 5.1.

5.4.1 Lme models

Determinants of variance in nitrogen were species (lme, $F_{1,462} = 20.58$, $p < 0.0001$), colony (lme, $F_{5,196} = 44.46$, $p < 0.0001$) tissue type (lme, $F_{2,462}=8.0$, $p = 0.004$), and year (in some, but not all years; lme, $F_{3,462} = 4.14$, $p = 0.007$) with significant interactions between species*tissue type (lme, $F_{2,462} = 107.31$, $p < 0.0001$) and colony*group (i.e. control vs geolocator; lme $F_{5,462} = 2.81$, $p = 0.02$). Sex was not a significant determinant of nitrogen (lme, $F_{1,462} = 2.37$, $p = 0.13$).

Determinants of variance in carbon included species (lme, $F_{1,463} = 161.2$, $p < 0.0001$), colony (lme, $F_{5,196} = 39.4$, $p < 0.0001$), tissue type (lme, $F_{2,463} = 698$, $p < 0.0001$) year (in some, but not all years; lme, $F_{3,463} = 20$, $p < 0.0001$), and sex (lme, $F_{1,463} = 21.3$, $p < 0.0001$; however there was extensive overlap of 95% CI) with a significant interaction between species*tissue type (lme, $F_{2,463} = 54.7$, $p < 0.0001$).

To better understand the details of these differences, lme for each species were run separately and are discussed below, in the context of seasonal (tissue type), inter-specific, and intra-specific (colony) differences.

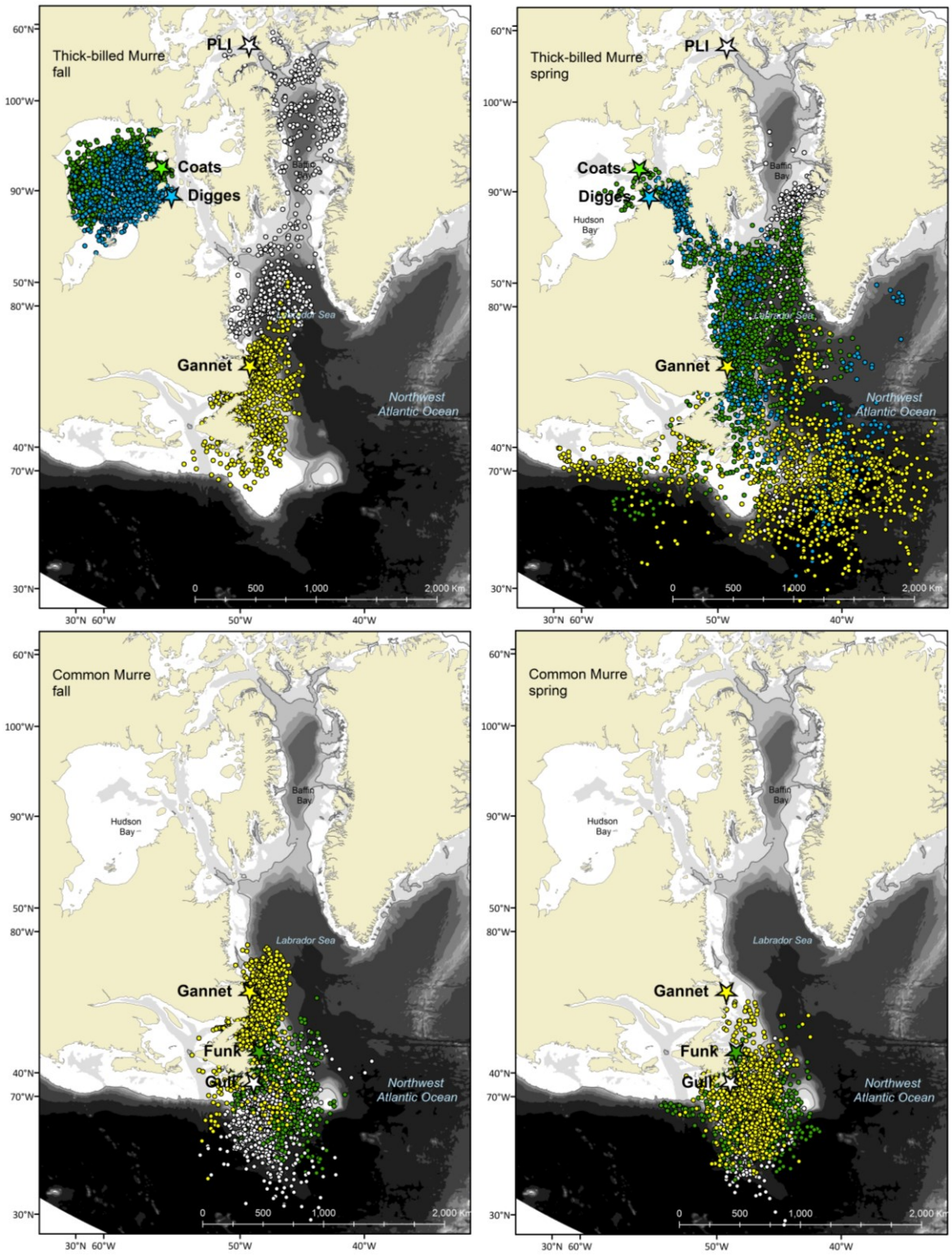

Figure 5.1. Spatial distributions of Thick-billed (top) and Common Murres (bottom) during the nonbreeding period when feather moult occurs (fall flight feather moult, August-September, left panels; and spring breast feather moult, March – April, right panels). Colored stars indicate individual breeding colonies and match the color of colony-specific tracking data.

5.4.2 Isotopic analyses

Raw values of stable nitrogen and stable carbon isotopes (without correction for fractionation) for each colony and tissue type are presented (Table 5.1) to facilitate direct comparison with other studies. Discrimination factors were applied to these values (see methods) to further describe spatial connections, seasonal trophic shifts, and inter- and intra-specific relationships. All further analyses (below) use isotopic values corrected for fractionation.

5.4.3 Geologger effects

At most colonies, isotope values for control and geologger birds were pooled because no differences were detected (nitrogen lme, $t_{1,459} = 0.15$, $p = 0.70$; carbon lme, $t_{1,459} = 0.8$, $p = 0.34$). Similarly, isotopic variance (NR, CR) and trophic niche width (TA) did not differ between control or logger groups in either species (ANOVA, all $p > 0.2$; Table 5.2).

However, a significant interaction among colony*group for nitrogen only (lme, $F_{5,459} = 2.8$, $p = 0.01$) prompted investigation of which colony showed a difference in control and geologger birds. At the Gannet Island colony only, geologger birds of both species had lower $\delta^{15}N$ (12.4 $\pm$ 0.7 Common Murre, 11.1 $\pm$ 0.93 Thick-billed Murre) than controls (12.8 $\pm$ 0.9 Common Murre, 11.4 $\pm$ 0.9 Thick-billed Murre; lme, $t_{1,122} = -3.4$, $p = 0.001$). These differences were more pronounced in blood (lme, $t_{1,16} = -2.4$, $p = 0.03$) and breast feathers (lme, $t_{1,12} = -3.5$, $p = 0.004$). Despite this difference, the direction of isotopic shifts between tissues were the same for control and geologger birds, so groups were pooled at the Gannet Islands to test isotopic shifts among tissues.

Table 5.1. Raw mean values (without corrections for isotopic discrimination) and standard deviation (SD) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in blood (BL), flight (F1) and breast feathers (F2) of Thick-billed Murres and Common Murres from 6 colonies in the eastern Canadian Arctic and eastern Canada.

Species	Colony	Tissue type	$\delta^{15}N \pm SD$	$\delta^{13}C \pm SD$
Thick-billed Murre	Prince Leopold	BL	17.41 ± 0.6	-19.60 ± 0.3
		F1	15.26 ± 1.4	-19.4 ± 0.70
		F2	14.22 ± 0.9	-18.42 ± 0.3
	Coats	BL	15.15 ± 0.6	-19.50 ± 0.4
		F1	16.88 ± 0.6	-20.92 ± 0.6
		F2	15.37 ± 1.1	-18.53 ± 0.8
	Digges	F1	16.89 ± 0.7	-20.96 ± 0.7
		F2	16.41 ± 1.5	-19.25 ± 1.5
	Gannets	BL	14.01 ± 0.6	-19.23 ± 0.5
		F1	15.31 ± 0.6	-19.35 ± 0.4
		F2	14.54 ± 1.4	-18.83 ± 0.9
Common Murre	Gannets	BL	15.46 ± 0.6	-18.95 ± 0.2
		F1	15.92 ± 0.7	-19.25 ± 0.5
		F2	16.39 ± 1.0	-18.71 ± 0.8
	Funk	BL	14.91 ± 0.7	-19.30 ± 0.4
		F1	15.47 ± 0.5	-19.41 ± 0.5
		F2	16.33 ± 0.6	-18.55 ± 0.4
	Gull	BL	15.99 ± 0.5	-19.70 ± 0.6
		F1	15.56 ± 0.9	-19.32 ± 0.3
		F2	16.52 ± 0.8	-18.65 ± 0.7

Table 5.2. Mean isotopic values (corrected for fractionation), trophic niche widths (TA), and isotopic variance for nitrogen (NR) and carbon (CR) of geologger and control Thick-billed Murres (4 colonies) and Common Murres (3 colonies).

				Trophic niche width			
Species	Group	$\delta^{15}N \pm SD$	$\delta^{13}C \pm SD$	n	TA.mean	NR.mean	CR.mean
Thick-billed Murre	geologger	12.50 ± 0.77	-20.78 ± 0.79	166	5.49	2.03	3.40
	control	12.49 ± 0.93	-20.76 ± 0.88	233	5.08	2.12	3.04
Common Murre	geologger	11.99 ± 1.49	-21.29 ± 1.23	226	2.43	1.70	2.21
	control	12.15 ± 1.24	-21.07 ± 1.24	250	3.49	2.09	2.81

5.4.4 Characterizing spatial and trophic connections

Carbon and nitrogen did not vary consistently by latitude, distance to coast or bathymetry (glm, all $p > 0.10$) for either species. However, nitrogen was weakly related to longitude for Thick-billed Murre only (glm, $F_{1,36} = 9.39$, $p = 0.004$, $R^2 = 0.21$), with higher $\delta^{15}N$ values at locations farther west. This followed a general pattern of isotopic enrichment that was connected with Hudson Bay, the upper Labrador Sea, and the high Arctic (near Prince Leopold Island) especially in fall.

Flight feathers - Neighborhood statistics to describe isotopic characteristics of Thick-billed Murres occupying similar space (Figure 5.2) in fall (from flight feathers) showed enriched $\delta^{15}N$ (range 9.8 to 13.7) and depleted $\delta^{13}C$ (range -20.3 to -24.3) signatures in Hudson Bay, the upper Labrador Sea/Davis Strait and the area of the Arctic Archipelago (near PLI), with lower nitrogen and more enriched carbon in the south of the study area (Figure 5.2, upper panels). For Common Murres, elevated $\delta^{15}N$ (range 10.7 to 13) and depleted $\delta^{13}C$ (range -20.5 to -21.7) in fall tended to be on the Grand Bank and just past the 500m isobaths, and on Labrador Bank (near the Gannet Island colony; Figure 5.2, lower panels).

Breast feathers - Neighborhood statistics showed high trophic level input for Thick-billed Murres in more northern areas (upper Labrador Sea, near Davis Strait, in Hudson Strait) and the Scotian Shelf and SW shoal of the Grand Bank (Figure 5.3, upper panels) in spring (breast feathers). Lower trophic level input occurred at the southern Labrador Sea, and offshore toward the Mid-Atlantic Ridge area (δ^{15}N range 8.9 – 13.2). Common Murres had overall high nitrogen signatures, particularly along the shelf edges (500m isobaths) on the Newfoundland Bank, Grand Bank, and St. Pierre Bank (δ^{15}N range 11.4 – 13.6; Figure 5.3, lower panels). For both species, more depleted carbon signatures occurred in Hudson Strait and in the mid-Labrador Sea, and around the edges of the SW Grand Bank Newfoundland/Laurentian Channel (Figure 5.3; δ^{13}C range – 20.8 to – 22.7 in Common Murres; range – 20.1 to – 22.8 in Thick-bills). A striking pattern of the species' spring distribution is the apparent exclusion of Thick-billed Murres (Figure 5.3, upper panels) from the productive area on the Grand Bank that is occupied by Common Murres (Figure 5.3, lower panels).

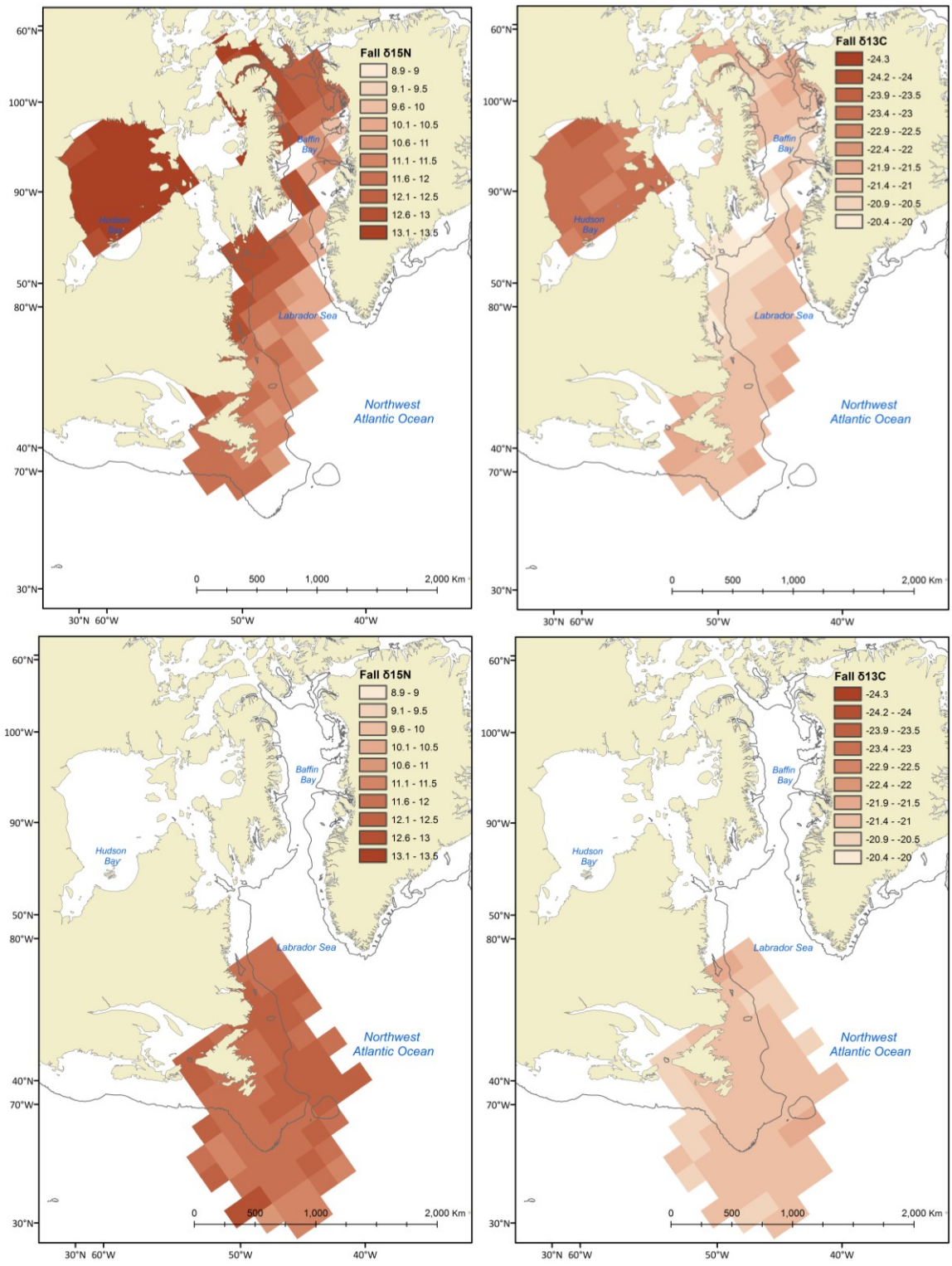

Figure 5.2. Fall neighborhood statistics (summing values in 180-km bins), depicting spatial patterns of nitrogen (left) and carbon (right) in primary feathers of tracked Thick-billed Murres (top) and Common Murres (bottom). The 500 m bathymetric contour is shown for reference. Color intensity indicates increasing enrichment of nitrogen and increasing depletion of carbon.

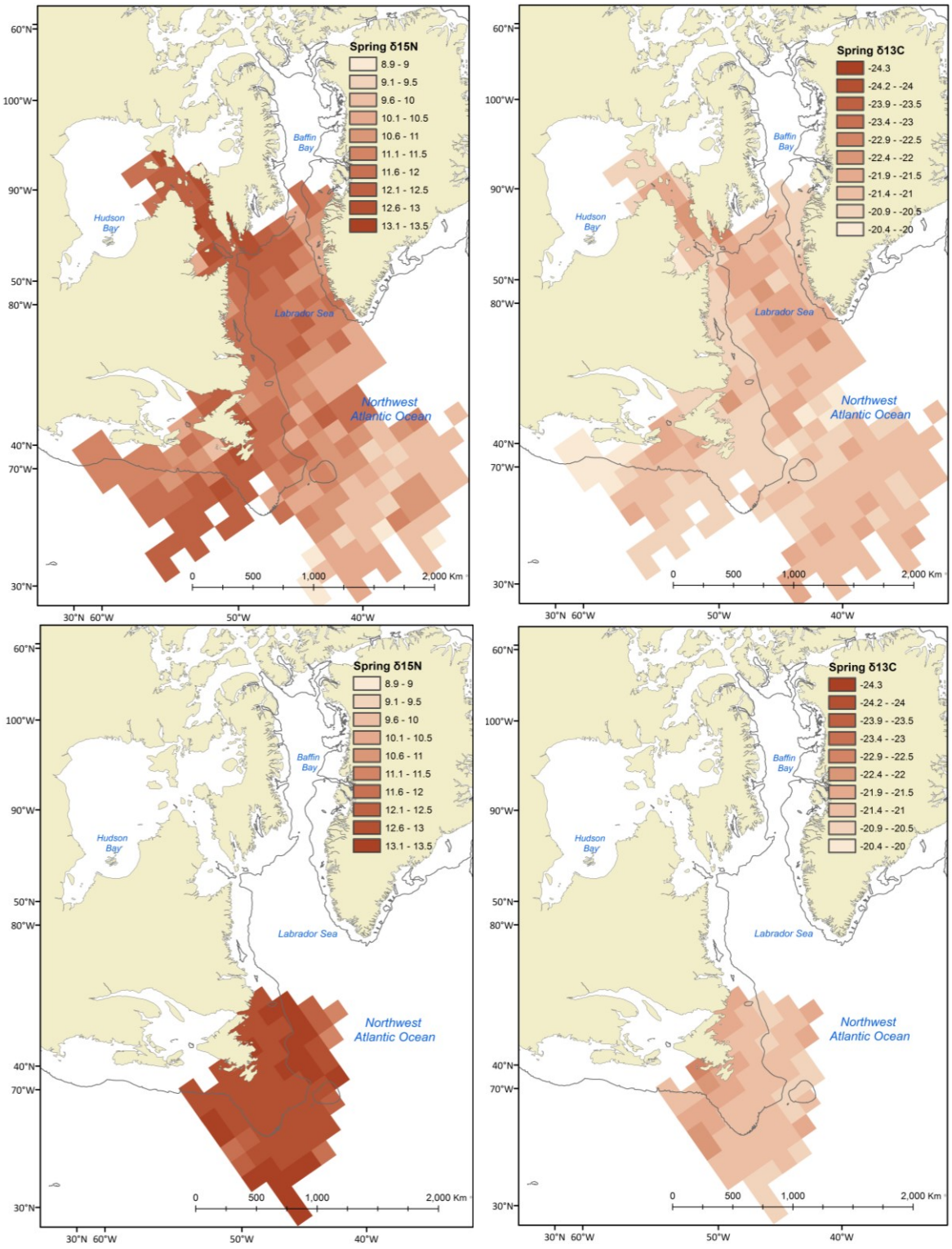

Figure 5.3. Spring neighborhood statistics (summing values in 180 km bins), depicting spatial patterns of nitrogen (left) and carbon (right) in alternate feathers of tracked Thick-billed (top) and Common Murres (bottom). The 500 m bathymetric contour is shown for reference. Color intensity indicates increasing enrichment of nitrogen and increasing depletion of carbon.

Kernel home range area – To test how isotopic niche width was related to space use, trophic variance was compared to spring kernel home range areas for all colonies. Kernel home range area (km^2) for both species combined was positively correlated with niche width (TA, Total Convex Hull Area, lm, $F_{1,5} = 9.52$, $p = 0.03$, $R^2 = 0.7$; Bayesian standard ellipse area SEA.B; lm $F_{1,5} = 7.6$, $p = 0.04$, $R^2 = 0.6$; Figure 5.4) and the variance of carbon (CR; $F_{1,5} = 15.6$, $p = 0.01$, $R^2 = 0.8$) but the relationship was not significant for variance of nitrogen (NR; lm, $F_{1,5} = 2.12$, $p = 0.20$, $R^2 = 0.3$).

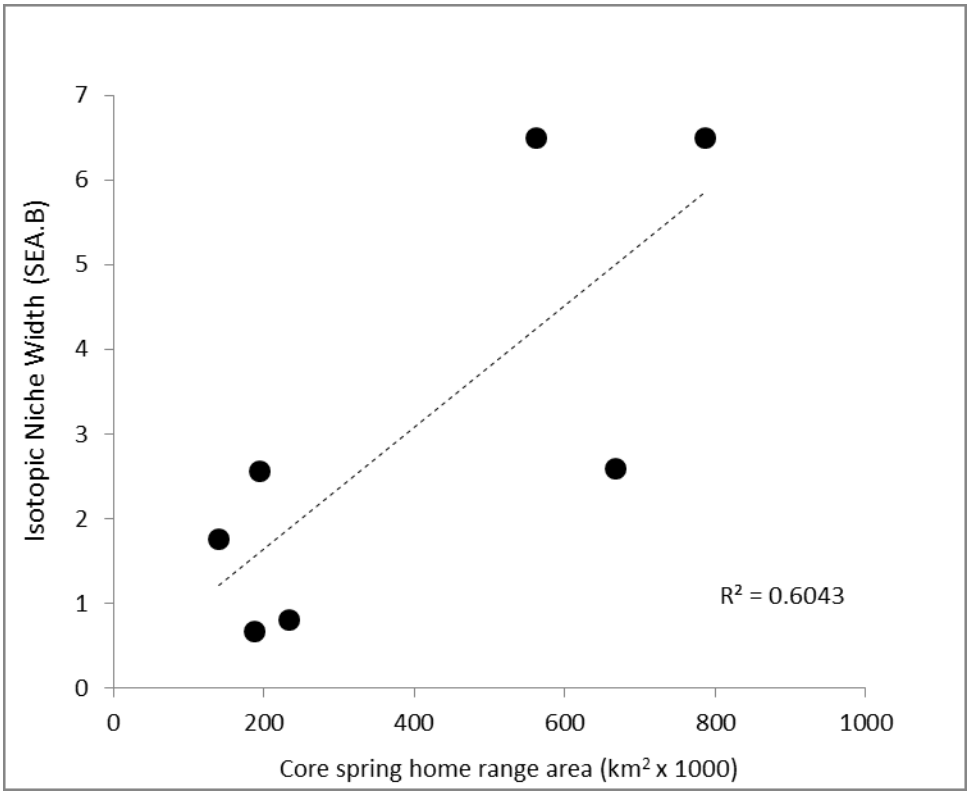

Figure 5.4. Kernel home range area of Common and Thick-billed Murres correlates with niche width, as measured by including Bayesian standard ellipse area (SEA.B; see also results).

5.4.5 Seasonal shifts in trophic associations

Isotopic analysis of three tissues in each bird allowed a comparison of seasonal trophic shifts. Descriptively, trophic variance (in both $\delta^{15}N$ and $\delta^{13}C$; see NR, CR, Table 5.3) was greatest during the nonbreeding period, particularly during prebreeding (alternate feathers; Table 5.3). This is also highlighted by greater distance between isotopic neighbors (MNND, SDNND, Table 5.3) during the nonbreeding period. Due to contrasting directions in seasonal shifts between the species (i.e. interaction term, species*tissue type; nitrogen lme, $F_{2,462} = 107.31$, $p < 0.0001$, carbon lme, $F_{2,463} = 54.7$, $p < 0.0001$), seasonal isotopic shifts are better understood in a separate analysis for each species.

Thick-billed Murres – Isotopic shifts between tissues were somewhat variable among Thick-billed Murre colonies, but for three common aspects: 1) $\delta^{15}N$ was consistently lowest in breast feathers (lme, $t_{2,24\,3} = -6.26$, $p < 0.0001$), 2) $\delta^{15}N$ was elevated in flight compared to breast feathers (as determined by 95% CI), and 3) $\delta^{13}C$ in blood was consistently enriched compared to both flight and breast feathers (lme, $t_{2,243} = -31.72$, $p< 0.0001$; lme, $t_{2,243} = -14.9$, $p < 0.0001$; Figure 5.5a). Only at PLI was $\delta^{15}N$ was substantially higher in blood (lme, $t_{2,34} = -10.2$m $p < 0.0001$; $t_{2,34} = -19$, $p < 0.0001$); at Coats and Gannet Islands, $\delta^{15}N$ in blood was lower than flight feathers (lme, $t_{2,126} = 9.2$, $p < 0.0001$; lme, $t_{2,58} = 2.4$, $p = 0.02$, respectively; Figure 5.5a). Although mean isotopic value varied by year, the direction of isotopic shifts among tissues was similar across years (Figure 5.5a).

Table 5.3. Seasonal changes in $\delta^{15}N$ and $\delta^{13}C$ (corrected for fractionation), and trophic niche width, for Thick-billed Murres and Common Murres. Layman's metrics (Layman et al. 2007) and SIBER (Jackson et al. 2011) describe isotopic variance and niche width as follows: NR, $\delta^{15}N$ range; CR, $\delta^{13}C$ range; TA, total area of convex hull; CD, mean distance to centroid; MNND, mean nearest neighbor distance; SDNND, standard deviation of nearest neighbor distance; SEA.B, Bayesian standard ellipse area.

				Layman's metrics							SIBER
Species	Season	$\delta^{15}N \pm SD$	$\delta^{13}C \pm SD$	n	NR	CR	TA	CD	MNND	SDNND	SEA.B
Thick-billed Murre	fall	12.5 ± 1.1	-22.1 ± 1.0	123	4.21	7.05	15.89	1.33	0.17	0.17	2.82
	spring	11.5 ± 1.3	-21.2 ± 0.9	125	5.78	6.41	21.71	1.37	0.16	0.17	3.88
	summer	12.4 ± 0.7	-19.8 ± 0.4	121	1.65	6.08	6.51	1.11	0.12	0.13	1.82
Common Murre	fall	11.9 ± 0.7	-21.2 ± 0.4	142	2.56	4.38	6.58	0.71	0.11	0.11	1.05
	winter/spring	12.8 ± 0.8	-21.1 ± 0.7	142	4.66	4.39	12.57	0.81	0.14	0.15	1.79
	summer	12.9 ± 0.7	-19.7 ± 0.5	92	2.17	3.64	5.38	0.79	0.08	0.07	1.36

Common Murres – Isotopic shifts between tissues followed the same general pattern among all Common Murre colonies: 1) $\delta^{15}N$ in blood was consistently higher than flight feathers (lme, $t_{2,218} = -9.1$, $p < 0.001$) but not higher than breast feathers (lme, $t_{2,218} = 0.37$, $p = 0.71$), 2) $\delta^{13}C$ was significantly enriched in blood compared to both flight and breast feathers (lme, $F_{3,218} = -29.2$, $p < 0.001$, $F_{3,218} = -22.7$, $p < 0.001$, respectively) and 3) $\delta^{13}C$ did not differ between feather types (as determined by 95% CI; Figure 5.5b). Although mean isotopic value varied by year (lme, $F_{3,218}$, $p < 0.0001$), the direction of isotopic shifts among tissues was similar across years (Figure 5.5b).

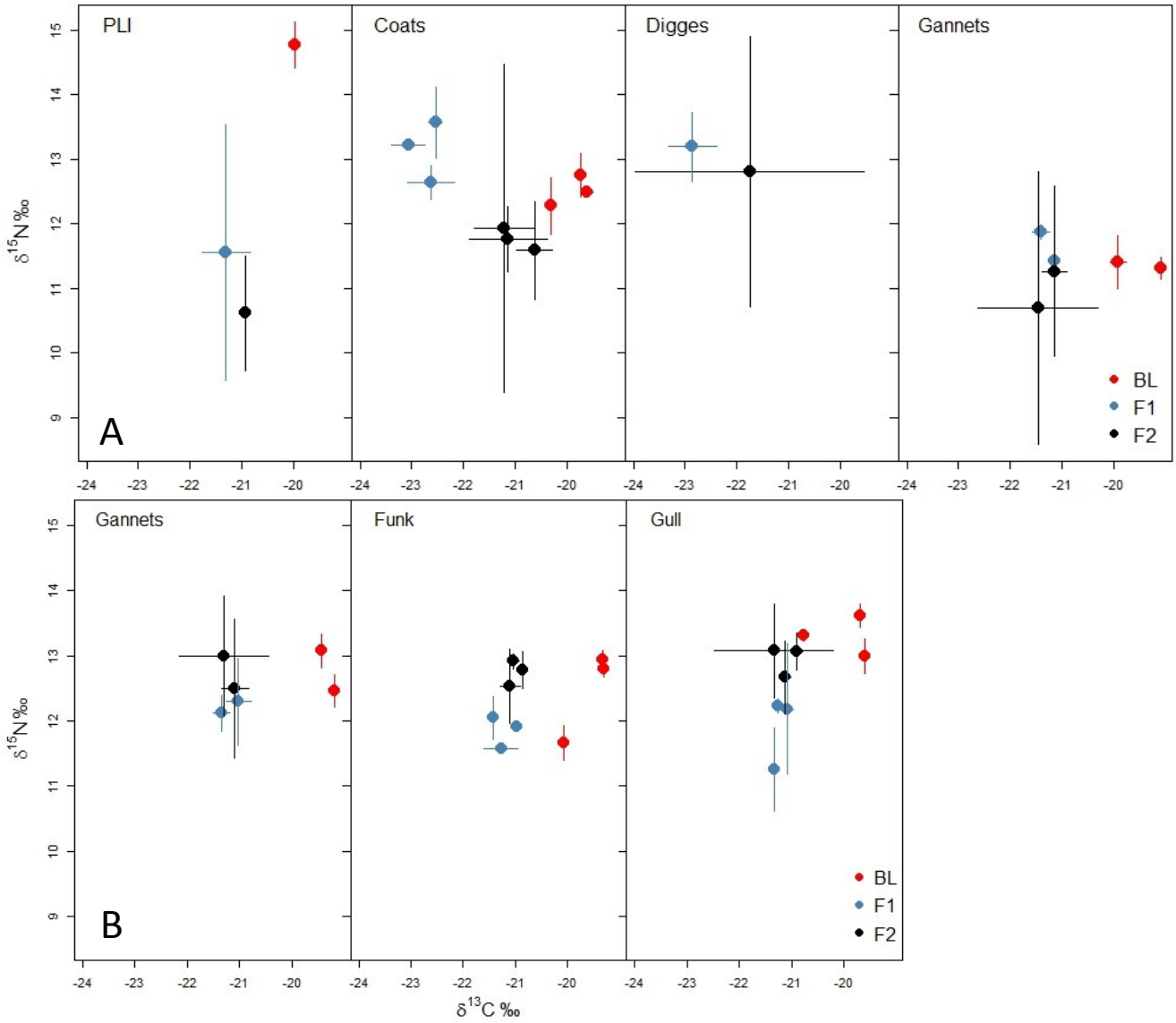

Figure 5.5. Seasonal isotopic changes ($\delta^{15}N$, $\delta^{13}C$) among colonies of (A) Thick-billed Murres (n = Prince Leopold (PLI) 75, Coats 189, Digges 54, Gannets 123) and (B) Common Murres (n= Gannets 131, Gull 96, Funk 148). Legend indicates blood (BL – breeding), flight feather (F1- post-breeding), breast feather (F2 - pre-preeding). Values take into account tissue-specific discrimination factors to facilitate direct seasonal comparison.

5.4.6 Inter-specific comparisons

Strong species differences were detected in both nitrogen (lme, $F_{1,462} = 20.58$, $p < 0.0001$) and carbon isotopes (lme, $F_{1,463} = 161.2$, $p < 0.0001$). Isotopic niche width was consistently larger for Thick-billed Murres in every season (Table 5.3). In general, Thick-billed Murres had lower nitrogen and more depleted carbon than Common Murres, but not at all colonies or in all tissue types.

At the Gannet Islands, where the species breed sympatrically and inter-specific overlap is highest, isotopic differences between the species were the most pronounced (lme, $F_{1,158} = 154$, $p < 0.0001$). Compared to Common Murres at the Gannet Islands, Thick-billed Murres had lower $\delta^{15}N$ in blood (lme, $t_{1,36} = -10.2$, $p < 0.0001$), flight feathers (lme, $t_{1,11} = -3.5$, $p = 0.005$) and breast feathers ($t_{1,40} = -5.5$, $p < 0.0001$). Thick-billed Murres also had more depleted $\delta^{13}C$, but only in blood (lme, $t_{1,36} = 32.8$, $p < 0.0001$; Figure 5.6).

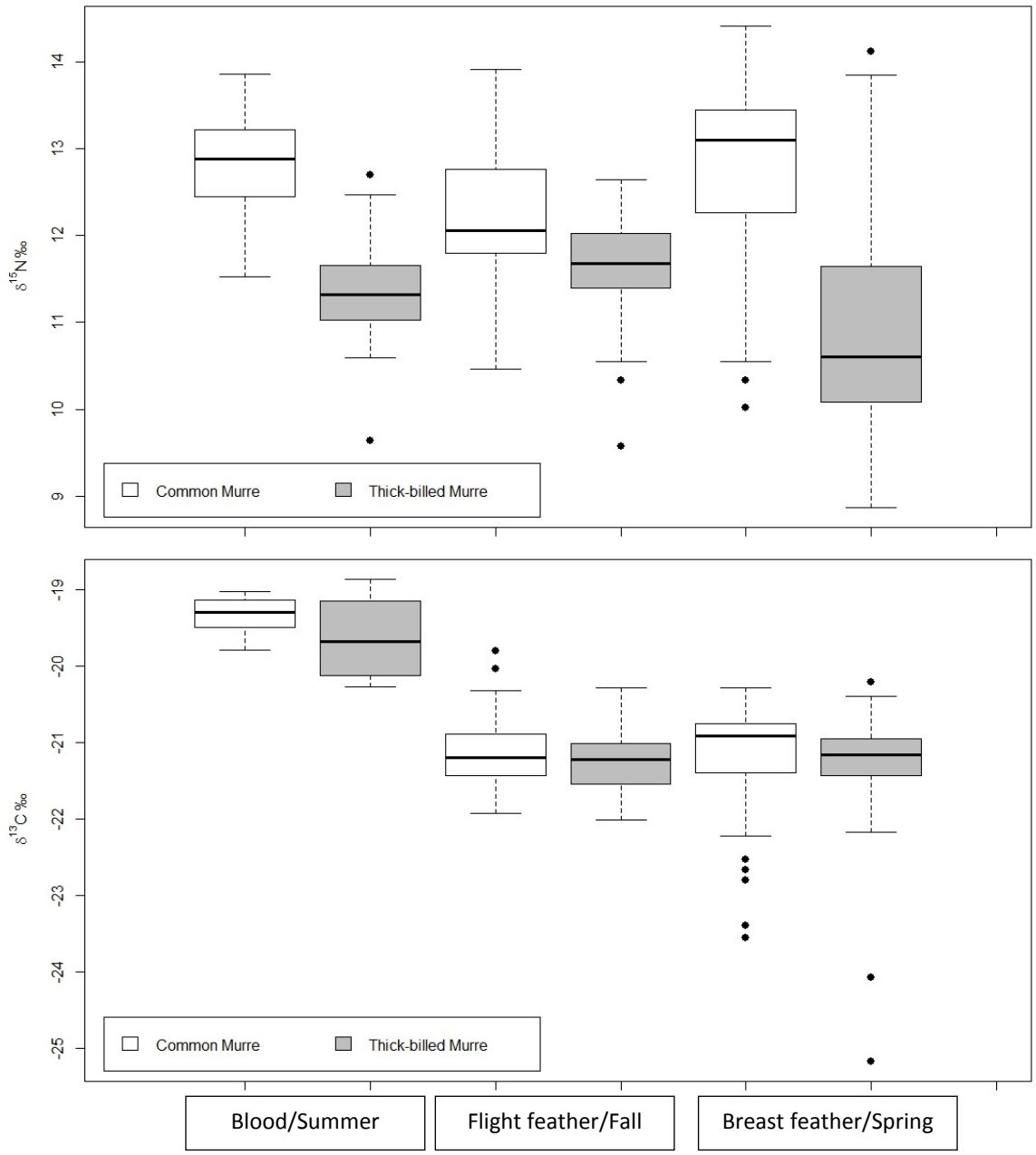

Figure 5.6. Species comparison of seasonal shifts in isotopes (corrected for fractionation; upper panel, δ^{15}N‰; lower panel, δ^{13}C‰) among Thick-billed Murres and Common Murres breeding sympatrically at the Gannet Islands, Labrador. Boxplots indicate lower (25%) and upper (75%) quantiles, whiskers indicate minimum and maximum values, and points indicate outliers.

5.4.7 Intra-specific comparisons

Blood - Due to differences in location of breeding colonies it is not surprising that considerable isotopic differences occurred among all the colonies. Isotopic signatures of $\delta^{15}N$ and $\delta^{13}C$ in blood differed significantly among all colonies of Thick-billed Murre (except Digges where no blood was taken; lme, $t_{2,67} = 108$, $p < 0.0001$; lme, $t_{2,67} = -2.5$, $p = 0.02$, respectively; Figure 5.5a). Similarly, isotopic signatures of $\delta^{15}N$ and $\delta^{13}C$ were significantly different between all colonies of Common Murre (lme, $t_{2,73} = 95.7$, $p = 0.0001$; lme, $t_{2,73} = 82.2$, $p < 0.0001$, respectively; Figure 5.5b), despite their relative spatial proximity.

Flight feathers – Similar to during the breeding season, there was considerable difference in post-breeding locations of most Thick-billed Murre colonies (Figure 5.1). $\delta^{15}N$ in flight feathers of Thick-billed Murre differed significantly between all colonies (lme, $t_{3,114} = 62.4$, $p < 0.0001$), but not between the two colonies that overlapped spatially during post-breeding (Coats and Digges in Hudson Bay, 95% CI). Flight feather $\delta^{13}C$ for Thick-billed Murres grouped into two significantly different pairs: $\delta^{13}C$ for Coats-Digges were the same and for PLI-Gannets were the same, but the pairs differed from each other ($t_{3,114} = 67.5$, $p < 0.0001$; Figure 5.5a). Common Murres overlap extensively in post-breeding locations (Figure 5.1; see also Chapter 4). For Common Murres, flight feather $\delta^{15}N$ (lme, $t_{2,77} = 8.7$, $p = 0.0004$) differed between Gannets and Funk/Gull, and $\delta^{13}C$ did not differ among colonies (lme, $t_{2,77} = 1.9$, $p = 0.15$; Figure 5.5b).

Breast feathers – Species and colonies were more likely to overlap spatially during pre-breeding than other times of the year (Figure 5.1), however, colonies still showed particular pre-breeding movement strategies (see also Chapter 4). For Thick-billed Murre breast feathers, $\delta^{15}N$ (lme, $t_{3,114} = 18.9$, $p < 0.0001$ with 95% CI) differed between all colonies except PLI-Gannets. Of note, this includes Thick-billed Murres with the greatest overlap in pre-breeding habitat (Digges-Coats; lme, $t_{3,114} = 2.5$, $p = 0.01$). $\delta^{13}C$

did not differ among colonies except between PLI-Digges (lme, $t_{3,114} = 3.32$, $p = 0.02$ with 95% CI; Figure 5.5). Notably, although PLI-Gannets had similar isotopic signatures (Figure 5.5), they did not overlap spatially (Figure 5.1). Breast feather isotopes of Common Murres colonies did not differ (nitrogen lme,$t_{2,79} = 1.7$, $p = 0.12$; carbon lme, $t_{2,79} = 0.57$, $p = 0.6$; see Figure 5.5b).

Trophic and spatial segregation - To help understand potential competitive interactions, the influences of home range overlap and inter-colony geographic distance on isotopic differences were investigated. No relationship was found between inter-colony isotopic distance (alternate feathers) and inter-colony geographic distance (lm, $F_{1,19} = 6.1x10^{-5}$, $p = 0.99$). There was an overall negative relationship between isotopic distance and percent core spring overlap (figure 5.7), however, this varied depending on the species being compared. For intra-specific comparisons between Thick-billed Murre colonies, there was no relationship (lm, $F_{1,4} = 0.09$, $p = 0.78$, $R^2=0.02$), and between Common Murre colonies, there was a negative relationship, suggesting that the greater the overlap, the shorter the isotopic distance (lm, $F_{1,1} = 290$, $p = 0.04$, $R^2 = 0.9$). For inter-specific comparisons, there no strong relationship between kernel overlap and isotopic distance (lm, $F_{1,10} = 3.7$, $p =0.08$, $R^2=0.3$; Figure 5.7).

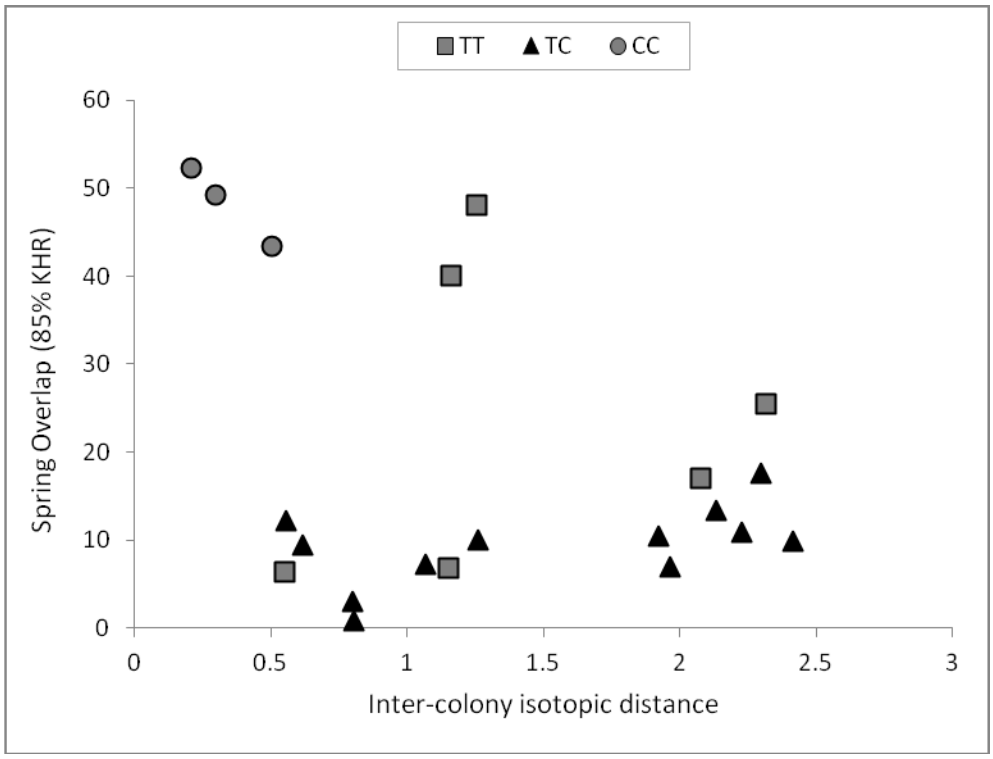

Figure 5.7. Relationship of isotopic distance with percent core spring overlap (85% KHR), between colonies of Thick-billed and Common Murres (TT =Thick-billed Murre colony pairs; TC =Thick-billed/Common Murre colony pairs; CC = Commmon Murre colony pairs).

5.5 DISCUSSION

The integration of tracking and isotopic approaches illustrates regional differences in isotopic signatures that reflect the trophic associations of Thick-billed and Common Murres. Besides regional differences, consistent patterns of variation in isotope signatures of particular tissues were detected within species, probably related to seasonal shifts in diet. Furthermore, the known distributions of tracked murres demonstrate areas of inter-specific overlap where shifts in trophic position could be influenced by competitive interactions.

Among Common and Thick-billed Murres breeding sympatrically, varied strategies of foraging, breeding phenology, and chick-provisioning can help reduce inter-specific competition (Birkhead and Nettleship 1987a,b,c, Barrett et al. 1997), with Thick-billed Murres generally foraging at lower trophic levels (or with wider diets; Gaston and Jones 1998) at greater distances from colonies (Barger and Kitaysky 2011). This study confirms a pattern of isotopic segregation at the Gannet Islands where the species breed sympatrically, not only during the breeding period, but year-round. Outside the breeding period, diet composition of both murres has not consistently been found to shift to different trophic levels (Tuck 1961, Elliot et al. 1990, compared to Lilliendahl 2009, Moody and Hobson 2007). Furthermore, few studies have compared murre winter diets in shared winter areas (Moody and Hobson 2007) and to our knowledge, none have compared winter and summer diets within the same individuals. For all past studies, the colony origins and seasonal movement patterns were unknown. We suggest that part of the equivocal nature of murre diet research to date stems from geographic variation in foraging conditions and regional differences in competitive interactions between the species in areas of spatial overlap. Comparative study of the movements of *Uria* murres and their trophic interactions during the non-breeding

period helps clarify when and where Thick-billed Murre and Common Murre differ in diet, and provides insight into their overwintering strategies and the degree of ecological segregation between them.

5.5.1 Geologger effects

Despite their small size, devices such as geolocators may in some cases influence mass, foraging behaviour, colony attendance or chick-provisioning of adults at breeding colonies (Paredes et al. 2005, Adams et al. 2009); and even when these aspects remain unaffected, physiological effects such as elevated corticosterone (Quillfeldt et al. 2012) or increased energy expenditure (Vandenabeele et al. 2012) are sometimes detected. In a concurrent study at our colonies, Elliott et al. (2012) found that after a year-long deployment of geologgers, Thick-billed and Common Murres had elevated corticosterone compared to controls, although levels were quite variable and were not significant at every colony. Adding to this story, we found decreased $\delta^{15}N$ only at the Gannet Islands, potentially indicating an effect of geologgers on foraging ecology at this site. Quillfeldt et al. (2012) also found increased corticosterone but no overall differences in stable isotope ratios of Thin-billed Prions (*Pachyptila belcheri*) after a year-long logger deployment. It is intriguing that the foraging ecology of loggered birds was only affected at the sympatric Gannet Islands. We recommend that other device effect studies should consider the potential compounding effects of inter- and intra-specific competition.

5.5.2 Spatial and trophic connections

We found strong inter- and intra-specific variation in $\delta^{15}N$ and $\delta^{13}C$ isotopes that likely incorporate regional differences in isotopic signatures of prey, true shifts in trophic association across seasons, and species-specific differences. From a geographic perspective, Thick-billed Murres $\delta^{15}N$ ratios in flight feathers were highest at the

northern end of the Labrador Sea and near Davis Strait, in Hudson Strait, at the Scotian Shelf and the SW edge of the Grand Bank. Lower trophic associations occurred at the mouth of the Labrador Sea, near the Grand Bank/Orphan Basin, and offshore toward the Mid-Atlantic Ridge. In contrast, Common Murres occupied fairly high and consistent trophic positions across the Grand Bank/Orphan Basin and beyond the shelf edges (500m isobath).

Using isotopes to describe spatial differences in distribution using isotopes depends on the isotopic distinctness of water masses where seabird tissues are grown (Ramos et al. 2009, Phillips et al. 2009). Pomerlau et al. (2011) documented regional variation in the eastern Arctic mesoplankton community, noting variable $\delta^{15}N$ isotopic signatures (but not $\delta^{13}C$) within particular prey species, according to water mass characteristics uniquely defining the Labrador Sea, Davis Strait, Baffin Bay, and Arctic Archipelago. Similarly, Hobson and Schell (1998) found repeated seasonal fluctuations in $\delta^{15}N$, but not $\delta^{13}C$, of eastern Arctic bowhead whales (*Balaena mysticetus*). In other regions (Antarctic, Pacific Oceans – Hobson et al. 1994, Quillfeldt et al. 2005, Gladbach et al. 2007, Phillips et al. 2009), increasing carbon depletion in the marine environment is used to characterize relative extent of offshore (pelagic source) foraging of nonbreeding seabirds. As well, Antarctic high-latitude waters are typically carbon-depleted due to increased CO_2 solubility in cold water (Rau 1989), and seabirds with very depleted $\delta^{13}C$ are assumed to moult in close association with the Antarctic ice edge (Rau et al. 1992, Phillips et al. 2009). However, in the NW Atlantic, carbon isotopic signatures are relatively invariant (Sherwood and Rose 2006, Pomerlau et al. 2011) and poorly describe relative movement of seabirds from nearshore to pelagic zones (Hedd et al. 2010). Despite the link to pelagic foraging area in other regions, we find carbon isotope depletion (the putative signal of "pelagic" distribution) in murres only weakly associated with offshore distribution, except for some carbon depletion observed in the central Labrador Sea. Rather, we found carbon depletion was strikingly associated with Hudson Bay and Hudson Strait. Murre-ice association in Hudson Bay and Hudson Strait

may partly explain the depleted carbon signatures among Coats and Digges birds, but is more likely related to complex and unique geochemistry of this large inland sea (Ferland et al. 2011, Guéguen et al. 2011, MacDonald and Kuzyk 2011). To a lesser degree, carbon depletion was also noted in murres associated with nearshore areas such as the Grand Banks of Newfoundland. Similarly, Hedd et al. (2012) found more depleted carbon in Sooty Shearwaters (*Puffinus griseus*) foraging SW of the Grand Banks compared to further offshore near the Mid-Atlantic Ridge. Also a potential complication is the seasonal distribution and lipid content of prey. Capelin (*Mallotus villosus*) and sandlance (*Ammodytes* sp.) have more depleted carbon signatures than other marine prey (Sherwood and Rose 2006, Sarà et al. 2009) and though these species are typically considered pelagic (Sarà et al. 2009), they make seasonal migrations to nearshore and demersal spawning sites where they attract predators such as cod, seabirds and whales (Davoren et al. 2003, 2007). Notably, capelin and sandlance have been increasingly prevalent Hudson Bay murre diets in recent years (Gaston et al. 2003). Higher lipid content also causes increased carbon depletion (Post et al. 2007), and lipid content increases in some species and age classes of fish (especially juvenile sandlance; Robards et al. 2011) and in zooplankton throughout summer (Falk-Peterson et al. 1981). Subsequent isotopic signatures of seabirds foraging on lipid-enriched prey may be carbon-depleted independent of a shift in foraging distribution (Thompson et al. 2000). Combined, these factors may help explain the depleted carbon signatures in nearshore environments in our study area, especially in fall (Figure 5.2).

Regional differences in prey communities may influence the timing and pattern of murre migration from particular colonies. Thick-billed Murres from Coats and Digges Islands remained within the region of their colonies (northern Hudson Bay), whereas birds from the high Arctic colonies (Prince Leopold, Minarets [Gaston et al. 2011, McFarlane Tranquilla et al. 2013]) moved quickly from breeding areas. Previous to this study (e.g. Gaston et al. 2011, McFarlane Tranquilla et al. 2013), Thick-billed Murres from all Arctic colonies were assumed to leave northern breeding areas and become

visible in coastal areas of Newfoundland from October – March (Tuck 1961, Gaston 1980, Elliot et al. 1990, Gaston and Hipfner 2000). The $\delta^{15}N$ signature of flight feathers grown in Hudson Bay in the fall helps to explain their unexpected stay-put strategy: remaining in Hudson Bay provides continued access to high trophic-level prey throughout fall.

In a similar fashion, the regional prey community on the Grand Bank may shape the foraging and movement strategy of Common Murres. Although they shift offshore during the nonbreeding season, $\delta^{15}N$ was high in all Common Murre tissues, suggesting they fed high in the marine food web throughout the year. Despite limited seasonal and colony diet variation, Common Murres have a narrower trophic niche (Figure 5.5; Table 5.3), supporting previous research identifying this species as a specialist for high trophic-level prey (Davoren and Montevecchi 2003). Our results extend this generalization year-round. Suitable prey seems available year-round on the Grand Bank. Securing an advantageous year-round foraging area, through foraging niche specialization, may require competitive exclusion of their abundant conspecific competitor (Thick-billed Murres) during the nonbreeding period, providing more reason for Common Murres to adopt a less migratory strategy. Year-round suitability of foraging habitat on the Grand Bank is further suggested by the winter influx of other Arctic and eastern Atlantic seabirds (Black-legged Kittiwakes *Rissa tridactyla,* Frederiksen et al. 2011; Dovekies *Alle alle*, Mosbech et al. 2012, Thick-billed Murres from Greenland, Iceland, and Svalbard, Kampp 1988, Bakken and Mehlum 2005, Fort et al. 2013), which Common Murres may also have to compete with during the nonbreeding season.

5.5.3 Seasonal changes in foraging strategy

Thick-billed and Common Murres exhibited clear, yet species-specific changes in isotope signatures during breeding, post-breeding, and pre-breeding periods. Despite inter-

colony variation in trophic signatures such as those for the Hudson Bay murres in fall, seasonal changes were consistent among multiple colonies and across years.

Like many marine birds and mammals (Atlantic Puffins, Hedd et al. 2010; penguins and fur seals, Cherel et al. 2007), both murres species appear to shift from more specialized trophic-level diets in summer to broader trophic level interactions during the nonbreeding period (see Figures 5.5, 5.6). Greater isotopic niche width and isotopic distance between neighbors (MNND; see Table 5.3) in the nonbreeding period suggests not just lowering, but expansion of isotopic niche in nonbreeding season. During breeding, murres are restricted to foraging near their colonies to allow timely chick-provisioning. Blood samples covering this precise period will reflect this spatial restriction and perhaps also will reflect trophic specialization of individuals (cf. Woo et al. 2008). By contrast, flight and breast feathers are grown over an extended period and reflect movement over a larger foraging range. Yet the relationship of kernel home range size with increased variance in *both* carbon (i.e. putative space) and nitrogen isotopes (i.e. trophic position; see results), suggests that both spatial movement and trophic position contribute to a wider trophic niche in the nonbreeding period. However, whether the wider niche is related to greater generalization of diets within individuals or a range of specialist strategies between individuals (cf. Woo et al. 2008) requires further investigation. Expansion of nonbreeding trophic niche, even when trophic signatures do not vary significantly between breeding and nonbreeding periods, is likely a common feature of seabird foraging ecology (Cherel et al. 2007; Hedd et al. 2010). Furthermore, for both murre species, this marks a shift from high diet overlap between breeding individuals, when individuals from the population are foraging mostly on the same prey (i.e. narrow trophic niche width; Bearhop et al. 2004), to lower dietary overlap between individuals and greater diversity during the nonbreeding period, reflective of a wider breadth of prey choices (Woo et al. 2008) and foraging locations (Wiley et al. 2012). Notably, trophic niche width was more variable (NR, CR) for Thick-billed Murres, suggesting greater variance in both foraging and movement strategies,

consistent with their wider spatial distribution during the nonbreeding period (Figure 5.1; see also McFarlane Tranquilla et al. 2013) and when individuals forage over a wider geographic range (Bearhop et al. 2004). By comparison, the variance in Common Murres isotopic niche width was much greater for nitrogen than for carbon, suggesting moderate flexibility in prey selection during the nonbreeding period and not in movement strategy.

Among both murre species, nonbreeding trophic signatures (post- and pre-breeding) were significantly depleted in $\delta^{13}C$, suggesting shifts to more pelagic/ice-associated sources, or inshore distribution of high-lipid prey (see above), compared to the breeding season. Contrary to expectation, the downward shift in $\delta^{15}N$ during the nonbreeding period was not consistent among colonies (except for Prince Leopold Island); for Thick-billed Murres, the consistent downward shift in $\delta^{15}N$ occurred only during pre-breeding, when murres were nearer winter areas. Seasonal increases in $\delta^{15}N$ enrichment at the base of the food web, due to changes in water mass structure or nutrient sources (Pomerlau et al. 2011) may explain the apparent upward trophic shift of Thick-billed Murres in Hudson Bay in fall. Similarly, a downward shift in $\delta^{15}N$ occurred consistently only during post-breeding for all Common Murre colonies. The consistent differences observed across years suggests species-specific differences in seasonal ecology between Thick-billed and Common Murres, with varying implications for each (see below).

5.5.4 Implications of seasonal shifts

The combination of an energetically-demanding moult (Guillemette et al. 2007, Hoye et al. 2011) with the challenging winter period creates a crucial “energetic bottleneck” in the life cycle of murres (Fort et al. 2009). For Thick-billed Murres in the Northwest Atlantic, it seems that this energetic bottleneck coincides with the late winter/early

spring, when seasonal ice extent is at its maximum (Canadian Ice Service[25]), when poor weather conditions might interfere with foraging (Finney et al. 1999), and when Thick-billed Murres are simultaneously molting and taking prey at a lower trophic level than at any other time of year. This is significant given that trophic position is positively related to body condition (mass) in Thick-billed Murres and kittiwakes (Moody et al. 2012). In contrast, Common Murres experience lowest trophic positions (and thus may be most energetically compromised) during fall, while also undergoing flight feather moult and providing post-fledging care of young (males), although at this time of year, water temperatures in the NW Atlantic are still warm. By late winter/spring, Common Murres are foraging at the same trophic levels as when breeding. This difference between species might partly explain the greater prevalence of late winter wrecks of Thick-billed Murres (McFarlane Tranquilla et al. 2010). Furthermore, the species may respond differently to climate change, depending on the season and the wintering area most affected (Cherel et al. 2006).

A greater proportion of high-energy prey in seabird diets enhances body condition and adult and chick survival (Sandvik et al.2005, Sorenson et al. 2008, Osterblom et al. 2011). As winter diet quality influences body condition for subsequent breeding attempts (Sorensen et al. 2008), differences in seasonal trophic shifts could also have species-specific consequences for birds returning to breeding colonies. Among migrant seabirds, the nutrients allocated to reproduction are derived along a continuum of exogenous (i.e. local foraging) or endogenous (i.e. stored in body tissue) sources in varying proportions (Klaassen et al. 2006, Bond and Diamond 2010). Although Common Murres, with ca. 85% exogenous nutrient contribution to egg production, have been considered mostly "income breeders" (Bond and Diamond 2010), it seems advantageous that they return to colonies in the spring after foraging at high trophic levels comparable to those that support breeding. By contrast, Thick-billed

[25] http://www.ec.gc.ca/

Murres return to northerly colonies after having foraged at their lowest trophic levels and made more extensive nonbreeding movements. Thick-billed Murres, like many other Arctic breeders (Klaassen et al. 2006) likely rely on endogenous reserves (i.e. "capital breeders") to produce first-laid eggs (Jacobs et al. 2009); and on the abundance and energetic composition (cf. Osterblom et al. 2008) of local food sources to for self-maintenance (Klaassen et al. 2006) and for replacement laying (Jacobs et al. 2009). Continued research to confirm spring body condition and endogenous reserves upon colony arrival would help clarify the relative consequences of spring trophic associations for these congeneric species.

5.5.6 Intra-specific and Inter-specific segregation

During breeding, inter-colony differences in murre diets reflect differences in local foraging conditions near colonies (Gaston and Bradstreet 1993), and this is confirmed by the large differences in $\delta^{15}N$ and $\delta^{13}C$ among colonies we studied (both Thick-billed and Common Murres). As well, we were able to confirm inter-colony differences in movement and diets throughout the year, but only for Thick-billed Murres. Winter colony segregation, in space, time, and diet, has also been found for Cape Gannets (Jaquemet et al. 2008), petrels (Cherel et al. 2006) and penguins (Thiebot et al. 2012). In contrast, the movement patterns of Common Murre colonies converged during the nonbreeding period; and isotopic segregation was limited to post-breeding (in flight feathers) at only one colony. The reasons why dietary segregation between Common Murre colonies is so limited, despite extensive year-round range overlap, deserves further study. Such information is critical to understanding the potential impact of winter foraging conditions on populations, dependent on the degree of spatial mixing (Esler 2000, Gonzáles-Solís et al. 2007, Frederiksen et al. 2011), and illustrates a potentially important differences between the two species.

A striking feature of the spatial distribution of murres during late winter/spring is very low species overlap on Newfoundland's Grand Bank (Figure 5.1), despite that area offering high trophic level prey ($\delta^{15}N$). The Grand Banks is occupied primarily by Common Murres, which may partially exclude Thick-billed Murres. Thick-billed Murres tend to forage on higher trophic prey in places where Common Murres are not present (Figures 5.2, 5.3); whereas in places where the species do overlap (e.g. on the Orphan Basin/Grand Bank), Thick-billed Murres take lower trophic level prey. Segregation of dietary niches is most clearly demonstrated by murres from the Gannet Island colony, where inter-specific spatial overlap is greatest, both in breeding and wintering periods (see also Chapter 2). Barger and Kitaysky (2011) found similar flexibility in trophic overlap among murres, apparently depending on annual availability of resources. This flexibility in foraging strategy, particularly of increased diversity in resource use (i.e. "niche expansion" cf. Agashe and Bolnick 2010; also "resource polymorphisms" cf. Smith and Skúlason 1996) when there is greater range overlap and subsequent inter-individual competition (Svanback and Bolnick 2007, Reifová et al. 2011), is evidence for active ecological segregation, that is, occurring in current space and time through behavioural plasticity (Pfennig and Pfennig 2012) and is also reflective of past mechanisms of ecological diversification among species (Diamond 1978, Woo et al. 2008). Research has also indicated that the magnitude of dietary variation depends on the level of inter - and intra -specific competition, expressed as increased individual specialization within generalist populations (Svanback and Bolnick 2007, Araujo et al. 2011), including among Thick-billed Murres (Woo et al. 2008). We contend that for Thick-billed Murres, a wider ecological niche (than Common Murres) is expressed through more varied movement and foraging strategies, and is related both to range of available habitat and prey, and to inter-specific interactions with Common Murres.

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CHAPTER 6 – MULTIPLE-COLONY WINTER HABITAT USE BY MURRES *URIA* SPP. IN THE NORTHWEST ATLANTIC CEAN: IMPLICATIONS OF MARINE RISK ASSESSMENT

CHAPTER 6 - MULTIPLE-COLONY WINTER HABITAT USE BY MURRES (*URIA* SPP.) IN THE NORTHWEST ATLANTIC OCEAN: IMPLICATIONS FOR MARINE RISK ASSESSMENT[#]

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6.1 SUMMARY

1) 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.

2) Using geolocators, we identified winter habitat use patterns of 115 adult murres (*Uria* species) from 7 colonies spanning the eastern Canadian Arctic to Newfoundland, 2007-2010.

3) Thick-billed Murres (*U. lomvia*) dispersed throughout the region (Davis Strait, Labrador Sea, Orphan Basin, Grand Bank) with 0-45% overlap of core use areas (50% Kernel Home Range) among breeding populations. Common Murres (*U. aalge*) concentrated on the Grand Bank and Orphan Basin, with 50-67% overlap among breeding populations. For both species, most individuals (up to 70%) wintered in shelf (≤500m) and oceanic zones (>500m); fewer than one-third (30%) of individuals used nearshore zones (≤ 50km to shore).

4) Tracked Common Murres 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 Murres, representing ~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 Murres. Both species from many colonies converged on the Grand Bank and Orphan Basin, with the implications for each breeding population dependent on its particular dispersal pattern.

5) We demonstrate the utility of tracking data for highlighting areas of risk, and improving the targeting of broad-scale marine conservation efforts.

6.2 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 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 and 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. 2008b, 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 ca. 1.7 million and 3.9 million birds respectively (Gaston & Hipfner 2000, Ainley et al. 2002, S. Wilhelm, Canadian Wildlife Service, 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* populations have occurred 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. 2008a, Harris et al. 2010) or forcing 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 gillnets (Benjamins et al. 2008, Stenson et al. 2011). The risks associated with these activities depend on their spatio-temporal 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 three other marine subregions (Davis Strait, Labrador Shelf, Orphan Basin) where there is intense human activity (AMAP 2010, CNOLPB 2010, GeoExpro 2010) and potentially high use by wintering seabirds (Merkel & Barry 1998, Merkel et al. 2002, Mosbech et al. 2006). We deployed bird-borne tracking devices at seven widely-dispersed sites from high to low arctic regions in eastern Canada (Figure 6.1) 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 four oceanic subregions with ongoing and increasing human activities; and 4) evaluate potential interactions between wintering birds and these activities.

6.3 MATERIALS AND METHODS

Study Colonies and Device Attachment - This research was carried out on Thick-billed Murres (TBMU) and Common Murres (COMU) at seven seabird colonies in Eastern Canada ranging from 74-47°N: Prince Leopold Island in the high Arctic (2008-2010; TBMU), the Minarets on Baffin Island (2007-2008; TBMU), Coats Island in Hudson Bay (2007-2009; TBMU), East Digges Island in Hudson Strait (2008-2009; TBMU), Nunavut; the Gannet Islands in Labrador (2008-2009; TBMU, COMU); and Funk Island (2007-2010; COMU) and Witless Bay Islands (2007-2009; COMU) in Newfoundland (Table 6.1, Figure 6.1). British Antarctic Survey (BAS; Mk5/Mk7, 3.6 g; Mk 13, 1.4 g, n = 220) or Lotek 2500 (3.6 g, n=17) geolocation-immersion loggers were attached to 237 breeding murres (134 TBMU, 103 COMU) at colonies during July/August 2007-2009, using leg bands and cable ties (total weight $\leq$ 5.4 g, ~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 (87 TBMU, 41 COMU; 54%) were retrieved at the same sites in following years (Table 6.1). Most loggers (92%) were collected in the year following deployment; nine were retrieved two years after deployment, and hence the number of year-round tracks exceeds the number of loggers retrieved (Table 6.1). Seventeen loggers failed to download. In total, we obtained year-round data from 111 loggers (46% of those deployed; Table 6.1); including repeated tracks, this provided 115 annual tracks and 75,122 individual geolocator or global location sensor (GLS) locations, or 37,561 tracking-days (2 locations per day). Recent estimates of colony sizes (Gaston et al. 2012; S Wilhelm, Environment Canada, unpubl. data, 2011; Table 6.1) were used to scale potential presence based on tracking data (see section below) and population estimates were made as described by Gaston (2002) using a combination of aerial photography, ground-truthing, and plot monitoring. Estimated breeding populations of Thick-billed Murres in eastern Canada total ~3.9 million (Gaston & Hipfner 2000, Wiese et al. 2004). The tracked murres were from five colonies representing about one-third (34%) of the

Table 6.1. Tracking of winter habitat use by Thick-billed Murre and Common Murre from colonies in eastern Canada: details of sites, 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 x 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 because loggers held > 2 yr of data. See Figure 6.1 for location of colonies

Species tracked	Site	Location	Colony Size (bp x 2)[1]	Year Deployed	Loggers Deployed	Annual Loggers Retrieved	Total Loggers Successfully Downloaded[2]	Total Annual Tracks[3]
Thick-billed Murre	Prince Leopold	74°02'N, 90°00'W	172,000[a]	2008	24 (BAS)	16		
				2009	5 (Lotek)	5	18	18
	Minarets	66°57'N, 61°50' W	260,000[a]	2007	20 (BAS)	14	14	14
	Coats	62°53'N, 82°00' W	36,000[b]	2007	20 (BAS)	18		
				2008	20 (BAS)	16	29	30
	Digges	62°32'N, 77°45' W	872,000[a]	2008	31 (BAS)	10	10	10
	Gannets	53°56'N, 56°32'W	3,700[c]	2008	14 (BAS)	8	5	5
Common Murre	Gannets	53°56'N, 56°32'W	62,420[c]	2008	16 (BAS)	12	8	8
	Funk	49˚45'N, 53˚11'W	825,048[c]	2007	20 (BAS)	10		
				2008	20 (BAS)	0		
				2009	12 (Lotek)	3	13	13
	Witless Bay	47°16'N, 52°46'W	500,000[c]	2007	5 (BAS)	5		
				2008	30 (BAS)	16	16	17
	Total		*2,731,168*		*237*	*128*	*111*	*115*

[a]2011, A.J. Gaston unpublished data; [b]2010, Gaston and Robertson; [c]2011, S. Wilhelm [Environment Canada] unpublished data

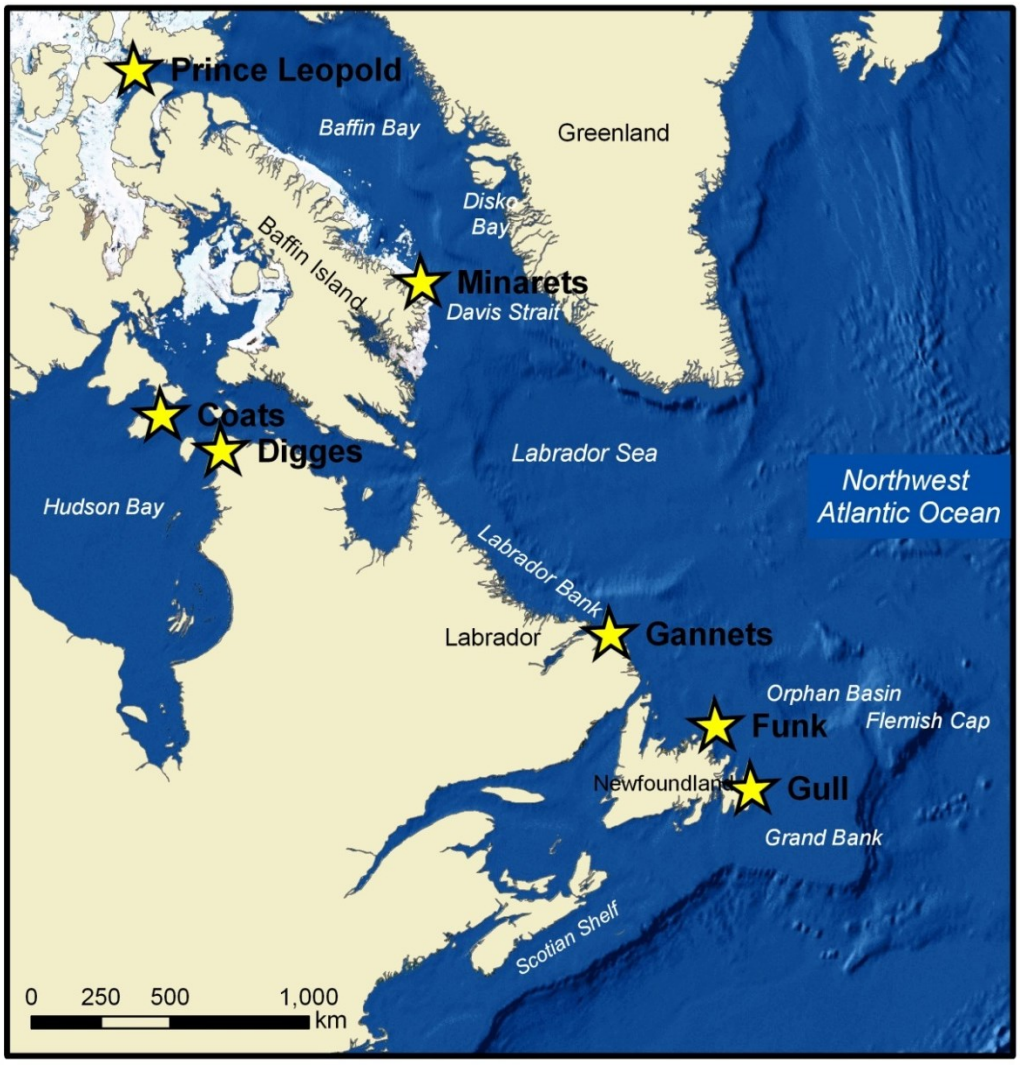

Figure 6.1. Map of study area and (☆) breeding colonies where global location sensor (GLS) loggers were deployed on Thick-billed and Common Murres.

total Canadian population. The estimated breeding population of Common Murres in eastern Canada is ~1.7 million, the colonies of origin of the tracked birds represent ~ 82% of the total population.

Data processing- Data from each BAS GLS 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 three decision-making criteria: 1) the distribution of logger positions during stationary ground-truthing at the southernmost colony (Witless Bay; Figure 6.1); 2) travel past obvious topographic features (eg. 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 murres 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 two 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 (LMT, 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, and show a high degree of consistency in core areas and individual distances traveled (LMT, 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/day) 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 sea surface temperature (SST) images. We used NOAA Modis A nighttime SST averaged over 8 days at a 4-kilometre 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 km north or south between successive positions. As such, temperature-based latitude estimates for the murres contributed very little new information (8% of total detections; LMT 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 were Sept-early Oct and late Feb -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-day 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 that 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 Kernel Home Range (KHR) contours were considered to represent the core areas used during the winter. 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, ver. 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^2. Percent overlap between colonies A and B was calculated as:

[1] Habitat Overlap = A_O / ($Area_A + Area_B - A_O$)

Proportional Use– For this analysis, KHRs were assessed separately for each bird, allowing evaluation of variation among individuals from each colony. We determined presence of all individual murre KHRs, proportional to the total tracked from their respective colony, within three marine zones of the Northwest Atlantic (nearshore $\leq$50 km from the coast), shelf (<500m deep, excluding waters <50 km from shore) and oceanic (> 500m deep). As a second exercise, we determine presence of individual murre KHRs intersecting with the same three marine zones within four relevant subregions (Davis Strait Area, Labrador Shelf, Orphan Basin, Grand Bank; Figure 6.2). Three marine zones were chosen based on bathymetry and biological relevance, for example, seabirds are hunted within 50km from shore (Merkel & Barry 1998); and often associate with bathymetric features such as the continental slope or shelf (Brown 1986, Kenyon et al. 2009). We included the upper slope of the continental shelf, and defined the shelf as all waters between 50km from shore to the 500m isobath. Oceanic subregions (Davis Strait, Labrador Shelf, Orphan Basin, Grand Bank) were selected on the basis of known concentrations of anthropogenic activity (references in Table 6.2).

Subregion boundaries were hand drawn (in ArcMap) to approximate conventional characterizations according to bathymetry (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, Figure 6.2). 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:

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

where *Pij* is the presence (binary, i.e. 0/1) 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 three 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 study area. As a separate exercise, the same approach was to standardize individual presence of birds from each colony wintering in zones of particular subregions.

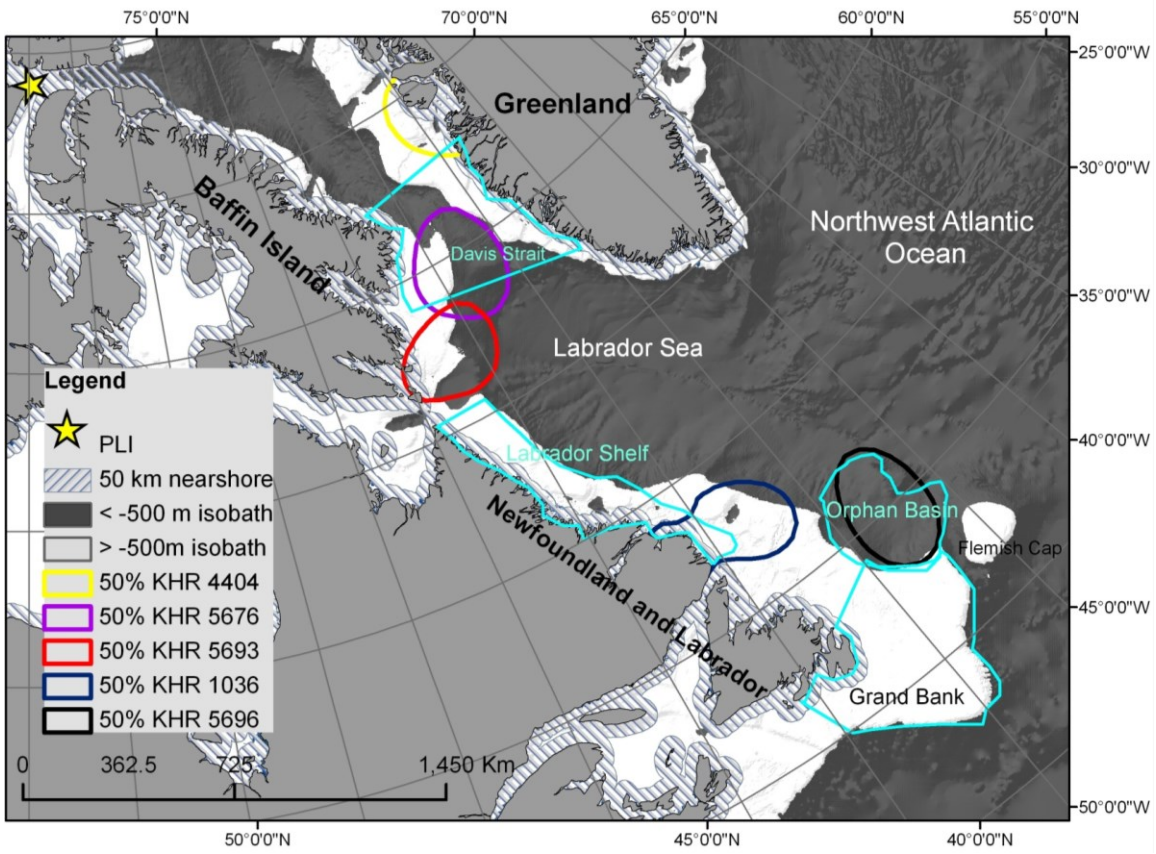

Figure 6.2. Location of marine zones in the Northwest Atlantic Study Area: nearshore (< 50 km) shelf (< 500 m deep, excluding waters < 50 km from shore) and oceanic (> 500 m deep). Location of subregions (Davis Strait Area, Labrador Shelf, Orphan Basin, Grand Bank) within the study area affected by human activity. Examples core (50%) wintering kernel home ranges (KHR) of 5 individual Thick-billed Murres (BAS loggers 4404, 5676, 5693, 1036, 5696) from Prince Leopold Island (PLI).

Table 6.2. Presence/absence (+/-) of anthropogenic threats affecting the Northwest Atlantic Study Area overall and within particular subregions during winter (see Figure 6.2). Relative presence is based on a literature review of anthropogenic threats in subregions[a]. 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 nearshore (≤ 50 km from coast), shelf (≤ 500 m deep) and oceanic (>500 m deep). na: the marine zone is not present in the area (e.g. the Grand Bank has no oceanic zone).

		Occurrence in Winter (+/-)[a]		
		nearshore	shelf	Oceanic
NW Atlantic Study Area	Hunt	+	-	-
	Gillnet/fishing gear	+	+	-
	Oil production/exploration	-	+	+
	Shipping /chronic oiling	+	++	++
Davis Strait Subregion	Hunt	+	-	-
	Gillnet/fishing gear	-	-	-
	Oil production/exploration	+	+	+
	Shipping /chronic oiling	-	-	-
Labrador Shelf Subregion	Hunt	+	-	na [b]
	Gillnet/fishing gear	+	-	na
	Oil production/exploration	-	+	na
	Shipping /chronic oiling	-	-	na
Orphan Basin Subregion	Hunt	na	-	-
	Gillnet/fishing gear	na	-	-
	Oil production/exploration	na	+	+
	Shipping /chronic oiling	na	++	++
Grand Bank Subregion	Hunt	++	-	na
	Gillnet/fishing gear	+	+	na
	Oil production/exploration	-	++	na
	Shipping /chronic oiling	++	+++	na

[a]References: (Bakken & Falk 1998, Wiese et al. 2001, Merkel et al. 2002, Wiese et al. 2004, Bakken & Mehlum 2005, Mosbech et al. 2006, Benjamins et al. 2008, Merkel & Barry 2008, Wilhelm et al. 2009, AMAP 2010, CNLOPB 2010, GeoExpro 2010, Stenson et al. 2011)

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 subregions *k* by each colony:

[3] Proportion Tracked to Zone *j* (P_{iz}) =avg(O_{ij})

[4] Proportion Tracked to Subregion *k* (P_{ik}) =avg(O_{ik})

To determine P_{iz} and P_{ik} for each species overall, O_{ij} and O_{ik} were averaged across colonies *i*. Note KHRs for some individuals did not intersect with any of the identified subregions, and thus were grouped in "Other".

Potential Presence – To estimate the number of birds from each colony present in a particular marine zone/subregion, we scaled the Proportions Tracked to Zone (P_{iz}) and to Subregion (P_{jk}) to colony size (Table 6.1) by simple multiplication. We assume that the behavior of our sample of tracked birds is representative of all birds at the colony. There will also be birds in each zone or region from other breeding colonies where devices were not deployed.

6.4 RESULTS

6.4.1 Wintering Areas and Proportional Use

Thick-billed Murres - Core wintering areas stretched over 27° of latitude from waters off West Greenland (~70°N), south to the Scotian Shelf (~43°N; Figure 6.3). Birds from Arctic colonies (representing >95% of the Canadian breeding population) were mainly north of 45°N. Proportional Use was spread across the three marine zones but was highest in the oceanic zone (58%) compared to offshore shelf (27%) and nearshore (15%) zones (Table 6.3). Among colonies Proportional Use of the

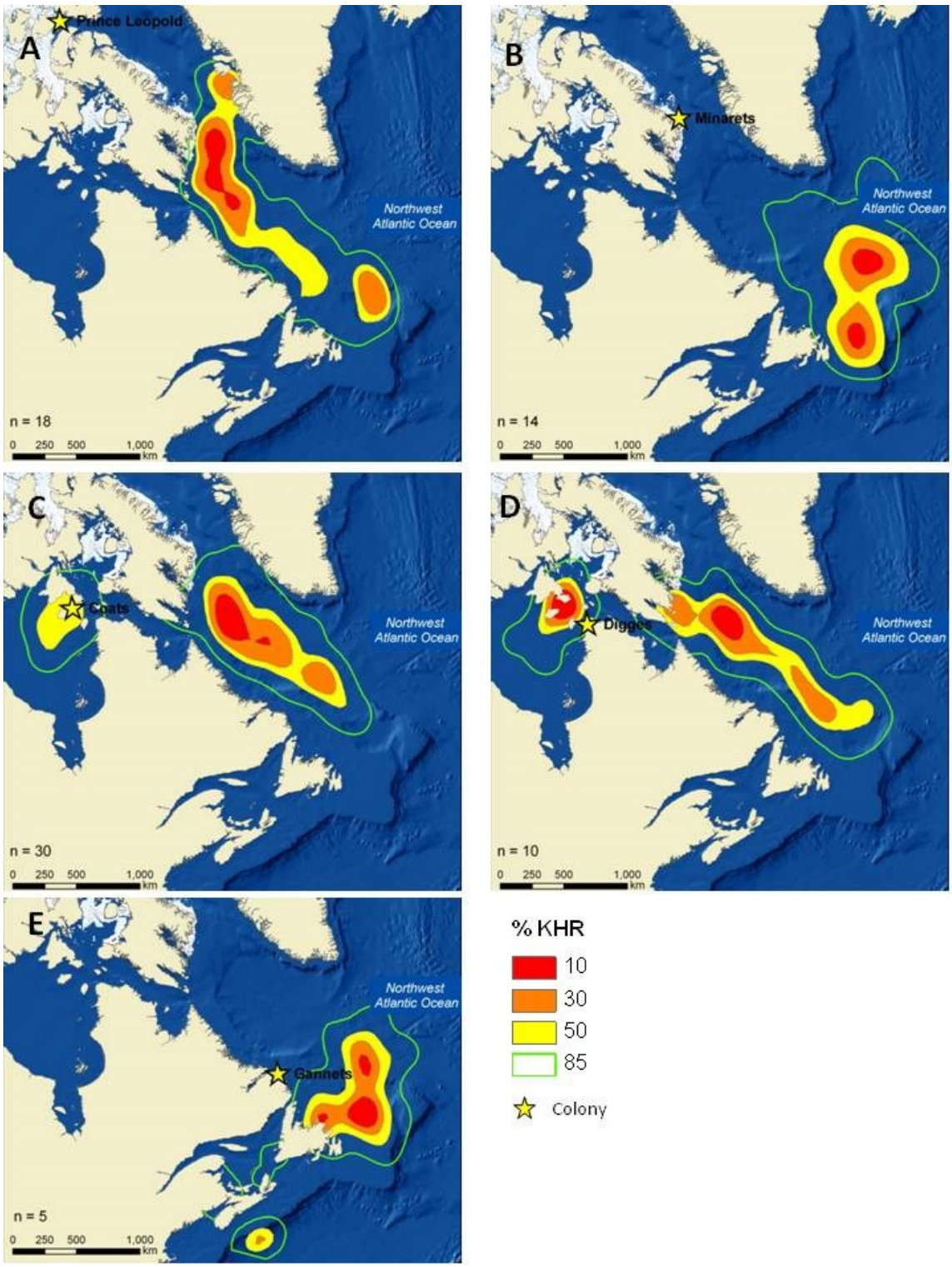

Figure 6.3. Winter distribution (10-85% Kernel Home Range contours, Nov-Feb) for five colonies of Thick-billed Murres breeding in eastern Canada: A) Prince Leopold B) Minarets C) Coats D) Digges E) Gannet Islands.

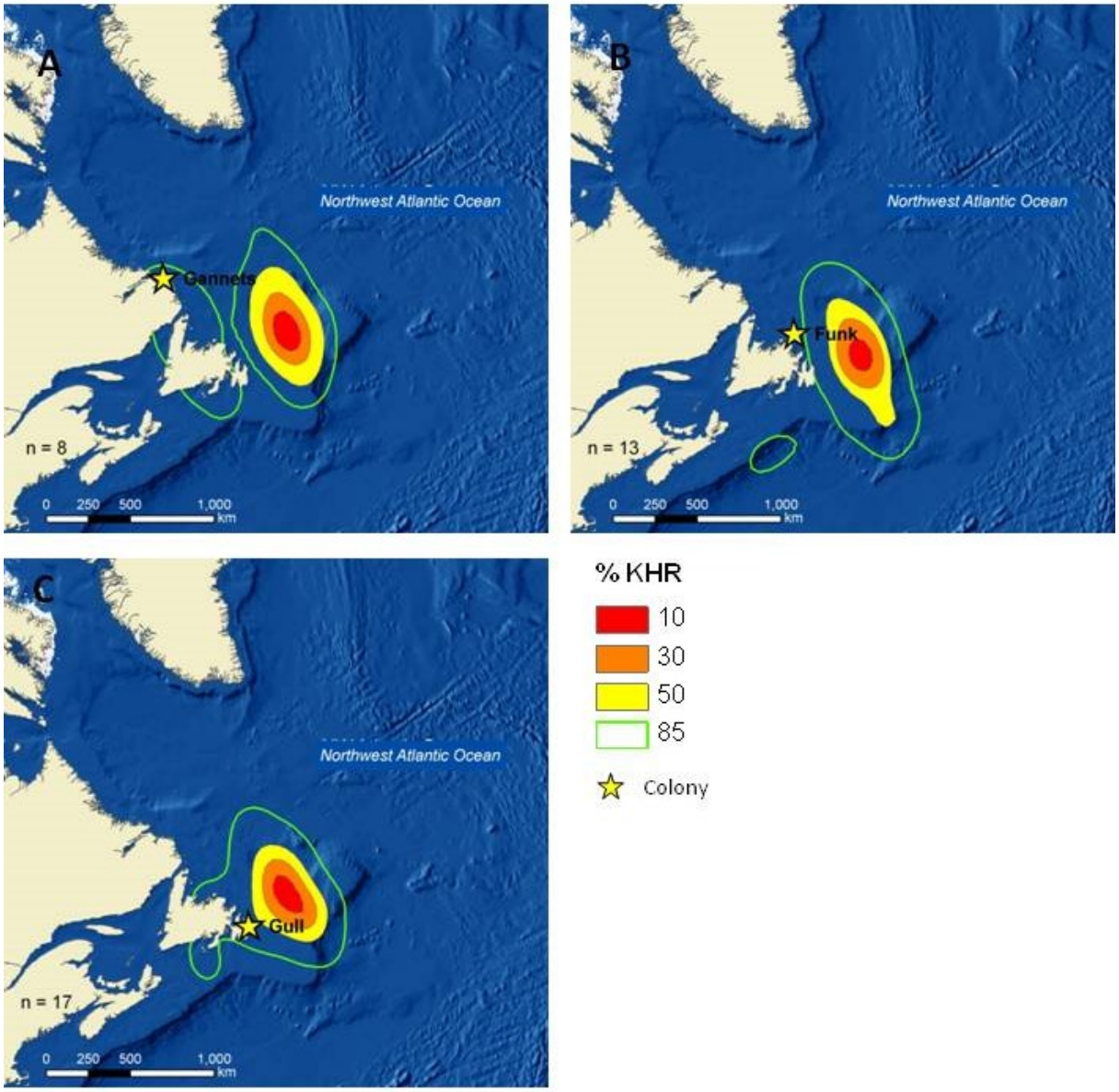

Figure 6.4. Winter distribution (10-85% Kernel Home Range contours, Nov-Feb) for three colonies of Common Murres breeding in eastern Canada: A) Gannet Islands B) Funk Island C) Witless Bay (Gull) Islands

Table 6.3. Proportional Use by tracked Thick-billed Murres and Common Murres, as determined by proportion of individual 50% KHRs per colony that intersected with marine zones (nearshore, shelf, oceanic; see Figure 6.2) in the Northwest Atlantic Ocean Study Area. Species summary data are indicated in gray; numbers in bold indicate zones of highest use per colony. See also Figure 6.5 for colony-specific details.

			NW Atlantic Marine Zone		
Species	Colony	Total N	Nearshore	Shelf	Pelagic
Thick-billed Murre	Prince Leopold	18	0.31	**0.39**	0.31
	Minarets	14	0.06	0.24	**0.70**
	Coats	30	0.08	0.18	**0.74**
	Digges	10	0.13	0.33	**0.53**
	Gannets	5	0.17	0.37	**0.47**
	Overall	*115*	*0.15*	*0.27*	***0.58***
Common Murre	Gannets	8	0.24	0.36	**0.40**
	Funk	13	0.04	**0.65**	0.31
	Witless Bay	17	0.11	**0.52**	0.37
	Overall	*38*	*0.11*	*0.53*	*0.36*

oceanic zone was high for birds from Minarets, Coats, and Digges; whereas birds from Prince Leopold Island (and to a lesser extent, the Gannet Islands) instead exhibited high Proportional Use of nearshore zones (Table 6.3, Figure 6.5).

Colony-specific core wintering areas (pooled individuals and years) showed considerable variation by colony (Figure 6.3). For Prince Leopold Island (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 (Figure 6.3a). For the Minarets (n = 14, winter 2008), two centers were identified over the eastern Grand Bank and the northern Orphan Basin/southern Labrador Sea (Figure 6.3b). For Coats Island (n = 30, winters 2008, 2009, 2010), multiple centers were in Hudson Bay (representing habitat use until Dec), and in the northern and central/south Labrador Sea, where birds resided Jan-Feb (Figure 6.3c). Similarly for Digges Island (n = 10, winters 2009 and 2010) multiple centers were in Hudson Bay (prior to winter migration (up to late Nov-early Dec), and then in the northern/central Labrador Sea, and over the Orphan Basin (in Dec – Feb; Figure 6.3d). For the Gannet Islands (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 (Figure 6.3e).

Analysis of colony-specific Proportional Use of inshore, shelf, and oceanic zones, within subregions, showed that individuals from Prince Leopold Island were distributed widely throughout the study area and used all identified subregions (Figure 6.5), with the highest Proportional Use in the shelf zone (Table 6.3). Individuals from the Minarets, Coats, Digges, and Gannets used slightly fewer subregions, with the highest Proportional Use in the oceanic zone (Table 6.3), particularly in the Orphan Basin (Figure 6.5).

Common Murres - Core winter areas spanned 10° of latitude over ~43-53°N and were much more restricted than those of Thick-billed Murres (Figure 6.4; colony details

below). Differences among colonies were more apparent in the patterns of habitat use (inshore vs. offshore) than in the regions visited (LMT unpubl. data). Proportional Use was highest in the shelf (53%), followed by oceanic (36%) and nearshore (11%) zones (Table 6.3). Among colonies, the highest Proportional Use of the shelf zone was by birds from Funk Island, and the highest Proportional Use of the nearshore zone by murres from the Gannet Islands (Table 6.3, Figure 6.5).

Colony-specific core wintering areas (pooled individuals and years) for each colony were as follows: For the Gannet Islands (n=8, winter 2009), core habitat was centered over the northeastern Grand Bank/Orphan Basin (Figure 6.4a). For Funk Island (n=13, winter 2008 and 2010), core area was mainly over the eastern Grand Bank/southern Orphan Basin (Figure 6.4b). For Witless Bay Islands (n=17, winter 2009 and 2010), core area had a single center on the northeastern Grand Bank/Orphan Basin (Figure 6.4c).

Analysis of colony-specific Proportional Use 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 (Figure 6.5). For both Funk and Witless Bay Islands, the highest Proportional Use was in the shelf zone, particularly on the Grand Bank (Table 6.3, Figure 6.5).

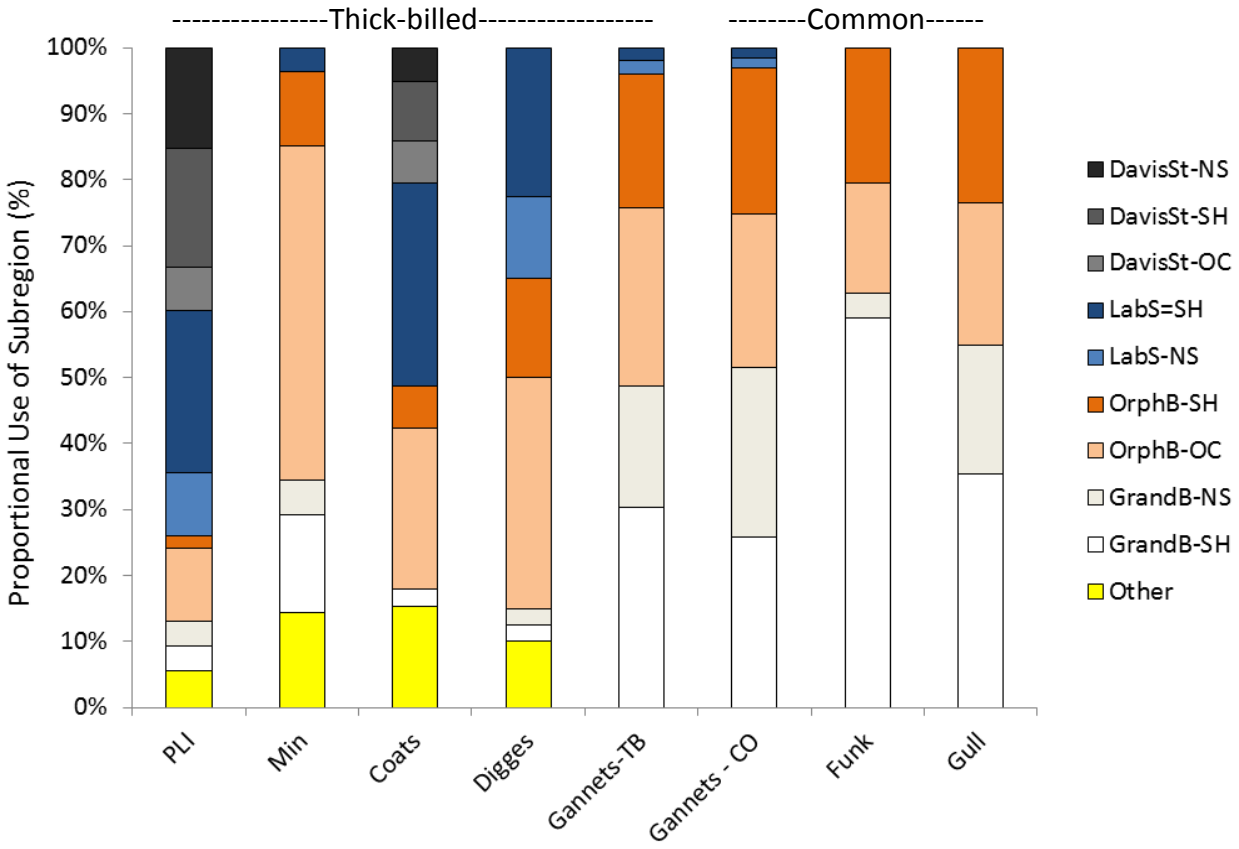

Figure 6.5. Proportional Use (per colony) of Thick-billed Murres and Common Murres in 3 marine zones (NS=nearshore, SH=shelf, OC=oceanic) and 4 subregions of the study area (Davis Strait, Labrador Shelf, Orphan Basin, Grand Bank) in winter. "Other" indicates that the birds were tracked to areas outside the 4 subregions. Murres originate from Prince Leopold (PLI), Minarets (Min), Coats, Digges, Gannets (TB – Thick-billed, CO – Common), Funk, and Witless Bay (Gull) Islands.

6.4.2 Range overlap

Average population/colony level 50% core winter range (KHR) for Thick-billed Murres (550,892 $\pm$ 41,895 km^2 se) was significantly larger than that of Common Murres (202,107 $\pm$ 11,414 km^2 se; ANOVA, $F_{1,6} = 38.14$, $p < 0.001$; see Table 6.4). Core use areas of Thick-billed Murre colonies overlapped by an average of 17%, ranging from 0.2% (Coats and Gannet Islands) to 47% (Coats and Digges Islands). Core use areas of the three tracked Common Murre colonies overlapped by an average of 60% (49-67% for each colony pair; Table 6.4). Areas of KHRs were 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.

Table 6.4. Area of Core Winter Range (50% kernel home range) of Thick-billed and Common Murres and percent overlap of core range between different colonies.

Species	Colony	Core Winter Range (km^2)	Winter Range Overlap (%)			
			PLI	Minarets	Coats	Digges
Thick-billed Murre	PLI	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
Overall		*550,892 ± 41,895 s.e.*		$\bar{x}$ = *17.4% ± 1.7 s.e.*		
Common Murre			Gannets	Funk		
	Gannets	224,803	--	--		
	Funk	192,879	49.4	--		
	Witless Bay	188,640	67.9	64.1		
Overall		*202,107 ± 11,414 s.e.*		$\bar{x}$ = *60.5% ± 3.3 s.e.*		

6.4.3 Composition of subregions

The composition of the birds within each subregion was based on the proportion of tracked individuals (P_{ik}), scaled to colony size (Figure 6.6). In Davis Strait, all three zones (nearshore, shelf, oceanic) were occupied solely by Thick-billed Murre from Prince Leopold and Coats Islands. On the Labrador Shelf, the nearshore zone was occupied by Thick-billed Murre from PLI and Digges (Figure 6.5, 6.6a); and by Common Murres from the Gannet Islands (Figure 6.5, 6.6b). Birds from these three colonies also used the Labrador Shelf, as did Thick-billed Murres from Coats and the Minarets. In the Orphan Basin, all colonies of both species were represented in both the shelf and oceanic zones, with murres from the Gannet Islands in the smallest proportion (Figures 6.6). All colonies and species were present to some extent on the Grand Bank (least abundant were Thick-billed Murre from Coats; Figure 6.6). Among tracked Thick-billed Murres, those from the Gannet Islands made highest proportional use of the Grand Bank (Table 6.3, Figure 6.5); however, after scaling to colony size, the nearshore zone of the Grand Bank was used most heavily by Thick-billed Murres from Digges, Minarets, and PLI (see below; Figures 6.6, 6.7). The shelf zone of the Grand Bank was dominated by Common Murres from Funk Island (Table 6.3; Figures 6.6, 6.7).

6.4.4 Potential Presence

We used Proportional Use (P_{ij}) of each zone (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; murres were least numerous in the nearshore zone of the Grand Bank and throughout Davis Strait (Figure 6.7). 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 Island); and over 680,000 Common Murres on the Grand Bank (shelf) during winter (driven by the large colony at Funk Island; see Figures 6.5, 6.6). 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.

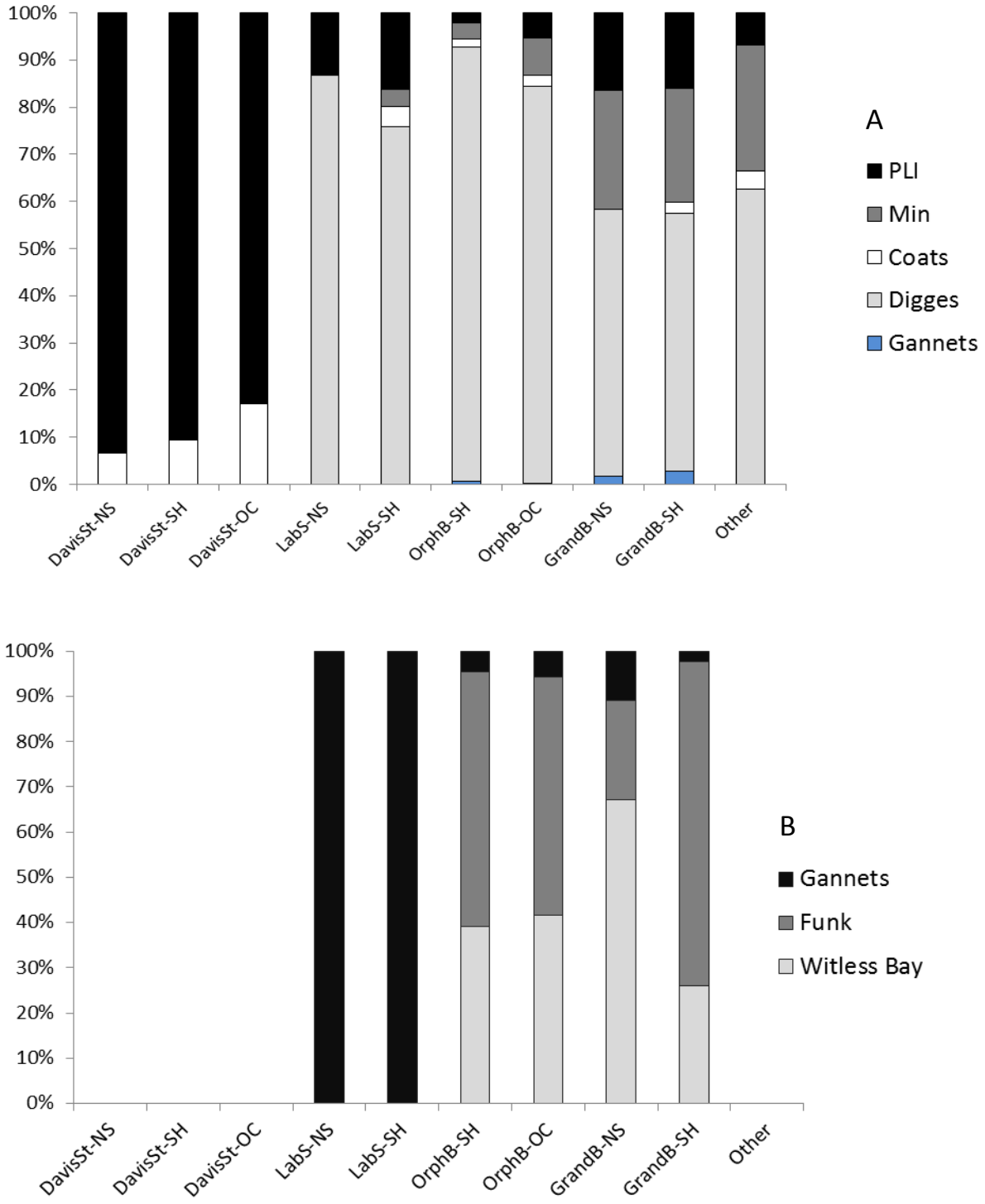

Figure 6.6. Composition of subregions (%) by populations from different colonies of (A) Thick-billed Murres and (B) Common Murres, based on Proportional Use and scaled to colony size. Only populations from the study colonies are included (i.e other murre populations potentially using these areas are not considered). NS: nearshore; SH: shelf; OC: oceanic.

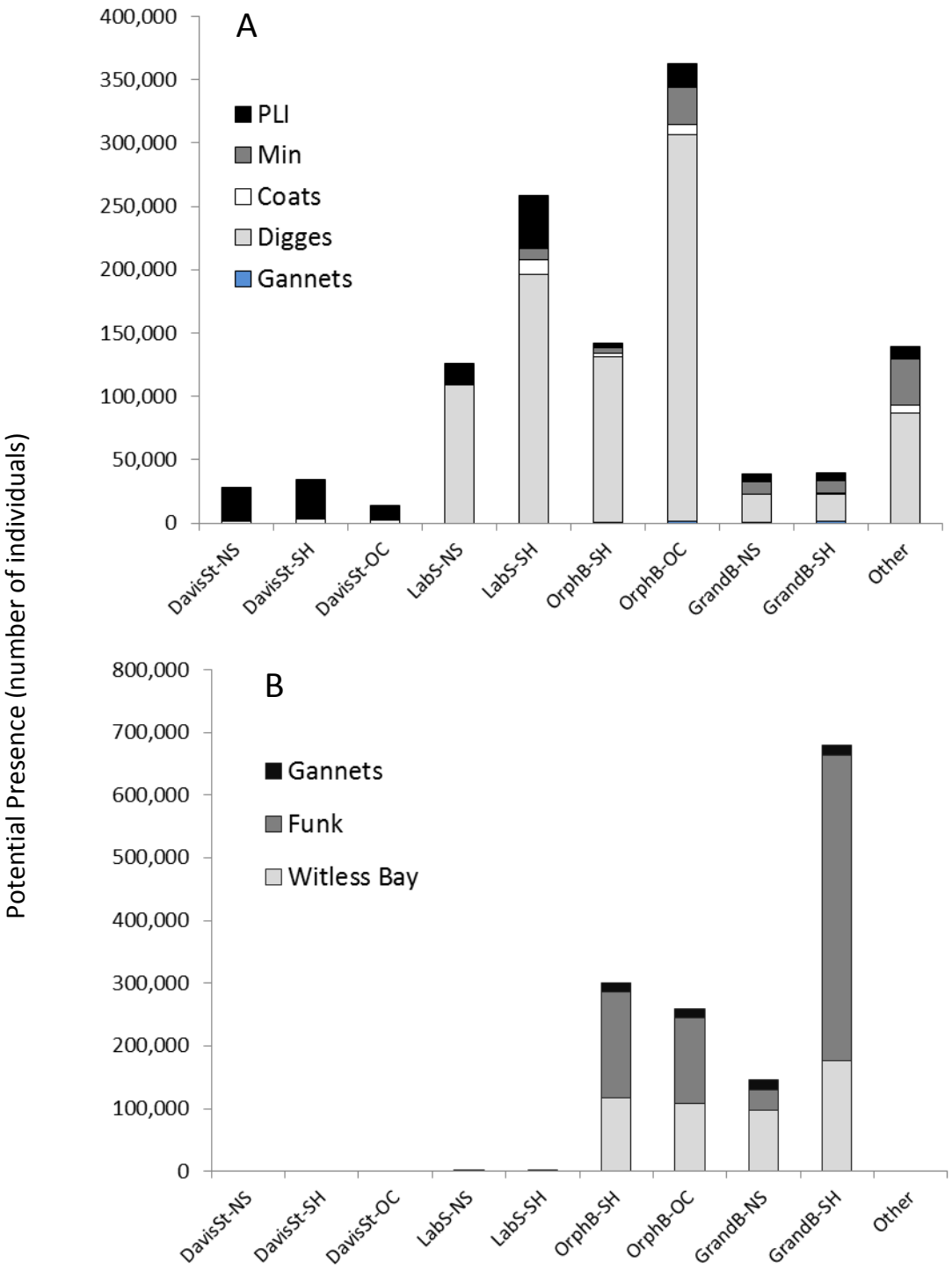

Figure 6.7. Potential presence in winter of (A) Thick-billed Murres and (B) Common Murres in the 3 marine zones (NS: nearshore; SH: shelf; OC: oceanic) of the 4 subregions in the study area (Davis Strait, Labrador Shelf, Orphan Basin, Grand Bank). Numbers are scaled to colony size.

6.5 DISCUSSION

6.5.1 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 has suggested that, within and between murre species, 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 the Gannet Islands where the two species breed sympatrically.

The extent to which individuals show plasticity in migratory strategy will likely determine colony- and species-specific vulnerabilities to anthropogenic 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 (eg. 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 warrants further study.

6.5.2 Winter 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 Gannet Islands (coastal areas of Newfoundland and Labrador) and Prince Leopold (coastal areas of West Greenland in the Davis Strait area). These findings contrast with previous conclusions 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 Thick-billed Murres 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 the Gannet Islands 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 those of earlier researchers could reflect recent changes in murre winter distributions of 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 Island, 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 islands exit Hudson Bay only as freeze-up occurs – 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 PLI and The Minarets move south well in advance of freeze-up (LMT 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 coldwater 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.

6.5.3 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 (Figure 6.5). 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 spp. on the northern edges of the Grand Bank, bycatch is no longer 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 paper; 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 6.2), and the number and variety of birds using the area (Table 6.3, Figure 6.5, 6.6). If anthropogenic risk affects ages, sexes, and breeding populations indiscriminately (Robertson et al. 2006), then the potential for encountering risk depends entirely on spatio-temporal 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. 2010) 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 sub-region (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 (eg. 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 seven colonies studied; Figure 6.6). 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 6.2). 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 (Gonzáles-Solis et al. 2007, Block et al. 2011, Frederiksen et al. 2012, Montevecchi et al. 2012, Croxall et al. 2012). Furthermore, public access to spatially-explicit maps of marine 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.

6.6 ACKNOWLEDGEMENTS

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CHAPTER 7 - CONCLUSIONS and SYNTHESIS

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7 CONCLUSIONS AND SYNTHESIS

This study is the first to integrate tracking and stable isotopic analyses to investigate and compare winter ecology among multiple North American colonies of closely-related Thick-billed and Common Murres. The strengths of this study are threefold: (1) comparative investigation of winter habitat use and of ecological segregation between these congeneric species; (2) assessment of connectivity between colonies and in previously undetermined marine winter areas; and (3) analyses of colony- and individual-specific movements and isotopes to highlight differences in species' behavior and relative vulnerability to anthropogenic activity.

7.1 ECOLOGICAL SEGREGATION

Inter- and intra-specific comparisons were used to build a picture of ecological segregation among murres through patterns of wintering strategies and habitat use. The picture that emerges is one of a different approach to winter strategy between the species. In all aspects of time, space and diet, Thick-billed Murres employ a greater diversity of strategies, compared to their evolutionary counterparts, Common Murres. Thick-billed Murres travelled farther to winter areas; had larger winter core ranges; travelled across a wider range of latitudes and habitats; showed more seasonal variation in distribution and timing of movements; used a wider assortment of movement strategies; and diets were more varied and more dynamic across seasons. Not only was this pattern of greater variation in Thick-bills found when comparing colonies spanning a wide latitudinal range (i.e. at study colonies from High to Low Arctic regions) but it was also evident between the species breeding sympatrically at the Gannet Islands. Yet despite this variability, many individuals showed remarkable consistency in winter movements and fidelity to wintering sites, with a degree of behavioural flexibility within

a few individuals that shifted winter sites between years. Furthermore, birds from particular colonies converged on similar wintering patterns. The pattern of increased variability may originate through a combination of phenotypic variation (i.e. genetics) among individuals and behavioural flexibility within individuals, potentially compounded by colony-specific cultural effects.

Whether studies of ecological segregation are documenting current mechanisms of resource partitioning, or merely reflecting the "ghosts of competition past" (Connell 1980) is a difficult question. Clues to ecological partitioning can be derived from comparative study of the niche occupied by species in allopatric and sympatric parts of their range. Where geographic ranges overlap, ecological partitioning among sympatric populations can be more marked than among allopatric populations of the same species (Diamond 1978, Reifová et al. 2011). In sympatry, divergence (of character or behaviour) may act to contract a species' potential niche, and interestingly, divergence may be asymmetric (Reifová et al. 2011). For murres, this was most obvious in their trophic relationships, which were most divergent in areas of high spatial overlap from the sympatric colony at the Gannet Islands, with dietary adjustment evident only among Thick-billed Murres. Partitioning can also occur through flexible individual behaviours that diversify (Svanback and Bolnick 2007) or specialize (Bolnick et al. 2002, Woo et al. 2008) resource use among competing individuals or populations. For murres, niche partitioning occurs, at least partly, through diversification of movement strategies, which in other species can maintain genetic differentiation among subpopulations (Helbig 1996, Irwin et al. 2011). And, in areas where *Uria* distributions overlap, segregation in their diet is more evident. *Uria* exhibit partially- and unequally-overlapping niches between the species, in which Thick-billed Murres occupy a broad ecological niche that includes, but extends beyond, the narrow, specialized niche of Common Murres, and which is adjusted where direct inter-specific contact occurs. According to Agashe and Bolnick (2012), niche expansion is facilitated both through competition and through genetic variation that increases individual variation in niche

use. We suggest that, for the *Uria* species, ecological segregation is expressed through the niche expansion of Thick-billed Murres, and is related to both the range of available habitat and prey, and to inter-specific competitive interactions with Common Murres.

7.2 MURRE WINTER ECOLOGY AND CONNECTIVITY

Through the use of bird-borne tracking devices, year-round movements and core wintering areas were identified for five colonies of Thick-billed Murres and three colonies of Common Murres. Thick-billed Murres exhibited a moderate-to-low degree of migratory connectivity (partially dependent on colony) between breeding and wintering grounds, and low overlap between colonies. In sharp contrast, Common Murres displayed a high degree of migratory connectivity, and high overlap between colonies. These divergent patterns carry clear implications for population demography and risk.

Thick-billed Murres from all colonies dispersed widely (~ 3600 km from breeding colonies) throughout the Labrador Sea during the nonbreeding season, with concentrations of murres from particular colonies in Davis Strait, Orphan Basin, Grand Bank, and east of the Flemish Cap near the Mid-Atlantic Ridge. Thick-billed Murres from particular colonies tended to follow similar wintering strategies and overlap of core wintering areas between colonies was low, yet there was considerable individual variation in winter strategy.

By contrast, Common Murres from all three colonies concentrated on the Orphan Basin and Grand Bank and remained within ~580 km of breeding colonies throughout the year. Common Murres from particular colonies also tended to follow similar wintering strategies but there was considerable overlap among populations, and little individual variation in winter strategy.

The contrasting use of nonbreeding habitat between the species implies that overall population vulnerability to spatially-concentrated risk or conditions in wintering areas will be greater for the relatively concentrated Common Murres than for more dispersed Thick-billed Murres. On the other hand, the wider-ranging Thick-billed Murres may encounter a wider variety of risks across the seascape.

Although the differences in spatial distribution and movement strategy between the two murre species are robustly demonstrated in this thesis, it is important to keep in mind that the use and segregation of wintering areas in this thesis represent only a fraction of the murre population that may be wintering in the North Atlantic (McFarlane Tranquilla et al. 2013; Chapter 6). Future collaborative study that incorporates winter distributions for other significant colonies in the region (similar to that done for breeding colonies of Northern Gannets surrounding the UK; Wakefield et al. 2013) would improve our understanding of segregation and connectity at the *Uria* species level.

7.3 MIGRATION AND WINTER STRATEGIES

We were able to confirm previous findings that Thick-billed Murres migrated farther to wintering sites than did Common Murres. Interestingly, there was no appreciable southward movement for Common Murres, as suggested in the reviews by Gaston and Jones (1998) and Brown (1985). This study's findings concur with those of Fort et al. (2013) who tracked Thick-billed and Common Murres from Svalbard, and help to consolidate a consistent inter-specific comparison. Furthermore, we were able to document consistency in individual migration patterns across 2-3 years of study.

Most individual wintering areas were found in deep oceanic waters. This movement from coastal to offshore areas, on or beyond the continental shelf, occurred more than expected from previous study. Previous information on the coastal

distribution of murres comes from hunt mortality, mostly young (first-year) murres (Elliot 1991, Donaldson et al. 1997). The adults we tracked may be more likely than young birds to remain in offshore areas, particularly in recent years when the leading edge of seasonal ice cover does not extend as far southward in winter as it used to (Gaston and Robertson 2010).

Migration is usually considered to be primarily under environmental control (Sinclair 1983, Newton 2008). Southward migration from northern breeding areas is generally viewed as a strategy to avoid seasonal reduction in food and/or harsh wintering conditions at high latitudes. The energetic gain in a milder or more productive environment outweighs the energetic expense of long-distance travel (Sinclair 1983). As Thick-billed Murres generally breed at more northern latitudes than Common Murres, their migrations are expected to be longer-distance. On the surface, Thick-billed Murres appear to fit this pattern in which seasonal changes in environment influence southward migration; yet some discrepancies occur. As in our study, Fort et al. (2013) tracked the southward migration of Thick-billed Murres from Bjørnøya (Bear Island), Svalbard, documenting their widespread winter distribution through the North Atlantic, in areas off southwest Greenland and between Iceland and the UK. In contrast, Linnebjerg (2012) found that Thick-billed Murres from Kitsissut Avalliit, Southwest Greenland, made little southward migration but remained throughout the nonbreeding season off the coast of southwest Greenland, a well-known and important wintering area for many seabirds (Mosbech and Johnson 1999, Mosbech et al. 2006, Linnebjerg 2012).

In marked contrast, Common Murres, which breed sympatrically with Thick-billed Murres at a wide range of latitudes, from 53^{o}N (this study, Gannet Islands), to 60^{o}N (Linnebjerg 2012, Kitsissut Avalliit) to 74^{o}N (Fort et al. 2013, Bjørnøya) make only limited southward migrations in winter and appear relatively unresponsive to the environmental influences that are considered to drive migration in Thick-billed Murres. In all three studies, Common Murres consistently wintered near breeding colonies regardless of latitude or associated “harshness” of winter conditions. Why? Fort et al.

(2013) calculated that overall winter energy expenditure was similar for the two species, and suggested that both tactics, migration and residency, represent suitable strategies for overwinter survival. Yet this begs the question, why might migration be more strongly under environmental control for Thick-billed Murres than for Common Murres? Could the differences in migratory strategy have deep-seated roots elsewhere, originating instead through inter-specific competitive interactions? If phenotypic plasticity in movement strategy played a role in character displacement and divergence (Pfennig and Pfennig 2012) of Thick-billed and Common Murre species, the tendency for increased movement among Thick-billed Murres may be under stronger genetic than environmental control. Understanding of how genetic and environmental components influence the control of migratory strategy will provide further insight into ecological segregation between the species, and importantly, will allow better prediction of how the species are and will be influenced by ocean climate and anthropogenic changes in winter habitat.

7.4 FUTURE DIRECTIONS

Advances in understanding the winter ecology of Thick-billed and Common Murres have been dramatic with just a few years of tracking from multiple colonies. Yet understanding the persistence of wintering areas and individual migratory flexibility requires longer-term study. Few tracking studies have gone beyond the collection of 2-3 years of data, yet repeat tracking of individuals will be invaluable in helping to record and predict responses to changing environments over time. Similarly, much will be gained by comparing winter ecology of these two species throughout their range (in the Atlantic, cf. this study, Linnebjerg 2012, Fort et al. 2013), and particularly in the Pacific where inter-specific studies are very limited. The ability to track young birds will also be invaluable to better understand how migratory strategies develop in young birds through natal dispersal and exploration (Alderman et al. 2010, Guilford et al. 2011,

Votier et al. 2011), to create a suite of alternative movement strategies that long-lived birds can draw upon when responding to environmental changes.

In this thesis, *Uria* spatial distributions were compared at a coarse-scale, but could not address small-scale local enhancement cues or multi-species interactions among multiple predators (Ainley et al. 2009, Fauchauld 2009). Yet the evidence for increased isotopic segregation in areas of increased spatial overlap suggests that inter-specific segregation also operates at smaller scales, through diet partitioning. Integrating fine- or meso-scale information from vessel-based surveys with coarse-scale tracking data (cf. Louzao et al. 2009) would provide increased understanding of the mechanisms of inter- and intra-specific spatial segregation operating at multiple hierarchical scales.

Several components of the dataset collected in this thesis remain unexplored in detail, such as GLS activity data (to determine time spent flying and on water during migration), details for individual migratory strategies, and a more in-depth analysis of environmental variables to describe habitat selection. Future research can continue to benefit from the data legacy of this project.

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APPENDICES

Appendix 1. Colony depatures, colony arrivals, and repeat distances to mean centre of wintering area (January) for individual Thick-billed and Common Murres across two, three, or four consecutive years. Red font indicates individuals that shifted core (KHR) wintering areas from the previous year.

Species	Colony	Bird ID	Colony Departures (dd/mm/yy)*	Colony Arrivals (dd/mm/yy)	Distance travelled to January mean centre (km)			
					Track# 1	Track 2	Track 3	Track 4
Thick-billed Murre	Prince Leopold	GLS5696	28/08/08 23/08/09	17/05/09 09/05/10	3269	3346	na	na
	Coats	80560	23/08/07 25/08/08	08/05/08 unk	3366	1254	na	na
		97041	25/08/07 17/08/08	27/04/08 02/05/08	1275	1183	na	na
		97045	26/08/07 21/08/08	29/04/08 15/05/09	3933	4039	na	na
		97046	26/08/07 20/08/08	08/05/08 08/05/09	4005	1908	na	na
		68756	07/08/07 27/08/08 31/07/09	01/05/08 unk unk	3553	3600	3308	na
		71378	15/08/07 24/08/09	03/05/08 05/05/09	1615	1625	na	na
		76601	22/08/07 18/08/08	01/05/08 unk	2800	1230	na	na
		80559	29/08/07 unk 25/08/09	30/04/08 unk 03/05/10	3845	2240	na	na
	Digges	190507530	31/08/08 24/08/09	19/04/09 24/05/10	711	1168	na	na
		190520112	22/08/08 20/08/09	unk 24/04/10	2115	1290	na	na
		190520118	20/08/08 31/08/09	22/04/09 03/05/10	698	1003	na	na
	Gannets	99666385	25/08/08 22/08/09	27/05/09 13/05/10	857	932	na	na

Species	Colony	Bird ID	Colony Departures (dd/mm/yy)*	Colony Arrivals (dd/mm/yy)	Distance travelled to January mean centre (km)			
					Track# 1	Track 2	Track 3	Track 4
			31/08/10*	unk				
		99696001	20/08/09	14/05/10	971	844	na	na
			26/08/10*	14/05/11				
		99696006	25/08/08	09/05/09	443	1043	1028	na
			28/08/09	14/05/10				
			01/08/10*	29/05/11				
		99696007	20/08/08	21/05/09	942	750	943	na
			23/08/09	02/05/10				
			30/08/10*	08/05/11				
		99696014	31/08/09	unk	900	981	na	na
			15/07/10*	09/05/10				
				unk				
		99696037	25/08/09	10/05/10	1189	1100	na	na
			unk	unk				
		99696038	31/08/09	13/05/10	1073	935	na	na
			17/08/10*	20/05/11				
		99696044	04/09/09	07/05/10	920	1062	na	na
			31/08/10*	17/05/11				
Common Murre	Gannets	99696008	25/08/08	11/05/09	958	1163	1228	na
			28/08/09	26/04/10				
			24/08/10*	30/04/11				
		99696010	30/08/08	30/05/09	879	1231	1232	na
			28/08/09	10/05/10				
			28/08/10*	12/05/11				
		99696013	26/08/08	unk	1128	1098	na	na
			23/08/09	10/05/10				
			24/08/10*	07/05/11				
		99696051	29/08/09	08/05/10	1296	1194	na	na
			10/08/10*	18/05/11				
		99696053	02/09/09	03/05/10	697	1197	na	na
			01/08/10*	18/05/11				
		99696055	23/08/09	20/05/10	858	837	na	na
			18/08/10*	13/05/11				
		99696080	26/08/09	unk	786	781	na	na
			31/07/10*	01/05/11				
	Funk	88646037	29/08/07	30/04/08	449	509	349	na
			09/09/08	12/05/09				
			11/09/09*	15/04/10				

Species	Colony	Bird ID	Colony Departures (dd/mm/yy)*	Colony Arrivals (dd/mm/yy)	Distance travelled to January mean centre (km)			
					Track[#] 1	Track 2	Track 3	Track 4
		88646043	17/08/07	02/05/08	569	433	483	(661)
			23/08/08	17/05/09				
			12/08/09*	24/05/10				
			20/08/10*	07/05/11				
		88646047	19/08/07	02/05/08	407	289	156	na
			unk	unk				
			15/08/09*	12/04/10				
			unk	unk				
		96630128	09/08/08	14/05/09	430	228	628	na
			08/08/09*	unk				
			unk	unk				
		96630131	20/08/08	14/05/09	418	469	508	na
			03/08/09*	12/04/10				
			unk	unk				
		96630132	09/08/08	14/05/09	347	205	na	na
			28/08/09*	13/05/10				
			unk	unk				
	Gull	75618251	10/08/08	12/08/09	141	111	na	na
			17/08/09	11/05/10				
		75618252	04/09/09	01/06/10	153	279	na	na
			unk	unk				
		75618253	17/08/08	12/05/09	384	471	na	na
			18/08/09	unk				
		75618254	11/08/08	13/05/09	278	342	na	na
			27/08/09	10/05/10				
		75618267	23/08/08	14/05/09	335	343	na	na
			07/08/09	28/05/10				
		75618273	30/08/08	9/06/09	297	407	na	na
			unk	unk				
		75618275	10/08/08	29/05/09	370	213	na	na
			15/08/09	26/05/10				

*Asterisk indicates year when polar bear present on colony, potentially influencing departure date; subsequently excluded from analyses

#"Track" indicates one-way distance to mean centre of January wintering area

Appendix 2. Repeat winter core home range areas (50% KHR, January) for individual Thick-billed and Common Murres across two, three, or four consecutive years. Average % change in size calculated for consecutive years.

			Kernel Home Range area (km^2)				
Species	Colony	Bird ID	KHR 1	KHR 2	KHR 3	KHR 4	Avg % change in size
Thick-billed Murre	Prince Leopold	unk	72,260	70,007	na	na	3%
	Coats	97041	112,705	128,253	na	na	12%
		97045	219,231	376,145	na	na	42%
		97046	197,798	362,139	na	na	45%
		68756	172,114	261,624	187,078	na	31%
		71378	156,959	138,347	na	na	12%
		76601	152,598	221,853	na	na	31%
		80559	239,201	105,933	na	na	56%
	Digges	190507530	212,663	504,546	na	na	58%
		190520112	169,716	159,873	na	na	6%
		190520118	149,122	163,737	na	na	9%
	Gannets	99666385	268,106	350,879	na	na	24%
		99696001	381,760	153,266	na	na	60%
		99696006	72,964	122,460	157,480	na	31%
		99696007	231,041	158,623	97,124	na	35%
		99696014	49,670	66,335	na	na	25%
		99696038	99,498	114,164	na	na	13%
		99696044	139,912	64,166	na	na	54%
Common Murre	Gannets	99696008	97,470	67,453	178,299	na	46%
		99696010	68,600	134,381	130,453	na	26%
		99696013	58,726	67,658	191,079	na	25%
		99696051	41,257	116,670	na	na	65%

Species	Colony	Bird ID	Kernel Home Range area (km^2)				
			KHR 1	KHR 2	KHR 3	KHR 4	Avg % change in size
		99696053	105,686	64,933	na	na	39%
		99696055	53,300	90,535	na	na	41%
		99696080	120,671	178,383	na	na	32%
	Funk	88646037	90,985	130,861	112,929	na	22%
		88646043	66,601	120,106	122,983	96,177	23%
		88646047	197,526	239,832	87,119	143,047	41%
		96630128	164,206	89,598	151,113	na	43%
		96630131	154,785	78,009	204,627	na	56%
		96630132	63,340	130,938	na	na	52%
	Gull	75618252	96,495	77,752	na	na	19%
		75618251	114,225	83,940	na	na	27%
		75618253	91,553	68,752	na	na	25%
		75618254	216,724	106,092	na	na	51%
		75618267	115,061	123,945	na	na	7%
		75618273	138,849	128,941	na	na	7%
		75618275	119,989	78,730	na	na	34%