Title

Comparative non-breeding foraging ecology of surface foraging kittiwakes (Rissa sp.) and deep diving thick-billed murres (Uria lomvia)

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COMPARATIVE NON-BREEDING FORAGING ECOLOGY OF SURFACE FORAGING KITTIWAKES (RISSA SP.) AND DEEP DIVING THICK-BILLED MURRES (URIA LOMVIA)

A dissertation submitted in partial satisfaction
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by

Rachael A. Orben

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Thesis Abstract

Comparative non-breeding foraging ecology of surface foraging kittiwakes (*Rissa sp*.) and deep diving thick-billed murres (*Uria lomvia*)

Rachael Ann Orben

The non-breeding period is a critical life history period for seabirds, as individuals need to regain body condition lost while breeding. Where animals move is driven by a myriad of factors that can be divided into intrinsic factors, which are linked to physiological and life-history traits, and extrinsic factors which occur as the result interactions with other animals or the environment. To better understand the challenges of wintering in the North Pacific marine ecosystem, I studied the migrations and foraging ecology of three species, surface foraging black-legged kittiwakes (*Rissa tridactyla*) and red-legged kittiwakes (*R. brevirostris*), and deep-diving thick-billed murres (*Uria lomvia*) from three colonies in the southeastern Bering Sea. I tracked birds with geolocation loggers and time-depth recorders over three winters with contrasting environmental conditions (2008-2011). Remotely-sensed environmental data was used to highlight the effects of changing conditions both intra- and inter-annually, while stable isotope values of carbon and nitrogen from feather tissue were used to infer dietary trophic level and niche partitioning. In Chapter 1, I contrasted red-legged and black-legged kittiwake wintering ecology across the spatial, behavioral and dietary niche dimensions and found significant partitioning; red-legged kittiwakes showed greater specialization across all niche dimensions and depended almost exclusively upon on the Bering Sea ecosystem. In Chapter 2, I assessed individual winter foraging strategies of thick-billed murres using a combination of spatial, stable isotope, and behavioral data. Both annual and body size differences largely determined strategies, with some larger bodied birds from St Paul using a deeper daytime diving and more residential strategy unexploited by smaller birds. In Chapter 3, I contrasted intrinsic drivers (e.g. sex, breeding colony and experience) with the influence of annual habitat conditions on black-legged kittiwake winter distributions. I found large annual differences in distributions that spanned the sub-arctic North Pacific, yet in consecutive winters individuals returned to the same regions more often than expected. Overall, environmental conditions played a significant role in influencing the movements and behavior of individuals, however life history characteristics in consecutive winters such as sex, dietary preference or body size sometimes constrain individual wintering ecology.

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Though they never liked me and they will never know, I am forever grateful to the birds that carried geolocation loggers and form the basis of this thesis. I hope that the advancement of knowledge that was derived from these loggers will help to insure the future of Bering Sea seabird populations.

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Thank you all.
Rachael Orben
Santa Cruz, 2014

They were indeed a queer-looking party that assembled on the bank--the birds with draggled feathers, the animals with their fur clinging close to them, and all dripping wet, cross, and uncomfortable.

The first question of course was, how to get dry again….

– *Alice's Adventures in Wonderland, Lewis Carroll*

The Beaches of Lukannon–the winter wheat so tall–
The dripping, crinkled lichens, and the sea-fog drenching all!
The platforms of our playground, all shining smooth and worn!
The Beaches of Lukannon–the home where we were born!
…
Wheel down, wheel down to southward; oh, Gooverooska, go!
And tell the Deep-Sea Viceroys the story of our woe;
Ere, empty as the shark's egg the tempest flings ashore,
The Beaches of Lukannon shall know their sons no more!

– *The Jungle Book, Rudyard Kipling*

These little Pribilof Islands, mere atoms in a storm swept sea, form the land home for myriads of birds.

– *1920, G Dallas Hanna*

Introduction & Synthesis

During the non-breeding period seabirds are freed from the constraints of attending colonies and provisioning their offspring (Orians & Pearson 1977; Costa 1991). The non-breeding period is a critical life history stage, since individuals may need to regain body condition or to mediate stress incurred during breeding (Croll, Gaston & Noble 1991; Satterthwaite, Kitaysky & Mangel 2012; Schultner *et al.* 2014), as well as needing to improve body condition in preparation for the following breeding attempt (Sorensen *et al.* 2009). Without the short-term constraints of central place foraging, non-breeding adults are free to choose preferred marine habitats either far away from breeding colonies or in the general vicinity. Marine habitats have predictable large-scale features characterized by heightened productivity and concentrated prey, such as upwelling zones and continental slope areas (Springer, McRoy & Flint 1996; Bost *et al.* 2009); however prey at small scales is often patchily distributed (Weimerskirch 2007; Benoit-Bird *et al.* 2013). How seabirds use habitats during the non-breeding season likely represents trade-offs between optimal foraging decisions; species-specific characteristics, such as vision or flight ability; individual traits, such as sex or ontogeny; competition, both intra- and inter-specific; predation risk; and time, since individuals still need to return to land to breed, typically on an annual or biannual schedule.

Some seabird species avoid the environmental challenges that come with spending a winter at sea by crossing the equator and perpetuating an endless summer (Shaffer *et al.* 2006; Egevang *et al.* 2010; Kopp *et al.* 2011; McKnight *et al.* 2013). Those species that remain in the same hemisphere during the winter are faced with light limitations at high latitudes (Ballard *et al.* 2010), stormy seas (Dehnhard *et al.* 2013), and changes in prey resource distributions and abundances (Fort *et al.* 2010; 2013). In the Bering Sea, sea-ice extent driven by prevailing winds changes annually and influences the timing and productivity of the spring bloom, making it an annually dynamic habitat for non-breeding seabirds

(Stabeno *et al.* 2012). Latitudes in the North Pacific just south of the Aleutian Islands often experience powerful storms, with higher productivity in the western subarctic relative to the east (Nagasawa 2000), while current-based ecosystems on the edges of the basin (the Kuroshio and Oyashio Currents to the west; the California and Alaska Currents to the east), are seasonally productive in the spring and fall (Figure 1). Regardless, numerous marine predators winter in these regions (Shuntov, 1974; Springer *et al.* 1999; Block *et al.* 2011).

The basis for this thesis is the simple, yet fundamental question: where do birds go during the non-breeding period? Traditionally, ship-based surveys provided approximate wintering distributions for a number of marine predators, however these observations lack the ability to understand how individuals got to a given observation point or to associate individuals with life history parameters such as breeding location. Additionally, for some species, observations at sea are simply limited due to cryptic behavior (e.g. frigate birds fly at high altitudes; Barbraud, Chastel & Weimerskirch 2003), lack of observation effort in wintering areas (Ballard *et al.* 2010), or similarity to other more common species (Landers *et al.* 2011); furthermore some species are attracted to ships, resulting in over estimates of abundances (Hyrenbach 2001). Until recently, movements across the open ocean have been a black box for many marine predators. The development and subsequent miniaturization of electronic data-loggers has allowed us to quantify how individual marine predators interact with their environment (Jouventin & Weimerskirch 1990; Prince *et al.* 1992). There has been previous work on non-breeding migrations of seabirds breeding in the Bering Sea and Gulf of Alaska (Hatch *et al.* 2000; Hatch, Gill & Mulcahy 2010; 2011; McKnight *et al.* 2011; 2013), but this thesis marks the first comprehensive study of individual migrations for three abundant seabird species breeding in the southeastern Bering Sea.

The three study species, black-legged kittiwakes (*Rissa tridactyla*), red-legged kittiwakes (*R. brevirostris,* Figure 2) and thick-billed murres (*Uria lomvia,* Figure 3), are important upper trophic level predators in the Bering Sea ecosystem during the summer (Paredes *et al.* 2012; Harding *et al.* 2013; Paredes *et al.* 2014). Both black-legged kittiwakes and thick-billed murres have numerous colonies throughout the region, while red-legged kittiwakes are concentrated at a few colonies. All three species serve as useful indicators of environmental change in the Bering Sea (Sinclair *et al.* 2008; Renner *et al.* 2012; Zador *et al.* 2013; Springer & van Vliet 2014; Renner *et al.* 2014). Kittiwakes are surface foraging seabirds that rely on prey located in the top meter of the water column, thus they are sensitive to horizontal changes in prey abundance and also to environmental shifts that cause prey to move deeper in the water column. In contrast, thick-billed murres are capable of diving to depths over 200 m (Croll *et al.* 1992), but this comes with a trade-off as murres have high wing loading and subsequently high cost flight (Pennycuick 1997; Elliott *et al.* 2013). Therefore, murres are less susceptible to changes in prey depth, but more susceptible to horizontal changes in prey fields. Because of these life history differences, we can examine murre foraging behavior to understand local changes in prey depths (Takahashi *et al.* 2008; Benoit-Bird *et al.* 2011), while we can look to kittiwakes to understand changes in prey abundance horizontally across their foraging range.

The three study colonies are located along a north-south line in the southeastern Bering Sea. At the north, the Pribilof Island group is composed of two main islands located on the continental shelf: St. Paul to the north and St. George near the Bering Sea slope. St. George has the largest colony of thick-billed murres in the North Pacific as well as the largest colony of red-legged kittiwakes, while the colony on St. Paul is substantially smaller. Three-hundred kilometers to the south of the Pribilof Islands, Bogoslof Island is home to increasing populations of northern fur seals and multiple seabird species (Lee, Burkanov & Neill 2014). The timing of breeding, productivity, and population levels of kittiwakes and murres has been monitored on the Pribilof Islands since the early 1970s (Byrd, Schmutz & Renner 2008a; Byrd *et al.* 2008b). Black-legged kittiwake and thick-billed murre populations on St. George have remained relatively stable over the last 30-years, while red-legged kittiwake populations underwent a severe decline in the 1980s and have subsequently largely recovered. In contrast, at the smaller colony of St. Paul, populations of both kittiwakes and thick-billed murres have undergone almost continual declines since population counts were initiated (Hunt, Eppley & Schneider 1986; Byrd *et al.* 2008a). The reasons for these contrasting population trends are likely a complex combination of factors (Kitaysky, Piatt & Wingfield 2002; Kitaysky *et al.* 2006; Paredes *et al.* 2012; Harding *et al.* 2013; Paredes *et al.* 2014); therefore, a thorough investigation of wintering ecology is necessary to disentangle potential drivers of population trends.

Thesis Summary

In Chapter 1, I compare the wintering niche of the Bering Sea endemic red-legged kittiwake to that of its cogener species the sympatrically breeding black-legged kittiwake. Species that breed sympatrically often occupy different foraging niches to mitigate competition for prey and these differences may or may not carry-over into the non-breeding period when competition relaxes. I found that the two kittiwake species have contrasting wintering ecology. Red-legged kittiwakes remained largely in the Bering Sea, where they experienced colder conditions and shorter days; individual birds used multiple habitats, including continental shelves, the sea-ice edge and pelagic waters. In contrast, black-legged kittiwakes migrated to the subarctic North Pacific, where they dispersed laterally across the basin; the majority of birds travelled to the western subarctic. Red-legged kittiwakes spent less time actively foraging and consumed higher trophic-level prey than black-legged kittiwakes. The disparate wintering ranges and foraging behavior of black-legged kittiwakes and red-legged kittiwakes suggest distinct environmental factors, specific to each species, drive overwinter survival. A strong association with sea-ice and specialization both in diet and foraging behavior may make red-legged kittiwakes particularly vulnerable to climatic change.

In Chapter 2, I assess the influence of body size differences on the wintering foraging strategies of thick-billed murres. For marine birds that fly and dive, body size constraints may be particularly important for migratory decisions as smaller bodies reduce flight costs whereas larger bodies are advantageous for diving deeper. I used geolocation time-depth recorders and stable isotopes to examine individual migratory behaviour of thick-billed murres from St. Paul, St. George and Bogoslof Island in the southeastern Bering Sea during three non-breeding periods, 2008-11. Structural body size differed both by colony and sex and the larger birds from St. Paul had higher wing-loading. Larger bodied birds dived to deeper depths and spent more time in the Bering Sea. A hierarchical cluster analysis then identified three foraging strategies based on movement, diving, and stable isotope data. These strategies were significantly related to both body size and annual conditions. One strategy was composed of large bodied birds from St. Paul (32%), who remained in the Bering Sea and foraged, mainly during the day. In contrast, birds from all colonies used the main strategy in both 2008/09 and 2009/10. This strategy was characterized by high residency areas south of the Aleutian Islands, where birds dove mainly at night to forage. The third strategy occurred only during 2010/11 when birds dove more frequently and deeper, suggesting limited prey resources or a change in targeted prey. These results suggest a complex regulation of overwinter survival of birds originating from St. Paul. As this colony is in a continued state of decline, the behavioural flexibility exhibited by murres, though constrained by body size, may not be enough to adapt to changing conditions in the Bering Sea.

In Chapter 3, I assess the relative importance of sex, colony, past experience, and habitat use on black-legged kittiwake migrations. Black-legged kittiwakes from the Pribilof Islands primarily wintered areas in pelagic, sub-arctic waters, however distributions spanned seven ecoregions of the North Pacific. There was a high degree of similarity in the area use of birds from the two closely situated colonies, while females were more dispersive than males. Birds tracked during two consecutive years showed higher fidelity to wintering areas than occurred at random. Annual changes were apparent, as 70% of birds remained in the Bering Sea in October and 45% stayed until November in 2009/10, while the southern boundary of distributions was farther north in 2010/11. The change in distributions in 2009/10 corresponded to lower October sea surface temperatures in the Bering Sea than the other two years. It appears that a balance between intrinsic and extrinsic factors mediates migration patterns; however, my analysis suggests that under current conditions black-legged kittiwakes have a high capacity to alter winter migrations relative to local environmental conditions.

Synthesis of Ecological Implications

For all three study species and colonies, wintering ecology does not appear to be the sole driver of population changes. However, this study enables us to begin to understand how conditions in wintering areas influences population trends. The apparent niche separation and extreme spatial segregation in red-legged and black-legged kittiwake wintering ecology suggest that changes during the wintering period could be a potential driver of the population decline in red-legged kittiwakes observed in the 1980's (Byrd *et al.* 1997). However, more efforts are needed to identify possible mechanistic links. The combined evidence from my thesis and recent summer foraging studies (Paredes *et al.* 2012; Harding *et al.* 2013; Paredes *et al.* 2014) suggest that the cross-species declines observed on St Paul may have different drivers. I did not find substantial differences in colony-level distributions of black-legged kittiwakes, suggesting that if there are differences in overwinter survival between the colonies, these may be driven by annual differences in the cost of breeding at each colony (Satterthwaite *et al.* 2012; Schultner *et al.* 2014). However, for thick-billed murres, colony level differences suggest that over winter survival of murres from St Paul may be a complex interaction between body size and individual wintering strategies, where there is again potential for interactions from breeding carry-over effects.

Both thick-billed murres and black-legged kittiwakes were tracked for three non-breeding periods, allowing for an assessment of changes in annual conditions on wintering distributions and to contrast the responses of a surface forager and a diver. The thick-billed murres responded strongly to apparently lower prey availability during the winter of 2010/11 by diving ~2 times more frequently. The most substantial annual change in wintering distributions of black-legged kittiwakes occurred in 2009/10 when birds remained in the

Bering Sea longer. There is some evidence that black-legged kittiwakes, like thick-billed murres, also increased foraging time in 2010/11 (% time actively foraging, residency time increase); however, spatial distributions were not substantially different than in 2008/09. There were no significant differences in thick-billed murre wintering behavior, determined by cluster analysis of foraging behavior, between 2009/10 and the other two winters. Combined, these results suggest that prey availability, in time and space, was markedly different during the three study winters, but divers were able to compensate during 2009/10, while surface foragers were able to compensate in 2010/11.

Study Limitations

Modern technological advances in biologging enabled this study, but these methods still have limitations. Geolocation loggers provide much needed, and hitherto unknown information; however, the locations derived from geolocators are associated with comparatively large errors (±180 km of error; Phillips *et al.* 2004; Shaffer *et al.* 2005) when compared to other biologging devices (e.g. Argos satellites or GPS). Additionally, during the solar equinoxes, latitudes must be informed by other variables, such as sea surface temperatures. State-space models, like the one used in Chapter 3 (Sumner, Wotherspoon & Hindell 2009), likely reduce location error; however, more efforts are needed to quantify the errors from these models. The geolocation dataloggers are still large enough to produce measurable negative effects on individuals in some species (Vandenabeele *et al.* 2011; Elliott *et al.* 2012; Robinson & Jones 2014), so continued efforts to miniaturize and streamline these devices are needed to further decrease impacts on study animals.

From the perspective of the birds, this study represents a three-year snapshot of winter migrations for individuals that may live upwards of 30 years. This study was limited to three study colonies, albeit one major one, among the hundreds of breeding colonies that surround the North Pacific basin. Due to the challenges of catching and recatching birds, the birds that were chosen to carry loggers were breeding birds that typically occupied nests at the edges of breeding colonies (e.g. low cliffs and cliff tops). Finally, we were only able to retrieve data from birds that successfully completed a winter migration as recovering the logger, via recatching the bird, is necessary to recover data.

Future Directions

There are numerous future directions for studies of seabird wintering ecology. For Bering Sea seabirds, a multi-species synthesis of wintering regions and habitat preferences derived from tagging data is just becoming possible and would be a valuable aid in understanding wintering hot spots. In addition, this would provide a starting point for predicting how wintering seabirds may be influenced by climate change. On the individual level, connecting reproductive stressors to wintering ecology and, ultimately, to survival will help to elucidate mechanisms behind population trends. Finally, continued efforts to track birds will build upon this effort though the development of multi-year data sets that can be used to understand how long-term environmental change influences seabird winter foraging ecology and ocean ecosystem structure.

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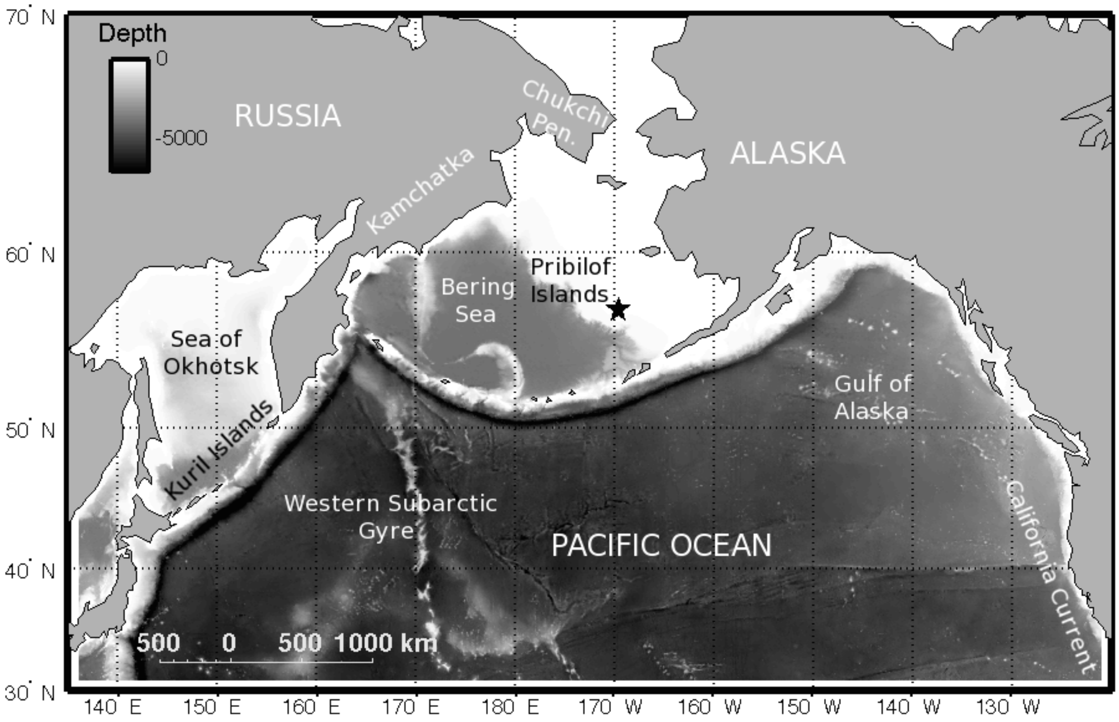

Figure 1. Map of the study region, the North Pacific and its marginal seas.

Figure 2. Red-legged kittiwake carrying a geolocation logger roosting on St. Paul Island.

Figure 3. Thick-billed murre with a geolocation logger (Photo credit: Thibaut Vergoz).

CHAPTER ONE

North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations

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Abstract

Species that breed sympatrically often occupy different foraging niches to mitigate competition for prey. When resource availability declines at the end of the breeding season, some animals migrate to regions with more favorable environmental conditions. When these life-history traits combine, foraging habitat preferences may continue to influence migration patterns and habitat utilization. The Bering Sea is home to the red-legged kittiwake (RLKI), *Rissa brevirostris*, which is endemic, and the black-legged kittiwake (BLKI), *Rissa tridactyla*, which has a circumpolar breeding distribution. Since the 1970s, numbers of RLKIs at the largest colony have declined and then recovered, whilst the BLKI population has remained stable. Knowledge of the migration ecology of kittiwakes is key to understanding differences in population trajectories, and predicting possible future responses of these species to climate change. Using geolocation loggers, we tracked adult RLKIs and BLKIs, from the Pribilof Islands, Alaska, during their non-breeding migrations. We used iterative methods to assess suitable sample sizes for determining space use. Kittiwakes are surface foragers; therefore we used wet–dry data to distinguish active foraging behavior and to test the species' responses to environmental conditions. Stable isotope ratios of feathers grown during the non-breeding period were used to assess dietary niche. RLKIs remained largely in the Bering Sea, where they experienced colder conditions and shorter days; individual birds used multiple habitats, including the continental shelves, the sea-ice edge and pelagic waters. In contrast, BLKIs migrated to the subarctic North Pacific, where they dispersed laterally across the basin; the majority of birds travelled to the western subarctic. RLKIs spent less time actively foraging than BLKIs, and consumed higher trophic-level prey. The disparate wintering ranges and foraging behavior of BLKIs and RLKIs suggest distinct environmental factors drive variation in overwinter survival. A strong association with sea-ice, and specialization both in diet and foraging behavior, may make RLKIs particularly vulnerable to climatic change.

1.1 Introduction

Species that breed sympatrically often occupy different foraging niches to mitigate competition for prey (Ashmole, 1968; Kappes *et al.*, 2010; Jeglinski *et al.*, 2013). However, few studies have addressed whether niche specialization during breeding has an influence, in turn, on the migration ecology of marine species (e.g. Thiebot *et al.*, 2013). During migration, individuals must adjust to changes in niche space, not only in terms of the physical environment, but also in food-web structure, including the composition of prey and predator communities and the presence of competitors. Because specialist predators need to track particular prey resources year-round, they are likely to be especially vulnerable to changes in prey distributions and community composition (Hückstädt *et al.*, 2012). In the marine environment, anthropogenic climate change continues to affect temperature and wind regimes, the strength and routes of ocean currents, and to increase the pH of the oceans, altering prey fields and therefore influencing the distribution of upper trophic-level organisms (Hazen *et al.*, 2012; Weimerskirch *et al.*, 2012; Pinsky *et al.*, 2013). Understanding the importance of migration strategies for life histories is essential for assessing how highly mobile species may cope with environmental change.

The physical environment of the Bering Sea is annually variable, as sea-ice influences the timing of the spring bloom, water column temperature and stratification. This results in a dichotomy between warm and cold years, in which different primary producers and secondary consumers are favored (Hunt *et al.*, 2011). Open-water spring blooms are higher in net primary productivity, occur in warmer water than ice-associated blooms, and over the long term will probably increase the carrying capacity of this ecosystem (Brown & Arrigo, 2013); however, warmer regimes disfavor *Neocalanus* copepods and their predators (Mueter *et al.*, 2011; Dorresteijn *et al.*, 2012). As the global climate changes, conditions in the Bering Sea are predicated to transition to current subarctic conditions, with greater stratification during the summer months likely to affect primary producers and have knock-on effects at upper trophic levels (Hunt *et al.,* 2011; Brown *et al.*, 2011).

Red-legged kittiwakes (RLKIs), *Rissa brevirostris* (Bruch, 1853), and black-legged kittiwakes (BLKIs) *Rissa tridactyla* (Linnaeus, 1758), breed sympatrically on a few islands in the Bering Sea. St George Island, of the Pribilof Island group, on the south-eastern Bering Sea shelf, is home to approximately 70% of all RLKIs and a large population of BLKIs (in 1977, 220,000 pairs of RLKIs and 72,000 pairs of BLKIs; Byrd *et al.*, 2008a). RLKIs are currently listed as 'Vulnerable' by the World Conservation Union (BirdLife International, 2013). On St George, the population trends of these two species have diverged. RLKIs decreased by roughly 44% between 1976 and 1986, but subsequently increased such that recent counts suggest populations have recovered to levels recorded in the mid-1970s (Klosterman *et al.*, 2011). In contrast, the BLKI population has remained relatively stable (Byrd *et al.*, 2008a; Klosterman *et al.*, 2011). The differing population trends of the two species, despite strongly correlated breeding productivity (Byrd *et al.*, 2008b), suggest that some degree of non-breeding niche separation may play a role in population regulation; however, basic life-history differences, such as longevity, may also contribute. At the smaller colony on St Paul Island, populations of both kittiwake species are declining, although here the causes are likely to be a combination of low local food availability (Paredes *et al.*, 2012) and targeting of RLKIs for subsistence hunting (Byrd *et al.*, 2008a).

During the breeding period the two kittiwakes species appear to occupy different foraging niches. On St George: diet and trip duration indicate that RLKIs forage predominantly over the basin and tend to specialize on lipid-rich myctophid fishes (Lance & Roby, 1998), while BLKIs feed on a broader suite of prey from both the basin and shelf (Paredes *et al.*, 2012; Renner *et al.*, 2012). There is evidence that RLKIs have the capacity to forage on neritic prey (Hunt *et al.*, 1981); however, since the 1990s, myctophids have increased in occurrence in the diet of both species, probably increasing interspecific competition (Sinclair *et al.*, 2008; Renner *et al.*, 2012). It is unknown how the release of the central-place breeding constraint affects RLKI foraging, particularly whether they continue to act as specialized foragers. Compared with BLKIs, RLKIs have physiological adaptations for their particular foraging style, including shorter bills and larger eyes, that suggest specialization for foraging at low light levels is an important life-history strategy (Storer, 1987). Outside the breeding period, the habitat use and diet of RLKIs is largely unknown, but they are thought to be highly pelagic; limited at-sea survey data indicate that they could range from the pack-ice edge to south-east Alaska, California and the Kuril Islands (Byrd & Williams, 1993). In contrast, BLKIs from coastal Alaska migrate south along the coast of North America (McKnight *et al.*, 2011).

In the present study, we characterized and compared the non-breeding foraging ecology of these two sympatric kittiwake species to determine whether niche partitioning occurs in space, time or dietary trophic level. For both species on the Pribilof Islands, we determined the distribution, habitat utilization, activity patterns and trophic partitioning based on stable isotope analysis. We used remotely sensed environmental data to examine how these species respond to habitat conditions. In light of these results, we speculate on the potential mechanisms that could drive population regulation in these congeners.

1.2 Materials and Methods

Global location sensor (GLS) loggers (2.5 g, Mk9/Mk19; British Antarctic Survey, Cambridge, UK) were attached to leg bands on kittiwakes in July 2010, on St Paul Island (57°11’ N 170°15’ W; BLKI = 31, RLKI = 5) and St George Island (56°34’ N 169°37’ W; BLKI = 28, RLKI = 22) of the Pribilof Islands, Alaska, USA. The birds were captured when attending nests, which typically contained one chick, using a telescoping noose pole or foot snare. Birds were recaptured using a foot snare or hand-held CO_2-powered net gun (Super Talon Animal Catcher; Advanced Weapons Technology, La Quinta, CA, USA). Body measurements were taken from all birds. Wing loading was calculated as body mass divided by the wing area. The latter was twice the area of the right wing (plus the rootbox, the area of the body between the wings), which was traced in the field then a cut-out weighed (accuracy 0.001g) and a standard curve used to calculate area (Pennycuick, 2008). Sex was determined from DNA extracted from blood samples (Fridolfsson & Ellegren, 1999).

All data processing and spatial analyses were conducted using MATLAB 2009a (The Mathworks, Natick, MA, USA). Statistical tests were run in R 3.0.0 (R Core Team, 2013). The results are shown as means ± SD. Significance was set to $P < 0.05$.

1.2.1 Movement and area utilization

Loggers were used to record light levels, and TRANSEDIT and LOCATOR (British Antarctic Survey) were used to identify dawn and dusk transitions using a threshold of 10, and to calculate locations based on a Sun angle of –3.5 for the Mk9 loggers and –3.0 for the Mk19 loggers (values selected on the basis of stationary calibration data). Locations were calculated following Phillips *et al.* (2004), by smoothing locations twice and then applying an iterative forward/backward averaging speed filter based on a maximum travel speed of 48 km h^{-1} sustained over 12 h (Coulson, 2011). Geolocation has an error of approximately 180–200 km that increases around the equinoxes (Phillips *et al.*, 2004; Shaffer *et al.*, 2005), therefore analysis was restricted to the period 15 October–27 February. Smoothed tracks were used to identify the furthest location (maximum range) from the colony, as well as the date and bearing of that location. To calculate departure and return dates, sea-surface temperatures (SST) were used to estimate latitudes for those loggers that recorded temperature (BLKI = 27, RLKI = 8) and then the tracks were speed filtered (Shaffer *et al.*, 2005).

Utilization distributions (UDs) were calculated using smoothed locations for the pooled samples by year and month to show general movement patterns, and for each bird using the IKNOS toolbox (Y. Tremblay, University of California Santa Cruz, Santa Cruz, unpublished data). The grid cell size was set at 80 km. To enable comparisons between species and iterations, the smoothing parameter was selected using the entre dataset (latitude 0.0171, longitude 0.0068; Sheather & Jones, 1991). Portions of UDs overlapping land were subtracted from area calculations. The 50% and 95% UDs were considered to represent the core area and overall range, respectively.

Bootstrapping was used to calculate standard deviations for area estimates, to determine whether enough individuals were tracked to make reasonable inferences of area use (Hindell *et al.*, 2003; Soanes *et al.*, 2013) and to assess overlap between groups (Breed *et al.*, 2006). To assess whether sample sizes were sufficient, the areas of the 50% and 95% UDs were calculated with the addition of a new bird selected at random until all individuals were included. This was repeated for 1000 iterations. To determine spatial partitioning between species, colonies (BLKIs only, due to small sample size of RLKI from St Paul) and sexes, the amount of overlap between observed distributions was compared with the overlap from 1000 bootstrapped selections from the pooled dataset. The area of overlap divided by the area of the 95% UD of the overall dataset was used as the test statistic, and the *P*-value was determined as the proportion of iterations that resulted in a smaller overlap than observed (Breed *et al.*, 2006).

1.2.2 Habitat

Habitat use was characterized in terms of oceanographic, topographical, astronomical and atmospheric variables extracted at a grid scale of 2° latitude by 1° longitude. SSTs were extracted as an 8-day blended product from National Oceanic and Atmospheric Administration (NOAA)'s Environmental Research Division (Pacific Grove, CA) (http://oceanwatch.pfeg.noaa.gov/thredds/catalog.html). Sea-surface height (SSH) and surface currents used to calculate eddy kinetic energy (EKE) were extracted from the Navy Layered Ocean Model (http://www7320.nrlssc.navy.mil/global_nlom/) using the nctoolbox (https://github.com/nctoolbox/). The distance to the coast was calculated using mean high water (National Geophysical Data Center, NOAA, Boulder, CO). The distance to the sea-ice edge (5% contour) was calculated from daily Advanced Microwave Scanning Radiometer - EOS (AMSR-E, National Space Development Agency of Japan) georeferenced images captured aboard the Aqua satellite (National Aeronautics and Space Administration, USA) projected using ArcGIS 9.0 (ESRI, Redlands, CA, USA). Bathymetry was extracted from 2-minute gridded global relief data (Smith, 1997). Day and twilight length (nautical) were calculated for each estimated location (Reda & Andreas, 2003). The fraction of the Moon illuminated was extracted from the US Naval Observatory (Washington, DC). Surface values of air temperature, wind speed, relative humidity, precipitation and barometric pressure were extracted from the NCEP/NCAR reanalysis I and NCEP/DOE reanalysis II datasets (Kanamitsu *et al.*, 2002; Kemp *et al.*, 2011).

1.2.3 Activity patterns

Kittiwakes are surface foragers, and immersion (wet–dry) sensors are particularly suited to monitoring their activities, as frequent switches between wet and dry indicate periods of more intensive foraging behavior. Following Paredes *et al.* (2012), activity data, recorded in 10-min blocks, was classified into three categories: (1) active foraging, with periods of frequent switches between wet and dry; (2) on water, delineated when a bird spent 100% of a 10 min period on the water as well as sequential periods of ≥ 90% of 10 min on the water; and (3) dry, when the logger spent > 99% of a 10 min interval dry, indicative of flight or roosting behavior. Light levels recorded by the logger were used to classify behaviors into daylight or darkness activities.

Linear mixed models were used to relate active foraging (as a percentage of 24 h) to environmental characteristics. The following variables were excluded because inclusion resulted in variance inflation factors > 3 (Zuur *et al.*, 2009): distance to coast and colonies, precipitation, and day and twilight length. SSH and EKE were excluded because they were unavailable on the Bering Sea shelf. Bathymetry was included as a categorical variable (shelf, < 200 m; shelf break, 200–1000 m; continental slope, 1000–2000 m; oceanic, > 2000 m) and day and twilight length were combined into one variable. Therefore, the full models contained 10 variables. To meet conditions of normality, Moon illumination and cloud cover were logit transformed, and distance to sea-ice and the response variable, the percentage time spent actively foraging, were square-root transformed. Best-fit models, constructed using a reductive approach, were identified from Akaike information criterion (AIC) scores based on restricted maximum likelihood estimates (Zuur *et al.*, 2009), and marginal and conditional R^2-values were used to assess the variance explained by the fixed effects and the combined fixed and random effects, respectively (Nakagawa & Schielzeth, 2012).

1.2.4 Stable isotope analysis

We sampled head feathers, which are grown in late winter as birds molt into their breeding plumage (Gabrielson & Lincoln, 1959), and body feathers, which were probably replaced over a broader time frame during the non-breeding period. Feathers were washed with 2:1 chloroform : methanol for 24 h, rinsed twice, allowed to dry for > 48 h, and cut finely. The feathers were analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Carbo-Elba elemental analyzer interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, University of California Santa Cruz, Santa Cruz, CA, USA). Data were corrected for sample mass and instrument drift. Measurement precision (standard deviation), based on within-run replicate measures of the laboratory standard (pugel), was 0.08 for $\delta^{13}C$ and 0.08 for $\delta^{15}N$ ($n = 24$).

1.3 Results

Overall, 86% of tagged birds were resighted in the following breeding season (St Paul, BLKI 87%, RLKI 60%; St George, BLKI 92%, RLKI 82%). These may be underestimates of survival as there was almost complete breeding failure of BLKIs during incubation and poor overall hatching success of RLKIs (Klostermann *et al.*, 2011; Thomson & Drummond, 2012). Overall, 71% of loggers were recovered; nine loggers failed. Complete datasets were available for analysis from 34 BLKIs (St Paul, 15; St George, 19) and 17 RLKIs (St Paul, 2; St George, 15). Mean mass at recapture was not significantly different from that at deployment (paired *t*-test, $P > 0.05$).

1.3.1 Morphometrics

Male BLKIs were larger than female BLKIs in all measurements except wing area, whereas male RLKIs were larger than female RLKIs in only head plus bill length ($F_{1,30} = 4.70$, $P = 0.038$). There were no significant differences between the sexes in either species regarding aspect ratio and wing loading (Table 1.1). BLKIs were larger than RLKIs in all measurements; however, there was no significant difference in aspect ratio or wing loading (Table 1.2).

1.3.2 Movements and area utilization

During the non-breeding period, both species migrated away from their colonies. Their distributions were spatially segregated, with almost no overlap of 50% UDs (Figure 1.1). The core areas for BLKIs were between 40° N and 50° N, while those of RLKIs were largely in the Bering Sea (Figure 1.1). There were overlaps between the 95% UDs of the two species in the south-east Bering Sea, the Western Subarctic Gyre (WSG) and along the northern edge of the BLKI distribution (Figure 1.1). Both species remained in the Pribilof region until late September. Although there were no significant differences in the maximum range, departure or arrival date between species, the ranges of individual RLKIs were further west and significantly smaller than those of BLKIs (Table 1.3). The furthest locations of males were further to the west than those of females, but no other significant effects of sex were observed.

High densities of BLKIs were consistently present in the central subarctic North Pacific (Figure 1.2). In February, BLKIs were highly dispersed, with a distribution that spanned the North Pacific from the Kuril Islands to the California coast. A total of 23 BLKIs (68%) travelled to the WSG. Overall BLKIs spent minimal time in the Gulf of Alaska, with three birds (8%) travelling to the California Current system in February (6 February ± 6 days), where they remained for 30 ± 8 days until departure in March (9 March ± 5 days). In contrast, 82% of RLKIs remained in the eastern Bering Sea through December, largely foraging over the shallow shelf, north to the Chukchi Peninsula. In November, two RLKIs (12%) flew to the northern Kuril Islands. By January, the remaining birds left the eastern Bering Sea as the sea-ice extended south, and rapidly crossed the basin or moved south along the coast of Kamchatka, where high densities occurred into February (Figure 1.2). By this time, all RLKIs had briefly visited the western subarctic and, when the birds began returning north, four birds made brief forays into the Sea of Okhotsk.

The total area occupied during the non-breeding period appeared to approach saturation (i.e. an asymptote) with the number of birds tracked; for RLKIs, an asymptote was reached at a lower sample size, indicating little variation between individuals (Figure 1.3). The species differed significantly in spatial extent, with BLKIs using a larger area (Figure 1.3). The species' distributions showed significantly less overlap than occurred randomly at both the core and range scales (50% UD, 10% overlap; 95% UD, 68.5% overlap; $P < 0.001$). BLKIs originating from the two study colonies showed significantly less overlap than occurred at random, indicating spatial differences (50% UD, 17% overlap, $P < 0.001$; 95% UD, 67% overlap, $P = 0.022$). There was less overlap between sexes than occurred at random in BLKIs for the 50% UDs (14% overlap, $P = 0.002$) but not the 95% UDs (59% overlap, $P = 0.065$); for RLKIs, there was less overlap for both the 50% UDs (10% overlap, $P < 0.001$) and 95% UDs (69% overlap, $P < 0.001$; Figure 1.4). Females appeared to be more widely dispersed; however, sample sizes were small. Because it was not possible to account for inter-colony variation for RLKIs, the colonies were combined in the following analysis.

1.3.3 Habitat

The physical characteristics of the habitats used by RLKIs and BLKIs in their core areas differed significantly for all environmental variables except mean sea level pressure and SSH (Table 1.4). RLKIs encountered, on average, significantly colder water and air temperatures and lower humidity, whereas BLKIs encountered higher winds and more cloud and precipitation. BLKIs experienced more hours of daylight but fewer hours of twilight. RLKIs were closer to the sea-ice edge; however, not all core areas were associated with sea-ice. Core areas of RLKIs had higher EKE; this difference reflected the pelagic portion of the respective distributions, as satellite remote-sensing limits the measurement of EKE to off-shelf regions. RLKIs remained closer to the Pribilof Islands and the coast, and hence in shallower water.

1.3.4 Daily activity patterns

BLKIs actively foraged more than RLKIs throughout the non-breeding period; RLKIs spent more time in flight or roosting in October–December and more time on the water in December–January than BLKIs (Figure 1.5; percentage of 24 h). Both species engaged in their most active foraging in October (RLKIs 15%, BLKI 25.3%) and the least in January (RLKIs 11.5%, BLKI 19.1%). The majority of the night was spent sitting on the water (BLKI 84.8 ± 8.5%, RLKI 91.1 ± 1.4%, $F_{1,46} = 4.66$, $P = 0.036$), with < 5% of darkness spent in flight; however, BLKIs spent a higher percentage of the night engaged in active foraging behavior than RLKIs (BLKI 10.3 ± 4.1%, RLKI 6.1 ± 2.1%, $F_{1,46} = 21.54$, $P < 0.001$).

For the linear models relating active foraging (percentage of 24 h) to environmental characteristics, the inclusion of a temporal autocorrelation term improved the AIC scores. For RLKIs, the best-fit model included six significant factors (Table 1.5); air temperature and combined daylight and twilight length were all positively related to active foraging, while SST, distance to the sea-ice, cloud cover and wind speed were negatively related. For BLKIs, the best-fit model included seven significant factors (Table 1.5); active foraging was related positively to SST, mean sea level pressure, air temperature, moonlight, humidity and cloud cover, and negatively to distance to sea-ice.

1.3.5 Stable isotope analysis

Compared with BLKIs, the head feathers of RLKIs had higher δ^{15}N ($F_{1,62} = 27.29$, $P < 0.001$), lower δ^{13}C ($F_{1,62}$ = 10.38, P = 0.002) and less variance for both δ^{15}N ($F_{42,18}$ = 11.91, P < 0.001) and δ^{13}C ($F_{42,18}$ = 3.14, P = 0.011; Fig. 5). δ^{15}N of body feathers was higher for RLKIs ($F_{1,62}$ = 9.41, P = 0.003); neither δ^{13}C nor variances of body feathers were significantly different, but variance was higher between body feathers than head feathers for both species (Figure 1.6). δ^{15}N of body feathers was higher head feathers of BLKIs (t = –2.56, P = 0.032) but not RLKIs (t = –1.774, P = 0.093). There was a significant difference in δ^{13}C of head feathers of individual RLKIs sampled in two consecutive years (2010, –18.56 ± 0.32‰; 2011, –18.34 ± 0.21‰; t = –2.2, n = 17, P = 0.043) but not in those of individual BLKIs (2010, 14.94 ± 0.96‰; 2011, 14.32 ± 1.50‰; t = 2.73, n = 37, P = 0.01); within individuals, there were no significant differences between years in δ^{15}N of head feathers and δ^{13}C and δ^{15}N of body feathers.

1.4 Discussion

We found that both kittiwake species made long-distance migrations and showed a substantial degree of spatial and dietary niche partitioning during the non-breeding period. Contrary to expectations, RLKIs were more coastal whereas BLKIs migrated to more pelagic areas and therefore experienced very different physical environmental conditions. Overall, BLKIs foraged more actively, were more active at night and foraged more in moonlight. The lower variance in stable isotope ratios suggested that RLKIs tended to be dietary specialists during the late winter, whereas BLKIs were generalists. Our data suggest that RLKIs are particularly adapted to exploitation of the Bering Sea ecosystem, and that changes in the oceanographic regime here will more strongly influence population trends of this species.

1.4.1 Spatial niche

The two kittiwake species showed marked segregation in spatial distribution and associated environmental conditions during the non-breeding period, which was independent of the colony of origin (BLKIs from the two study colonies showed extensive overlap in distribution).

By utilizing both the eastern and western Bering Sea, RLKIs exploited a diversity of habitats, including the shallow continental shelf, sea-ice edge and pelagic regions of high EKE. The use of the Bering Sea shelf in the autumn is supported by at-sea data (March–October), as the relative abundance of RLKIs increases over the shelf break, and to some extent over the shelf, during both the early autumn and spring, following the general trend for surface foragers in the region to move nearer to the shore during these periods (Hunt *et al.*, 2013). The sea-ice edge is likely to be a key habitat for RLKIs, although from our large-scale geolocation data it is impossible to resolve the exact association. As well as the extensive coastal sea-ice present for much of the winter, the Kamchatka Current is characterized by areas of relatively high EKE. Eddy activity may make prey more available for surface-foraging seabirds and provide predictable spatial structure for locating prey (Bost *et al.*, 2009). Although the diversity in non-breeding habitats used by RLKIs might be expected to result in dietary shifts, our data on activity budgets, and the low variance in stable isotope ratios in feathers grown during the non-breeding season, suggest they maintain similar levels of foraging specialization throughout this period.

BLKIs showed a preference for westerly and central areas in the subarctic North Pacific and RLKIs also utilized waters of the WSG. This preference is similar to large-scale patterns observed for other marine predators, including migratory shearwaters and some cetacean species (Springer *et al.*, 1999). It is likely that resources are more abundant or predictable here, as high primary productivity supports higher winter zooplankton biomass and a greater diversity of myctophid fishes than in the eastern North Pacific (Beamish *et al.*, 1999; Nagasawa, 2000). None of the tracked kittiwakes utilized the Gulf of Alaska, one of the stormiest regions of the North Pacific (Wilson & Overland, 1986). Nevertheless, this is likely to be an important wintering area for a proportion of Alaskan BLKIs; birds from Prince William Sound have ranged there during some years (McKnight *et al.*, 2011). Many kittiwakes breeding in the north-east Atlantic also cross the basin to winter in cold waters off Newfoundland and Labrador, suggesting a commonality in winter resource availability where cold waters, the Kamchatka Current (North Pacific) and Labrador Current (North Atlantic) move south (Frederiksen *et al.*, 2012).

1.4.2 Behavioral niche

Both species were largely diurnal in their use of active foraging, which is similar to BLKIs tracked in the eastern North Pacific (McKnight *et al.*, 2011). Environmental conditions were only able to explain a small portion of the variance in the percentage of time the two species spent actively foraging, reflecting the large amount of individual variation in both species. In general, BLKIs were more active, even during darkness, and, unlike RLKIs, BLKIs increased their active foraging when the Moon was fuller. Specialist predators are sometimes more efficient at catching and handling prey (Heinrich, 1976). However, it is surprising RLKIs were not more active during darkness, as suggested previously on the basis of their relatively large eyes (Storer, 1987). This does not refute the hypothesis that larger eyes are an adaptation for foraging at night, as this species could be employing a less energetically costly sit-and-wait strategy for night foraging (Jodice *et al.*, 2003). RLKIs experienced more hours of twilight than BLKIs, but the activity patterns of both species suggest that they do not use all the daylight hours to meet their energetic needs.

1.4.3 Dietary niche

Our data suggest that RLKIs are foraging predominantly on higher trophic-level prey than BLKIs. Elevated $\delta^{15}N$ values do occur for other reasons, including as a result of fasting or spatial differences in baseline values. The latter are particularly important when considering large geographical ranges; however, for head feathers grown in the late winter the geolocation data suggest both species were using off-shore resources, supporting the idea of higher trophic foraging by RLKIs. Nevertheless, higher $\delta^{15}N$ of body feathers from some RLKIs is probably the result of movement to the northern Bering Sea, as the baseline $\delta^{15}N$ values increase 2–6‰ from south to north, whereas $\delta^{13}C$ values are more spatially heterogeneous (Schell *et al.*, 1998). Myctophids are not found in the shallow waters on the Bering Sea shelf (Beamish *et al.*, 1999), which in itself suggests that RLKIs are able to shift their diets from the types of prey exploited during the summer. Excluding the individuals with elevated δ^{15}N, the remaining RLKIs showed a low degree of variance in stable isotope ratios in their body feathers (δ^{15}N variance = 0.257‰), indicating a diet specialization that is maintained for long periods.

Dietary specialization during the non-breeding period appears to be rare, and instead an expansion in trophic niche is more common (Cherel *et al.*, 2007; González-Solís *et al.*, 2011; but see Bodey *et al*., 2013). RLKIs appear to be specialists during the pre-nuptial molt, as the variance in isotope ratios among individuals was less than 1‰ (Jaeger *et al.*, 2009). This specialization may make them vulnerable to changes in prey populations, and indeed fluctuations in breeding success are evident at St George that relate to a negative competitive interaction with pink salmon, *Oncorhynchus gorbusch* (Springer & van Vliet, 2014). How these interactions influence distributions is unknown, as we only tracked individuals during one year. However, individual RLKIs showed a slight, but significant, shift of 0.22‰ in δ^{13}C in head feathers grown in consecutive years, which could relate to annual differences in spatial habitat use.

1.4.4 Population regulation

The striking non-breeding niche separation between these kittiwake species may help to explain the divergent population trends observed on St George, although other differences in life-history factors may also be important. Regardless, as RLKIs spent a large portion of the non-breeding period in the Bering Sea, it seems reasonable to expect that changes in year-round prey resources in this region will influence overwinter survival. Declines in RLKIs followed the 1976–77 regime shift in the Bering Sea (Hare & Mantua, 2000); however, how winter prey availability changed during this time period is unclear. Winter conditions in the Bering Sea show a high degree of annual variability, because of changes in sea-ice extent and the timing of ice retreat (Overland & Stabeno, 2004), whereas the subarctic North Pacific may provide a more stable wintering habitat (Bograd, 2004). Our data relate to a single year of tracking and hence the degree of annual variation in migration patterns and distributions is unknown; however, for RLKIs the lack of any significant change within individuals in the isotopic ratios of body feathers grown during consecutive winters of extensive sea-ice suggests a high degree of fidelity in both habitat use and diets under these conditions.

The restricted range of the RLKI and its greater dietary specialization may make this species vulnerable to future declines in sea-ice extent, as the eastern Bering Sea is predicted to be ice-free year-round by 2050 (Wang *et al.*, 2012). Our study highlights a close association between RLKIs and sea-ice; however, it is unknown to what extent RLKIs rely on pagophilic prey. Kittiwake reproductive success is linked to sea-ice extent and timing of retreat at lagged time-scales (Zador *et al.*, 2013); hatch dates have become progressively earlier, which is also thought to be related to prey availability and changes in sea-ice dynamics (Byrd *et al.*, 2008b). In this study, both species returned to the Pribilof Islands around the spring equinox, when there was still sea-ice in the south-eastern Bering Sea. Independent time series data for observed return dates are not available, but on 8 April 1914, G D. Hanna observed the first RLKIs returning to St George (Gabrielson & Lincoln, 1959), which hints that the reliance on springtime resources in the Bering Sea has existed for at least the last 100 years.

1.5 Conclusions

Our study provides new insights into the non-breeding distribution and ecology of two important avian predators in the Bering Sea ecosystem. Specifically, the division of range and habitat use of these two congeneric kittiwake species during this time implies that different environmental factors will influence foraging success and survival. The lower levels of activity shown by the RLKIs, as well as the high degree of similarity in stable isotope values, suggest that this species employs a specialized foraging strategy, which may increase their susceptibility to environmental change. Warming temperatures may allow BLKIs to use more of the Bering Sea during the winter, while the RLKIs' preferred habitat may shift further north. The degree of individual flexibility in migratory patterns may be an important factor in how well these two species will adapt to future climate change.

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Table 1.1 Morphometric characteristics (mean ± SD) of male and female red-legged kittiwakes (RLKIs), *Rissa brevirostris*, and black-legged kittiwakes (BLKIs), *Rissa tridactyla* from colonies on St George and St Paul islands of the Pribilof Islands, Alaska, USA. Significant differences are highlighted in bold. Sample sizes are shown in parentheses.

Size metric	**Female**	**Male**	**SSD**	***F***	***P***
RLKI					
Mass (g)	365.6 ± 45.9 (14)	379.1 ± 24.2 (18)	3.69	77.63	0.800
Culmen (mm)	29.0 ± 1.8 (14)	29.8 ± 1.4 (18)	2.76	1.89	0.180
Head + bill (mm)	81.8 ± 3.9 (14)	84.3 ± 2.7 (18)	**3.06**	**4.70**	**0.038**
Tarsus (mm)	31.8 ± 1.9 (14)	31.5 ± 1.5 (18)	–0.94	0.21	0.650
Natural wing chord (mm)	308.5 ± 6.8 (14)	310.8 ± 6.6 (18)	0.75	0.96	0.336
Wing span (B, cm)	95.15 ± 3.24 (4)	96.13 ± 6.70 (3)	1.03	0.068	0.804
Wing area (S_{wing}, cm^2)	898 ± 106 (4)	939 ± 81 (3)	4.57	0.308	0.603
Wing chord [c_m, (S_{wing}/B), cm]	9.44 ± 0.81 (4)	9.78 ± 0.27 (3)	3.60	0.477	0.521
Wing loading (N/m^2)	40.41 ± 5.4 (4)	39.67 ± 3.04 (3)	–1.83	0.044	0.842
Aspect ratio (B/c_m)	10.12 ± 0.58 (4)	9.83 ± 0.61 (3)	–2.87	0.415	0.548
BLKI					
Mass (g)*	380.6 ± 30.8 (24)	435.3 ± 36.3 (26)	**14.37**	**26.66**	**<0.001**
Culmen (mm)	38.5 ± 1.4 (24)	40.8 ± 1.6 (26)	**5.97**	**23.35**	**<0.001**
Head + bill (mm)	93.5 ± 2.2 (24)	98.5 ± 2.2 (26)	**5.35**	**45.87**	**<0.001**
Tarsus (mm)	34.5 ± 1.6 (24)	36.7 ± 1.7 (26)	**6.38**	**18.26**	**<0.001**
Natural wing chord (mm)*	311.4 ± 7.4 (24)	320.9 ± 6.1 (26)	**3.08**	**17.45**	**<0.001**
Wing span (B, cm)	101.4 ± 2.5 (17)	105.0 ± 2.4 (10)	**3.55**	**7.72**	**<0.001**
Wing area (S_{wing}, cm^2)	1063 ± 77 (17)	1125 ± 77 (10)	5.83	4.046	0.055
Wing chord [c_m, (S_{wing}/B), cm]	10.50 ± 0.59 (17)	10.72 ± 0.60 (10)	2.10	0.90	0.351
Wing loading (N/m^2)*	35.71 ± 4.85 (17)	38.64 ± 4.07 (10)	8.20	2.578	0.121
Aspect ratio (B/c_m)	9.67 ± 0.44 (17)	9.82 ± 0.49 (10)	1.55	0.601	0.444

*Colony significantly different: mass, St Paul 419 ± 40.7 (19), St George 387.9 ± 38.2 (22), *F* = 13.66, *P* < 0.001; natural wing chord, St Paul 317.9 ± 7.7 (19), St George 312.9 ± 8.1 (22), *F* = 7.10, *P* = 0.011; wing loading, St Paul 38.3 ± 4 (18), St George 33.7 ± 4.7 (9), *F* = 6.91, *P* = 0.015).

Table 1.2 Comparison of species morphometric characteristics between red-legged kittiwakes (RLKIs), *Rissa brevirostris*, and black-legged kittiwakes (BLKIs), *Rissa tridactyla* from the Pribilof Islands, Alaska. Results are from two-way ANOVAs with species and sex as factors. Significant differences are highlighted in bold.

Size metric	***F***	***P***
Mass (g)	**13.25**	**<0.001**
Culmen (mm)	**768.07**	**<0.001**
Head + bill (mm)	**88.02**	**<0.001**
Tarsus (mm)	**356.69**	**<0.001**
Natural wing chord (mm)	**11.42**	**0.001**
Wing span (B, cm)	**31.87**	**<0.001**
Wing area (S_{wing}, cm^2)	**24.85**	**<0.001**
Wing chord [c_m, (S_{wing}/B), cm]	**15.35**	**<0.001**
Wing loading (N/m^2)	2.87	0.101
Aspect ratio (B/c_m)	1.72	0.200

Table 1.3 Migration characteristics (mean ± SD) of red-legged kittiwakes (RLKIs), *Rissa brevirostris*, and black-legged kittiwakes (BLKIs), *Rissa tridactyla*, from the subarctic North Pacific; *P*-values indicate species differences and are the result of two-way ANOVAs with species and sex as factors. ANOVAs did not assume that variances were equal. Sample sizes are given in parentheses. Significant differences are highlighted in bold.

		RLKI	**BLKI**	***F*** ***P***
Departure date	28 September ± 21 (8)	24 September ± 17 (26)	0.36	0.058
Return date	22 March ± 3 (8)	26 March ± 23 (25)	0.24	0.626
Trip duration (days)	175 ± 22 (8)	183 ± 30 (25)	0.51	0.480
Maximum range (km)	2,600 ± 400 (17)	2,800 ± 800 (34)	0.85	0.361
Date at maximum range	16 January ± 15 (17)	25 January ± 27 (34)	1.51	0.224
Bearing to maximum range (°)	259 ± 11 (17)	220 ± 43 (34)	**14.62**	**< 0.001***
Individual area of 50% UD (km^2)†	468,000 ± 202,000 (17)	674,000 ± 249,000 (34)	**8.59**	**0.005**
Individual area of 95% UD (km^2)†	2,212,000 ± 672,000 (17)	3,197,000 ± 1,062,000 (34)	**11.80**	**0.001**
Area of 50% UD (km^2)	1,281,000 (17)	2,219,000 (34)	–	–
Area of 95% UD (km^2)	5,534,000 (17)	9,874,000 (34)	–	–

*Bearing to maximum range (location at the maximum distance from the colony), female 224.5 ± 45.7, male 248.5 ± 22.1, *F* = 6.81, *P* = 0.012.

†Average area of utilization distribution (UD) for individual birds.

Table 1.4 Habitat characteristics (mean ± SD) of red-legged kittiwakes (RLKIs, *n* = 17), *Rissa brevirostris*, and black-legged kittiwakes (BLKIs, *n* = 34), *Rissa tridactyla*, in the subarctic North Pacific in the 50% utilization distributions (UDs) for the period 15 October–27 February; *P*-values are the result of ANOVAs with sex and species as factors, and indicate species differences. No significant differences between sexes were found.

	RLKI	BLKI	*F*	*P*
SST (°C)	1.96 ± 0.91	6.85 ± 0.68	468.64	< 0.001
Depth (m)	–862 ± –805	–5516 ± –92	1195	< 0.001
EKE ($cm^2 s^{-2}$)	239 ± 156	79 ± 19	34	< 0.001
SSH (cm)	–11.00 ± 3.06	–11.75 ± 3.45	0.58	0.451
Distance to coast (km)	93 ± 26	670 ± 104	485	< 0.001
Distance to sea ice (km)	122 ± 41	1052 ± 207	323	< 0.001
Distance to Pribilofs (km)	855 ± 318	1559 ± 337	51	< 0.001
Air temperature (° C)	–1.8 ± 2.2	5.9 ± 1.0	290.3	< 0.001
Cloud cover (%)	64.5 ±7.3	74.5 ± 2.3	56.6	< 0.001
Humidity (%)	84.3 ± 2.6	85.6 ± 1.8	4.4	0.042
Precipitation ($kg\ m^{-2}$)	7.8 ± 1.1	13.6 ± 1.5	192.3	< 0.001
Sea level pressure (mb)	1008.5 ± 3.2	1010.5 ± 3.8	3.4	0.071
Wind speed ($m\ s^{-1}$)	6.29 ± 0.77	9.47 ± 1.23	90.45	< 0.001
Day length (h)	7.67 ± 0.71	9.55 ± 0.30	182.35	< 0.001

SST, sea surface temperature; EKE, eddy kinetic energy; SSH, sea surface height.

Table 1.5 Summary statistics for linear mixed models of environmental influences on time spent actively foraging for red-legged kittiwakes (RLKIs), *Rissa brevirostris* (n = 17, observations = 1927), and black-legged kittiwakes (BLKIs), *Rissa tridactyla* (n = 32, observations = 4202), in the subarctic North Pacific. All models include a temporal correlation term [corCAR1(form = ~date|id)]. Akaike information criterion (AIC), change in AIC relative to the best-fit model (ΔAIC) and marginal R^2 [$R^2(m)$] and conditional R^2 [$R^2(c)$] values are presented. For both species, AIC indicated that model 4 (in bold) was the best-fit model.

Model		d.f.	AIC	ΔAIC	$R^2(m)$	$R^2(c)$
RLKI						
Full	SST+d2ice+cloud+wind+BP+air+light+moon+humid+bathy	14	–5184.1	7.0	0.054	0.130
1	SST+d2ice+cloud+wind+BP+air+light+moon+bathy	13	–5186.1	5.0	0.054	0.131
2	SST+d2ice+cloud+wind+BP+air+light+moon	12	–5187.9	3.2	0.054	0.131
3	SST+d2ice+cloud+wind+air+light+moon	11	–5189.6	1.5	0.054	0.131
4	**SST+d2ice+cloud+wind+air+light**	**10**	**–5191.1**	**0**	**0.053**	**0.131**
5	d2ice+cloud+wind+air+light	9	–5190.3	0.8	0.053	0.131
6	d2ice+cloud+air+light	8	–5188.8	2.3	0.051	0.130
7	d2ice+cloud+air	7	–5187.6	3.5	0.047	0.126
BLKI						
Full	SST+d2ice+cloud+wind+BP+air+light+moon+humid+bathy	14	–9997.0	3.6	0.070	0.201
1	SST+d2ice+cloud+wind+BP+air+light+moon+humid	13	–9998.8	1.8	0.070	0.200
2	SST+d2ice+wind+BP+air+light+moon+humid	12	–9999.5	1.1	0.070	0.200
3	SST+d2ice+wind+BP+air+moon+humid	11	–10000.2	0.5	0.069	0.200
4	**SST+d2ice+BP+air+light+moon+humid**	**10**	**–10000.6**	**0**	**0.068**	**0.200**
5	SST+d2ice+BP+light+moon+humid	9	–9999.2	1.4	0.065	0.199

SST, sea surface temperature; d2ice, distance to sea-ice edge; cloud, cloud cover; wind, wind speed; BP, mean sea level pressure; air, air temperature; moon, moonlight; humid, humidity; bathy, bathymetry.

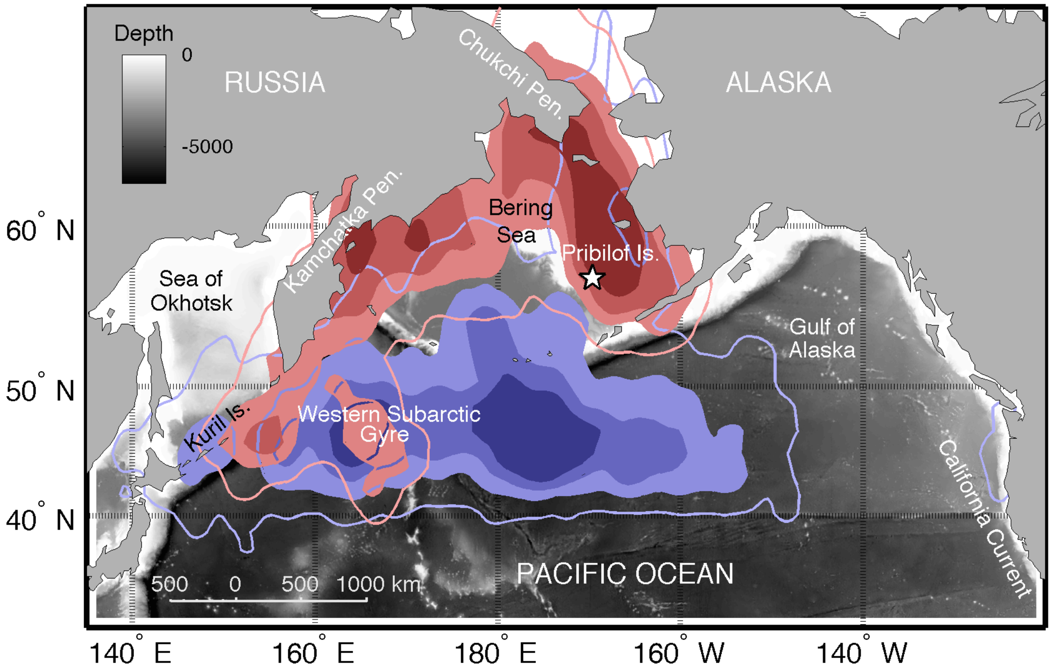

Figure 1.1 At-sea utilization distributions (UDs) for red-legged kittiwakes (RLKIs), *Rissa brevirostris* (shades of red, *n* = 17), and black-legged kittiwakes (BLKIs), *Rissa tridactyla* (shades of blue, *n* = 34), in the subarctic North Pacific, from 15 October 2010 to 27 February 2011. The 25%, 50% and 75% UDs are represented by continuously lighter shades, and the solid line represents the 95% UD.

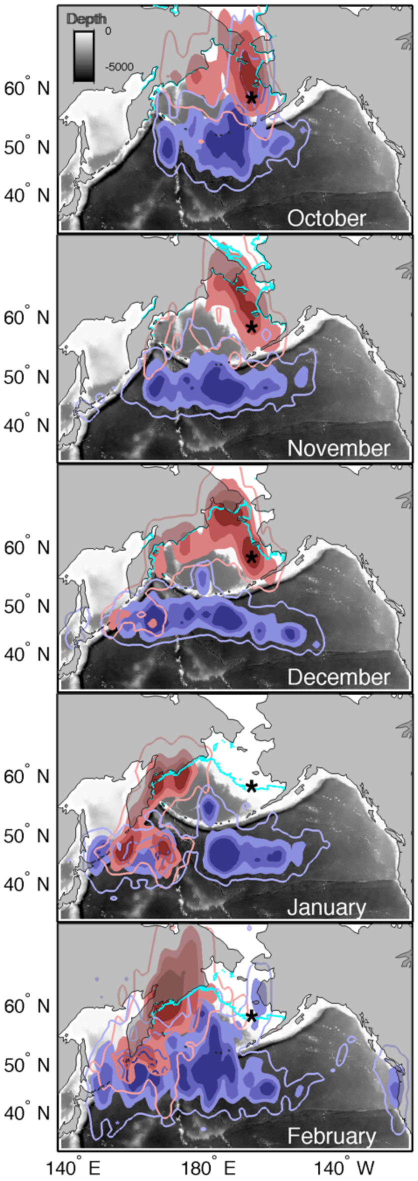

Figure 1.2 Monthly utilization distributions (UDs) derived from smoothed locations for red-legged kittiwakes (RLKIs), *Rissa brevirostris* (shades of red, *n* = 17), and black-legged kittiwakes (BLKIs), *Rissa tridactyla* (shades of blue, *n* = 34), in the subarctic North Pacific. The 25%, 50% and 75% UDs are represented by continuously lighter shades, and the solid line represents the 95% UD. The Bering Sea ice edge (5% contour) at the end of each month is shown in light blue.

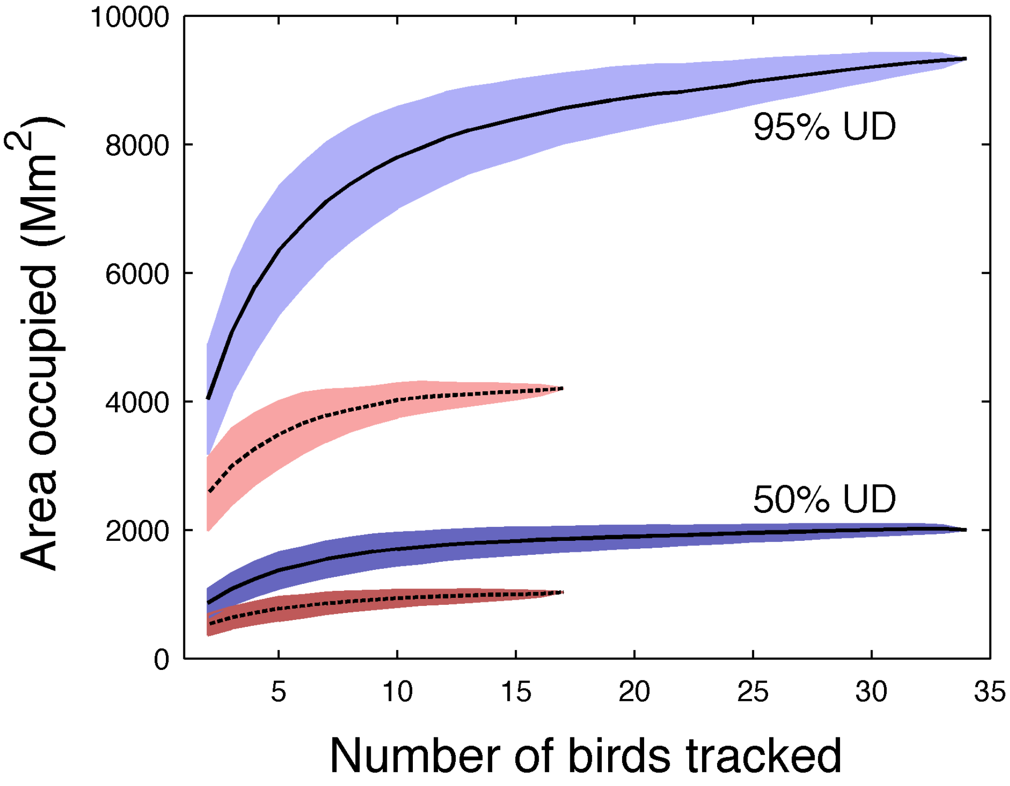

Figure 1.3 Area of the 95% utilization distributions (UDs) and 50% UDs relative to sample size from 1000 iterations of sequential area estimates for red-legged kittiwakes (RLKIs), *Rissa brevirostris* (dashed line, red), and black-legged kittiwakes (BLKIs), *Rissa tridactyla* (solid line, blue), based on their presence in the subarctic North Pacific.

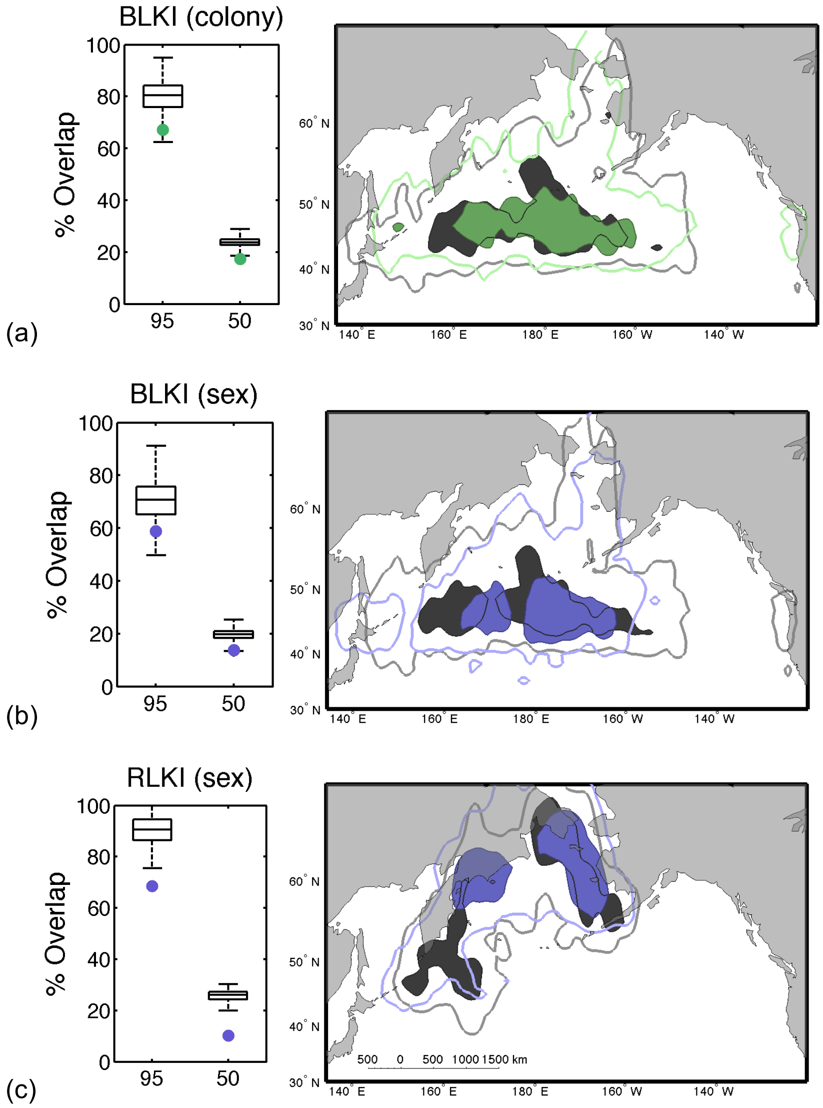

Figure 1.4 Bootstrap area of overlap for 1000 iterations at 50% and 95% utilization distributions and kernel density plots of observed distributions in the subarctic North Pacific between (a) colonies of black-legged kittiwakes (BLKIs), *Rissa tridactyla* (St Paul Island, green, *n* = 15; St George Island, grey, *n* = 19), (b) sexes of BLKI (male, blue, *n* = 10; female, grey, *n* = 24) and (c) sexes of red-legged kittiwakes (RLKIs), *Rissa brevirostris* (male, blue, *n* = 10; female, grey, *n* = 7). Colored circles on box plots correspond to the percentage of area overlapped by the observed groups.

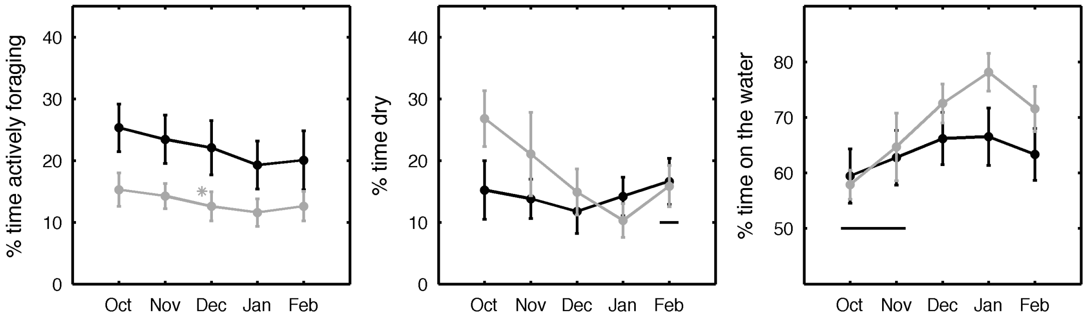

Figure 1.5 Activity budgets of red-legged kittiwakes (RLKIs), *Rissa brevirostris* (grey), and black-legged kittiwakes (BLKIs), *Rissa tridactyla* (black), for the non-breeding period, October–February, in the subarctic North Pacific. Percentages are of 24-h periods. Months when species are not significantly different, as determined by monthly linear mixed effects models with individual as a random effect, are indicated by a horizontal line. An asterisk indicates differences between sexes within a species. Means ± SD.

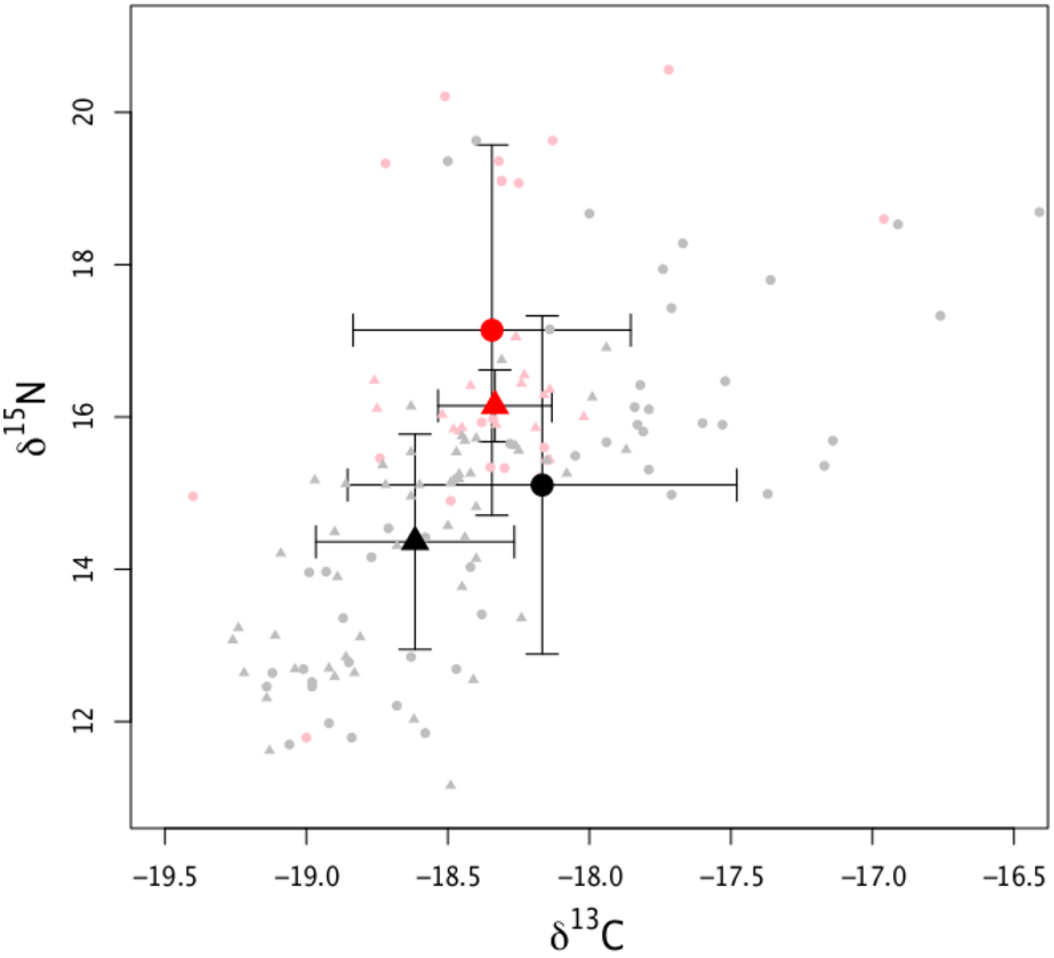

Figure 1.6 Stable carbon and nitrogen isotope values from subarctic North Pacific red-legged kittiwakes (RLKIs), *Rissa brevirostris* (red, *n* = 19), and black-legged kittiwakes (BLKIs), *Rissa tridactyla* (black, *n* = 49), from head feathers (triangles) and body feathers (circles). Error bars are ± SD and lighter shaded markers indicate values of individual birds.

CHAPTER TWO

Body size predicts individual winter foraging strategies of thick-billed murres (*Uria lomvia*) in the Bering Sea

Rachael A. Orben, Rosana Paredes, Daniel D. Roby, David, B. Irons, and Scott A. Shaffer

Abstract

1. Both migration and niche specialization can evolve in response to resource limitation. Within populations, individual foraging strategies can reduce competition, however seasonal changes in environmental conditions and subsequent responses of prey populations can alter the relative effectiveness of strategies.

2. For marine birds that fly and dive, body size constraints may be important for migratory decisions as smaller bodies reduce flight costs whereas larger bodies are advantageous for diving deeper. This study tests the hypothesis that body size influences individual migratory strategies in the deep diving thick-billed murre (*Uria lomvia*).

3. We used geolocation time-depth recorders and stable isotopes to examine individual migratory behaviour of thick-billed murres from St Paul, St George and Bogoslof Island in the south-eastern Bering Sea during three non-breeding periods, 2008-11.

4. Structural body size differed by colony and sex and the larger birds from St Paul had higher wing-loading. Larger bodied birds dived to deeper depths, spent more time in the Bering Sea, and had higher δ^{15}N and δ^{13}C values from throat feathers grown in the late winter. A hierarchical cluster analysis identified three foraging strategies based on the movement, diving, and stable isotope data. One strategy was composed of only birds originating from St Paul (31%), who remained in the Bering Sea and foraged, mainly during the day, and had elevated late winter δ^{15}N and δ^{13}C values. In contrast, the main strategy, employed by birds from all colonies in 2008/09 and 2009/10, was characterized high residency areas south of the Aleutians, where birds dove largely at night. The third strategy occurred during 2010/11 when birds dove more and deeper, suggesting limited prey

resources. Stable isotope analysis of throat feathers indicates that St Paul individuals exhibit annual flexibility in the use of their colony specific foraging strategy.

5. Foraging strategies were linked to body size associated with the three breeding colonies and partitioned with respect to annual differences, presumably in relationship to shifts in prey distributions. Our results suggest a more complex regulation of overwinter survival of birds originating from the colony on St Paul, than for birds from St George or Bogoslof.

2.1 Introduction

Both migration and niche specialization can evolve in response to resource limitation (Chase & Leibold 2003; Milner-Gulland, Fryxell & Sinclair 2011). Within populations, individual foraging strategies can reduce competition, however changing environmental conditions and subsequent responses of prey resources can seasonally alter the effectiveness of strategies. The use of individual foraging strategies, though widespread across taxa (Bolnick *et al.* 2003), appears to be especially common in diving marine predators including sharks (Kim *et al.* 2012), otters (Tinker *et al.* 2007), seals (Lea *et al.* 2002; Weise, Harvey & Costa 2010; Hückstädt *et al.* 2011), whales (Hoelzel, Dorsey & Stern 1989), penguins (Tremblay & Cherel 2000), and other diving seabirds (Kato *et al.* 2000; Woo *et al.* 2008; Sommerfeld *et al.* 2013). Many of these predators also make extended seasonal migrations (e.g. penguins, murres, fur seals, and elephant seals; Bost *et al.* 2009; Block *et al.* 2011; Gaston *et al.* 2011). The temporal scale of studies investigating individual foraging strategies varies widely (breeding season, migration, multiple years) and influences both the types of strategies observed and how they are quantified. Seasonal changes in available prey resources, particularly shifts in prey depth, as well as resource utilization of a new habitat may alter how individuals forage (Sims *et al.* 2005; Harding *et al.* 2013). Long time frames are necessary to understand how individuals are able to adjust foraging behaviour to changing conditions to fulfil life history needs, especially in species that appear to employ specialized predatory strategies.

Body size is a fundamental characteristic that influences life history traits including animal movements, reproduction and longevity (Peters 1983; Schmidt-Nielsen 1984). Within a species, body size differences arise through a number of mechanisms, including ontogeny, sexual selection, and local adaptations (Bolnick & Doebeli 2003; Millien *et al.* 2006; Fairbairn 2010). In some marine predators individual foraging strategies are independent of body size (Le Vaillant *et al.* 2012), in others, body size constrains behaviours as the physiology of diving and flying are strongly related to allometic relationships (Costa 1991; Costa & Shaffer

2012). Diving-flying seabirds face body size constraints in two modes of movement. Larger body sizes generally equate to enhanced diving performance where durations are longer and depths are deeper (Burger 1991; Boyd & Croxall 1996). Additionally, wings with reduced surface area are better for propulsion underwater (Pennycuick 2008). These large bodies and small wings are not efficient for flying and result in high wing-loading, fast flight speeds and greater flapping rates to stay aloft (Pennycuick 2008). Within flying-diving species, differences in body size can facilitate niche partitioning and diet specialization between size classes (Wanless & Harris 1991; Paredes *et al.* 2008; Ratcliffe *et al.* 2013) or be the result of local adaptations to environmental conditions around breeding colonies (e.g. Hilton *et al.* 2000; Cook *et al.* 2013).

For flying-diving seabirds, the dual use of specialized locomotion through two mediums has required functional compromises that may vary in importance during breeding and migration. Migration necessitates relatively large-scale movements outside of home ranges and appears to be important in flying-diving seabird life histories (e.g. Gaston *et al.* 2011; Guilford *et al.* 2011); therefore body size also influences migratory ability and strategies, both in locomotion mode and in how animals fuel migrations (Milner-Gulland *et al.* 2011). Thick-billed murres (*Uria lomvia*) are at the extreme of this junction (Figure 2.1), physiologically adapted to dive to extreme depths for their body size (~210 m, (Croll *et al.* 1992), with lower than predicted costs, but with flight costs that are the highest recorded at 0.83 J/Nm (Elliott *et al.* 2013). Even with high flight costs, some birds make foraging trips of up to 70 km when breeding (Harding *et al.* 2013) and migrate from high Arctic colonies to lower latitudes to winter (Gaston *et al.* 2011; McFarlane Tranquilla *et al.* 2013; Fort *et al.* 2013). Murres are adaptable predators and adjust their diving behaviour relative to ocean stratification and both prey patch size and distribution (Takahashi *et al.* 2008; Benoit-Bird *et al.* 2011). However, individual learning and experiences are likely important for successful predatory strategies as these long-lived birds employ extended parental care and can specialize on prey species over many breeding seasons (Woo *et al.* 2008).

In this study, we tracked birds during the non-breeding period from the largest bodied subspecies of thick-billed murre (*U. l. arra,* Pallas, 1811) breeding at three colonies along a north-south transect in the south-eastern Bering Sea. Metrics of spatial distributions, diving behaviour and diet data inferred from stable isotopes of feathers were used to identify migratory foraging strategies. We hypothesized that body size differences, between sexes and colonies, constrain individual wintering strategies of thick-billed murres.

2.2 Materials and Methods

The Pribilof Islands, with St Paul (57°10'N 170°17'W) to the north and St George (56°34'N 169°36'W) ~70 km the south, are situated on the edge of the shallow continental shelf in the south-eastern Bering Sea at the limit of winter sea ice extent, while ~350 km to the south, Bogoslof Island (53°55′N 168°02′W) is surrounded by deep waters that remain ice free. At these colonies, chick-rearing murres were captured off ledges using a telescoping noose pole, however at recapture some failed breeders were caught with foot snares. A combined geolocation and time-depth logger (LAT2500, 3.6g, Lotek Wireless Inc., Ontario, CA) or a time-depth logger (LAT1500, 3.4g), weighing 0.3% of thick-billed murres (hereafter murres) body mass (n = 148, 1058 ± 112 g), was deployed attached to leg bands during July of 2008-2010, at St Paul ($n_{LAT2500}[n_{LAT1500}]$ = 13[0]/25[0]/19[10], per year respectively), St George ($n_{LAT2500}[n_{LAT1500}]$ = 15[0]16[0]/15[12]) and at Bogoslof in 2008 only ($n_{LAT2500}$ = 15). Blood samples were taken for molecular sexing (Fridolfsson & Ellegren 1999). To examine logger effects, 1) body mass of individual murres deployed with loggers at recapture was compared to mass at deployment and 2) body mass was compared between chick rearing uninstrumented controls and birds retrieved with loggers (2009 and 2010).

2.2.1 Body Size

A principal component analysis (PCA) integrated scaled body size metrics measured at deployment (head+bill, culmen, tarsus, and natural wing chord). The first principle component

(PC1) representing 51.4% of the variance was retained for comparison with foraging strategies as the other principal components had eigen values less than 1 (Table 2.1); PC1 was significantly positively correlated with body mass ($r^2 = 0.441$, $p < 0.001$). In 2011 only, we measured wing area using wing tracings to calculate aspect ratio ($[\text{wing span}]^2$ / wing area) and wing loading (weight / wing area) and these were compared between colonies and sexes (Shaffer, Weimerskirch & Costa 2001; Pennycuick 2008). To investigate the association of body size with foraging behaviour, PC1 was regressed against the metrics of foraging used to determine migratory strategies.

2.2.2 Migratory Strategies

To process locations calculated by the geolocation loggers (Ekstrom 2004), we used a generalized additive model (GAM) with thin plate regression splines to separately smooth both latitude and longitude over time (Mosbech *et al.* 2011). This allowed for both short and rapid long distance changes in location and provided tentative estimations during the equinox periods; full tracks are presented, however residency and associated behaviour analysis was limited to October thru February. We felt that the GAM approach was warranted, as there was a high degree of error in the tag-derived geolocations, likely due to periods when the sensor was obscured. For longitude we allowed gamma to remain at the default 1 to prevent over-smoothing, while the gamma for latitude was adjusted to 1.4 (Mosbech *et al.* 2011). Daily locations were then predicted using the GAM output.

The cumulative amount of time an individual animal spends within a circle of constant radius around each point, or residency time (Barraquand & Benhamou 2011), was calculated along each track. Ideally this radius is based on a biologically relevant characteristic such as sensory perception, but in our case we chose a radius (60 km) roughly equivalent to the standard error of the GAM models for latitude (± 0.66°) and longitude (± 0.53°). Because murres spent long periods of time in localized areas we used a temporal step length of one day. Areas of high residency were identified as the upper quartile of each individual's residency times (Torres *et al.* 2011). The percentage of high residency locations in the Bering Sea was calculated as a metric of large-scale habitat use. The maximum distance from the colony and the minimum convex hull area of high residency locations were used to determine individual spatial patterns and area use.

Loggers recorded pressure (dBar) conditionally every minute below 5 dBar, equivalent to 5 m. Average dive durations during the breeding season range from 89-120 s (Paredes *et al.* 2008), suggesting our sampling rate likely provided 1-2 samples per dive, however short shallow dives may be missed. Loggers independently recorded daily maximum dive depth. Sunrise and set times were determined from geolocations and matched to dive records to identify dives as day or night ('suncyle', air-sea toolbox 2.0). Dive bout end criteria were calculated using maximum likelihood estimates from a mixture of 2 random Poisson processes (DiveMove 1.3.4,(Luque & Guinet 2007). For the resolution of this dataset, dive bouts concluded when 25.7 ± 3.1 min (n = 80) transpired without a dive.

For $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis we sampled breast feathers grown in the fall and throat feathers from breeding plumage grown between February and March (Gaston & Jones 1998). Feathers were analysed using a Carbo-Elba elemental analyser interfaced with a Finnigan Delta Plus XP mass-spectrometer (Light Stable Isotope Lab, UCSC). Measurement precision (standard deviation), based on within-run replicates of the laboratory standard (pugel), was 0.13‰ for $\delta^{13}C$ and 0.14‰ for $\delta^{15}N$.

Migration foraging strategies were identified on the basis of individual spatial distributions, diving behaviour, and feather stable isotope values. Standard deviations of diving parameters were included to account for temporal variation. A PCA was run on the correlation matrix of scaled parameters (Lê, Josse & Husson 2008). Eight PCs, accounting for 78% of the variance (Table 2.2), were loaded into a hierarchical clustering algorithm using Ward's method and Euclidean distances to build the tree. Clusters were determined by minimizing inertia gain between potential clusters (Lê *et al.* 2008). *Post-hoc*, cluster composition was tested in relationship to body size (PC1), colony, sex, year, and breeding status at recapture (egg or chick vs. failed). To look at temporal variability in foraging effort within clusters, percent time diving at night was compared to the fraction of the moon illuminated (http://aa.usno.navy.mil/data/docs/MoonFraction.php). Likewise, seasonal changes in percent time diving were compared between strategies and stable isotope values from the two feather tracks were compared to test for seasonal changes.

All data processing and spatial analysis were conducted using MATLAB (The Mathworks, Natick, MA, USA). All statistical tests were done in R 3.0.0 (R Development Core Team, 2013). Significance was set to $p < 0.05$.

2.3 Results

Overall, 84% of birds were resighted each year (St George: 2009 = 80%, 2010 = 65%, 2011 = 85%; St Paul: 2009 = 92%, 2010 = 80%, 2011 = 84%; Bogoslof: 2009 = 93%). Logger recovery rates were 68% on the Pribilofs and 93% on Bogoslof. Logger failures were common, however 74 tracks and 83 dive records of various lengths were obtained, resulting in full datasets for 49 individuals (St Paul = 29, St George = 14, Bogoslof = 6). There was no significant difference in mass between deployment and recapture for all birds that carried a logger (paired-t = -0.584, $p = 0.561$, n = 105), but in 2010, birds retrieved with loggers, attending chicks, were significantly lighter than control birds ($\mathrm{F}_{1,101} = 7.76$, $p = 0.006$; Logger = 1043 ± 88, n = 14; Control = 1068 ± 118, n = 94); this effect was not different by sex or colony.

2.3.1 Body Size

Birds in this study ranged from 829 – 1318 g. Murres from St Paul were significantly larger, had lower aspect ratios and higher wing loading than murres from St George, whereas linear measurements of murres from Bogoslof overlapped with both colonies, but body mass was similar to only St George murres (Table 2.3). Significant sexual size dimorphism was apparent as males were heavier with larger structural size, but wing area did not differ (Table

2.3). Body size PC1 differed both by colony ($F_{1,47}$= 9.97, *p* < 0.001) and sex ($F_{1,47}$= 9.71, *p* = 0.003) and had a significant negative relationship to mean daily dive depth (r^2 = 0.157, *p* = 003), bout depth (r^2 = 0.200, p < 001) and a positive relationship to throat feather $\delta^{15}N$ (r^2 = 0.121, *p* = 0.011) and $\delta^{13}C$ (r^2 = 0.229, p < 0.001); a logistic regression of the location of high residency areas indicated that larger birds were more likely to be found in the Bering Sea than south of the Aleutian Islands (z = -16.18, p < 0.001; Figure 2.2). Sex differences were found in breast feather $\delta^{15}N$ (Males = 16.07 ± 1.12 ‰, Females = 16.74 ± 0.59 ‰, t = 2.92, *p* = 0.005), maximum distance of high residency locations (Males = 184 ± 35, Females = 205 ± 37, t = 2.13, *p* = 0.038), and percent time diving at night (Males = 6.7 ± 3.5%, Females = 10 ± 6.3%, t = -2.46, *p* = 0.0175.

2.3.2 Colony Differences in Winter Distributions

Murres predominantly wintered in the south-eastern Bering Sea and areas south of the Aleutian Islands (Figure 2.3). A few birds travelled away from common wintering areas; three St Paul birds moved into to the western Bering Sea and birds from Bogoslof and St George travelled eastward into the Gulf of Alaska (Figure 3, n = 7). Murres from St George and Bogoslof largely left the Bering Sea from November through January, while 88% of birds from St Paul spent some of this time in the Bering Sea.

2.3.3 Migration Strategies

Overall, 19 variables contributed significantly to the cluster analysis and three migration foraging strategies were identified (Table 2.4). Individuals in the first cluster had low $\delta^{15}N$ values from throat feathers, spent the most time diving, particularly at night, and had longer and more variable dive bouts (Table 2.4), therefore this cluster was termed high frequency divers (Cluster HF). Spatial distributions of Cluster HF were largely outside of the Bering Sea along the southern side of the Aleutian Islands (Figure 2.4a). Individuals in the next cluster had the highest values for throat feather $\delta^{15}N$ and $\delta^{13}C$ (Table 2.4). These birds spent the majority of their time in the Bering Sea (Figure 2.4a). They dove the least at night, diving deeper, mainly during the day, therefore this cluster was termed deep day divers (Cluster DD). The final cluster was characterized by low throat feather δ^{15}N and δ^{13}C, similar to Cluster HF, but birds dove to shallower depths spending less time diving during the day and during dive bouts; these birds spent the least amount of time in the Bering Sea (Figure 2.4a). This cluster was termed shallow night divers (Cluster SN). Maximum dive depth did not contribute to the clusters, but the deepest dive recorded was 207 m.

The three clusters related significantly to year (χ^2_4 = 41.93, p < 0.001) and colony (χ^2_4 = 12.03, p = 0.017), but not sex (χ^2_2 = 1.09, p = 0.579) or post-breeding status (χ^2_2 = 3.77, p = 0.152). Cluster SN contained birds from all three colonies and the majority of birds from 2008/09 (75%) and 2009/10 (81%). Cluster HF was composed of both St Paul and St George birds from only 2010/11, constituting 87% of birds from this year; the others were contained in Cluster DD. Cluster DD was composed entirely of birds from St Paul from all three study years; 31% of birds from St Paul. Body size, represented by PC1, was significantly related to Cluster DD and SN, with larger bodied birds comprising Cluster DD and smaller in Cluster SN (Table 2.4), however body size of birds in Cluster DD was not significantly different than birds from St Paul in other clusters ($F_{1,19}$= 2.21, p = 0.27*)*.

All clusters showed shifts in diving behaviour throughout the non-breeding period, along with shifts in isotopic values (Table 2.4, Figure 2.4b). For all three clusters, depth utilization was at a minimum in November, and then rapidly increased with the deepest dive depths occurring January through March (Figure 2.4b). Depth utilization showed strong monthly cycles in shallow dive depths for Cluster HF (Figure 2.4b). A significant positive relationship was found between percent time diving at night and the fraction of the moon illuminated for Cluster HF ($\mathrm{F}_{1,82}$ = 9.74, p < 0.001), but not for the other two clusters. Overall, time spent diving, was lower for birds in Clusters DD (6.3 ± 2.4%) and SN (6.9 ± 2.1%), whereas birds in Cluster HF increased time spent diving from 8.0 ± 2.3% in the fall (Oct-Nov) to 17.3 ± 4.0% in (Feb-Mar; Figure 2.5). Breast feathers (fall) were not a significant contributor in determining foraging clusters, however throat feathers (late winter) were (Table 2). Seasonal shifts were evident as breast feather $\delta^{15}N$ was significantly higher than throat feather $\delta^{15}N$ for Cluster HF (paired-t = 3.73, *p* = 0.002) and Cluster SN (paired t = 5.71, *p* < 0.001); however, $\delta^{15}N$ was not different for Cluster DD (paired-t = -1.04, *p* = 0.3282). Significant shifts in $\delta^{13}C$ occurred from fall to winter; decreasing for Cluster HF (paired-t = 2.32, *p* = 0.039) and Cluster SN (paired t =2.17, *p* = 0.040), while Cluster DD increased (paired-t = -3.44, *p* = 0.009).

Since isotope values in throat feathers significantly influenced foraging clusters, we analysed these from all birds sampled throughout the study (n = 211 winter trips) in a hierarchical cluster analysis to test association of foraging clusters with isotopic based clusters. Murres clustered into three groups significantly related to colony (χ^2_4 = 52.69, p < 0.001) and year (χ^2_4 = 27.63, *p* < 0.001), but not sex (χ^2_4 = 0.04, *p* = 0.978; Figure 2.6). Birds from St Paul dominated Cluster C (94%), characterized by high $\delta^{15}N$ and $\delta^{13}C$. All of the tracked birds from Cluster DD, were included in this elevated $\delta^{15}N$ group along with two birds from St George and two birds from Cluster HF, suggesting that this solely isotopic based cluster related strongly to the St Paul deep day diving strategy. We then assessed the prevalence of elevated $\delta^{15}N$ (Cluster C) and tested fidelity to this strategy between years (n = 28 birds). The proportion of birds in Cluster C differed by year (2008/09 = 57.7%, 2009/10 = 31.7%, 2010/11 = 46.4%), with 60% of individuals from St Paul using this foraging strategy in at least one year. Individuals were not always faithful to this strategy as 64% of birds changed isotopic clusters. The other isotope clusters did not separate according to foraging cluster (Figure 2.6).

2.4 Discussion

Wintering murres maintained a relatively large degree of spatial structure in both horizontal and vertical distributions relative to their breeding colony, which was associated with body size differences. We found metrics of foraging behaviour, specifically dive depth, late winter isotopic values, and residency in the Bering Sea, correlated significantly with body size and predicted the winter foraging strategies of individual thick-billed murres. A portion of the birds from the colony with the largest body size, St Paul, utilized a unique more residential deep day diving foraging strategy. Nonetheless, these birds were able to switch foraging strategies between years and birds seasonally adjusted foraging behaviour indicating high flexibility in response to environmental changes. Overall, winter foraging strategies appear to relate strongly to body size and annual changes rather than a random assortment of individual foraging strategies.

2.4.1 Logger Effects

Attaching instruments to a small diving flying seabird is challenging because attachment location and buoyancy, size and weight of instruments can all have measurable negative effects (Paredes, Jones & Boness 2005; Vandenabeele et al. 2011; Elliott et al. 2012), but see (Elliott, Davoren & Gaston 2007). In our study the majority of birds returned to breed, mass at recapture was not significantly different than at deployment, however following the winter of 2009/10 birds carrying geolocators (and raising chicks) were lighter than control birds. Birds from 2009/10 clustered with those from 2008/09 indicating that behavioral effects were minimal, were not measurable with our sampling rate or manifested after our study concluded. Both instrumented and control birds from St Paul had elevated $\delta^{15}N$ and $\delta^{13}C$ in throat feathers suggesting that this strategy is a fundamental characteristic of the population rather than an artifact of logger effects.

2.4.2 Body Size and Foraging Strategies

Flying is the most expensive foraging activity for murres (Elliott *et al.* 2013). The higher wing-loading of mures from St Paul, relative to those breeding at St George, may constrain these birds to fly less, thereby limiting distributions, however birds did not travel substantial distances, especially when compared to murres in the North Atlantic (Gaston *et al.* 2011; Fort *et al.* 2013). The resulting longer residence in the Bering Sea, is especially apparent for Cluster DD, but overall larger birds (predominantly from St Paul) spent more time in the Bering Sea. Allometry predicts that divers of larger body size will be able to dive deeper and longer due to increased O_2 stores (Boyd & Croxall 1996; Schreer & Kovacs 1997; Watanuki & Burger 1999; Halsey, Butler et al. 2006) and lower mass-specific metabolic rates (Kleiber, 1961). The larger birds that followed the daytime deep diving strategy (Cluster DD), did not dive to the deepest depths, but did spend the most time at deeper depths. Murres in cluster DD also spent the least amount of time diving overall, suggesting they were able to meet daily energetic needs with fewer dives, similar to cormorants wintering in Greenland (Grémillet *et al.* 2001). These larger birds also spent much less time diving than murres wintering in the western North Atlantic, (Fort *et al.* 2013), further suggesting that the birds following this strategy were able to reduce energy expenditure, despite the higher requirements of their larger bodies (Peters 1983).

Murre fathers accompany their flightless chicks out to sea and related differential distributions between the sexes are known to occur in Alaskan populations during the fall (Hatch *et al.* 2000). Additionally, males tracked from the high Canadian Arctic showed a tendency to remain farther north than females (Gaston *et al.* 2011). Despite these sex specific behaviours and the sexual size dimorphism of our study populations, we did not find differences in foraging strategies related to sex. We did find differences in breast feather $\delta^{15}N$, percent time diving at night and maximum distance, but these differences did not drive the cluster analysis. It appears that though sex differences in behaviour occurred, other factors associated with the colony of origin and body size might be more important in regulating winter distributions in the study colonies.

Differences in body size of birds from our three study colonies could have evolved due to summer foraging conditions, similar to blue-eyed shags (*Phalacrocorax verrucosus*) breeding in the Kerguelen archipelago where there are colony based differences in diets, foraging habitats and distances to foraging areas (Cook *et al.* 2013). Together, the long term differences in summer diets of murres at the Pribilofs (Sinclair *et al.* 2008; Renner *et al.* 2012) and recent tracking data (Harding et al. 2013), suggest that St Paul birds are constrained to shelf habitats and may have specialized to feed locally on benthic prey. Additionally, although murres from St George and Bogoslof both forage over the basin, St George birds must commute longer distances that may favour smaller body size whereas Bogoslof birds can access deep waters adjacent to the colony (Harding et al. 2013). Regardless of the mechanistic explanation of body size differences, these colony based size differences and foraging strategies appear to carry over to influence migratory strategies.

2.4.3 Diets, Foraging, and Distributions

Elevated δ^{15}N values can result from higher trophic level foraging, spatial changes in the baseline of the food web, and fasting. In the south-eastern Bering Sea there is a strong baseline gradient of δ^{15}N with lower values occurring the basin and higher on the shelf (Jones et al 2014), likewise baselines appear to be higher in the Bering Sea basin versus the Gulf of Alaska (Pomerleau *et al.* 2014), so a large part of the isotope differences could be due to spatial differences. Unlike the other clusters δ^{15}N increased from fall to winter for Cluster DD, while spatial distributions did not appear to substantially change. This difference, suggests that these birds could be consuming a more fish and squid-based diet, in the later winter than during the fall. Thick-billed murres wintering off the south-west coast of Greenland also appear to increase reliance on fish during the late winter (Linnebjerg *et al.* 2013).

In addition to forage fishes and squid, thick-billed murres consume euphausiids and amphipods, both during breeding and the winter months (Falk & Durinck 1996; Renner *et al.* 2012). Both Cluster SN and Cluster HF birds exhibited foraging behaviours, such as shallow night diving, that are associated with foraging on diel vertically migrating prey when these prey are close to the surface (Benoit-Bird *et al.* 2011; Benoit-Bird *et al.* 2013). Murres using these strategies wintered predominately in oceanic waters south of the Aleutians and along the continental slope. This off-shore area is influenced by the Alaska Stream and characterized by an oceanic zooplankton community, including the euphausiid, *Euphausia pacifica* (Coyle 2005). This oceanic euphausiid may be a predictable prey source, as they are omnivorous, can produce multiple broods in a year (Pinchuk & Hopcroft 2006), have continuous growth rates (Pinchuk & Hopcroft 2007) and showed little annual variation in abundance over 5 years in the Gulf of Alaska (Pinchuk, Coyle & Hopcroft 2008). However, despite this evidence of a predictable prey source, foraging behaviour changed in 2010/11.

The winter of 2010/11 was one of the strongest La Niña years on record, following closely after the central Pacific El Niño conditions of 2009/10 (Hu *et al.* 2014). Concomitantly, zooplankton biomass, survival estimates for age-1 pollock, and catch rates of juvenile pink salmon in the Gulf of Alaska were all low (Orsi *et al.* 2013; Zador (ed.), 2013). During this winter murres increased their foraging effort; notably through an approximately 2-fold increase in time spent foraging, particularly in the latter half of the winter, longer bout durations, and foraging associated with moonlight availability. Murres from Bogoslof were not tracked in 2010/11, however the high degree of spatial overlap between St George and Bogoslof birds in 2008/09, suggests that birds from Bogoslof likely responded similarly.

Within each cluster murres exhibited the capacity to adjust foraging behaviour in response to environmental changes. On the daily and monthly scales, foraging strategies related to preferences for foraging during the day or night. Like murres wintering in the North Atlantic, dives shoaled in the late fall and then deepened in the mid-winter, probably in response to seasonally driven shifts in prey availability within the water column (Fort *et al.* 2013). The HF cluster birds dove more with increasing moonlight, a behaviour observed in common murres, who displayed increased diving efficiency with moonlight versus starlight (Regular et al. 2011). Within the foraging clusters, standard deviations indicate a substantial amount of individual variation in behaviour. Spatially thick-billed murres wintering in the northwest Atlantic showed diversity in core wintering areas (McFarlane Tranquilla *et al.* 2014), similarly in this study individual tracks were dispersive though the wintering area.

Combined, this temporal plasticity in foraging behaviour and diversity of behaviours between individuals shows an impressive capacity to adjust behaviours in response to local conditions.

2.5 Conclusions

Constrained to relatively small winter ranges thick-billed murres exhibited remarkable seasonal flexibility in diving behaviour likely in relationship to seasonal changes in prey distributions. Broadly, foraging strategies were linked to body size differences associated with the three breeding colonies and partitioned with respect to annual differences, presumably in relationship to shifts in prey distributions. Our results suggest a more complex regulation of overwinter survival of birds originating from the colony on St Paul. As this colony is in a continued state of decline, the behavioural flexibility exhibited by murres, constrained by body size, may not be enough to adapt to changing conditions in the Bering Sea.

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Table 2.1 Loadings Matrix for PCA analysis of body size components. Only PC1 had an eigen value greater than 1. Percentage of variance incorporated by each PC is given.

	PC1 51.1%	PC2 23.0%	PC3 19.9%	PC4 6.0%
Culmen (mm)	0.589	-0.443	-0.029	0.675
Head+bill (mm)	0.626	-0.269	-0.095	-0.726
Tarsus (mm)	0.373	0.499	0.782	0.035
Wing cord (mm)	0.350	0.695	-0.616	0.125

Table 2.2 Loading matrix of principle components of winter foraging strategies. Only first eight components with eigenvalues greater than 1 are shown as these were used in the hierarchical cluster analysis. Percentage of variance incorporated by each PC is show given.

	PC1 22.8%	PC2 14.8%	PC3 11.3%	PC4 9.7%	PC5 6.0%	PC6 5.1%	PC7 4.7%	PC8 4.0%
Diet								
Throat δ^{15}N	-0.143	0.299	-0.221	0.001	-0.201	0.177	0.084	-0.130
Throat δ^{13}C	-0.052	0.338	-0.173	0.075	-0.116	0.270	-0.124	-0.036
Breast δ^{15}N	0.026	0.142	-0.221	0.273	-0.168	-0.283	0.135	0.156
Breast δ^{13}C	0.135	0.080	0.169	-0.051	-0.175	0.040	0.488	-0.164
Spatial								
% HR in	-0.096	0.280	-0.181	0.145	0.324	0.095	0.243	-0.057
convex hull	-0.029	-0.008	0.333	-0.104	0.037	-0.037	0.193	-0.408
Max.	0.014	0.068	-0.286	0.193	0.459	0.173	0.040	0.234
Temporal								
date of max.	-0.006	-0.096	0.304	-0.006	0.244	0.005	0.42	0.018
date at max.	-0.099	-0.173	-0.016	-0.074	0.175	-0.077	0.303	0.566
Dive								
max. dive	0.147	0.072	0.342	0.164	0.324	-0.045	-0.181	0.085
% 24hr day	0.263	0.177	-0.168	-0.088	0.159	-0.132	0.226	-0.144
% 24hr night	0.297	-0.188	-0.114	-0.122	-0.053	0.022	-0.117	-0.048
day mean	0.045	0.408	-0.014	-0.061	0.220	-0.173	-0.089	-0.137
night mean	-0.066	0.211	0.243	-0.305	-0.117	-0.31	-0.128	0.138
SD day depth	0.309	0.101	0.189	0.084	-0.048	0.162	-0.132	0.241
SD night	0.026	0.312	0.309	0.088	-0.128	0.154	-0.017	0.200
SD % 24hr	0.319	0.146	-0.147	-0.105	-0.050	-0.078	0.133	-0.010
SD % 24hr	0.326	-0.104	-0.152	-0.073	-0.134	0.076	-0.173	0.050
Dive Bouts								
bout duration	0.249	-0.095	-0.110	-0.355	0.263	0.108	0.043	-0.172
bout depth	-0.128	0.378	0.041	-0.216	0.121	-0.264	-0.116	0.015
% bout diving	0.326	0.136	-0.111	-0.056	-0.171	-0.193	0.152	0.141
post bout	-0.116	0.075	0.009	-0.043	-0.268	0.434	0.286	0.053
# of bouts /	0.038	-0.088	-0.03	0.485	0.057	-0.181	-0.063	-0.367
SD bout	0.316	0.003	-0.003	-0.163	0.144	0.277	-0.066	-0.061
SD % bout	0.254	-0.030	-0.029	0.212	-0.189	-0.311	0.179	0.099
SD # bouts /	0.189	-0.011	0.163	0.405	-0.015	0.067	0.018	-0.081
SD bout	0.222	0.203	0.278	0.128	0.010	0.204	-0.081	0.102

Table 3. Morphometric comparison of thick-billed murres (*Uria lomvia algae*) from colonies in the south-eastern Bering Sea. Bold sexual size dimorphism (SSD) values indicates sexes are significantly different (SSD = (male-female)/female x 100). Three-way colony comparisons are results of t-tests. Sample sizes are indicated in parentheses. Means ± SD.

	St Paul (P)			St George (G)			Bogoslof (B)			Colony Comparison
	♂ (39)	♀ (36)	SDD	♂ (53)	♀ (29)	SDD	♂ (17)	♀ (15)	SDD	
Body Mass (g)	1184 ± 101	1106 ± 96	**7.65**	998 ± 61	960 ± 65	**4.27**	1038 ± 73	1003 ± 54	**3.39**	P > B = G
Culmen (mm)	42.8 ± 2.6	41.6 ± 2.0	**2.88**	41.1 ± 2.1	39.8 ± 2.0	**3.27**	42.1 ± 2.1	40.1 ± 1.8	**5.00**	P > G, P = B, G = B
Head + bill (mm)	117.1 ± 3.2	113.7 ± 2.4	**3.09**	112.0 ± 3.3	109.9 ± 2.9	**1.91**	114.9 ± 2.7	111.1 ± 3.4	**3.42**	P > G, P = B, G = B
Tarsus (mm)	40.7 ± 1.8	39.0 ± 1.9	**4.35**	38.9 ± 1.7	37.8 ± 1.3	**2.91**	40.1 ± 1.4	38.9 ± 2.5	**3.08**	P > G, P = B, G = B
Wing (mm)	227 ± 6	226 ± 5	0.44	223 ± 6	222 ± 4	0.45	223 ± 7	224 ± 5	-0.45	P > G, P = B, G = B
Wing Area (cm^2)*	719.4 ± 26.2	708.1 ± 50.0	1.60	679.5 ± 34.9	647.6 ± 45.8	4.93	-	-	-	P > G
Aspect Ratio*	9.12 ± 0.26	9.23 ± 0.24	-1.91	9.70 ± 0.30	9.50 ± 0.30	2.12	-	-	-	P < G
Wing Loading (Nm^2)*	163.6 ± 7.4	165.2 ± 14.7	-0.96	147.1 ± 8.1	140.7 ± 6.0	4.57	-	-	-	P > G

*St Paul ♂ (7), ♀ (8); St George ♂ (12), ♀ (5).

Table 2.4 Behavioural parameters (± SD) used to determine wintering foraging clusters of thick-billed murres. The importance of each variable in determining clusters was tested via an F test and variables that significantly contribute to each cluster ($p < 0.05$) are shown in bold. η^2 is presented as an index of the proportion of variance explained by each of the factors, bold η^2 indicate a significant contribution to the overall model. Sex, colony, year, and body size PC1 were not included as variables in the cluster analysis.

Table 2.4

	η^2	High Frequency	Deep Day	Shallow Night
n		13	9	27
Sex (♂ / ♀)	-	6 / 7	6 / 3	13 / 14
Colony (P / G / B)	-	7 / 6 / 0	9 / 0 / 0	13 / 8 / 6
Year (2008 / 2009 / 2010)	-	0 / 0 / 13	3 / 4 / 2	9 / 18 / 0
Body Size PC1	-	-0.02 ± 1.52	**1.20 ± 0.94**	**-0.42 ± 0.89**
Diet				
Throat δ^{15}N (‰)	**0.41**	14.82 ± 1.52	**17.05 ± 0.78**	**14.78 ± 0.89**
Throat δ^{13}C (‰)	**0.41**	-18.63 ± 0.31	**-17.89 ± 0.31**	**-18.96 ±**
Breast δ^{15}N (‰)	0.10	16.71 ± 1.04	16.69 ± 0.65	**16.09 ± 0.96**
Breast δ^{13}C (‰)	0.12	**-18.11 ± 0.48**	-18.60 ± 0.60	-18.60 ±
Spatial				
% HR in Bering Sea	**0.28**	27 ± 50	**82 ± 32**	**23 ± 35**
convex hull area (Mm^2)	0.00	43.2 ± 45.8	52.3 ± 74.7	50.4 ± 62.3
Max. distance (km)	0.03	189 ± 27	207 ± 31	190 ± 43
Temporal				
date of maximum depth	0.08	Jan 20 ± 26	Jan 13 ± 44	Jan 31 ± 29
date at maximum distance	**0.21**	**Nov 18 ± 42**	Nov 11 ± 42	**Jan 1 ± 45**
Dive				
maximum dive depth (m)	0.13	**161.8 ± 22.7**	143.6 ± 14.2	152.3 ± 13.7
% 24 hr day diving	**0.37**	**10.2 ± 3.6**	7.4 ± 2.5	**5.7 ± 2.0**
day mean depth (m)	**0.35**	50.5 ± 6.0	**54.1 ± 3.6**	**44.1 ± 6.3**
SD % 24 hr day diving	**0.56**	**7.1 ± 1.2**	4.6 ± 2.1	**3.6 ± 1.1**
SD day depth (m)	**0.65**	**20.5 ± 2.8**	**11.1 ± 1.9**	**13.1 ± 2.8**
% 24 hr night diving	**0.31**	**13.0 ± 6.8**	**4.5 ± 2.3**	7.9 ± 3.7
night mean depth (m)	0.02	32.3 ± 4,1	33.6 ± 7.3	31.4 ± 6.5
SD % 24 hr night diving	**0.47**	**15.1 ± 6.7**	**4.1 ± 1.8**	**7.2 ± 3.5**
SD night depth (m)	**0.16**	**13.9 ± 3.2**	12.9 ± 2.9	**11.2 ± 2.6**
Dive Bouts				
bout duration (min)	**0.13**	**80.5 ± 23.3**	65.4 ± 10.3	67.9 ± 12.3
bout depth (m)	**0.39**	40.0 ± 4.1	**47.0 ± 4.3**	**39.6 ± 5.1**
% of bout diving	**0.64**	**59.1 ± 3.7**	41.4 ± 11.8	**39.0 ± 5.6**
post bout interval (min)	0.12	333 ± 224	622 ± 651	310 ± 194
# of bouts / day	0.02	4.0 ± 0.5	3.9 ± 0.5	4.1 ± 0.7
SD bout duration (min)	**0.42**	**105.4 ± 26.5**	68.0 ± 13.6	**68.1 ± 18.0**
SD bout depth	**0.39**	**21.4 ± 3.6**	16.8 ± 1.7	**16.9 ± 2.3**
SD % of bout diving	**0.31**	**30.1 ± 4.3**	**20.9 ± 5.2**	23.9 ± 5.3
SD # bouts / day	**0.21**	**1.72 ± 0.35**	**1.34 ± 0.26**	1.48 ± 0.24

Figure 2.1 A thick-billed murre in flight at St Paul Island, Alaska (photo: Dan Cushing).

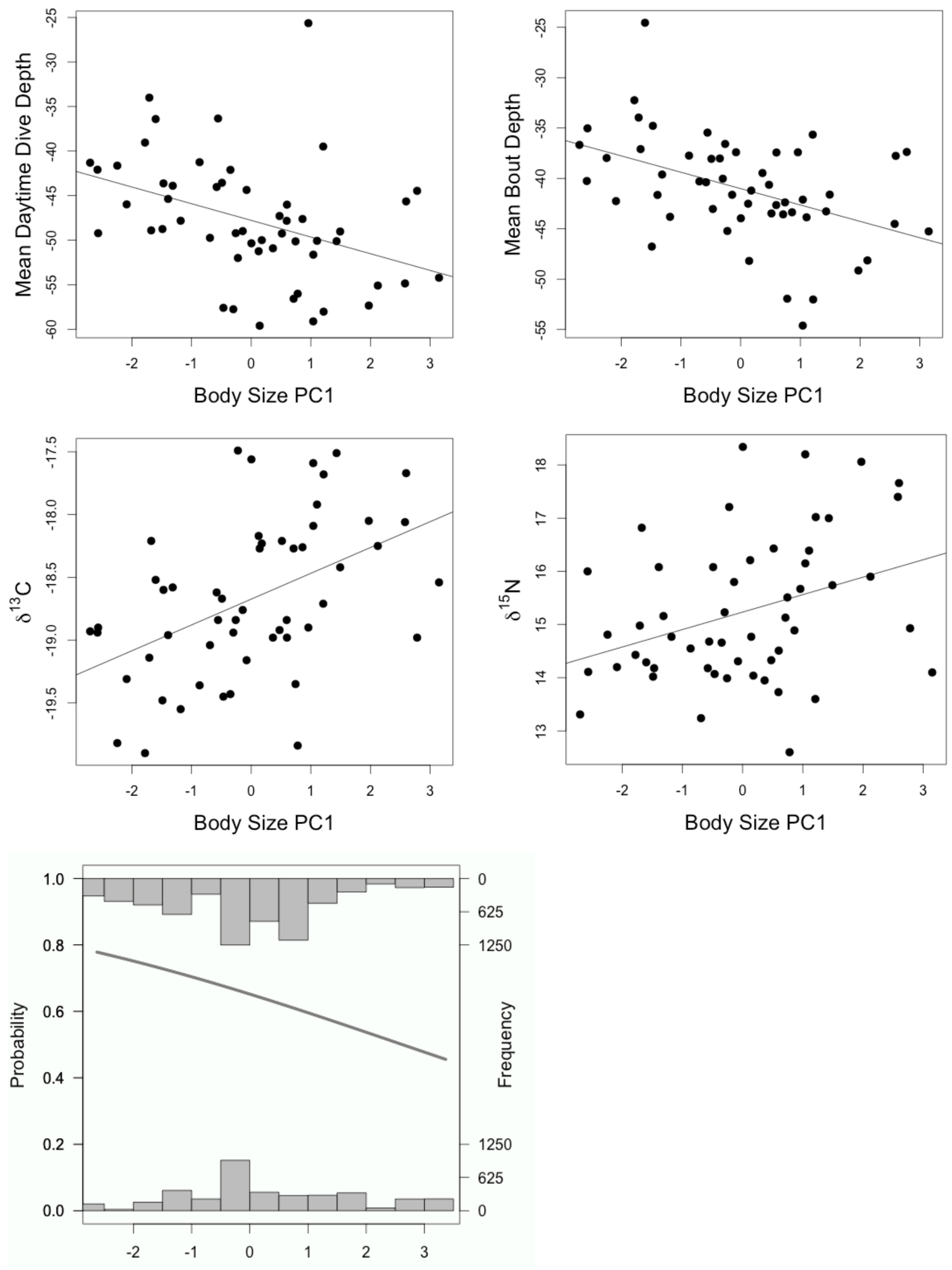

Figure 2.2 Relationship between body size (PC1 of culmen, head+bill, tarsus and wing length) and parameters describing winter foraging strategies a) mean daytime diving depth, b) mean bout depth, c) throat feather δ^{13}C (‰), d) throat feather δ^{15}N (‰), and e) logistic regression of locations in the Bering Sea (0) versus locations in the North Pacific south of the Aleutians (1).

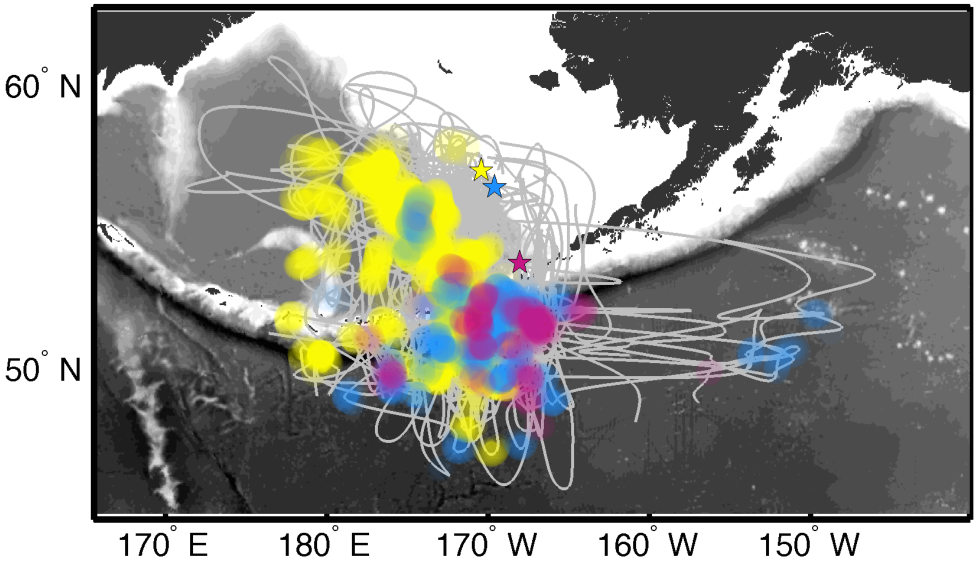

Figure 2.3 Winter distributions of thick-billed murres in the Bering Sea and North Pacific. High residency locations of birds from St Paul (yellow, n = 40), St George (blue, n = 23) and Bogoslof (pink, n = 11), are shown from October thru February with complete tracks in grey, the radius of the circles is scaled to the search area of residency time (60 km). Stars of corresponding colours label the colonies.

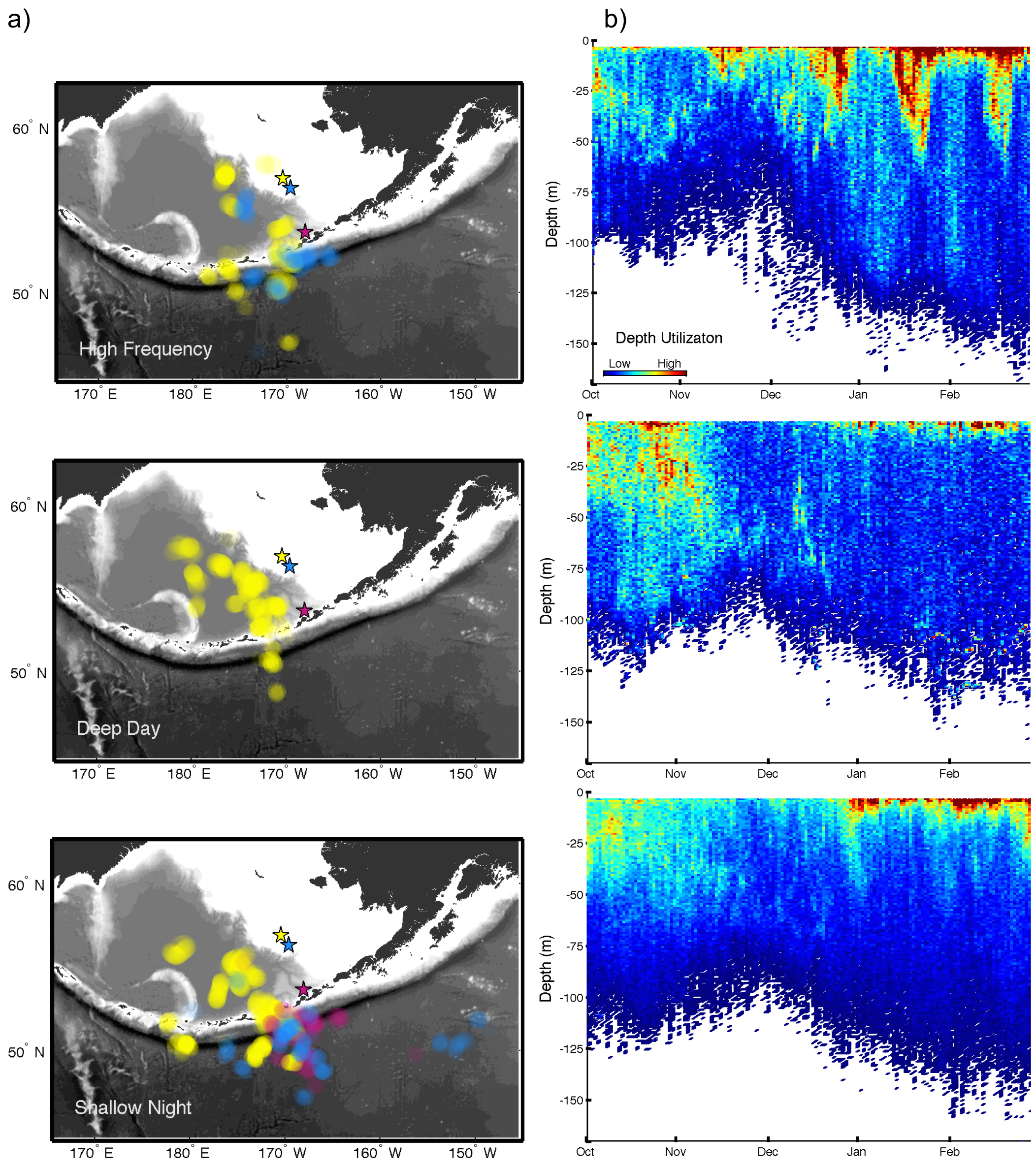

Figure 2.4 Winter distributions and depth utilization of thick-billed murres, October thru February, by foraging cluster with a) spatial extent, (high residency locations; St Paul [yellow], St George [blue] and Bogoslof [pink]) and b) depth utilization of the three foraging clusters. Depth utilization is normalized by the number of birds tracked daily.

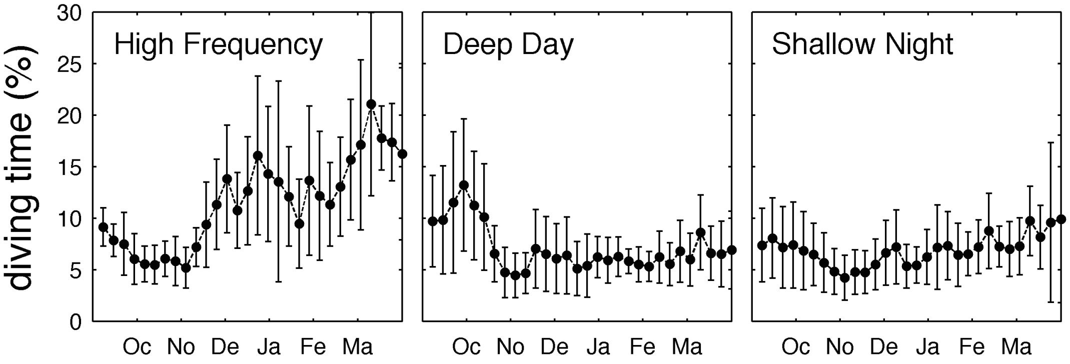

Figure 2.5 Weekly proportion of time (24 hrs) spent diving ± standard deviation for thick-billed murres from the three winter foraging clusters.

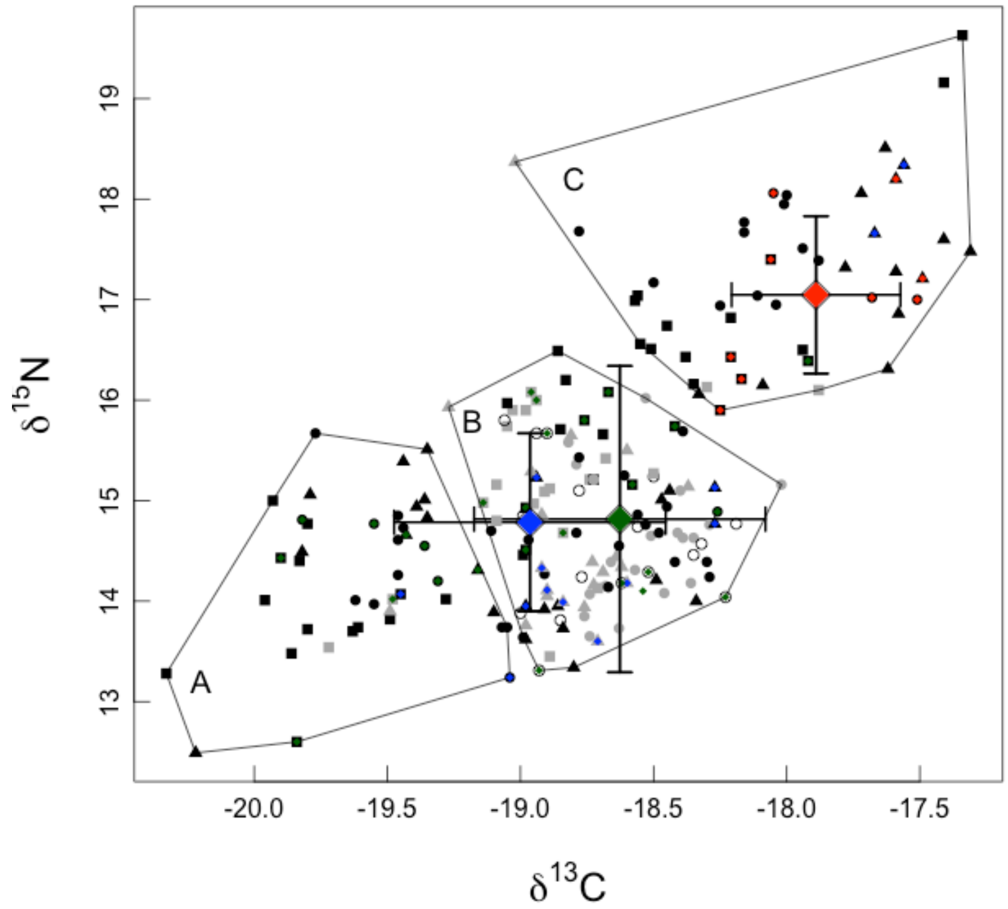

Figure 2.6 Isotopic Clusters A, B, & C from throat feathers (n = 211), overlaid with isotopic values from foraging clusters HF, DD, & SN (cross plot ± SD). Sampling years (summer) are indicated by circles (2009), squares (2010), and triangles (2011), while colonies are shown by black (St Paul), grey (St George), and white (Bogoslof). Points corresponding to individuals included in the foraging cluster analysis are overlaid with a circle, coloured according to cluster (HF = blue, DD = red, and SN = green).

CHAPTER THREE

Factors influencing annual variation of winter migrations of black-legged kittiwakes (*Rissa tridactyla*) in the sub-arctic North Pacific.

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Abstract

Background: Understanding the importance of factors that affect animal movements is critical for delineating energetic bottlenecks within population dynamics. Intrinsic factors (e.g. sex, colony, adult quality, prior experience) may impact only subsets of a population, whereas extrinsic factors are broader and change overtime (e.g. prey availability, weather and competition). Here, we attempt to understand the interaction of these factors on the winter migrations of a surface-feeding seabird in the North Pacific, Between 2008 and 2011, we tracked 99 black-legged kittiwakes (*Rissa tridactyla*) breeding at St. Paul and St. George in the Pribilof Islands, Alaska using geolocation loggers. We tested for colony and sex differences in winter distributions, and individual differences in spatial fidelity (n = 17) over two consecutive winters. Then, we linked tracking data to associated environmental conditions as proxies of prey availability (e.g. sea surface temperature, mesoscale eddies, chlorophyll a, and wind) to understand their influence on space use at an ocean basin scale.

Results: Black-legged kittiwakes from both Pribilof Islands primarily wintered in pelagic sub-arctic waters, however, distributions spanned seven ecoregions of the North Pacific. Although there was a high degree of similarity in the areas used by birds from the two closely situated colonies, females were more dispersive than males. Birds tracked over consecutive years showed higher fidelity to wintering areas than occurred randomly. Annual changes were apparent, as distributions were further north in 2009/10 than 2008/09 or 2010/11. The winter of 2009/10 was anomalous compared to the other seasons because kittiwakes remained in the Bering Sea during October and November, which corresponded to lower sea surface temperatures.

Conclusions: Although intrinsic factors appear to influence the movement patterns, our results suggest that under current conditions black-legged kittiwakes have a high capacity to alter winter migrations relative to local environmental conditions

3.1 Introduction

Where and how animals move across a landscape is driven by a myriad of factors than can simplistically be divided into intrinsic or extrinsic factors (Holyoak *et al.* 2008; Nathan *et al.* 2008). Intrinsic determinates of animal movements are inherently linked to physiological and life-history traits of species (e.g. reproductive status, past experience, physiological needs and capacity, navigation abilities), while extrinsic influences occur as the result of an animal's interactions with either other animals or the environment (e.g. competition, predation, habitat quality and prey availability). Disentangling multiple factors and understanding how they can interact is inherently difficult, such that in many cases measuring relevant influencing factors on movement is challenging or impossible (Tremblay *et al.* 2014). In some cases, longitudinal studies have been able to delineate apart these relationships (Delgado *et al.* 2010; Martin *et al.* 2012; Plante, Colchero & Calmé 2013; Daunt *et al.* 2014), while the majority of animal movement studies focus on particular factors (reviewed in Holyoak *et al.* 2008). Understanding how these drivers interact to influence animal movements is paramount to understand population trends and spatial capacity, particularly in highly mobile species that have strong intrinsic constraints (e.g. Martin *et al.* 2012).

For seabirds, intrinsic constraints may weaken during the non-breeding period when the constraint of central-place foraging is relaxed. However, intrinsic factors do appear to continue to play a role, as age, sex, and breeding colony are known to influence seabird migrations (Rayner *et al.* 2011; Thiebot *et al.* 2013b; Riotte-Lambert & Weimerskirch 2013; Weimerskirch *et al.* 2013; Perez *et al.* 2014). Moreover, these differences provide a mechanism for portions of populations to be differentially affected by spatially distributed extrinsic effects such as prey availability. For wintering seabirds, understanding the importance of intrinsic factors can help us to understand how populations may be impacted by environmental variation such as storms or low prey availability. In some species, individuals choose migratory destinations at an ocean basin scale, presumably without knowledge of current local conditions (Shaffer *et al.* 2006;

McKnight *et al.* 2013). These life-history characteristics are adaptive as oceanic prey resources are predictable at large and meso-scales (Weimerskirch 2007), however climate change will lead to shifts in ecosystems at scales that will likely influence the large-scale predictability of resources (Polovina *et al.* 2011; Hazen *et al.* 2012; Pinsky *et al.* 2013).

There is undoubtedly an influence of past experience and learning that shapes some portion of migratory paths, wintering areas, and prey preferences in long-lived seabirds (Phillips *et al.* 2005; Croxall 2005; Guilford *et al.* 2011; Gutowsky *et al.* 2013; Yamamoto *et al.* 2014; McFarlane Tranquilla *et al.* 2014). However over a lifetime, individuals may exhibit flexibility in their foraging choices as oceanic habitats are dynamic and conditions change from one season to the next (Dias *et al.* 2011, Baylis *et al.* 2014). For example, black-legged kittiwakes show spatial and dietary variability in foraging habitats both within and between colonies, and throughout the annual cycle (Bogdanova *et al.* 2011; McKnight *et al.* 2011; Paredes *et al.* 2012; 2014), however individuals are also known to display marked fidelity to locations and foraging in concert with tidal cycles (Irons 1998).

In the present study, we compare the winter ecology of two black-legged kittiwake populations from the Pribilof Islands, Alaska. First, we examined intrinsic effects resulting in differences related to sex and individual spatial fidelity. Then, we link winter distributions in three consecutive years to associated environmental conditions to understand how habitat conditions influence space use at an ocean basin scale in each population

3.2 Methods

To study black-legged kittiwake (hereafter kittiwake) wintering ecology geolocation loggers (Mk13/Mk9/Mk19, British Antarctic Survey, Cambridge UK) were deployed on 164 kittiwakes during July of 2008-2010 at two colonies in the Pribilof Islands, Alaska (St. Paul Island, 57.17N 169.60W, n = 87 and St. George Island, 56.60N 169.60W, n = 77).

Over the three study winters, 17 birds carried loggers for 2 winters. All birds were captured off active nests using a noose pole or foot snare supplemented with a CO_2 powered net gun (Super Talon Animal Catcher, Advanced Weapons Technology, California) at recapture. At deployment and recapture birds were weighed and measured, nest contents were recorded and blood samples for DNA sexing were taken (Fridolfsson & Ellegren 1999). Data processing, spatial analyses and statistical tests were conducted using MATLAB (v2014a, The Mathworks, Natick, MA) and R v3.1.1 (R Development Core Team, 2014). Significance was set to $p<0.05$.

3.2.1 Geolocation processing

Geolocations were estimated from September 1 thru May 30 with the colony as a fixed start and end location using the 'TripEstimation' package in R to implement a Bayesian model that incorporates a land mask, flight speed, and locations from light levels using the 'template-fit' method into the prior distribution (Ekstrom 2004; Sumner, Wotherspoon & Hindell 2009; Thiebot & Pinaud 2010). We used a mean speed of 33 km hr^{-1} (Hatch 2010), however tag derived activity data (time spent dry, Orben *et al. in press*) indicated that birds only spent 15 ± 9% of each 24 hr period flying, therefore, as a conservative estimate we chose to assume that birds spent 33% (two standard deviations from the mean) of their time in flight, restricting an individual's range over 12 hours, on average, to 130km. Thus a mean speed of 10.89 km hr^{-1} and speed variance equal to half this were entered into the model to parameterize a log-normal distribution. The most probable track was then obtained using a state-space model with a Kalman filter with six Markov Chain Monte Carlo (MCMC) simulations of 1000 iterations each, after a 500-iteration burn in period. Tracks were visually compared and found to be similar to locations calculated following the smoothing and filtering methods of Phillips et al. (2004), with errors of 186 ± 114 km. Subsequently, all analysis were constrained to October-February to avoid greater errors inherent in locations estimated around the equinox period.

3.2.2 Distributions

How birds share space over large scales relates to the size of individual ranges, the distribution of these ranges, and the density of birds. Individual range size was calculated as the number of 45 km x 45 km grid squares occupied by the last chain of the MCMC estimation (1000 iterative tracks). To assess how variable each group (colony, sex, year) was in the areas they used as well as a quantitative assessment of sample sizes, the cumulative number of grid cells occupied was calculated with the addition of each track randomly selected for 10,000 iterations (Hindell *et al.* 2003). Groups with less variability or higher amounts of area shared between individuals, have shallower curves than groups with high individual variability in area use (Hindell *et al.* 2003). To assess the amount of shared area, an index of similarity was calculated as the ratio of the number of shared grid cells (45 km) occupied by the last chain of the MCMC estimation to the total grid cells used by both groups, where identical groups would be equal to 1. To test these indexes against what similarity might randomly occur, birds were randomly assigned to groups and the index of similarity was calculated 10,000 times with the same number of individuals in each group as the original dataset. *P*-values were calculated as the percentage of iterations that resulted in an similarity index smaller than observed (Breed *et al.* 2006; Orben *et al.* 2014). Finally, to assess relative density of birds and overall distributions, densities were calculated from the last chain of the MCMC estimation for each individual over a 5 x 5 km grid (to aid in visualization). This method incorporates the uncertainty in the location estimates and negates the reasons to use a method such as a kernel density estimate (Sumner *et al.* 2009; Ratcliffe *et al.* 2014).

3.2.3 Individual Spatial Fidelity

Area fidelity can occur at varying spatial scales. To identify the spatial scales in which kittiwakes showed fidelity to wintering areas we calculated a monthly index of similarity, a measure of the number of shared grid cells, between all estimated locations for repeat trips from individual birds (n = 17) at a series of grid sizes ranging from 10 - 400 km.

Then to quantify a random measure of overlap we calculated the percentage of overlap between 59 random pairs, from consecutive years and between individuals of the same sex and colony.

3.2.4 Annual difference in large marine ecosystem use

To better understand annual changes in large-scale distributions and habitat use of Pribilof kittiwakes we assessed the use of oceanic biogeographical provinces of the North Pacific (Longhurst 2010). For each province, at the scale of 45 km grid cells, we calculated the percentage of the biogeographic province occupied by kittiwakes (again incorporating location error by using the last chain of the MCMC estimates) (# grid cells occupied / total grid cells in province), average density of occupied grid cells, and the proportion of the overall bird distribution in each province (# grid cells occupied inside region / total # grid cells occupied). We also assessed how individuals used these regions by calculating the number of ecoregions used by individual birds and ecoregion use by sex.

3.2.5 Annual habitat conditions

Habitat variables were extracted along the best-fit tracks at a 1° grid scale. Sea surface temperatures (SST) were extracted as an eight-day blended product from data hosted by NOAA’s Environmental Research Division (http://oceanwatch. pfeg.noaa.gov/thredds/catalog.html). Bathymetry was extracted from the ETOPO1 dataset (Smith 1997), and bathymetric slope calculated. As eddies are known to condense prey for surface foraging predators including kittiwakes (Bost *et al.* 2009; Paredes *et al.* 2014), we extracted sea surface height (SSH) and surface currents used to calculate eddy kinetic energy (EKE) were extracted from the Navy Layered Ocean Model (1/32°, http://www7320.nrlssc.navy.mil/global_nlom/) using the nctoolbox (https://github.com/nctoolbox/). We also calculated the distance to eddy edge using mesoscale eddy trajectories (Chelton, Schlax & Samelson 2011). Distance to productive seamounts or knolls, defined as those within 1500m of the sea surface, was calculated for each bird location, as these features are also known to enhance biological productivity (Yesson *et al.* 2011; Bouchet *et al.* 2014). Monthly composites of MODIS-Aqua chlorophyll a, spanning 2007-2012, were constructed using DINEOF 3.0 to interpolate regions where clouds obscured satellite data. Locations were matched to monthly composites, with the first week of each month assigned to the previous month. Wind speed was extracted from the RNCEP Reanalysis II data sets for surface values (Kanamitsu *et al.* 2002; Kemp *et al.* 2011).

3.2.6 Residency Time

We used residency time to understand the influence of habitat variability on individual movements. Residency time can be defined as the cumulative amount of time an individual animal spends within a circle of constant radius over a period of time (Barraquand & Benhamou 2011). In our case, we chose a radius of 45 km, as this is rougly equivelant to the mean daily distance kittiwakes traveled over the whole wintering period (Sept-May), and a time constraint of 1 month to avoid false positives if individuals crossed over their own path months later on the return trip. High residency locations, indicating periods of intense search effort, were then chosen as the upper quartile of each individuals residency times (Torres *et al.* 2011).

3.2.7 Habitat selection models

Linear-mixed models were used to relate residency time to oceanic habitat characteristics for each winter migration in the top four biogeographic regions frequented by kittiwakes. Variance inflation factors were calculated, but all were <3, so all explanatory variables were retained (Zuur *et al.* 2009). To meet the conditions of normality for linear models residency time and chlorophyll a were log transformed and distance to eddy and bathymetric slope were square-root transformed. Best-fit models for each ecosystem were constructed using a reductive approach and identified from Akaike Information Criterion (AIC) scores based on restricted maximum likelihood estimates (Zuur *et al.* 2009). Marginal R^2 values were used to the variance explained by the fixed effects and conditional R^2 values, the combined fixed and random effects (Xu 2003; Nakagawa & Schielzeth 2012).

3.3. Results

Loggers were recovered with a 78% recovery rate (St Paul n = 66, St. George n = 63). Seven loggers failed during data recovery and 13 loggers failed before recapture. A total of 113 complete winter migration trips were recorded from 99 kittiwakes.

3.3.1 Wintering Distributions

Kittiwakes from the Pribilof Islands wintered predominantly in the deep oceanic waters of the central and western subarctic North Pacific all three years (Figure 3.1). Area use of individual birds did not significantly differ between years, sexes, or colonies (1,557,000 ± 358,000 km^2, $p > 0.05$; Table 3.1). As a group, females covered more area than males (Figure 3.2). There was no difference in the size of cumulative area covered by birds from the two study colonies up to 40 individuals (n = 40, St Paul: 12,328,000, St George: 12,235,000), however at that point the lines diverge suggesting more low level variation in area use occurs among St. Paul birds (n = 53, St Paul: 13,241,000, St George: 12,235,000; Figure 3.2). The amount of overlap between groups was not different than random for colonies (72% overlap, $p = 0.113$) and marginally different between sexes (70% overlap, $p = 0.06$). However yearly combinations all showed less overlap between the observed distributions than randomly grouped tracks (2008/09 vs. 2009/10, 63% overlap, $p < 0.001$; 2009/10 vs. 2010/11, 56% overlap, $p < 0.001$; 2008/09 vs. 2010/11, 61% overlap, $p = 0.001$).

3.3.2 Scale of Individual Spatial Fidelity

Birds that were tracked for two winter migrations showed a tendency to return to the same regions and, for example, had on average 9% overlapping grid squares for 100 x 100 km grid squares. During the peak winter migration period (October - February) birds showed site fidelity at all scales, as the amount of shared grid cells was higher for individual bird repeat trips than for randomly paired tracks (Figure 3.3). Some individuals repeated very unique migrations routes, for instance, one bird traveled to the northern Bering Sea in the fall and then foraged along the Emperor Sea Mounts before heading back to the vicinity of the Pribilof Islands (Figure 3.3).

3.3.3 Annual difference in large marine ecosystem use

Pribilof kittiwakes used seven biogeographical regions of the North Pacific during their winter migrations (Table 3.2). On average 89.3 ± 4.4% of the area kittiwakes used occurred in four of these, Epicontinental Seas (Bering Sea and Sea of Okhotsk – with little use of the Sea of Okhotsk), Western Subarctic Gyre (PSAW), Eastern Subarctic Gyre (PSAE), and the Polar Front (NPPF). Though geographically close to the Pribilof Islands, kittiwakes hardly used the Alaska Coastal Downwelling region (< 3% of bird distributions). In all three years, kittiwakes used almost the entire area of the PSAW, while distributions only occupied a portion of all other biogeographical regions (Table 3.2). The highest densities of tracked kittiwakes also occurred in the PSAW (Table 3.2). Annual differences were apparent in regards to when kittiwakes occupied each of the main ecoregions; specifically in October and November of 2009/10 there was a notable increase in the continued use of the Bering Sea (Figure 3.4). In both 2008/09 and 2009/10, Dec-Feb, over 30% of bird locations were in the NPPF, whereas in 2010/11 the majority of locations during these months were father north in the PSAW (Figure 3.4).

On average individual kittiwakes used 4.9 ± 1 ecoregions and this did not differ between sex, or year, however birds from St Paul used fewer ecoregions (4.6 ± 1) than birds from St George (5.3 ± 0.08; Figure 3.5). Only birds from St. Paul used areas of the northwestern Bering Sea (Figure 3.6). A small number of birds, all females (n = 5), traveled east to the California Current System.

3.3.4 Habitat conditions and selection

Throughout the winter, kittiwakes experienced a broad range of habitat conditions. Sea surface temperatures were on average 6.3 ± 2.6˚C (daily individual range: -1.7˚C –

14.8˚C), chlorophyll a 1.32 ± 4.08 mg m^{-3} (0.25 mg m^{-3}– 62.67 mg m^{-3}), EKE 63.9 ± 45.4 $cm^2\ s^{-2}$ (5.8 $cm^2\ s^{-2}$ – 437.2 $cm^2\ s^{-2}$), SSH -8.9 ± 8.3cm (-26.3cm – 20.2cm). Annual differences in habitat conditions were dwarfed by differences between ecoregions (Table 3.3). In October of 2009, sea surface temperatures in habitat encompassed by kittiwake ranges inside the Bering Sea were lower than in the other two study years (Table 3.4). Habitat variables were not a good predictor of residency in each ecoregion, with the best models only explaining <15% of the variation (Table 3.5).

3.4 Discussion

Kittiwakes from the Pribilof Islands underwent extensive pelagic migrations to diverse subarctic biogeographical regions in North Pacific. Both sex and past experience appear to influence where individuals wintered. However, individuals exhibited a large amount of flexibility and annual variation in distributions were larger than those observed between sexes or colonies.

3.4.1 Interplay of intrinsic influences

The reasons for colony specific wintering areas are not always clear. In some cases these colony differences may arise as the result of differing local conditions, altering the phenology of migrations, or simply be the result of a range expansion from geographically separated colonies as birds are still tied to these at an annual or biennial time scale (Rayner *et al.* 2011; Frederiksen *et al.* 2011; Thiebot *et al.* 2012; McFarlane Tranquilla *et al.* 2013; Ratcliffe *et al.* 2014). Alternatively there are examples where birds from different colonies winter in the same region (Shaffer *et al.* 2006; González-Solís *et al.* 2007; McFarlane Tranquilla *et al.* 2013). The Pribilof colonies are only 70 km apart and the timing of breeding is highly synchronous (Byrd *et al.* 2008); thus it is not surprising that distributions of kittiwakes are similar. Yet, they are almost entirely distinct from areas frequented by other Alaskan kittiwakes such as in Prince William Sound (McKnight *et al.* 2011). Thus, there is likely a large amount of colony-specific variability in wintering areas across the North Pacific basin similar to that seen in kittiwakes in the North Atlantic (Frederiksen *et al.* 2011).

Sex differences in distributions are often linked to differences in timing relative to nest defense or breeding roles (Thiebot *et al.* 2013a; 2014; Hedd *et al.* 2014), intersexual competition (Gonzáles-Solís et al. 2000) and niche partitioning in sexually dimorphic seabirds (Shaffer et al. 2001; Weimerskirch *et al.* 2014). There is ample evidence of sexual differences in behavior of kittiwakes during the breeding season (Roberts & Hatch 1993; Jodice *et al.* 2006; Paredes *et al.* 2012), and that breeding outcome or elevated stress levels may carry over to affect the non-breeding distributions of one but not the other sex (Bogdanova *et al.* 2011; Schultner *et al.* 2014). We found an effect of sex on wintering distributions; though area use was largely similar females appear to be more dispersive and only individuals traveling to the California Current System. Although sexual size dimorphism is slight in kittiwakes, the smaller bodies of females and associated lower flight costs may facilitate the more dispersed distribution of females that we observed (Orben *et al.* 2014), however there were no clear differences in wind regimes that might further support this conclusion.

Fidelity during periods when individuals are constrained by central-place foraging, for instance in breeding seals and seabirds, appears to be relatively high in some instances (Call *et al.* 2008; Sumner *et al.* 2009; Baylis *et al.* 2011; Patrick *et al.* 2014). Much less is known about spatial fidelity when predators undergo migrations, often at the scale of ocean basins. Both flexibility and fidelity have been observed in migrating shearwaters, suggesting that individuals are able to explore and utilize multiple suitable wintering areas during a life-time (Dias *et al.* 2011; Yamamoto *et al.* 2014). Like migrating Atlantic puffins (Guilford *et al.* 2011), black-legged kittiwakes displayed a tendency to return to areas that they frequented the year before. Both puffins and kittiwakes show characteristics of a dispersive migration, as routes often move gradually away from the breeding colony, rather than traveling to a distinct destination (Figure 3.7). However for kittiwakes, the amount of fidelity individuals showed was relatively small compared to the fidelity quantified for Atlantic puffins (Guilford *et al.* 2011). Kittiwakes are generalist predators that can only access the top 1 m of the water column, and they are much better fliers than puffins, and perhaps it is the combination of these life-history traits that limits the amount of spatial fidelity that is advantageous, as prey resources can be patchy in pelagic environments (Weimerskirch 2007). Like puffins, it is unlikely that kittiwakes socially learn migration routes as there is both individual fidelity and a high amount of variability in migratory paths within the population (Figure 3.7), instead it seems more likely that individuals rely on past experience and spatial memory to inform travel paths. Our dataset is dominated by comparisons to 2009/10 when population level distributions were distinctly different, these contrasts likely lead to less individual fidelity than may be observed under similar conditions and more research is needed to understand how individuals respond to the range of oceanographic conditions they may encounter.

3.4.2 Oceanographic habitats and annual conditions

During all three of our study years, kittiwakes from the Pribilof Island colonies used the entire Western Subarctic Gyre (PSAW). The PSAW has higher primary productivity than the Gulf of Alaska (Saito *et al.* 2010), more intense eddy activity (Bograd *et al.* 1997), and supports a greater diversity of marine predators (Springer *et al.* 1999); potentially providing a more predictable winter habitat than the other ecoregions. Annual changes in kittiwake distributions occurred at a much higher magnitude, measured by the amount of overlap, than differences between intrinsic groups (colony and sex), and this reflects the contrasting conditions that occurred during the three-study years.

In 2009/10, El Niño Modoki conditions occurred (central Pacific El Niño), characterized by a weakened Aleutian Low which is strengthened during a typical El Niño winter (Weng, Behera & Yamagata 2008). During this winter the western sub-arctic experienced anomalously high sea surface temperatures, while the central subarctic had anomalously cool sea surface temperatures (Ratnam *et al.* 2011). The distribution of wintering kittiwakes in 2009/10 had a restricted longitudinal range and birds stayed much longer in the Bering Sea, potentially facilitated by colder sea surface temperatures (see Figure 4 and Table 4), than during 2010/11, classified as strong La Niña year or 2008/09 classified as neutral conditions (National Weather Service Climate Prediction Center). This shift to more northerly distributions was also noted for wintering kittiwakes from a colony in Prince William Sound (McKnight *et al.* 2011). This similar response, suggests that during this year conditions suitable for wintering kittiwakes shifted northward across the North Pacific. The occurrence of El Niño Modoki is thought to be induced by anthropogenic climate warming and the frequency of its occurrence has increased since the late 1970s (Ashok *et al.* 2007; Yeh *et al.* 2009), suggesting that its impacts on wintering North Pacific kittiwakes will increase in the future.

The winter of 2010/11, switched to one of strong La Niña conditions (Hu *et al.* 2014). In the Gulf of Alaska, zooplankton biomass, survival estimates for age-1 pollock, and catch rates of juvenile pink salmon were all low (Orsi *et al.* 2013; Zador (ed.), 2013). Wintering murres increased their foraging effort; notably through an approximately 2-fold increase in time spent foraging, particularly in the latter half of the winter, longer bout durations, and foraging associated with moonlight availability (Chapter 2). In 2010/11, kittiwakes spent much less time in the Polar Front region, however birds that did venture there did not experience conditions that were notably different from either of the other years, except for a marked decrease in EKE. Eddies and surface currents are known to condense and facilitate prey capture for surface foraging seabirds (Paredes *et al.* 2014; Scales *et al.* 2014), thus is may be that this difference is linked to lower use. The more northerly distributions, relative to 2008/09, both in 2009/10, when birds used the Bering Sea more, and in 2010/11 when kittiwake range in the subarctic was decreased, could be closer to what kittiwake wintering distributions may be like in the future. Climate change is predicted to shift the North Pacific Transition Zone farther north, causing the subarctic zone south of the Aleutians to shrink in size (Polovina *et al.* 2011). This shift in habitats is likely to be challenging for Hawaiian albatrosses as it moves preferred foraging areas farther from breeding colonies (Kappes *et al.* 2010; Hazen *et al.* 2012). For kittiwakes, these changes will shrink the area of available wintering habitat, initially to a greater extent than what will open up to the north (due to the presence of land). This could then lead to density dependent regulation of kittiwake populations, particularly if winter day length limits how far north kittiwakes can remain during the winter (Ballard *et al.* 2010), but see (Grémillet *et al.* 2005).

In the North Pacific, Russian stocks of pink salmon (*Oncorhynchus gorbuscha*) currently follow a predictable alternation between large and small cohorts and numbers of the large cohort have increased exponentially in the last decade (Springer & van Vliet 2014). During large cohort years, prey availability is suppressed and black-legged kittiwakes respond though later hatch dates, lower laying success, smaller clutch size, and lower overall reproductive productivity –these effects appear to diminish in colonies in the eastern Gulf of Alaska (Springer & van Vliet 2014). There is likely to be a large amount of spatial overlap between Eastern Kamchatka pink salmon stocks and wintering kittiwakes, presumably kittiwakes originating from colonies from roughly the Pribilofs westward (Springer & van Vliet 2014). In 2010/11, the competitive influence of pink salmon was likely amplified by additional poor wintering conditions, leading to extremely low breeding productivity at both Pribilof Islands (Klostermann, Drummond & Scopel 2011; Thomson & Drummond 2011). In general, bimodal increased competition in wintering regions, during the late winter and early spring, could be helping to facilitate kittiwake responses during the breeding season. Finally, though kittiwakes are flexible in their wintering habitats and movements, the combination of increased competition due to increasing abundances of pink salmon in response to a warming subarctic and the predicted shrinkage of the subarctic do to climate change may combine to change the wintering dynamics for black-legged kittiwakes in the North Pacific.

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Table 3.1 Yearly summary of winter space use for black-legged kittiwakes from the Pribilof Islands (Oct – Feb, 2008-2011).

	2008/09	**2009/10**	**2010/11**
# of birds St Paul [male / female]	19 [7/12]	26 [12/14]	15 [3/12]
# of birds St George [male / female]	17 [7/10]	18 [10/8]	18 [6/12]
Daily distance traveled (km)*	35.4 ± 3.5	32.1 ± 2.3	34.5 ± 2.8
Max distance from colony (km)	2,573 ± 682	2,508 ± 625	2,601 ± 798
Individual Area use (# 45 x 45 km cells)	811 ± 226	726 ± 120	781 ± 172
Residency (days)	2.17 ± 0.35	2.45 ± 0.45	2.09 ± 0.37

*year: F = 14.25, $p < 0.001$

Table 3.2 Annual occupancy of marine biogeographical ecoregions by migrating black-legged kittiwakes from the Pribilof Islands (October thru February). Marine biogeographical ecoregions are those defined by Longhurst (2010).

	Average bird occupancy (# birds / $45km^2$)			**% Ecoregion occupied**			**% bird distribution**		
	2008/09	**2009/10**	**2010/11**	**2008/09**	**2009/10**	**2010/11**	**2008/09**	**2009/10**	**2010/11**
Epicontinental Seas:	3.9 ± 3.0	6.6 ± 5.3	4.9 ± 3.0	38.8	56.2	62.9	16.1	24.4	25.6
Bering Sea	4.3 ± 3.2	7.4 ± 5.5	5.6 ± 3.0	55.1	77.2	81.7	13.2	19.4	19.3
Sea of Okhotsk	1.9 ± 1.0	3.4 ± 2.2	2.6 ± 1.3	14.9	29.0	35.5	2.8	5.7	6.6
Subarctic Gyre (West)	8.5 ± 4.3	9.2 ± 5.2	7.6 ± 4.0	99.7	98.5	99.7	22.0	22.7	21.5
Subarctic Gyre (East)	6.6 ± 5.0	5.3 ± 5.6	5.4 ± 4.4	58.0	39.2	79.9	16.5	11.6	22.2
Alaska Coastal Downwelling	4.1 ± 2.4	1.4 ± 1.0	2.2 ± 1.4	20.5	12.1	34.5	1.4	0.8	2.2
Polar Front	4.5 ± 4.0	4.9 ± 4.2	2.3 ± 1.8	53.4	53.2	25.6	34.0	35.3	15.9
California Current	1.1 ± 0.3	0	1.5 ± 0.7	16.8	0	22.9	3.7	0	4.9
Kuroshio Current	3.3 ± 2.4	1.9 ± 1.1	1.1 ± 0.3	21.1	12.4	22.6	5.5	3.4	5.8

Table 3.3 Habitat characteristics of wintering locations for black-legged kittiwakes from October thru February in 2008/09, 2009/10, and 2010/11. Yearly means ± SD are calculated from individual bird means in each ecoregion.

	2008/09	**2009/10**	**2010/11**
Bering Sea			
Residency Time (d)	2.1 ± 1.0	2.8 ± 1.0	2.0 ± 0.8
SST (˚C)	4.65 ± 2.2	5.23 ± 0.94	5.87 ± 1.85
Distance to Seamount (km)	455 ± 285	242 ± 133	362 ± 230
SSH (cm)	-9.12 ± 3.78	-8.34 ± 2.06	-10.96 ± 3.35
EKE (cm^2 s^{-2})	70.4 ± 35.9	39.1 ± 15.9	54.6 ± 27.2
Distance to Eddy Edge (km)	143 ± 71	131 ± 48	169 ± 84
Chl a (mg m^{-3})	1.40 ± 0.99	1.68 ± 2.21	2.25 ± 2.79
Wind speed (m s^{-1})	9.17 ± 1.39	8.94 ± 0.70	8.49 ± 1.48
Subarctic Gyre (West)			
Residency Time (d)	2.0 ± 0.7	2.2 ± 0.9	2.0 ± 0.5
SST (˚C)	7.75 ± 1.95	5.61 ± 1.78	5.33 ± 1.17
Distance to Seamount (km)	392 ± 130	357 ± 118	348 ± 114
SSH (cm)	-17.99 ± 3.28	-14.83 ± 2.15	-15.49 ± 3.0
EKE (cm^2 s^{-2})	49.4 ± 19.1	58.9 ± 18.2	59.0 ± 28.4
Distance to Eddy (km)	127 ± 29	124 ± 21	114 ± 11
Chl a (mg m^{-3})	0.63 ± 0.22	0.55 ± 0.13	0.66 ± 0.32
Wind speed (m s^{-1})	8.85 ± 1.52	9.64 ± 1.25	9.46 ± 0.90
Subarctic Gyre (East)			
Residency Time (d)	2.02 ± 0.65	2.06 ± 0.81	1.83 ± 0.73
SST (˚C)	7.82 ± 1.34	6.33 ± 1.54	6.58 ± 1.22
Distance to Seamount (km)	766 ± 221	770 ± 228	744 ± 192
SSH (cm)	-14.78 ± 5.39	-10.79 ± 3.48	-13.55 ± 2.89
EKE (cm^2 s^{-2})	38.6 ± 12.6	58.9 ± 76.0	44.3 ± 34.4
Distance to Eddy (km)	152 ± 35	163 ± 40	147 ± 37
Chl a (mg m^{-3})	0.64 ± 0.28	0.48 ± 0.20	0.50 ± 0.21
Wind speed (m s^{-1})	9.31 ± 1.70	9.49 ± 2.13	9.77 ± 2.07
Polar Front			
Residency Time (d)	2.13 ± 0.55	2.0 ± 0.48	1.90 ± 1.28
SST (˚C)	9.67 ± 1.22	8.50 ± 1.43	8.83 ± 1.68
Distance to Seamount (km)	119 ± 390	122 ± 324	131 ± 325
SSH (cm)	2.78 ± 6.72	5.30 ± 7.91	-0.89 ± 4.72
EKE (cm^2 s^{-2})	75.2 ± 23.8	67.7 ± 18.9	55.3 ± 32.5
Distance to Eddy (km)	119 ± 21	122 ± 22	131 ± 42
Chl a (mg m^{-3})	0.35 ± 0.05	0.32 ± 0.05	0.32 ± 0.06
Wind speed (m s^{-1})	9.76 ± 0.95	9.91 ± 0.84	9.19 ± 2.61

Table 3.4 Habitat characteristics of wintering locations for black-legged kittiwakes in the Bering Sea during from October (2008, 2009, 2010). Means ± SD are calculated from individual bird means.

	2008	**2009**	**2010**
Residency Time (d)	2.3 ± 1.0	2.9 ± 1.1	2.3 ± 1.3
SST (˚C)	6.2 ± 0.8	5.8 ± 0.9	7.1 ± 1.4
Distance to Seamount (km)	474 ± 241	284 ± 144	438 ± 329
SSH (cm)	-7.9 ± 2.45	-7.3 ± 2.56	-9.6 ± 3.54
EKE (cm^2 s^{-2})	66.8 ± 34.7	42.5 ± 27.1	48.3 ± 23.1
Distance to Eddy (km)	154 ± 62	139 ± 76	206 ± 121
Chl a (mg m^{-3})	1.61 ± 1.30	1.88 ± 2.63	3.0 ± 4.44
Wind speed (m s^{-1})	8.72 ± 1.33	8.71 ± 1.02	7.79 ± 0.99

Table 3.5 Summary statistics for linear mixed models of environmental influences on residency time for black-legged kittiwake in each ecoregion. All models include a temporal correlation term (corCAR1(form = ~date|id)). Summary statistics of each full model (SST+depth+d2ed+slopetrn+eketrn+ssh+d2hill+wind+ chla) are presented first, followed by the best-fit model for each ecoregion. Akaike Information Criterion (AIC) were used to identify the best-fit model and marginal R^2 (R^2 (m)) and conditional R^2 (R^2 (c)) are presented. Abbreviations for the environmental variables used in the table are: sea-surface temperature (SST), distance to mesoscale eddy center (d2ed), sea-surface height (SSH), eddy kinetic energy (EKE), distance to productive seamounts and knolls (d2hill), monthly chlorophyll a (chla), bathymetric slope (slope) and bathymetry (bathy).

	df	**AIC**	**ΔAIC**	**R^2 (*m*)**	**R^2 (*c*)**
Bering Sea					
Full model	13	5504	7	0.005	0.149
dist2ed+eketrn+d2hill+wind	8	5497	-	0.004	0.150
Subarctic Gyre (West)					
Full model	13	13051	8	0.019	0.098
SST+dist2ed+wind	7	13043	-	0.019	0.098
Subarctic Gyre (East)					
Full model	13	6129	10	0.028	0.071
SST+d2hill	6	6119	-	0.028	0.071
Polar Front					
Full model	13	8765	7	0.005	0.078
dist2ed+d2hill+chla	7	8757	-	0.004	0.076

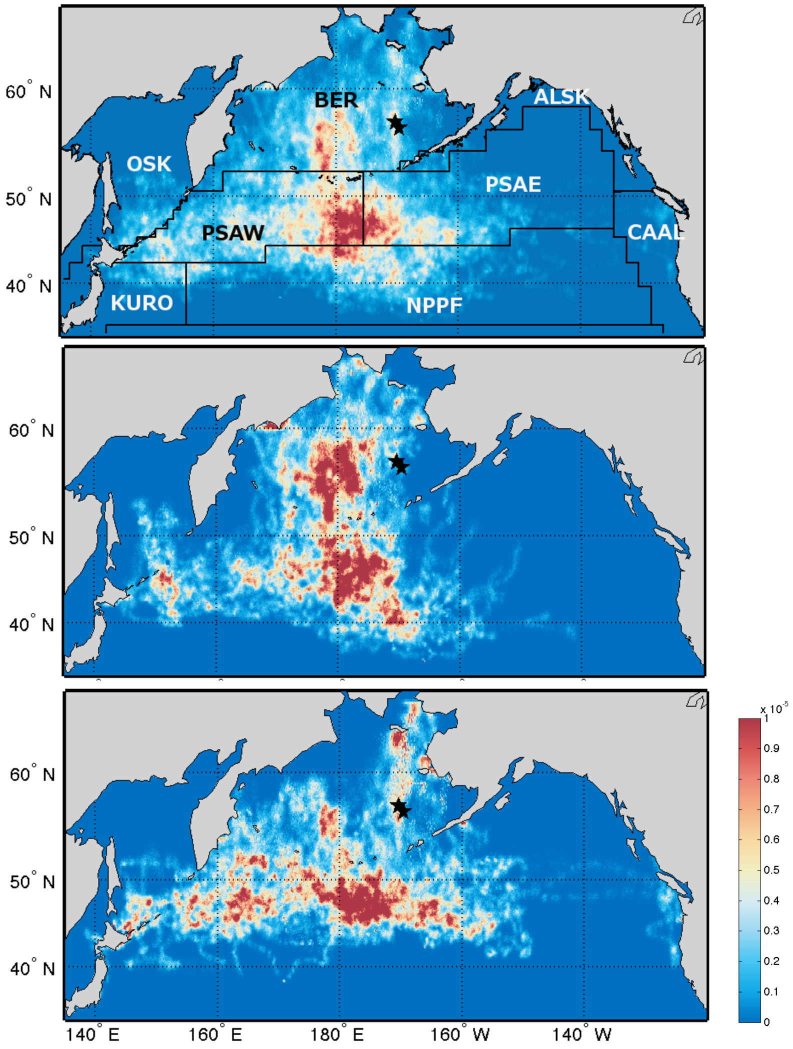

Figure 3.1 Annual distribution of black-legged kittiwakes (*Rissa tridactyla*) from the Pribilof Islands during their central wintering period (October thru February). In a) 2008/09 (n = 38), b) 2009/10 (n = 44), and c) 2010/11 (n = 33). The boundaries of the ecoregions are shown following Longhurst, 2010, with the Bering Sea [BER] and Sea of Oskhosk [OSK] separated into two subregions. Remaining abbreviations are as follows: ALSK = Alaska Coastal Downwelling Zone, CAAL= California Current, KURO = Kuroshio Current, NPPF = North Pacific Polar Front, PSAE = Eastern Subarctic Gyre, PSAW = Western Subarctic Gyre.

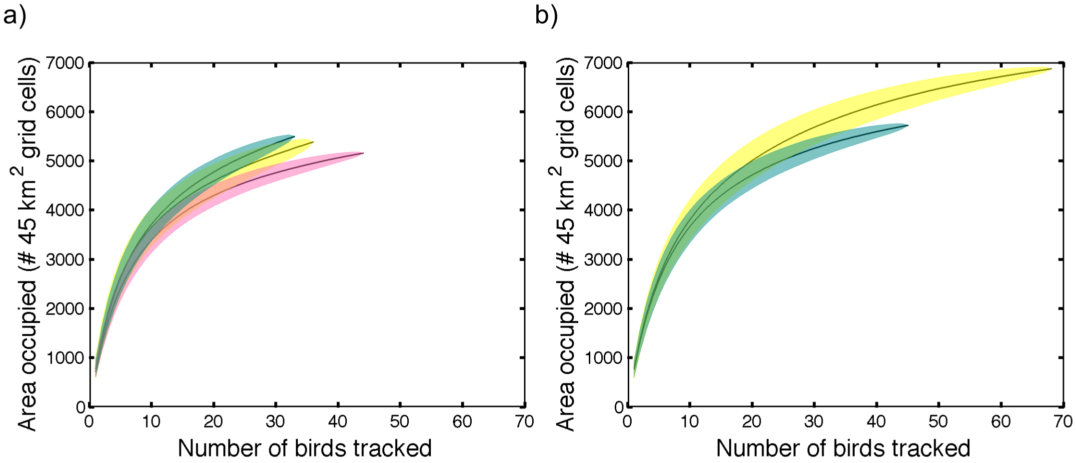

Figure 3.2 Area occupied, in terms of number of 45km^2 grid cells, by migrating black-legged kittiwakes from October thru February. By a) year where 2008/09 = yellow, 2009/10 = pink, and 2010/11 = green and b) sex (female = yellow, male = green).

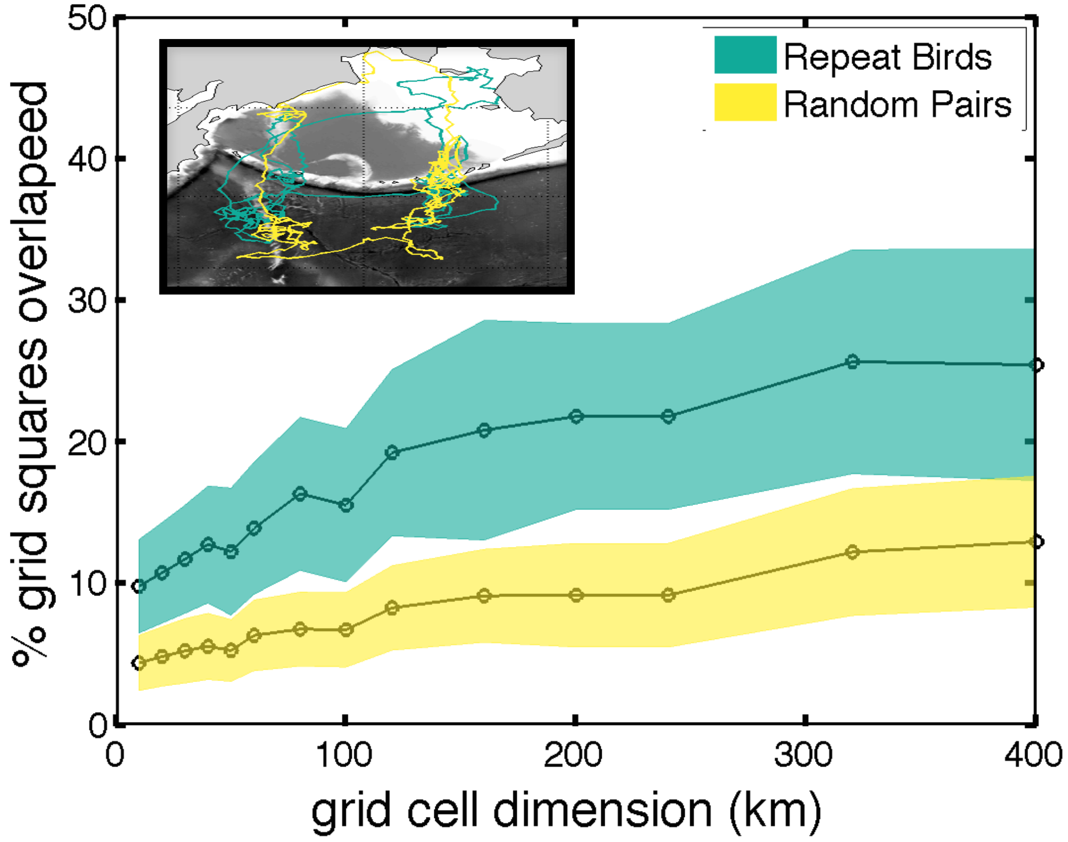

Figure 3.3 Higher site fidelity in repeat migrations of black-legged kittiwakes (n = 17) during Oct-Feb than randomly paired tracks (n = 59), of the same colony and sex. Inset is an example track from a kittiwake breeding at St Paul, yellow is 2009/10 and green is 2010/11.

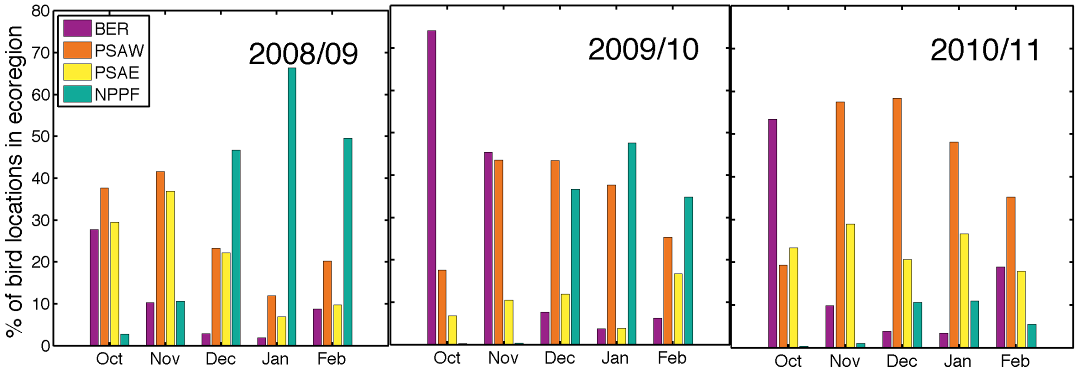

Figure 3.4 Percentage of monthly bird locations in the four North Pacific ecoregions frequented most by wintering black-legged kittiwakes from the Pribilof Islands in 2008-2011, where NPPF = North Pacific Polar Front (green), PSAE = Eastern Subarctic Gyre (yellow), PSAW = Western Subarctic Gyre (orange), and BER = Bering Sea (purple).

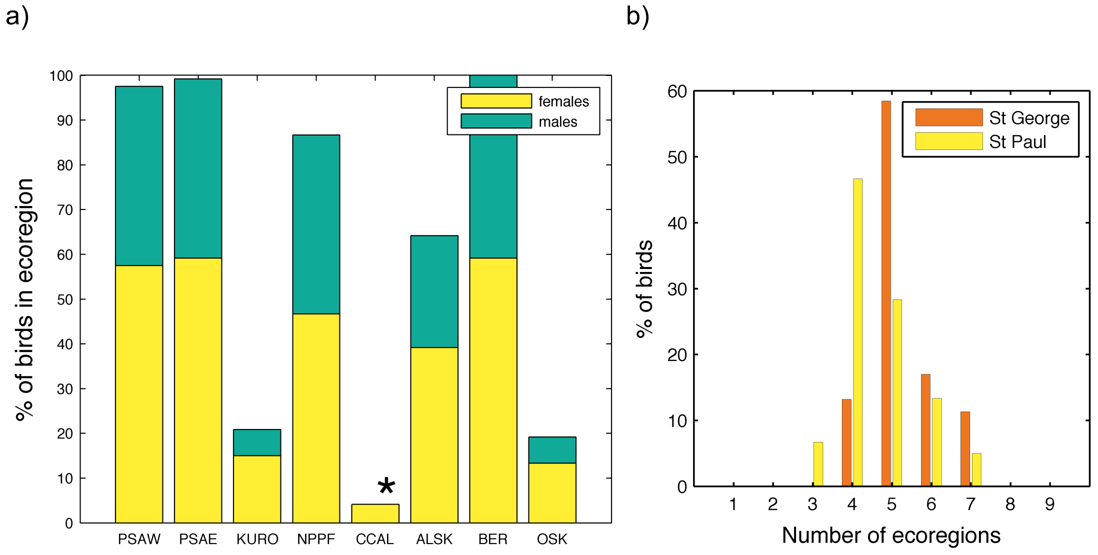

Figure 3.5. Ecoregion use of blacklegged kittiwakes. a) Percent of black-legged kittiwakes using each ecoregion, proportion of males (green) and females (bottom, yellow) is shown. The California Current (CCAL), denoted by an asterisk, was visited exclusively by female kittiwakes. Counts of males and females in each ecoregion are not significantly different than the overall sample (Chi squared, *p* > 0.05). b) Number of ecoregions used by individual birds from St Paul (yellow) and St George (orange).

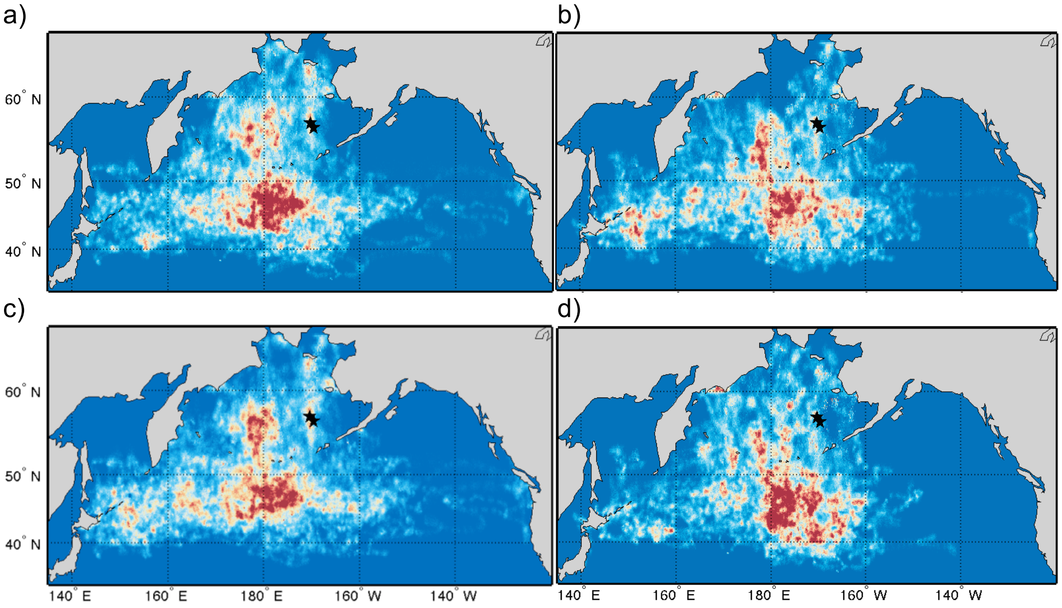

Figure 3.6 Distributions of black-legged kittiwakes (*Rissa tridactyla*) from the Pribilof Islands during their central wintering period (October thru February) for colonies and sexes. From a) St. Paul (n = 60), b) St. George (n = 53), c) females (n = 76) and d) males (n = 56).

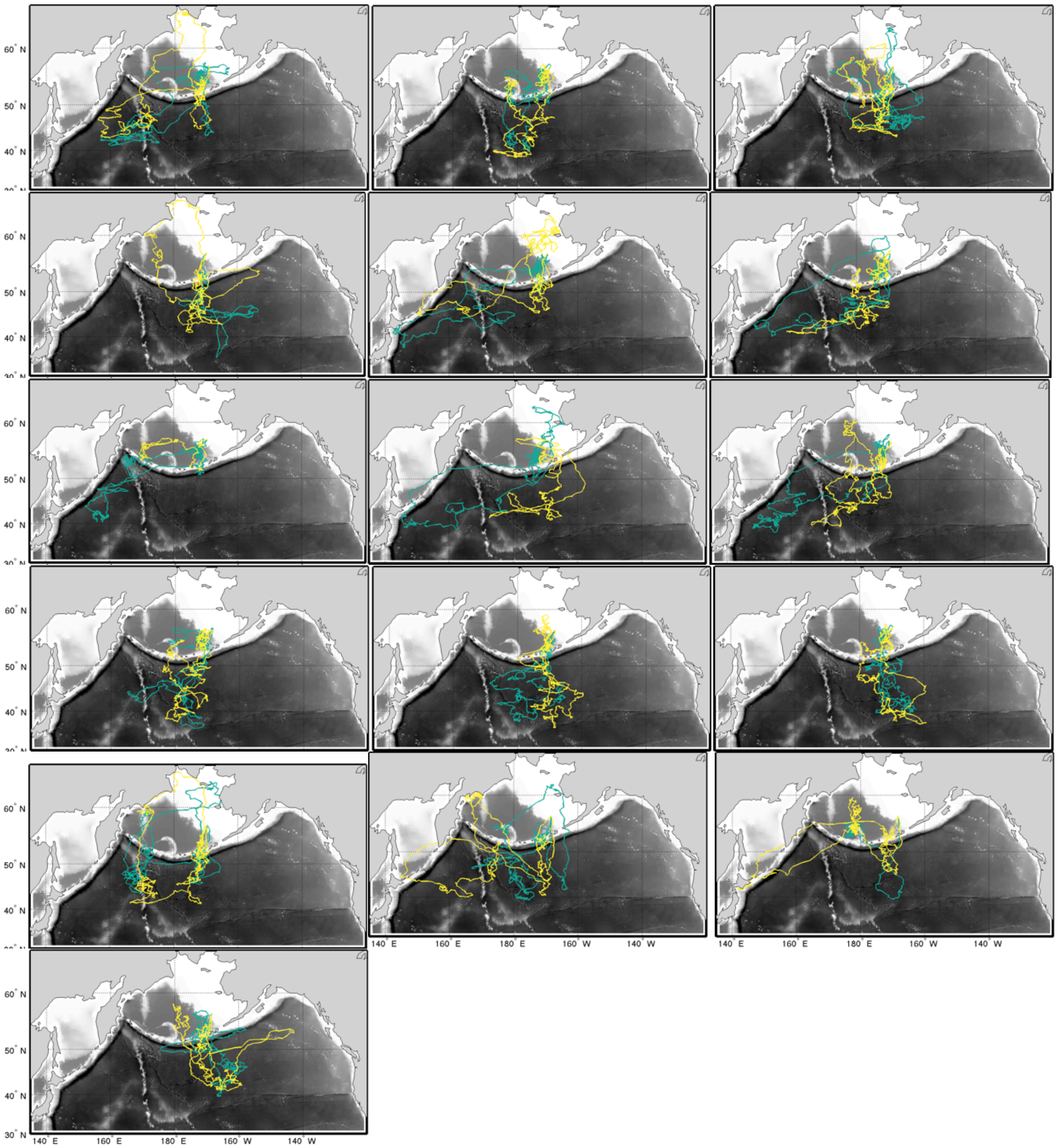

Figure 3.7 Repeat wintering tracks from 16 individual black-legged kittiwakes breeding on the Pribilof Islands. Tracks are from winters 2008/09, 2009/10 and 2010/11.