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Migration and Winter Movement Ecology of Red-Throated Loons (Gavia Stellata) in Eastern North America

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MIGRATION AND WINTER MOVEMENT ECOLOGY OF RED-THROATED LOONS (*GAVIA STELLATA*) IN EASTERN NORTH AMERICA

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

May 2021

Advisory Committee:

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MIGRATION AND WINTER MOVEMENT ECOLOGY OF RED-THROATED LOONS (*GAVIA STELLATA*) IN EASTERN NORTH AMERICA

By Carrie E. Gray

Dissertation Advisor: Dr. Brian Olsen

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
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May 2021

Migratory animals exploit multiple habitats across the extent of their range and conditions experienced can have considerable effects on individual survival and population size. Understanding where species are exposed to survival risks and evolutionary selection pressures and how connected are different portions of the range requires defining a complete annual movement network with all major seasonal sites—e.g., breeding, migratory stopovers, staging, and wintering—and describing where populations may or may not overlap in space and time.

I used movement data collected from satellite-tagged Red-throated Loons (*Gavia stellata*) to provide new and more accurate information about spatial use during the full annual cycle for this species in eastern North America. I examined whether specific behavioral states could be inferred from raw spatiotemporal data, and explored the degree to which environmental cues cause variation in migratory movements, to understand how they will respond to environmental changes in different areas of their migratory corridor. Lastly, I estimated winter home ranges of individual loons and quantified how selection of these areas varied in relation to environmental conditions to better describe important winter habitat for the species within the Mid-Atlantic Bight.

Four primary migration routes were used to travel between mid-Atlantic wintering and arctic breeding grounds. The major sites identified as core use areas included lower Hudson Bay and James Bay, the lower Great Lakes, the Gulf of St Lawrence, Nantucket Shoals, and the major bays of the mid-Atlantic region, where birds were captured in winter, including Delaware Bay, Chesapeake Bay, and Pamlico Sound. Individuals differed in their tendency to be intensive versus extensive in their movement behaviors, which corresponded with individual differences in the scale of their use of the landscape. Photoperiod was an important indicator of increased movement at the onset of migration and wind speed was indicative of whether conditions were conducive to migratory flights. Stopover habitat and winter home ranges were associated with warmer, shallow, coastal waters with higher surface current velocities and chlorophyll *a* concentration. Overall, however, Red-throated Loons exhibited a high degree of individual variation in their movement behavior and responses to environmental conditions.

DEDICATION

To Jackson,

my darling boy,

may this body of work be a reminder that you can do whatever you set your mind to,

and that dedicating yourself to a cause is time well spent.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Brian Olsen, for his guidance and scholarship on this journey. His encouragement, good humor, and friendship made the process so very enjoyable, and helped motivate me through the more difficult periods of my PhD study. I would also like to thank my committee members—Dr. Erik Blomberg, Dr. Brian McGill, Dr. Jeffrey Runge, Dr. Joel Schmutz, and Dr. Iain Stenhouse—for taking the time to share their knowledge and help me become a better scientist. I also thank the School of Biology, as well as the Department of Wildlife, Fisheries, and Conservation Biology, for providing the financial support to undertake my studies at the University of Maine.

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TABLE OF CONTENTS

Chapter

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Some birds undertake spectacular migrations covering vast distances between summer breeding and wintering areas. Over the course of their annual cycle, migratory birds may occupy a broad range of landscapes and the conditions experienced can have considerable effects on individual survival and population size (Alerstam et al. 2003, Newton 2004). Indeed, demographic events experienced during one time or in one place during the annual cycle may result in carryover effects during subsequent seasons, including the timing or capacity to migrate, breed, or survive (Marra et al. 1998, Studds and Marra 2005). Migratory birds have evolved multiple behaviors in response to variations in habitat, prey availability and predation pressures, photoperiod, and climatic conditions they may experience as they traverse the globe. Movement is one such behavioral response, in which birds exhibit a wide range of flight speeds, degree of movement consistency, periodicity of stopover or staging behaviors, and complexity of migratory route.

The field of movement ecology recognizes that it is the response of individuals to their environment that ultimately shapes the spatial distribution of populations and the timing of their mass movements. One of the primary research objectives is to understand how individual movements vary in relation to environmental conditions. This can be a key factor both for predicting responses to changing climatic and habitat conditions and for identifying critical habitats or landscapes for conservation or management. The first step to understanding the ecological requirements of any species, and where to focus species conservation initiatives, is to obtain information regarding where and when individuals and populations are located throughout the year (Taylor and Norris 2010). For seabirds, however, limited information is available on their offshore distribution, foraging movements, and habitat requirements during the nonbreeding season (Schreiber and Burger 2001). Yet, effective conservation at the species scale necessitates a full annual cycle research approach (Rushing et al. 2016). As seabird populations experience rapid declines in many parts of the world (Paleczny et al. 2015), identifying important habitats for conservation, such as marine protected areas, has become a critical tool in seabird conservation (Thaxter et al. 2012, Lascelles et al. 2016).

Describing space use throughout the annual cycle has historically been limited due to the technical constraints of monitoring individuals and populations across often vast expanses of their annual range. Prior to the 1990s, obtaining distribution data on marine birds at sea was limited to ship-based surveys that were restricted in the spatiotemporal extent of their observations. Advances in satellite tracking technology, however, have made it possible to track the movements of individual birds. And the use of tracking technology on seabirds has proven an effective method in the identification of core use areas that provide important habitat at sea (Wakefield et al. 2009, Lascelles et al. 2016). Remote collection of relocation data also provides us with the means to examine how seabirds interact with the marine environment. The prey of many marine birds, forage fish, are patchily distributed and strong spatiotemporal variability in the oceanographic processes make favorable foraging conditions also variable in space and time (Wiens 1976, Kotliar and Wiens 1990). Yet, quantifying the variability of seabird responses to physical and biological conditions can help to foster our understanding of the physical processes and trophic transfer that promote optimal foraging conditions in the marine environment.

My dissertation seeks to address some of these data gaps in marine bird ecology during the nonbreeding season via a satellite tracking study on Red-throated Loons (*Gavia stellata*) in eastern North America. The Red-throated Loon is the smallest of the world's five loon species and the most distantly related, but like other Gaviidae species, they are piscivorous, long-lived with high annual adult survival, and exhibit delayed sexual maturity with low annual productivity (Johnsgard 1987). They have a circumpolar breeding distribution, where they breed primarily on freshwater or brackish ponds at high latitudes, and winter in temperate coastal ocean waters (Rizzolo et al. 2020). They have a global population estimate of 200,000 – 600,000 individuals and have an International Union for Conservation of Nature (IUCN) status of *Least Concern* (Bird Life International 2021). Populations are considered declining or unknown, however, and they are listed by the U.S. Fish and Wildlife Service (USFWS) as a species of conservation concern in much of its breeding range and wintering grounds in the Atlantic Flyway. Approximately 70,000 – 100,000 Red-throated Loons are estimated to winter along the U.S. Atlantic coast, and the core of this wintering range is reported to occur in the mid-Atlantic region (New Jersey to North Carolina), with the largest concentrations reported off the coasts of Delaware and North Carolina (Forsell 1999, Root 1988). However, data gaps exist regarding source breeding populations, wintering distributions, including concentration and timing of use, migratory routes and stopover areas.

In this dissertation, I will provide the first complete description of migration routes used by Red-throated Loons to move between wintering areas along the U.S. mid-Atlantic coast and their breeding grounds. I also describe distinct behavioral states during migration using metrics developed for analyzing movement tracks of individuals and explore how the expression of different behavioral classifications could be attributed to spatial, temporal, and individual effects. I explore relationships between migratory movements and a number of potential migration cues, including photoperiod, weather, and oceanic habitat characteristics, and quantify variability in how birds responded to cues throughout the migratory period. Lastly, I estimate individual home ranges to better describe important winter habitat for the species and identify individual variation in resource selection.

CHAPTER 2

A NETWORK APPROACH SHOWS MOVEMENT BOTTLENECKS AND ALTERNATIVE MIGRATORY ROUTES DESPITE TOTAL LACK OF MIGRATORY CONNECTIVITY FOR AN ARCTIC SEABIRD

Introduction

Animal populations may be limited by factors operating in any part of their annual cycle (Newton 2004), and the limiting factors with the greatest effect on individual vital rates will result in the greatest changes in annual and long-term abundance (Newton 2004). For migratory birds making large-scale seasonal movements between disparate breeding and wintering ranges, these effects interact across multiple spatial and temporal scales to influence population dynamics (Nichols 1996). Demographic events experienced during one time or in one place during the annual cycle may result in carryover effects during subsequent seasons, including the timing or capacity to migrate, breed, or survive (Marra et al. 1998, Studds and Marra 2005). The ability for these effects to propagate across an entire population or species, however, is determined by the degree of spatial interconnectivity achieved through individual movements. Effective conservation at the species scale therefore necessitates a full annual cycle research approach (Rushing et al. 2016), that elucidates (a) the seasonal variability in where individuals are most likely to be exposed to stressors (i.e., spatial distribution), as well as (b) how likely those stressors will propagate due to changes in individual movements among areas (i.e., connectivity).

Understanding how breeding and non-breeding populations are geographically linked across seasons (i.e., migratory connectivity) has important behavioral, demographic, and evolutionary implications for migratory animals (Webster et al. 2002*a*, Webster and Marra 2005, Taylor and Norris 2010, Kays et al. 2015). Migratory connectivity is strongest when populations are highly structured, and most individuals who reside near each other in one period of the year are similarly associated in other residential periods. Consequently, the effects of local environmental conditions will be unlikely to propagate across the entire species for species with high migratory connectivity (McKellar et al. 2013, Ouwehand et al. 2016). In contrast, individuals from migratory populations with weak connectivity diffuse across the species range between stationary phases, and individuals from any given locale during one phase may overlap with individuals from across the range during the opposite stationary phase (Webster et al. 2002*b*). The demographic effects of local habitat conditions from one season (and, in turn, the resultant evolutionary selective processes of those effects) are thus diluted across the range for the other season (Cresswell 2014).

Bird conservation has advanced greatly in the last twenty years by moving from a focus almost solely on breeding locations to one that includes the demographic impacts from the non-breeding stationary phase as well (Marra et al. 2015). Measures of migratory connectivity are generally based on the correlation of pairwise distances between breeding locations of sampled populations and the corresponding distances between wintering locations (Cormier et al. 2013, Trierweiler et al. 2014), with the expectation that individuals that breed near one another will also winter near one another for species with high connectivity (Ambrosini et al. 2009). Over the course of their annual cycle, however, migratory animals exploit multiple habitats between those two end points of their overall range (Alerstam et al. 2003). In fact, migration can occupy as much or more of the annual cycle than any stationary phase, and commonly, if not nearly always, involves a greater degree of habitat heterogeneity and risk to survival than the stationary phases of the year. Therefore, understanding where species are exposed to both survival risks and evolutionary selection pressures, and how connected different portions of the range are, requires us to define a complete annual movement network with all major seasonal sites—e.g., breeding, migratory stopovers, staging, and wintering—and describe where populations may or may not overlap in space and time (Taylor and Norris 2010). Variation in the use of particular migratory sites by individuals from different stationary-phase locations has much potential for demographic and evolutionary carryover effects as connectivity is in any other period of the annual cycle. Both high and low connectivity have potential conservation implications. While conservation at the migratory flyway level often focuses on migratory “bottlenecks” within the network (i.e., areas used by individuals from a large majority of stationary phase locations, (Brown et al. 2017, Studds et al. 2017, Sherry 2018, Cardenas-Ortiz et al. 2020), the probability of encountering risky habitats increases with the number of sites used (Cresswell 2014). Therefore, species that rely on a suite of sites to complete their annual cycle may experience greater risk of demographic effect and also be more likely to propagate impacts from many smaller sites across the species range.

Describing the complete annual movement network has historically been limited due to the technical constraints of monitoring individuals and populations across often vast expanses of their annual range (Marra et al. 2015). The advent of increasingly sophisticated tracking technology, however, has made it possible to remotely collect spatiotemporal data on the migratory and within-season movements of individual birds. Yet, merely tracking locations of animals on the landscape does not necessarily provide us with all the information we need to understand how events in one point in time and space can have impacts across the annual cycle and the species range.

Principles of network theory are increasingly being used to evaluate the importance of different sites that comprise the network that migratory populations rely on during the course of their annual cycle (Taylor and Norris 2010, Bastille-Rousseau et al. 2018, Knight et al. 2018, Lamb et al. 2019). The network analysis approach, in comparison to more traditional methods of characterizing animal space use, such as utilizations distributions (UDs), allows for the identification of movement corridors, which may either be hidden within the core use isopleth of a traditional UD surface (Benhamou and Riotte-Lambert 2012, Bastille-Rousseau and Wittemyer 2020) or may be associated with less intensive use and classified as areas of low importance by UD methods, even though they provide important bridges for connectivity within the migratory flyway.

I used movement data collected from satellite-tagged Red-throated Loons (*Gavia stellata*) to accomplish three goals. First, I provide new and more accurate information about spatial use during the full annual cycle for this species in eastern North America. The Red-throated Loon is listed by the U.S. Fish and Wildlife Service (USFWS) as a species of conservation concern in much of its breeding range and wintering grounds. Second, I examined the strength of migratory connectivity and the degree of population spread between breeding and wintering areas using traditional methods to compare this species to others that have been described in this way. Third, I used network theory and behavioral cluster analysis to construct a movement network for the species to obtain a better understanding of how spatial use and spatial connectivity might affect these birds throughout the annual cycle.

Methods

Data Collection and Management

I used Argos telemetry data (location classes 1, 2 and 3) collected from 36 adult Red-throated Loons, captured on their wintering grounds offshore of the U.S. mid-Atlantic coast, between January and late March in 2012 – 2015. Animal handling and satellite transmitter implantation details can be found in Appendix A. Prior to the analysis, I censored the first 16 days post-release of each bird to minimize the effects of capture, handling, and surgery on behavior (Blomberg et al. 2018; Appendix A). For this study, I include position data from one complete annual cycle for most birds, from capture on the non-breeding grounds to the establishment of breeding home ranges and return to the wintering range. I used R package *foieGras* to filter observed locations with a continuous-time state-space model to account for error in the Argos telemetry, to estimate true animal locations, and to regularize the filtered locations to a 24-h time interval (Jonsen et al. 2019).

Full Annual Cycle Spatial Use

Regularized tracks for each loon were uploaded into the R package *adehabitatLT* and stored as trajectory objects (Calenge 2006). Shapefiles of each trajectory were created using R package *rgdal* and exported for further analysis in ArcGIS (Keitt et al. 2010). Summaries of the general patterns of migratory routes were written after visually inspecting plots of each trajectory over the World Ocean Base map in ArcMap 10.8.1 (ESRI 2011).

Traditional Migration Connectivity

Mantel tests. Spatial distance matrices can be used to test for correlations in pairwise individual distances between two residential periods (Cormier et al. 2013, Trierweiler et al. 2014). For populations with high connectivity, the expectation is that individuals that breed near one another will also winter near one another (Ambrosini et al. 2009). I used R package *MigConnectivity* to measure associations between two $n \times n$ matrices of these pairwise distances using the Mantel test (Mantel 1967, Cohen et al. 2018). The entries in the first matrix are the Euclidean distances between all pairwise combinations of breeding territory locations, and the second matrix contains the distances between capture locations in the non-breeding range (Ambrosini et al. 2009). Breeding territory locations were centroids of breeding home ranges, which were polygons constructed using a simple minimum convex hull geometry of summer non-migratory relocations for each individual bird. The non-migratory period was defined as the time between when an individual bird stopped making northward movements in spring and began making southward movements in late summer. Daily movements were much smaller and confined to the area around the home range making nonmigratory locations easy to differentiate from migratory relocations. Population spread on the breeding and non-breeding grounds was estimated by calculating the range and mean of pairwise distances for both the breeding territory centroids and the winter capture locations. To test if birds that used the same migration route exhibited similar spatial structure on breeding and wintering grounds, Mantel correlations were also calculated among individuals within each of the four migration routes identified in this study.

Sampling Coverage. Capture of Red-throated Loons was limited to the mid-Atlantic region of their winter range, while the full winter range extends the length of the U.S. Atlantic Coast. Ideally, estimates of migratory connectivity are based on sampling that occurs across the entirety of one stationary range to limit potential sampling bias (Finch et al. 2017). To ascertain the degree of potential sampling bias in my migratory connectivity estimates, I compared the sampled winter range to an estimate of the percentage of the Atlantic Flyway breeding range occupied by my sampled birds. I defined the breeding range occupied by my sampled population as the area determined by a polygon of the minimum bounding geometry of the breeding home-range centroids. I used a simple minimum convex hull geometry type, where width is determined by measuring the shortest distance between any two vertices of the hull, and the length is the longest distance between any two vertices. The polygon was then clipped to a larger polygon for the full breeding range of North American Red-throated Loons in the Atlantic Flyway to calculate the percentage of overlap. Small overlap would indicate sampling bias. To estimate the Atlantic Flyway breeding range, I used a subset of the full North American breeding range (BirdLife International and Handbook of the Birds of the World 2020) that removed Alaska and British Columbia. Results from other tracking studies indicate that Red-throated Loons breeding in these areas are solely members of the North America-Pacific or Asia-Pacific flyways (McCloskey et al. 2018).

I employed a similar approach to estimate bias in the wintering range. Capture locations of the birds tracked were used to construct a minimum convex hull of the winter sampling area using the coordinates of each bird's capture location. The percentage of area overlap was then calculated between the winter capture area polygon and the polygon of the North American Atlantic portion of the non-breeding range (BirdLife International and Handbook of the Birds of the World 2020).

Network Connectivity

Principles of graph theory were employed to analyze the migratory network of Red-throated Loons in eastern North America. When applied to animal tracking data, the structural component of the network, or *nodes*, are the animal relocations on the landscape, and the connections within the network, or *edges*, represent movement between nodes (Jacoby and Freeman 2016, Bastille-Rousseau et al. 2018). Weighting the edges according to the frequency of movement between nodes can provide insight, either at the individual or population level, regarding the intensity of use of sites that make up the network (Jacoby and Freeman 2016). Other metrics, such as edge betweenness, measure the number of shortest paths connecting two sites, and can be used to identify movement "corridors" on the landscape that are critical for maintaining overall connectivity of the network.

I followed methods outlined in Bastille-Rousseau and Wittemyer (2020) and the associated R package, *moveNT,* to build the network. A gridded raster of the regularized and filtered location data for the 36 loon trajectories was used to build the network. Each pixel in the raster represented a node and movement between nodes represented edges. Nodes of the rasterized network were squares with sides equal to the median step length (19.6 km)—i.e., total distance moved between 24-h relocations—of all individual trajectories. In effect this defines a network where any two loon locations (of either the same or different loons) that are less than an average day's flight from each other are considered on the same node. From here, a weighted, undirected (i.e., omni-directional movement is allowed) adjacency matrix was developed to tally the population-level movements between any two nodes of the network among all sampled individuals during the study period. Node-level metrics were calculated for each pixel to assess intensity of use and its importance in connecting other nodes within the network. These included: (1) *weight* (total number of times any individual used a node); (2) *degree* (number of other nodes it is connected to); and (3) *betweenness* (the number of times a node bridges the shortest path between any two other nodes in the network). Movement metrics, including mean (4) *speed of movement* and (5) *turning angle*, were also calculated for each node to gain additional insight on movement behavior that could be used to differentiate whether the node served as a residential home range, a migration stopover, or a movement corridor.

I then used these five movement metrics to calculate the population-level probability that a node was used for a discrete type of behavior. Model-based clustering based on Gaussian mixture models of the metrics were conducted in *moveNT* to identify unique classifications of movement behavior among nodes in the network for each individual (Bastille-Rousseau and Wittemyer 2020). The cluster analysis was constrained to differentiate up to a maximum of 8 qualitative classifications: fast or slow movements in high use, medium use, or low use sites, and fast or slow movements in movement corridors. My primary interest was the identification of nodes in the network that were associated with the greatest intensities of use (e.g., residential ranges or migratory stopover locations) and those that served as movement corridors (e.g., areas with fast movements).

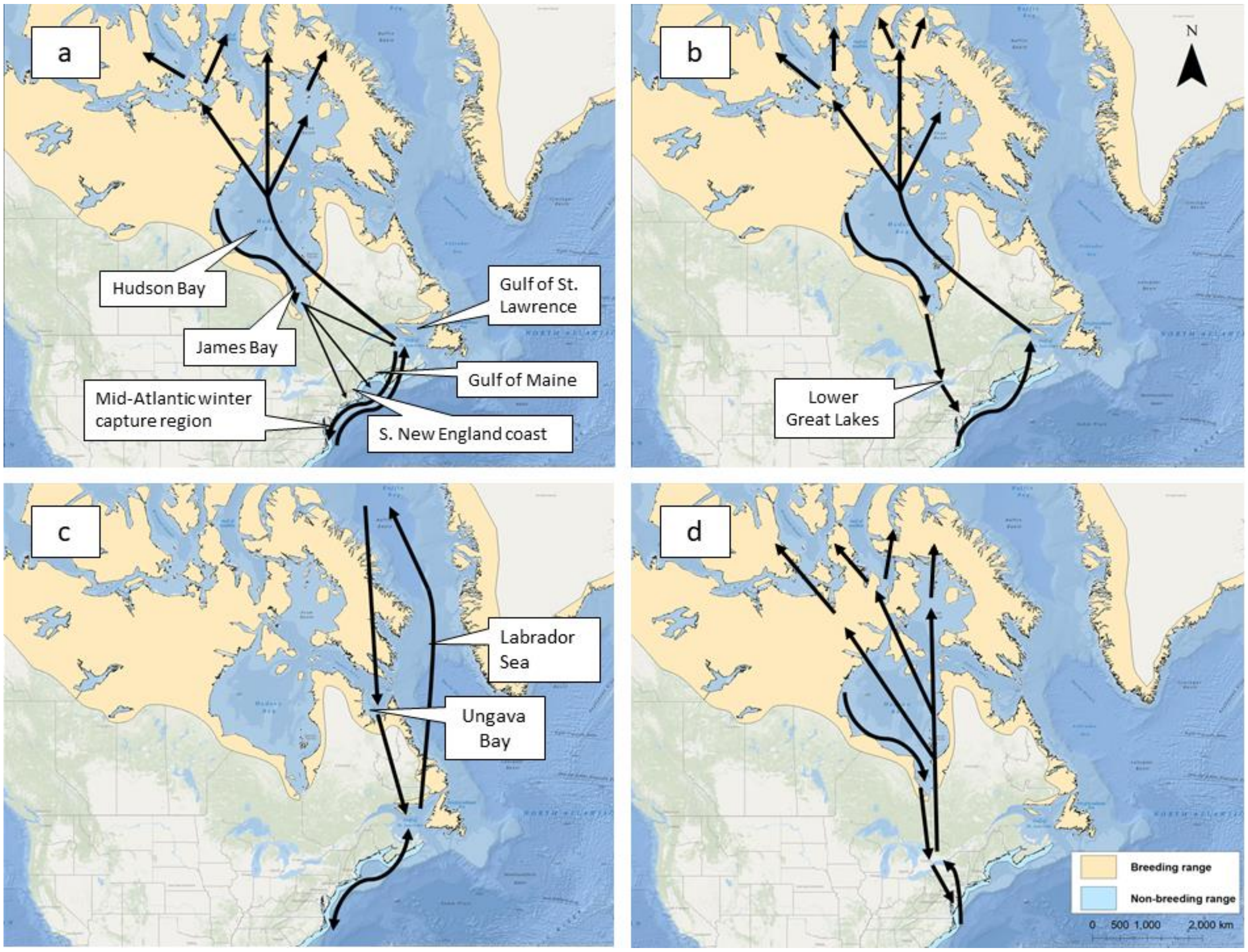
The cluster analysis first estimated the probabilities that each bird location (individual use of a node) belonged to each of the classification categories. To classify the type of use of the node at the population-level scale, I then averaged these individual probabilities across individuals for each node. The nodes of the network are pixels, so I created a raster for each behavioral classification cluster, where the raster values were the probability (x) of a given node (i.e., pixel) belonging to that classification category. To find the most probable classification category (k) for each node (i) of the network at the population level, I subtracted the probability of i belonging to the kth cluster from one ($1 - x$) for each individual, to create a raster surface of the probability of i not belonging to the kth cluster (i.e., $\{1 - x = z\}$). Next, for each k, I multiplied z_i, across all individuals to generate a raster of the mean probability of i not belonging to the kth cluster ($\overline{z}$). Last, I subtracted $\overline{z}_i$ from 1 to generate a raster for each k, where the values of each pixel contained the population mean probability of a node belonging to behavioral cluster ($\overline{x}$).

Results

Full Annual Cycle Spatial Use

Four primary migration routes were identified that Red-throated Loons used to move between wintering grounds offshore of the U.S. mid-Atlantic region and their Canadian breeding grounds (Figure 2.1). The most frequently traveled route (A), with 44% (n = 16) of birds using, followed the Atlantic coast north to the Gulf of St. Lawrence, before fanning north and northwest to breeding territories across Nunavut. Following breeding, birds then moved to the Hudson Bay before continuing south towards James Bay. From there, individuals made rapid flights overland to points along the northeastern Atlantic coastline, before continuing southward to return to the mid-Atlantic wintering grounds in early winter. The next most utilized route (B) followed a similar pattern, i.e., coastal route north in spring and autumn return through Hudson and James Bays; however, birds using this route (n = 10) departed James Bay earlier than route A birds, and traveled to the lower Great Lakes for extended stopovers, before making direct rapid flights over New York and Pennsylvania to the mid-Atlantic coast. Route c was used by 17% (n = 6) of sampled birds, that followed the coast north to the Gulf of St. Lawrence in spring, but then continued north along a more eastern route through the Labrador Sea and over Baffin Island to points north. These birds returned south through Ungava Bay, in lieu of Hudson Bay, before returning to the Gulf of St Lawrence and then south along the coast toward the mid-Atlantic. Route D (n = 4) took an inland route north through the Great Lakes before spreading to points north and northwest in the breeding range. Three of these birds returned through Hudson/James Bay before returning to the lower Great Lakes en route to the mid-Atlantic wintering area (i.e., like route B). One bird returning from a breeding location in the Northwest Territories, however, kept further south and west after departure from the breeding area, moving through Lake Winnipeg and the western Great Lakes before arriving in lower Great Lakes and continuing on to the mid-Atlantic.

Figure 2.1. Four primary spring and autumn migration routes of satellite-tracked Red-throated Loons (n = 38) captured on wintering grounds offshore of the U.S. mid-Atlantic coast: (a) Route a (n = 16) followed the Atlantic coast north in spring to the Gulf of St. Lawrence before spreading north over Hudson Bay to Arctic breeding territories. Birds returned to northern Hudson Bay in early autumn and moved south to James Bay, from where they made rapid flights overland to points along the east coast, before turning south to return to the mid-Atlantic region; (b) Route B (n = 10) followed a route similar to Route A in spring and early autumn, but made stopovers in the lower Great Lakes, before returning directly to the mid-Atlantic region; (c) Route C (n = 6) followed a more eastern route north when departing the Gulf of St. Lawrence and returned through Ungava Bay in autumn; (d) route D (n = 4) took an inland route north through the Great Lakes en route to the Arctic and returned through this area in autumn when returning to the mid-Atlantic.



Traditional Migratory Connectivity

Mantel tests. The distance between capture locations of individuals sampled in the mid-Atlantic portion of the wintering range ranged from < 1 km to 444 km ($\bar{x}$ = 195 km). The population spread of those individuals during the breeding season ranged from 37 km to 2,506 km ($\bar{x}$ = 943 km). Overall, the distance between two individuals during the non-breeding season was poorly correlated (-0.03) with the distance between the same individuals during the breeding season, suggesting low connectivity and random spatial structure in winter (Table 2.1). Mantel correlation coefficients by migration route were also low, ranging from -0.13 to 0.16. No significant structure was detected for the two routes that pass through the Great Lakes (B & D) when those birds were assigned to the same population; nor was any structure noted when the two populations that circumvent the Great Lakes (A & C) were combined.

Table 2.1. Mantel correlation coefficients for pairwise distances between Red-throated Loons (n = 36) at winter capture locations offshore of the U.S. mid-Atlantic coast and the pairwise distances between those same birds on Canadian Arctic breeding grounds. Mantel correlation coefficient values are unitless, range from – 1 to 1, and are an indicator of the strength of a population's migratory connectivity. Values less than 0.25 suggest no spatial structure, values 0.26 to 0.50 are representative of weak structure, 0.51 to 0.70 is reasonable structure, and > 0.71 is strong structure (Ambrosini et al. 2009). Positive values indicate birds are close together and negative values suggest greater population spread. The B and D migrants use the Great Lakes during migration, whereas A and C migrants do not. Route C migrants are the only migrants that do not use Hudson Bay.

Population	***N***	**Mantel Correlation Coefficient**
All birds	36	-0.034
Route A Migrants	16	0.033
Route B Migrants	10	-0.130
Route C Migrants	6	0.161
Route D Migrants	4	0.145
Route A & C Migrants	22	-0.051
Route B & D Migrants	14	-0.108

Sampling coverage. The area of the Red-throated Loon wintering range sampled due to capture locations (x = 22,284 km^2) comprised 5% of the total North American east coast winter range (x = 474,820 km^2) (Figure 2.2). The breeding territories of the birds that were captured spread out over an area of 15,012,145 km^2, comprising 65% of the total Atlantic flyway breeding range (x = 38,739,315 km^2). Source breeding locations ranged from -66°W to -110°W longitude and 58°N to 81°N latitude, and included the Northwest Territories, Nunavut, Manitoba, and northwest Greenland (Figure 2.3).

Figure 2.2. Capture locations of satellite-tracked Red-throated Loons (n = 36) wintering offshore of U.S. mid-Atlantic coastline in January to April, 2012 – 2015. Birds are color-coded according to one of four migration routes used to travel between breeding and non-breeding ranges. Sampling area coverage denotes the proportion of the east coast North American non-breeding range we sampled.

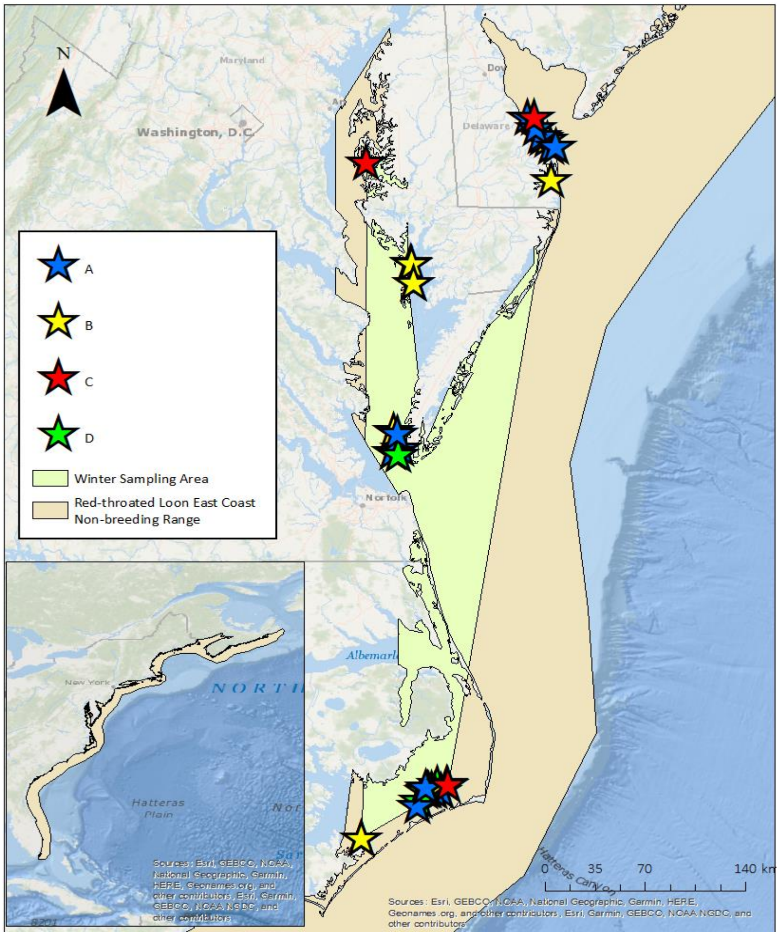
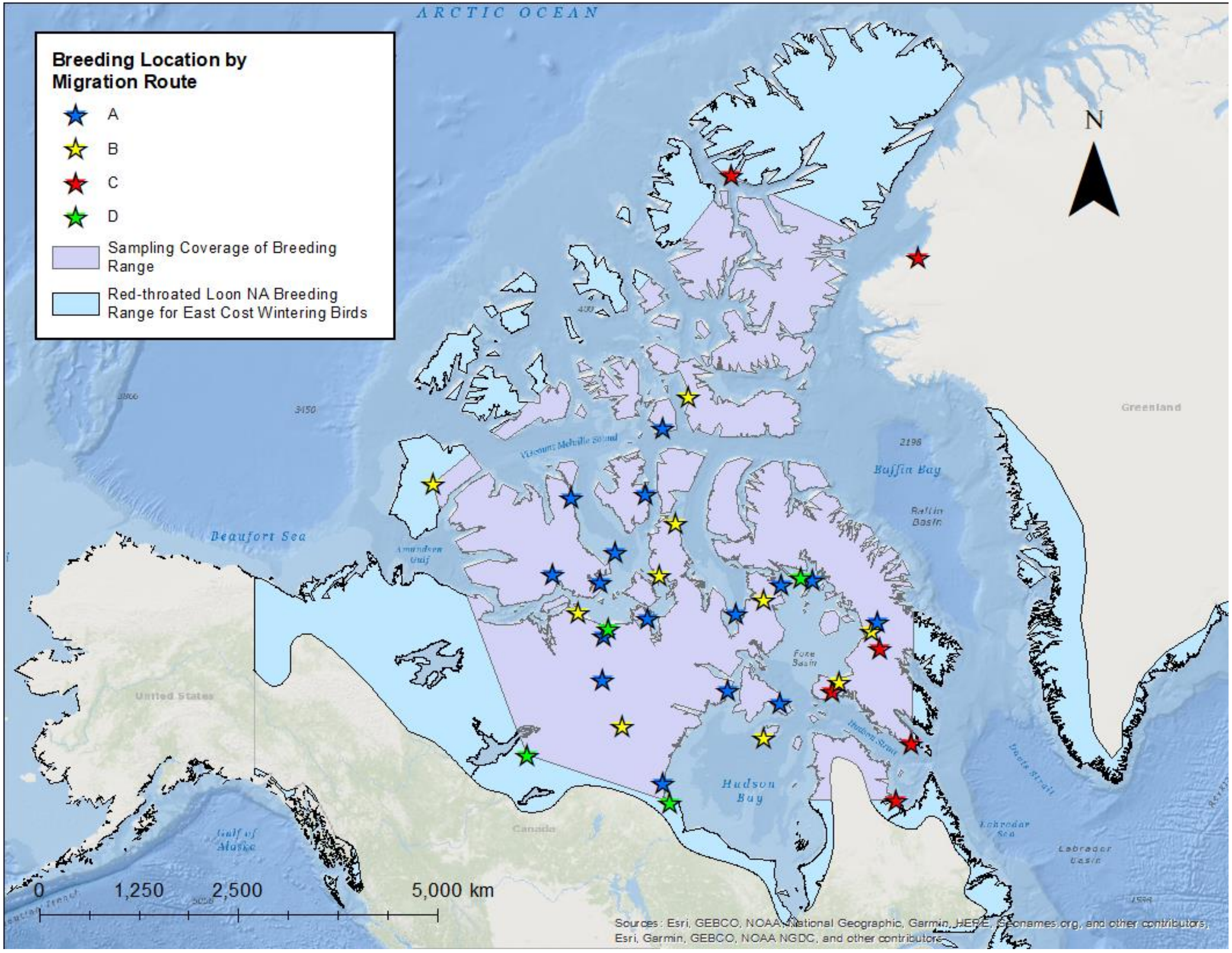


Figure 2.3. Breeding locations of satellite-tracked Red-throated Loons (n = 36) captured and released offshore of U.S. mid-Atlantic coastline in January to April, 2012 – 2015. Birds are color-coded according to one of four migration routes used to travel between breeding and non-breeding ranges. Sampling area coverage denotes the proportion of the North American breeding range (minus Alaska and British Columbia) the birds we sampled covered. Note: the individual with breeding territory in northwest Greenland was not included because it did not overlap with the officially mapped breeding range for this population.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Network Connectivity

Cluster analysis on the node-level metrics of weight, degree centrality, betweenness, speed, and turning angle resulted in the identification of seven types of movement behavior across the migratory network (Table 2.2). Map plots of each of the node-level metrics can be found in Appendix B. Nodes designated to clusters 2, 4, and 6 together comprised the majority of nodes in the network (35.1%, 3.4%, and 13.7%, respectively), and were indicative of sites with the highest use (weight) and moderate to high connectivity (degree). These were associated with Hudson and James Bay, the lower Great Lakes, the Gulf of St. Lawrence, northern Bay of Fundy, southern New England Atlantic coast, and the large bays of the mid-Atlantic winter capture region, including Delaware Bay, Chesapeake Bay, and Pamlico Sound (Figures 2.4 and 2.5). Clusters 2, 4, and 6 tended to co-occur in the same regions. Among the three high-use, high connectivity nodes, however, cluster two had the lowest use and degree of connectivity, suggesting more peripheral nodes in high-use areas. Cluster 4 was differentiated among these three clusters by faster relative movement behavior, higher betweenness, and more directed movement (i.e., less turning angle) values than clusters 2 and 6. This suggests that nodes designated as cluster 4 were end points for corridors, where birds typically departed from or arrived when engaging in stopover behavior. Speed, betweenness, and directed movement were even higher for clusters 5 and 7, which accounted for 8.2% and 12.6% of all nodes within the network. Together with their lower use, this indicates that that these sites are important corridors for facilitating movement between high-use areas. Nodes associated with corridors stretched between southern Hudson and James Bays, overland to the Gulf of St. Lawrence, and less so, to the southern Great Lakes. Corridors along the coast were evident across the extent of the New York/New Jersey Bight, Nantucket Shoals, and Gulf of Maine. Movement in corridors was directed and fast, with speeds being slightly slower in cluster 7 nodes than in cluster 5. Clusters 1 and 3, representing 15.5% and 11.5% of all nodes, represented sites of low use, low connectivity, and low importance.

Table 2.2. Summary of Gaussian mixture model classifications applied to network analysis and movement metrics of satellite-tracked Red-throated Loons (n = 36) in eastern North America, 2012 – 2015. Network metrics were based on gridded raster with pixel size of 19.6 km that classified pixels as one of seven clusters based on five metrics that included: *weight* – number of relocations in a pixel; *degree* – number of other pixels to which a pixel is connected; *betweenness* – number of shortest paths in pixel relative to total shortest paths, i.e., importance of pixel in facilitating flow of network; movement *speed* – average velocity of in a pixel; and *turning angle* - mean cosine of all turning angles in pixel.

Metric	**Cluster 1**	**Cluster 2**	**Cluster 3**	**Cluster 4**	**Cluster 5**	**Cluster 6**	**Cluster 7**
Weight	-0.361	0.427	-0.228	3.190	-0.284	3.162	-0.364
Degree	-0.499	0.889	-0.218	2.347	-0.323	2.754	-0.498
Betweenness	-0.116	-0.141	-0.254	0.155	0.422	0.052	0.642
Speed	-0.186	-0.381	-0.304	0.254	2.750	-0.450	0.896
Turning angle	0.073	-0.269	-0.877	-0.633	0.015	-0.187	0.601
% of network	0.155	0.351	0.115	0.034	0.082	0.137	0.126
Movement type	*low use (slow)*	*med. use (slowest)*	*low use (slowest)*	*high use (slow)*	*corridor (fastest)*	*high use (slowest)*	*corridor (fast)*

Figure 2.4. Map of the northern part of the migratory network of satellite-tracked Red-throated Loons (n = 36) in eastern North America, 2012 – 2015. Moderate to high intensity use areas characterized by slow rates of movement are represented by Clusters 2, 4, and 6. Movement corridors characterized by fast and slow rates of movement are represented by Clusters 5 and 7, respectively.

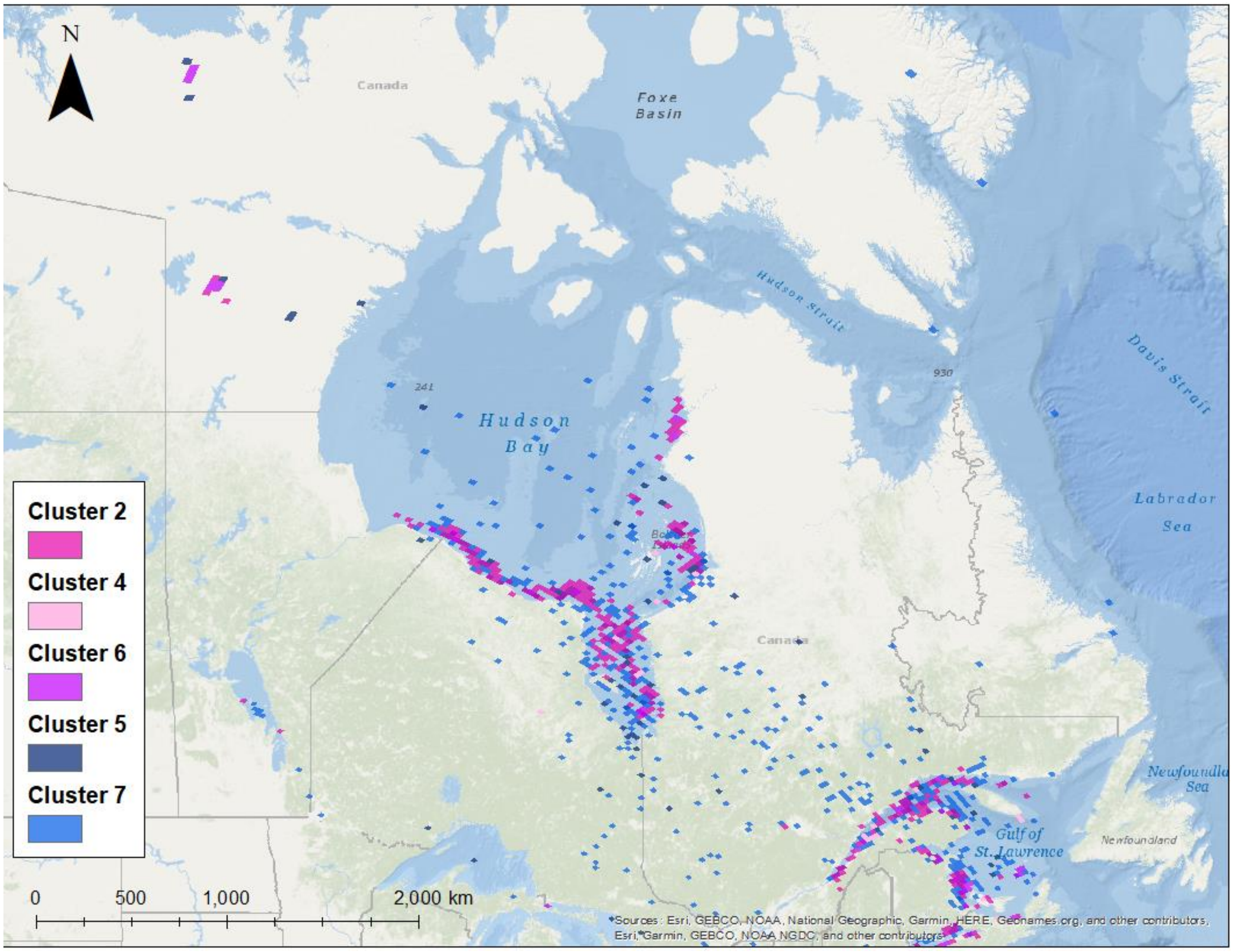
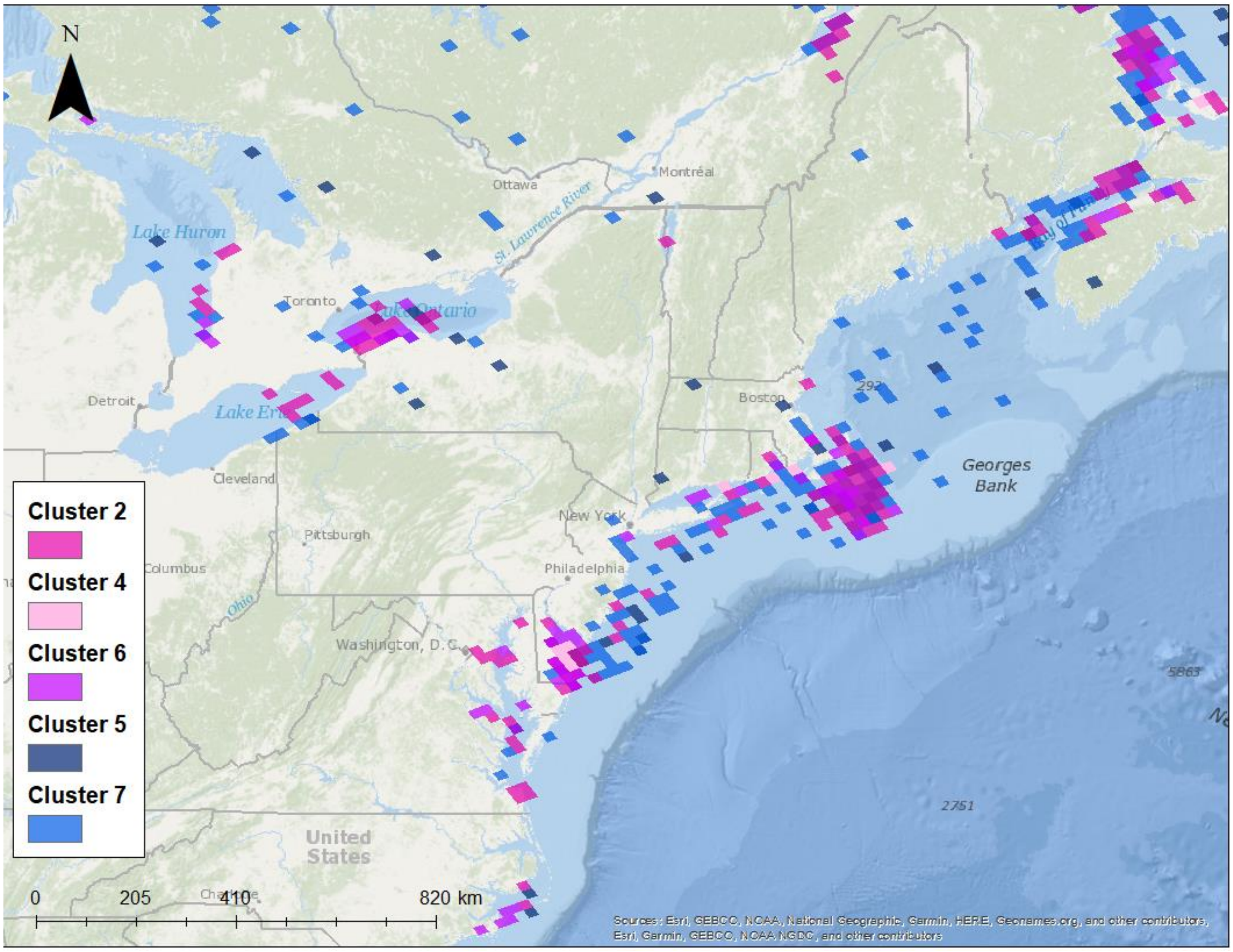


Figure 2.5. Map of the southern part of the migratory network of satellite-tracked Red-throated Loons (n = 36) in eastern North America, 2012 – 2015. Moderate to high intensity use areas characterized by slow rates of movement are represented by Clusters 2, 4, and 6. Movement corridors characterized by fast and slow rates of movement are represented by Clusters 5 and 7, respectively.



Discussion

This study presents the first complete description of four broad migration routes used by Red-throated Loons to move between wintering areas along the U.S. mid-Atlantic coast and their northern breeding grounds. Most birds followed the Atlantic Coast north to the Gulf of St. Lawrence in spring before fanning out in multiple directions to reach breeding grounds distributed across a wide swath of the Canada and Greenland. In autumn, birds associated with more eastern breeding locations, e.g., northwest Greenland, tended to track further east through Ungava Bay, but most birds across nearly the entire Canadian Arctic east of Yukon returned though Hudson and James Bay. The primary distinguishing factor in migration routes among the birds I sampled was whether they traveled from Hudson/James Bay directly to points along the Atlantic Coast or if they instead moved to the lower Great Lakes for extended stopovers. Those that moved through the Great Lakes exhibited an elliptical migration pattern, which has not been documented in other parts of the species' range; however, it has been observed in other Arctic-breeding birds that utilize the Atlantic Flyway (Brown et al. 2017).

The birds I sampled exhibited a high degree of population spread in the breeding range, occurring across 44 degrees of longitude and 23 degrees of latitude. It is unclear, however, if this represents a continuous breeding range or disjunct breeding populations that mix on the wintering grounds. When considered as one continuous population, the random spatial distribution of individuals during the breeding and nonbreeding seasons indicated a pattern of low migratory connectivity. Examining connectivity by assigning birds to one of four populations according to migration route did little to change those results. I should note that estimates derived from the Mantel test may not be robust to small sample size, uneven sampling efforts, and location error uncertainty (Finch et al. 2017, Cohen et al. 2018). New methods that account for variation in population abundance may help to fine-tune migratory connectivity estimates (Cohen et al. 2018). The Mantel test, however, was the most appropriate connectivity measure to use for this study, given that the data was based on individual animal relocation data and because abundance estimates were not available for the sampled population (Cohen et al. 2018). I attempted to reduce potential location error bias in the analysis by only including relocations of the highest quality (Argos location classes 1, 2, and 3) when calculating centroids of breeding territories. Sampling for this study occurred across just 5% of the North American Atlantic coast non-breeding range. Yet, despite sampling an area equal to just 0.001% of the presumed Atlantic flyway breeding range (i.e., not including Alaska and British Columbia), the birds spread out across 65% of that breeding range, yielding better than expected sampling coverage. These results support the notion that the mid-Atlantic region constitutes the core of the non-breeding range for Red-throated

Loons that winter on the Atlantic coast (Root 1988, Forsell 1998), and that demographic changes in this relatively small area could have consequences across the majority of the North American breeding range. Additional tracking efforts and the collection of abundance data for the species in this part of their range would provide greater sample sizes and information necessary for fine-tuning estimates on larger scale spatial structure and population size.

Network analysis of Red-throated Loon satellite tracking data allowed for the identification of core use areas across the annual cycle (clusters 2, 4, and 6) that provide critical stopover and wintering habitat, and, movement corridors (clusters 5, 7), which facilitate connectivity across the range. The major sites identified as core use areas included lower Hudson Bay and James Bay, the lower Great Lakes, the Gulf of St Lawrence, Nantucket Shoals, and the major bays of the mid-Atlantic region, where birds were captured in winter, including Delaware Bay, Chesapeake Bay, and Pamlico Sound. Movement corridors are also critical components of the network and link disjunct core use areas that are used for foraging and rest (LaPoint et al. 2013, Bastille-Rousseau and Wittemyer 2020). Prominent movement corridors were evident from southern Hudson Bay and James Bay extending to points south and southeast, primarily the lower Great Lakes and the Gulf of St. Lawrence. Hudson/James Bay provides important autumn core use stopover habitat but is also of high importance as a movement corridor during both the spring and autumn migrations. Most of the birds I tracked relied on the waters of southern Hudson and James Bays for one-quarter to one-third of their annual cycle. It was also the final staging area before they embarked on non-stop flights of more than 1,000 km across eastern Ontario and Quebec. This may have important conservation implications as conditions at population-specific bottlenecks can have considerable effects on individual survival, and potentially population size (Newton 2006).

Low migratory connectivity between wintering and breeding ranges (i.e., relative panmixia) and the use of several varied migration routes likely dilute the demographic impacts from any one residential location across the annual network. There are, however, multiple points in the network that may create geographic bottlenecks during migration. For example, 90% of the birds I tracked in spring and 61% in autumn relied on core use areas (and the corridors that connected them) along the Atlantic coast of the northeastern U.S. and Canadian Maritimes. Potential limiting factors on loon demography in coastal non-breeding areas include: inclement weather and oceanographic conditions (Schmutz 2014); exposure to contaminants (Schmutz et al. 2009, Evers et al. 2014) and oil spills (Sperduto et al. 2003, Evers et al. 2019, Paruk et al. 2019); risk of collision mortality and habitat displacement from offshore wind farms (Bradbury et al. 2014, Heinänen et al. 2020, Stenhouse et al. 2020); and the threat of bycatch mortality associated with fishing nets (Warden 2010, Žydelis et al. 2013). This highlights the possibility that species without strongly structured residential populations (i.e., without high traditional migratory connectivity) might still be sensitive to environmental changes in small portions of their migratory ranges, a finding that requires an annual cycle approach which includes the migratory period.

A smaller proportion (10%) of birds I tracked took an inland route north through the Great Lakes in spring, instead of following the Atlantic coast, and 40% of all birds passed through there in autumn. The Great Lakes pose a unique threat as they host sporadic, but often devastating, Type E botulism outbreaks that have been responsible for killing thousands of fish-eating waterbirds (Rocke 2006, Chipault et al. 2015). These outbreaks tend to overlap with the period of autumn migration, when Common Loons (*Gavia immer*) in particular have suffered extensive mortality (Brand et al. 1988, Rocke 2006). While Type E botulism mortality reports of Red-throated Loons are typically much less for this area, it is not clear if they are less affected due to differences in the timing of their movements through the area, differences in food items ingested during stopovers, or if they are being underreported due to observer difficulty in differentiating the two species or in finding carcasses.

Characterizing spatial distributions during the breeding, migration, and winter periods is often the first critical step to understanding the full annual cycle of a species. Identifying where and when individuals and populations are located throughout the year provides us with the necessary information for constructing movement networks. From there, we can identify the most important parts of the network that can be used to focus species conservation initiatives. The importance of a site may be based on how intensively it is used, the proportion of the population it supports, the demographic function it serves, and/or its role in maintaining overall connectivity of the network, particularly when alternate sites are not available. Intraspecific variation in the use of sites within the migratory network allows populations to exploit different habitats to maximize life history traits during different parts of the annual cycle. For example, when individuals are spread out over multiple sites during migration, as is seen in populations with multiple migration routes, is potentially buffered from the negative effects associated with smaller-scale habitat changes. This effect will be further enhanced for taxa that also spread out over the residential periods. Conversely, those that occupy smaller, more restricted seasonal residential ranges, have a higher probability of population decline (Gilroy et al. 2016).

This study revealed considerable sympatry of wintering Red-throated Loons from a wide swath of the breeding range and used a network approach to identify a number of migration bottlenecks in important movement corridors, despite multiple, clearly discrete, migration strategies. Identifying the impact of these patterns on population resilience will require further investigation. However, by documenting these locations, I hope to both inform the conservation of this species as well as to underscore the importance that large-scale migratory spatial structure might play for otherwise panmictic taxa.

CHAPTER 3

INTRINSIC AND SPATIOTEMPORAL VARIATION IN THE NON-BREEDING MOVEMENT BEHAVIOR OF A HIGH ARCTIC MIGRANT, THE RED-THROATED LOON (GAVIA STELLATA)

Introduction

Behavior reflects the internally coordinated responses of an organism to internal and external stimuli (Levitis et al. 2009). Movement is an example of a behavioral response to such physiological and environmental factors. The types of movement any single organism can exhibit, however, are incredibly varied, as internal state, navigational capacity, motion capacity, and environmental factors all combine to determine an animal's decisions (Nathan et al. 2008). To predict animal movements first requires an understanding of what movement components are generally co-associated. These so-called movement "states", from small-scale ranging to directed long-distance relocations, are each defined by a suite of correlated behaviors. Once we understand these states, their expression may be predicted by: (a) where an animal is, (b) what point in their circadian or circannual rhythm they are in, and (c) what their internal physiological state is.

How often individuals switch between movement states may be more variable during certain parts of the year than others, and variable times of the year may thus be more informative for our understanding of what causes behavioral state changes. Three broad categories of movement behavior have been widely described, including: (1) station-keeping, where the individual's movements are related to deriving resources necessary for breeding and survival within the periphery of a home range; (2) ranging, which are explorations of new areas, such as natal dispersal and nomadic movements, that often end with the establishment of a new home range; and (3) migratory relocation, when movement between distant sites is directed and in response to seasonal physiological stimuli (Dingle 2006). Importantly, all three of these movement states occur during the non-breeding periods of many animals, while many species show only a subset during breeding periods.

Migration, for example, is a complex behavioral phenomena that is made up of many different movement states that are all, in turn, strongly influenced by when, where, and who an individual is. Substantial proportions of animal phyla engage in migration, including insects, fish, reptiles, amphibians, and mammals (Luschi et al. 1998, Mate et al. 1999, Poole and Mowat 2005, Mehner and Kasprzak 2011), and each taxa, and sometimes each individual, can vary both the properties of their directed migratory movements as well as how frequently they alternate the expression of such behavioral states with other states along the migratory route.

Birds in particular often undergo spectacular migrations covering vast distances between summer breeding and wintering areas (Egevang et al. 2010, Battley et al. 2012). Consequently, multiple behavioral strategies have evolved among migratory birds in response to the broad range of landscapes, prey availability and predation pressures, photoperiod, and climatic conditions they may experience as they traverse the globe (I. Newton 2008, Egevang et al. 2010, Franke et al. 2011, Nilsson et al. 2015). They exhibit a wide range of flight speeds, degree of movement consistency, periodicity of stopover or staging behaviors, and complexity of migratory route.

Birds also vary considerably in how they enter into or exit out of the migratory program, with some species (e.g., obligate, long-distance migrators) switching tightly between the long-distance, directed movements of migration and into or out of consistent station-keeping behaviors on either end of the migratory route (González-Solís et al. 2007, Stutchbury et al. 2009, Egevang et al. 2010). Other species (e.g., facultative migrators) appear to flip into and out of the migratory program repeatedly during the full non-breeding period in response to a variety of internal or external cues (Hochachka et al. 1999, Cheveau et al. 2004, Newton 2012). The entire non-breeding period for some bird species is therefore the time with the greatest diversity in movement states and presents us with the best period to understand what drives behavioral diversity both between and within individuals.

Our ability to explain movement behaviors of migratory birds has historically been limited due to the technical constraints of monitoring individuals and populations across the often vast expanses of their annual range. The advent of tracking technology, however, has made it possible to remotely collect spatiotemporal data on individual birds (Higuchi 2012, Allen and Singh 2016), and behavioral states can in some instances be inferred from raw spatiotemporal data (Nathan 2008, Benhamou 2014). Specific behavioral states can be defined by distinctive types of movement, and so changes in movement pattern can also indicate shifts in underlying states (Morales et al. 2004). This ability to infer behavioral state changes from tracking data therefore allows for the testing of whether specific intrinsic and extrinsic factors influence movement processes (Jonsen et al. 2007). Here, I present an example of this approach that attempts to explain variance in behavioral states using an individual's spatial, temporal, and individual identities.

There is a wide array of literature supporting that behavioral states can be explained by an individual's particular location in space (Morales et al. 2004, Frair et al. 2005, Jonsen et al. 2006, McClintock et al. 2012). The switch between exploratory, non-oriented movement states and non-random, directed movements, for example, can be a response to habitat quality (Faaborg 2010, Fryxell et al. 2008). Further, an animal's position in space can explain switches between extensive (ranging and relocation) and intensive (area-concentrated) movement states (Barraquand and Benhamou 2008). Birds also change their behavioral states during migration as a function of their spatial location when, for instance, they encounter ecological barriers (Diehl et al. 2003, Strandberg et al. 2010, Buler and Moore 2011, La Sorte and Fink 2017). Migrating birds approaching coastal areas, for example, may enter the behavioral state necessary to attain fuel loads for long, non-stop flights over large waterbodies (Lindström and Alerstam 1986, Alerstam et al. 2003, Deutschlander and Muheim 2009, Smolinsky et al. 2013). Birds have also been observed to make detours running parallel to such barriers, frequently alternating between stopover and shorter migratory states to facilitate shorter barrier crossings (Alerstam 2001)

Changes in behavioral state can also be driven by characteristics that vary in time instead of space. Each spring and fall, for example, exogenous and endogenous circannual rhythms produce stimuli that initiate migratory behavior in birds that make seasonal movements between breeding and wintering ranges (Gwinner 1996). The behavioral traits of the migratory state are well-regulated in time and include the initial preparation phase, alternating periods of flight and stopovers, and a turning off phase upon arrival at the final destination (Ramenofsky and Wingfield 2007). Time of year and seasonal changes in ecological productivity play a strong role in influencing these behavioral transitions, particularly the shift from stationary to non-stationary movements involved in the onset of migration (Marra et al. 2005, La Sorte et al. 2015). Behavioral state diversity can also vary at a larger temporal scale, with different behaviors expressed by individuals during spring versus fall migration (Nilsson et al. 2013). There may also be considerably more behavioral variability, and not just different behaviors, during some periods of the year relative to others (Schmaljohann 2018). Movements during the non-breeding months, for instance, may alternate between relatively stationary states—e.g., foraging territories (Townshend 1985)—and more itinerant foraging strategies that require frequent relocation movements; this may be especially true for species that rely on ephemeral resources and must track changes in resource availability (Ruiz-Gutierrez et al. 2016).

Movement behaviors vary not only with changes in both space and time; there is also increasing evidence for a high degree of individual variation. Multiple studies have identified high degrees of intrinsic variation within movement patterns and space use that have been linked to, for example, personality type (Spiegel et al. 2016), foraging specializations (Patrick et al. 2013), energetic condition (Cohen et al. 2012), sex (Fudickar et al. 2013), age (Riotte-Lambert and Weimerskirch 2013), and ultimate breeding destination (Conklin et al. 2010). If this intraspecific variation in behavioral traits has at a partial genetic underpinning, it can have important evolutionary and ecological consequences. Certain phenotypes may be favored under particular environmental conditions, leading to evolutionary divergence and adaptation (Dingemanse et al. 2004, Smith and Blumstein 2008). Furthermore, individual variation within a species may allow it to occupy a wider range of spatiotemporal conditions and make it more resilient to extinction (Sih et al. 2012).

I examine behavioral complexity in the non-breeding movement paths of satellite-tagged Red-throated Loons to determine: (1) if distinct behavioral states could be identified using common methods and metrics developed for analyzing movement tracks of individuals, and (2) to what degree the expression of different behavioral classifications could be attributed to spatial, temporal, and individual effects. Red-throated Loons are long-distant migrants with an annual range encompassing approximately 40° of latitude. They are also opportunistic feeders that neither defend non-breeding territories nor closely follow a specialized prey item (Guse et al. 2009). Together, these traits make them an excellent species to capture large variation in movements and to examine how spatial, temporal, and individual circumstances influence behavioral state.

Methods

I used Argos telemetry data collected from 31 adult Red-throated Loons, captured on their wintering grounds offshore of the U.S. Mid-Atlantic Coast, between January and late March in 2012 – 2015. Animal handling and satellite transmitter implantation details can be found in Appendix A. Prior to the analysis, I censored the first 16 days post-release of each bird to minimize the effects of capture, handling, and surgery on behavior (Blomberg et al. 2018) (Appendix A). Next, I used R package *foieGras* to filter observed locations with a continuous-time state-space model to account for error in the Argos telemetry, estimate true animal locations, and to regularize the filtered locations to a 6-h time interval (Jonsen et al. 2019).

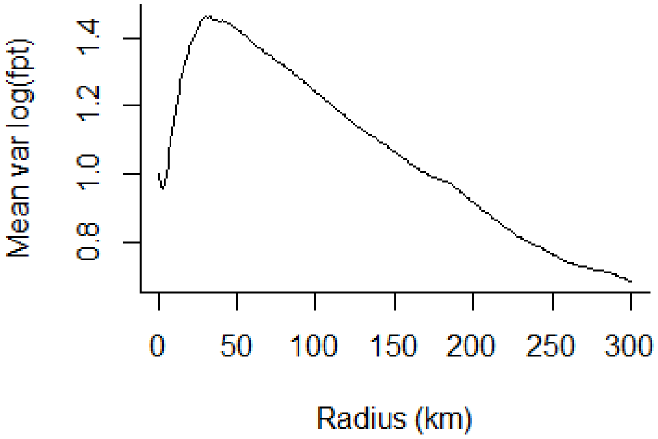
Regularized tracks for each loon were uploaded into the R package *adehabitatLT* and stored as trajectory objects for further analysis (Calenge 2006). Reduced data transmissions associated with the summer duty cycle (June 1 – August 31; see Appendix A for duty cycle details) resulted in spurious location estimates in the modeled tracks for this time period. Therefore, two trajectory objects were generated for each loon in *adehabitatLT*: one period representing late winter and spring migration (March 1 to May 31) and one for fall migration/early winter (September 1 to February 28); each will be referred to as “spring” and “fall”, respectively, from this point forward.

Calculating Movement Parameters

The following movement parameters were calculated for each individual’s seasonal trajectories using *adehabitatLT*: (1) step length: the Euclidian distance between consecutive locations; (2) relative (turning) angle: the angle between the current step and the consecutive one; (3) net squared displacement: the Euclidian distance between the current location and the first location of the trajectory; and (4) first passage time: the amount of time it takes for an individual to enter and leave a circle of fixed radius drawn around each location in the trajectory (Fauchald and Tveraa 2003).

First passage time summarizes both the velocity and tortuosity of an animal’s movements along the trajectory by measuring the amount of time it takes to pass through a circle of a given radius. Low first passage times indicate faster, more directed movement (e.g., commuting or migration behavior), while higher first passage times indicate more tortuous movement with higher turning angles—often termed area-concentrated search behavior (e.g., foraging; Barraquand and Benhamou 2008). The first step was to determine the appropriate scale of the analysis, i.e., the size of the radius around each location to measure passage time. I began by calculating first passage time for each location along each bird’s seasonal trajectories for radii ranging from 10 to 300 km by 1-km increments. The variance of the log-transformed first passage time was then computed and plotted against the corresponding radii to identify the peak in maximum variance. Area-concentrated search behavior, being the most tortuous of movement types, is associated with the greatest amount of variance in first passage time; therefore, the radius with the maximum variance is the scale that captures this behavior and is the scale used for the analysis. It is the scale at which the animal is interacting with its environment and within which the variance of many other classic movement types is captured (Fauchald and Tveraa 2003). I log-transformed first passage time to make the magnitude of the variance independent of the mean. I then identified a single scale to compare first passage times across all individuals and seasons by compiling the variances across both seasonal tracks of each bird and calculating the mean across all birds and tracks for each radius. The peak in those mean variances corresponded to a radius of 33 km (Figure 3.1); therefore, all first passage times in the results are based on a radius of 33 km in unit hours around each location.

Figure 3.1. Mean variance of log-transformed first passage times and corresponding radii (km) for the spring and fall analysis periods. The radius (x = 33 km) associated with the peak in mean variance was the scale used for calculations of first passage time, residence time, number of revisits, and time to return analyses.



Residence time, the time to return (each in hours), and the number of revisits were additional movement parameters calculated for each location at the 33-km scale using the R package *recurse*

(Bracis et al. 2018). Residence time is closely related to first passage time in that it measures time spent within a circle of a given radius around each location in an animal's trajectory; however, residence time allows for excursions outside of the circle that do not stop the measurement of time within the circle. The amount of time allowed outside of the circle before the clock is re-set is a user-defined threshold. It can be a useful comparison to first passage time to distinguish animals that are truly "encamped" within an area versus those that are patch foraging at larger scales. I selected 24 h as the cutoff time for the residence time analysis, given the temporal coarseness of the Argos data, to be certain that birds had truly left the area before resetting the clock. When an individual does not return to a given circle within 24 h, another clock is triggered: the time to return, which measures the amount of time it takes to re-enter the circle. Lastly, revisits are calculated for each point by counting the number of trajectory segments entering and exiting the circle; returns occurring within 24-h were not counted as new visits and all locations had a minimum of 1 "revisit" representing the initial visit.

Identifying Candidate Behavioral States

Estimated movement parameters described for all animal locations were compiled into two datasets according to seasonal trajectory: spring and fall. I then conducted a principal component analysis (PCA) on each seasonal dataset independently to simplify the metrics into uncorrelated dimensions using the R package *FactoMineR* (Lê et al. 2008). The data were standardized prior to the PCA so that the movement variables were on similar scales. To identify candidate behavioral states, I then conducted a hierarchical clustering analysis on the principal components using FactoMineR to identify groups of similar observations in each seasonal dataset, which I then defined as distinct behavioral states. I retained the number of principal components in each cluster analysis necessary to explain 80% of the original cumulative variation in behavior (Zuur et al. 2007). Ward's method was used to evaluate distances between clusters (Ward 1963).

Explaining Variance in Behavioral States

I used a random forest approach to explore how well spatial, temporal, and individual covariates predicted movement behavior state for each animal location in either the spring or fall tracks. Spatial candidates included latitude and longitude; temporal candidates included month and year; and individual characteristics included sex, subcutaneous fat level at capture (as an index of winter condition ranging from lowest level 1 to highest level 4), spring migration distance quartile (as an index of relative individual migratory distance), and individual identity (residual individual characteristics).

The random forest algorithm grows an ensemble of classification trees, each of which is based on a recursive, partitioning method that splits the data into smaller and smaller sets to identify a set of *if-then* logical conditions that can be used to predict or classify group membership. Each tree provides a classification for a given observation and the classification with the most "votes" across all trees in the forest "wins". My random forest analysis was based on unbiased conditional inference trees with subsampling (Hothorn et al. 2006), in the R package *party.* The data were first partitioned into a training set comprised of a random sample of 70% of the total observations that was used to train the model, and a test set made up of the remaining 30% of the dataset, which was used to validate the model. I assessed the ability of each of the candidate spatial, temporal, and individual predictors to classify behavioral state using variable importance values. Variable importance was assessed using R package *caret,* by calculating the difference in classification prediction accuracy of models with and without each predictor present (Strobl et al. 2007, Kuhn 2008).

Results

Location data was collected from 31 Red-throated Loons with abdominally implanted PTTs during the spring and fall periods of 2012 to 2015. The number of active transmitters varied across years: 2012 (n = 5); 2013 (n = 8); 2014 (n = 11); and 2015 (n = 7). The total number of locations for which reliable estimates of all movement metrics could be calculated was 7,919 for the spring period (March 1 to May 31) and 13,143 for the fall period (September 1 to Feb 28/9) across all years. Spring locations ranged from 34.9°N to 58.4°N and fall/winter locations ranged from 76.4°N to 34.0°N.

The first two principal components (PCs) of the spring and fall PCAs accounted for 52% and 48% of the total variation in their respective 7-variable datasets (Table 3.1). Residence time, first passage time, time to return, and number of revisits were the most important movement parameters in explaining variability in these first two dimensions across both seasons (Figures 3.2a and b). Net squared displacement and step length were weakly correlated with the first PC and similarly or more strongly correlated with PC4 and PC5 (Table 3.2). Relative angle was largely independent of the other movement parameters, being most correlated with and the only major contributor to PC3 in both the fall and spring. The first five PCs were needed to account for at least 80% of the cumulative variance in each season (spring: 89.5%; fall: 87.6%) and were retained for hierarchical cluster analyses.

Table 3.1. Eigenvalues, variance, and cumulative variance of principal components for spring and fall PCAs.

Season	Principal Component	Eigenvalue	Variance (%)	Cumulative variance (%)
Spring analysis	1	2.096	29.946	29.946
	2	1.536	21.937	51.883
	3	1.001	14.305	66.188
	4	0.867	12.388	78.576
	5	0.763	10.901	89.477
	6	0.512	7.313	96.790
	7	0.225	3.210	100.000
Fall analysis	1	2.255	32.212	32.212
	2	1.125	16.078	48.290
	3	0.999	14.267	62.557
	4	0.963	13.758	76.315
	5	0.790	11.291	87.606
	6	0.681	9.731	97.337
	7	0.186	2.663	100.000

Figure 3.2. Biplot of variables and their relationship with the first two principal axes in PCA analysis for the (a) spring and (b) analysis periods. Positively correlated variables are grouped together; negatively correlated variables are positioned on opposite sides of the plot origin. The distance of the arrows from the origin indicates how well each variable is represented by the first two PCs. Relative contribution (%) of variables in accounting for variability in each PC is indicated by the “contrib” gradient scale.

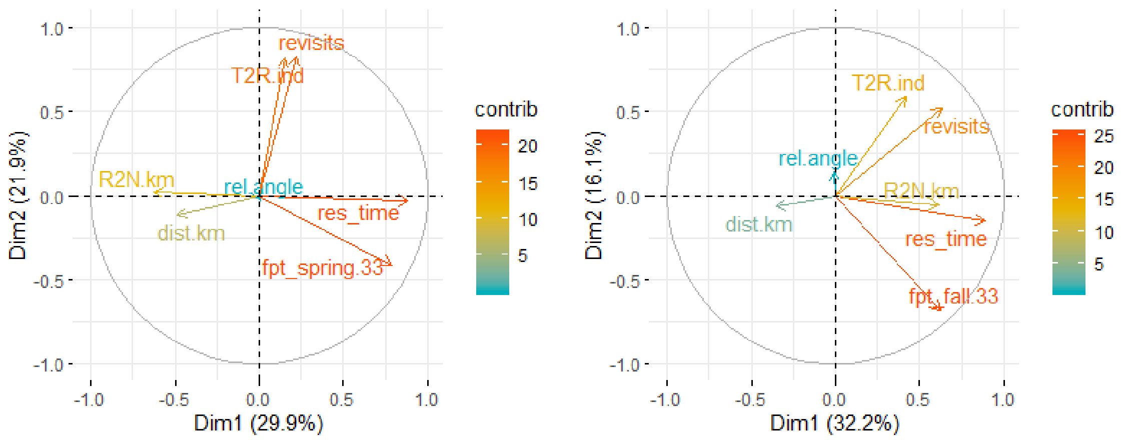

(a) (b)

Table 3.2. Contribution of variables in accounting for variability within each principal component (PC), expressed as a percentage.

	Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Spring	relative angle	<0.1	<0.1	99.0	0.7	0.2
	first passage time	29.3	11.2	<0.1	0.1	14.7
	number of revisits	2.4	44.4	0.1	4.1	0.7
	residence time	37.4	<0.1	<0.1	1.8	10.1
	time to return	1.1	43.4	<0.1	0.3	10.1
	net squared displacement	18.6	<0.1	<0.1	15.3	55.1
	step length	11.2	0.9	0.8	77.6	9.1
Fall	relative angle	<0.1	1.8	97.6	0.2	0.4
	first passage time	17.1	41.3	0.5	0.9	9.7
	number of revisits	17.8	23.7	0.2	5.2	11.8
	residence time	35.3	2.1	<0.1	0.4	1.2
	time to return	7.7	30.5	1.3	2.9	47.8
	step length	5.4	0.4	0.3	75.7	16.5
	net squared displacement	16.7	0.3	<0.1	14.6	12.7

Identifying Candidate Behavioral States

The cluster analysis identified three unique behavioral groups for spring and four for the fall season (Figure 3.3a and b). The spring period's cluster one (S1) was the most commonly exhibited behavior for the spring period and the spatial distribution of its occurrence was diffuse across the seasonal range for this part of the annual cycle (Figures 3.4 and 3.5). It can best be described as a "ranging and relocation" behavioral state, as it was characterized by step lengths of 5 to 23 km interspersed with stationary periods, at the 33-km scale, lasting 2 to 8 days, with mostly no returns to previously visited sites (Table 3).

Figure 2.3. Biplot of hierarchical cluster analysis of principal components results indicating three movement behaviors in (a) spring and four movement behaviors in (b) fall. Data points are color-coded according to movement behavior cluster classification.

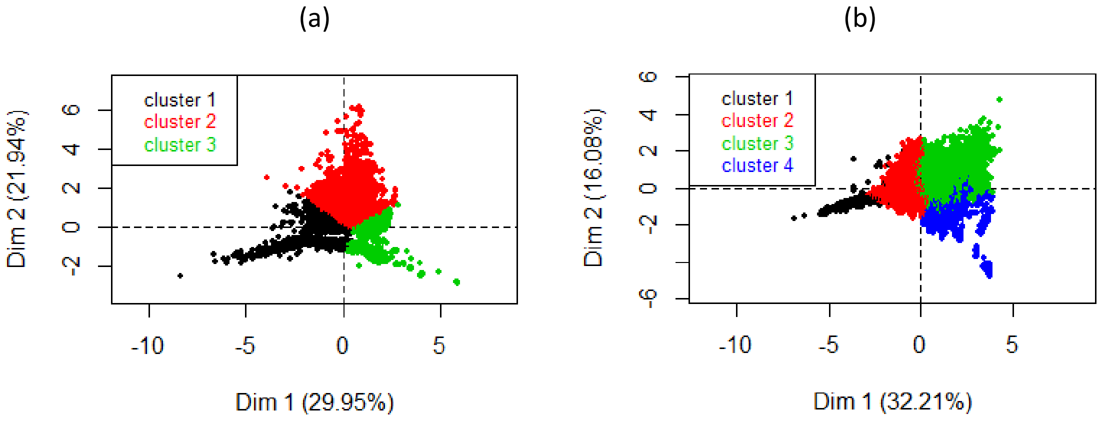


Figure 3.4. Frequency of spring movement behaviors by cluster (S1 = cluster 1, S2 = cluster 2, S3 = cluster 3) among all location points for the periods, March 1 to May 31, 2012 - 2015.

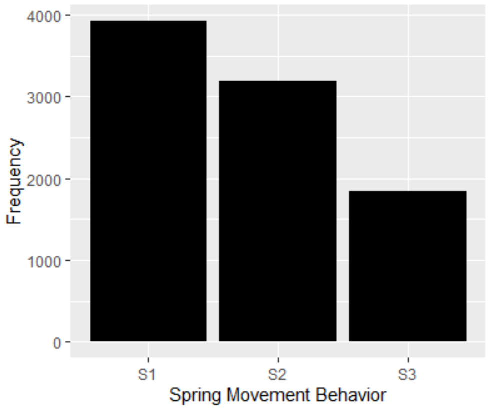


Figure 3.5. Spatial distribution of spring movement behavior one (S1) (N = 3,932) during the periods of March 1 to May 31, 2012 — 2015.

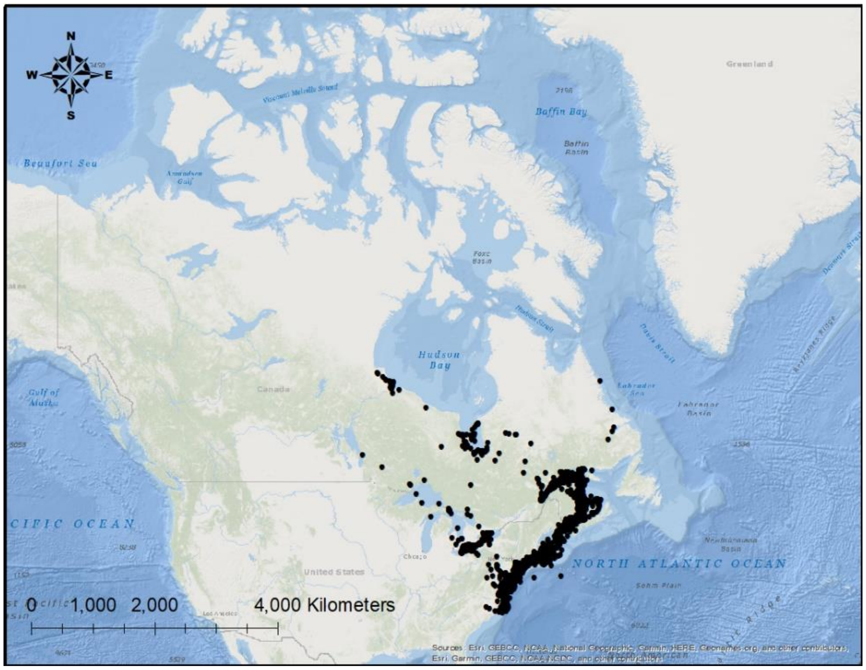
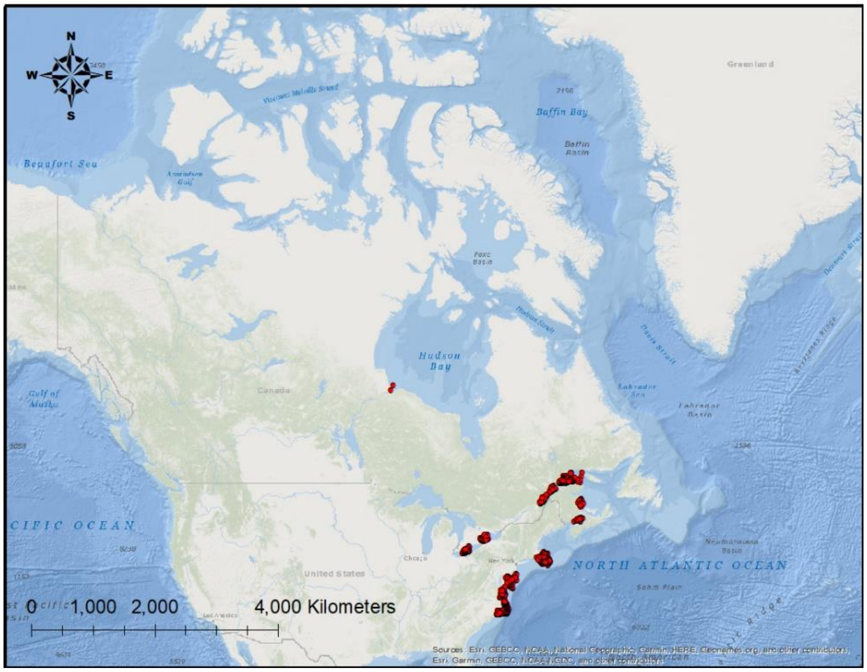


Table 3.3. Mean ± standard deviation and interquartile range of movement metrics by fall behavior class for Red-throated Loons in eastern North America during the periods of March 31 to May 31, 2012 — 2016.

	Spring Movement Behavior		
Movement Parameter	**S1 (n = 3,287)**	**S2 (n = 3,730)**	**S3 (n = 902)**
First Passage Time (hrs)	85.1 ± 74.5 (27.48 – 124.4)	143.9 ± 123.1 (61.10 – 180.6)	525.29 ± 292.5 (325.10 – 709.5)
Number of revisits	1.3 ± 0.6 (1.0 – 1.0)	3.6 ± 1.9 (2.0 – 4.0)	1.6 ± 0.9 (1.0 – 2.0)
Residence Time (hrs)	146.0 ± 136.3 (42.6 – 200.8)	462.2 ± 262.7 (239.2 – 703.1)	810.3 ± 232.9 (722.0 – 940.9)
Time to return (hrs)	115.3 ± 178.4 (81.1 – 224.1)	50.7 ± 103.7 (35.8 – 82.1)	138.6 ± 166.9 (131.0 – 254.4)
Step length (km)	28.6 ± 59.2 (4.7 – 22.6)	10.8 ± 17.1 (4.1 – 12.7)	5.9 ± 5.9 (2.5 – 7.4)
Relative angle (°)	(-0.1 ± 1.4 (0.6 – 0.6)	(-0.1 ± 1.5 (-0.8 – 0.7)	<0.1 ± 1.6 (-0.9 – 0.9)
Net squared displacement (km)	1170.1 ± 812.7 (460.9 – 1947.5)	682.3 ± 677.5 (63.1 – 1177.7)	282.4 ± 395.1 (19.0 – 259.6)

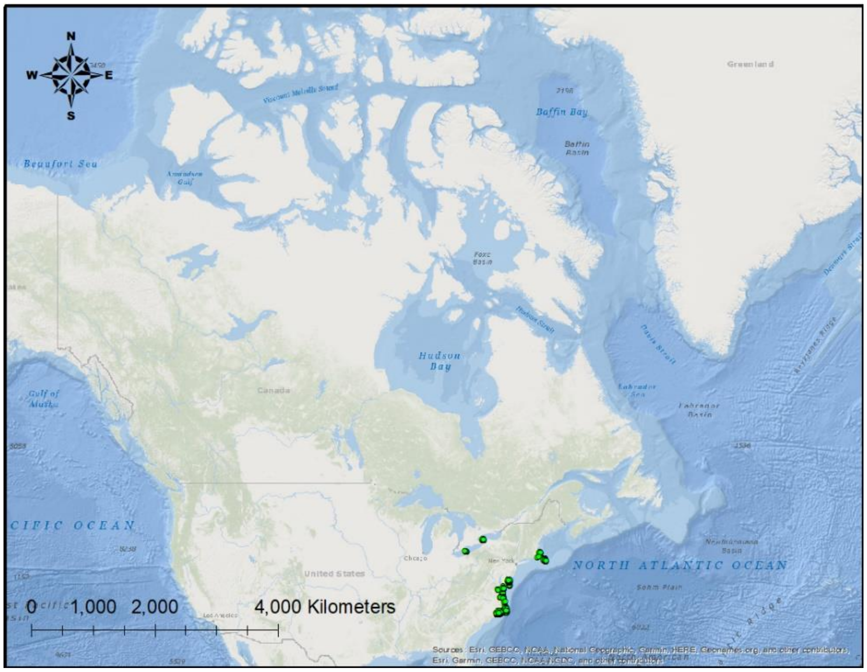
Cluster S2 was also commonly expressed, but was more clustered in its spatial distribution. It aligns best with an “area-concentrated search” behavioral mode (Figure 3.6). Most first passage times for birds in this behavioral mode were similar to S1 (between 2 and 7 days), while most residence times were longer (10 to 30 days). The difference between first passage and residence times indicates birds in this behavioral mode frequently ranged beyond the 33-km radius, thereby resetting the first passage time clock, but re-entered the circle within 24-hrs, which kept the residence time clock from resetting. Individuals also tended to range beyond the 33-km scale for periods longer than 24-hrs while in this behavioral mode, however, as is evidenced by the higher number of revisits and low time to return estimates. The lower step distance relative to the first cluster also reflects the lack of any relocation behaviors to more distant areas.

Figure 3.6. Spatial distribution of spring movement behavior two (S2) (N = 3,192) during the periods of March 1 to May 31, 2012 – 2015.



The third cluster in the spring analysis (S3) also resembled an area-concentrated search behavior mode and it overlapped spatially with cluster S2’s more southern distribution points; however, S3’s occurrences were even more tightly clumped at fewer, more southern locations (Figure 3.7). The scale of movements for individuals exhibited this behavioral mode was smaller than it was for S2. Individuals exhibiting S3 were generally stationary within the 33-km radius for periods of 2 to 4 weeks, while moving the smallest step lengths (~2.5 to 7 km) of the three spring clusters. Brief (< 24-hr) excursions outside the circle after the initial 2 to 4-week stationary period occurred (evidenced by residency times often lasting 4 to 6 weeks) but were infrequent, given the limited number of revisits associated with this behavior.

Figure 3.7. Spatial distribution of spring movement behavior three (S3) (N = 1,840) during the periods of March 1 to May 31, 2012 — 2015.



The first two clusters identified in the fall analysis were both consistent with ranging and relocation behavioral modes. The first cluster was similar to S1, yet occurred at a much larger spatial scale. It was characterized by long, unidirectional movements and high velocities based on first passage and residency times of 1 to 3 hours, minimal revisits, and typical step lengths of 200 to 400 km (Table 3.4). This behavior was exhibited infrequently, yet it was diffuse in its spatial distribution across the fall migration routes (Figures 3.8 and 3.9). Conversely, the second fall behavioral cluster (F2) occurred with high frequency and exhibited a dense spatial distribution throughout the migratory and winter range

(Figure 3.10). It was more directly comparable to the small-scale ranging and relocation behavior observed in spring (S1), in that step lengths were generally 4 to 13 km and interspersed with stationary periods lasting several days to two weeks.

Table 3.4. Mean ± standard deviation and interquartile range of movement metrics by fall behavior type for Red-throated Loons in eastern North America during the periods of March 31 to May 31, 2012 — 2016.

	Movement Behavior Category			
Movement Parameter	**F1 (n = 300)**	**F2 (n = 10,657)**	**F3 (n = 5,808)**	**F4 (n = 1,823)**
First Passage Time (hrs)	4.1 ± 12.1	114.9 ± 104.4	206.3 ± 157.9	1,070.6 ± 484.2
	(1.25 - 2.92)	(44.63 - 153.06)	(86.6 - 288.2)	(728.3 - 1,359.9)
Number of revisits	1.1 ± 0.8	2.2 ± 1.5	6.8 ± 3.5	2.6 ± 1.8
	(1.0 - 1.0)	(1.0 - 3.0)	(4.0 - 9.0)	(2.0 - 3.0)
Residence Time (hrs)	18.6 ± 106.1	241.6 ± 241.8	983.2 ± 548.2	1,404.6 ± 418.1
	(1.2 - 3.1)	(67.1 - 331.7)	(551.4 -1332.4)	(1,055.1 - 1,775.2)
Time to return (hrs)	73.5 ± 74.7	93.2 ± 111.2	81.4 ± 125.9	107.1 ± 123.2
	(44.2 – 865.6)	(71.3 – 224.19)	(64.5 - 143.6)	(65.1 - 681.5)
Step length (km)	312.1 ± 144.6	12.9 ± 19.1	7.9 ± 8.1	4.7 ± 3.9
	(207.2 - 370.2)	(4.1 - 13.1)	(3.2 - 9.8)	(2.1 - 6.3)
Relative angle (°)	(-0.1 ± 0.6)	(-0.1 ± 1.2)	0.1 ± 1.3	(-0.1 ± 1.2)
	(-0.1 - 0.1)	(-0.5 - 0.4)	(-0.5 - 0.5)	(-0.6 - 0.4)
Net squared displacement (km)	2231.3 ± 1,420.7	2,000.9 ± 1,417.5	4,363.2 ± 1,116.1	4,076.2 ± 1,170.1
	(1,030.6 – 3,339.3)	(1,024.6 – 2,775.4)	(3,709.0 – 5,175.8)	(3,300.5 + 4,861.1)

Figure 3.8. Frequency of fall movement behaviors by cluster (1 = large-scale (> 33 km) ranging and relocation; 2 = small-scale (< 33 km) ranging and relocation; 3 = large-scale area-concentrated search; 4= small-scale area-concentrated search among all location points for the periods, March 1 to May 31, 2012 - 2015.

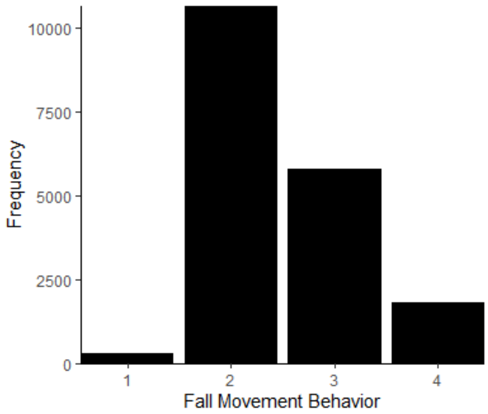


Figure 3.9. Spatial distribution of fall movement behavior one (F1) (N = 300) during the periods of September 1 to February 28, 2012 – 2016.

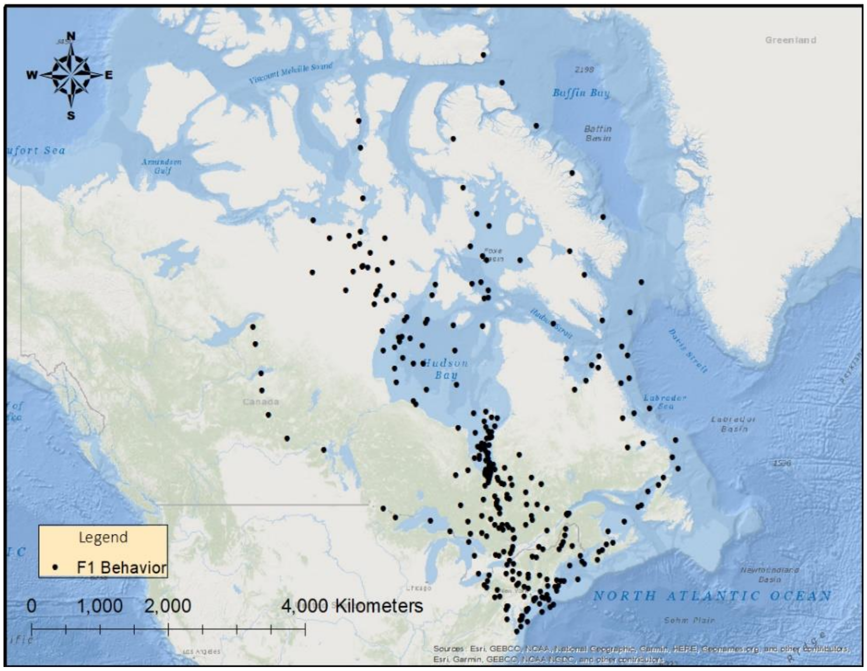
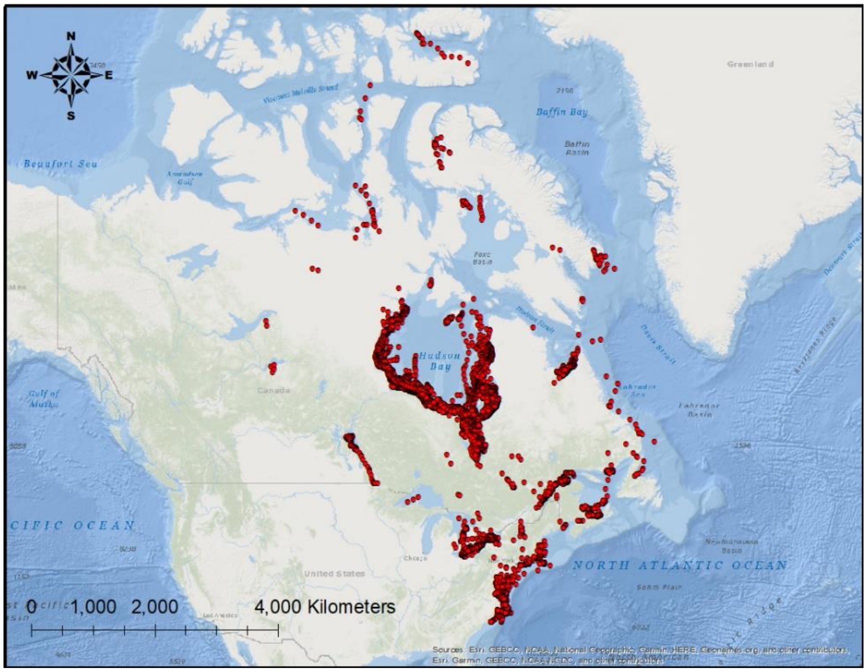
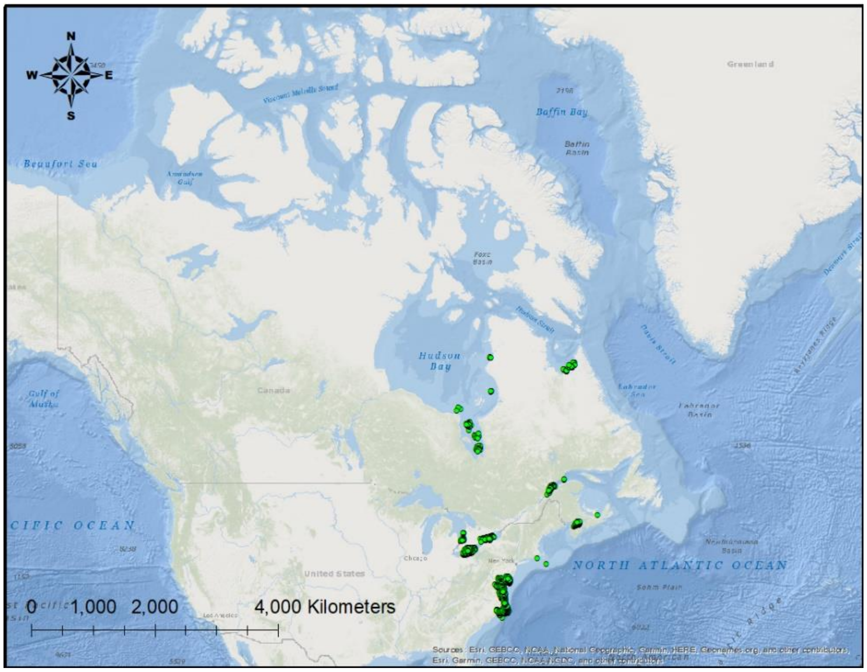


Figure 3.10. Spatial distribution of fall movement behavior two (F2) (N = 10,657) during the periods of September 1 to February 28, 2012 — 2016.



Cluster F3 was less common and more concentrated in its spatial distribution compared to cluster F2; however, the density of points was greater in the wintering area (Figure 3.11). It was similar to the larger-scaled area-concentrated search behavior in spring (S2), with slow first passage times of 4 to 12 days, and even longer residence times of 3 to 8 weeks, indicating that birds were moving beyond the 33-km radius within a given 24-hr period. Additionally, the high number of revisits and average time to returns of 3.5 days is suggestive of area-concentrated search behavior, but at a scale larger than 33-km.

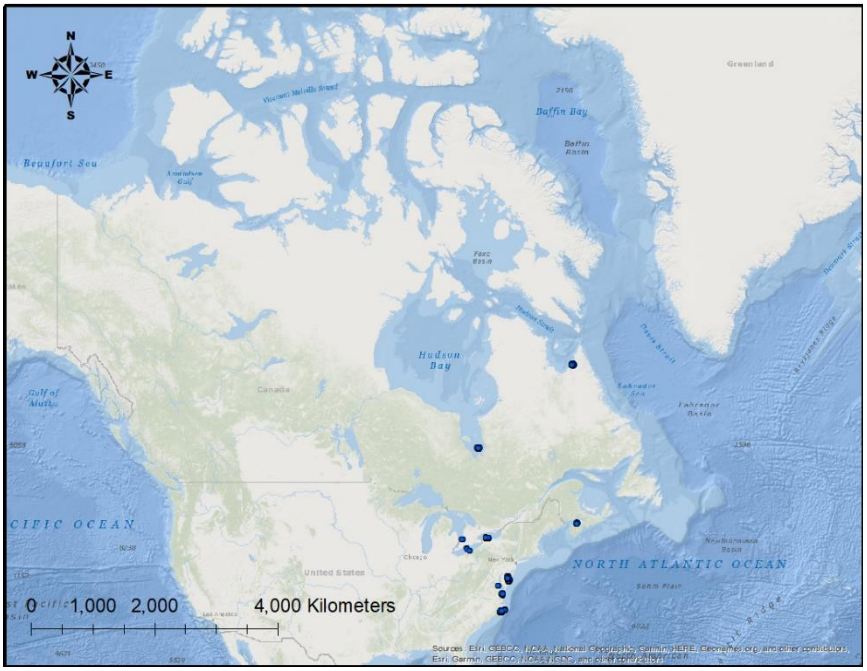
Figure 3.11. Spatial distribution of fall movement behavior three (F3) (N = 5,808) during the period of September 1 to February 28, 2012 — 2016.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

The fourth fall cluster (F4) occurred in smaller numbers and in tight clumps in only a few locations across the range (Figure 3.12). It was characteristic of the smaller-scale area-concentrated search also observed in spring (S3), with first passage times of 4 to 8 weeks, residency times of 6 to 11 weeks, limited revisits, and step lengths of 2 to 6 km. The similarity between first passage and residency times, as well as the small average number of revisits, suggests that individuals remained relatively stationary within the 33-km scale when exhibiting these behavioral modes.

Figure 3.12. Spatial distribution of fall movement behavior four (F4) (N = 1,823) during the periods of September 1 to February 28, 2012 — 2016.



Explaining Variance in Behavioral States

Individual identity and spatial location were important predictors of behavioral mode across both seasons. The random forest model for the spring period indicated that individual identity had the greatest importance among all of the intrinsic, spatial, and temporal variables. Permuting identity resulted in a 29% decrease in model accuracy. Both of the spatial predictors (latitude = 15%, longitude = 12%) and one of the temporal predictors (month = 14%) were the next best predictors, and the remaining variables (year, sex, total migration distance quartile, and wintertime subcutaneous fat level) had negligible effects on model accuracy (Figure 3.13). For the fall period, latitude had the greatest effect on prediction accuracy, with a 26% reduction in model accuracy upon permutation (Figure 3.14). Individual identity had the next greatest effect with a decrease in accuracy of 20%, while month (8%) and longitude (6%) had marginal effects, and the remaining variables had negligible effects. Interestingly, month had a stronger role in predicting spring behavioral states, even though the spring analysis only occurred over three months, while the fall analysis occurred over six.

Figure 3.13. Importance of variables used to predict spring movement behavior classification in random forest model. Variable importance represents the percentage decrease in model accuracy when the corresponding variable is permuted. Predictor variables included individual identity (ID), latitude (Lat), month, longitude (Lon), year, winter subcutaneous fat score (fat), sex, and the spring migration distance quartile (Q).

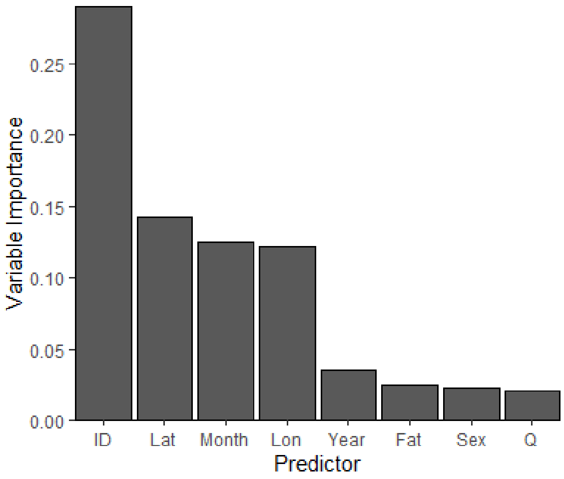
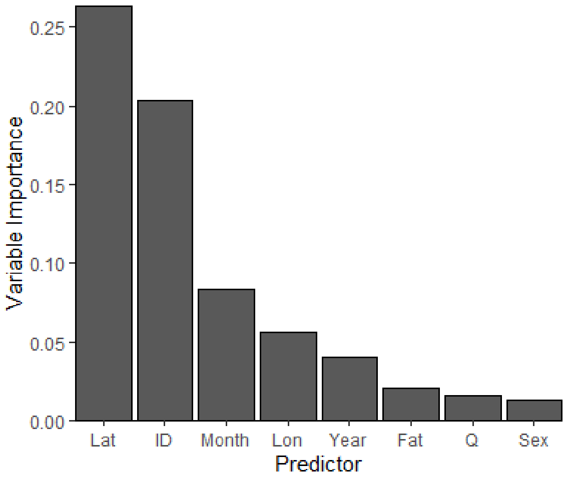


Figure 3.14. Importance of variables used to predict fall movement behavior classification in random forest model. Variable importance represents the percentage decrease in model accuracy when the corresponding variable is permuted. Predictor variables included identity (ID), latitude (Lat), month, longitude (Lon), year, winter subcutaneous fat score (Fat), sex, and one-way migration distance quartile (Q).



The four large modes of behavior were predicted partially by spatial and temporal variables. Large-scale ranging and relocation behavior (F1) (fall only) was limited in occurrence but was found generally equally across all latitudes and occurred most often in September and November (Figures 3.15 and 3.16), as would be expected of a migratory behavioral mode. Importantly, I identified no similar behavioral mode in the spring. The northward migration was instead accomplished using only the small-scale ranging and relocation behavior (S1), which had a positive relationship with increasing latitude, occurred more frequently in April and May, and generally increased as area-concentrated search behavior decreased (Figures 3.17 and 3.18). The same patterns were also true for the small-scale ranging and relocation behavior during the fall (F2), except that it occurred most frequently in September, October, and November.

Figure 3.15. Proportion of location points classified as each fall movement behavior type by latitude. Cluster 1 represents large-scale (> 33 km) ranging and relocation behavior, cluster 2 represents small-scale (< 33 km) ranging and relocation behavior, cluster 3 represents large-scale area-concentrated search behavior, and cluster 4 represents small-scale area-concentrated search behavior. The width of the bars is scaled according to sample size for each interval of latitude, i.e., latitudes with larger sample sizes have wider bars.

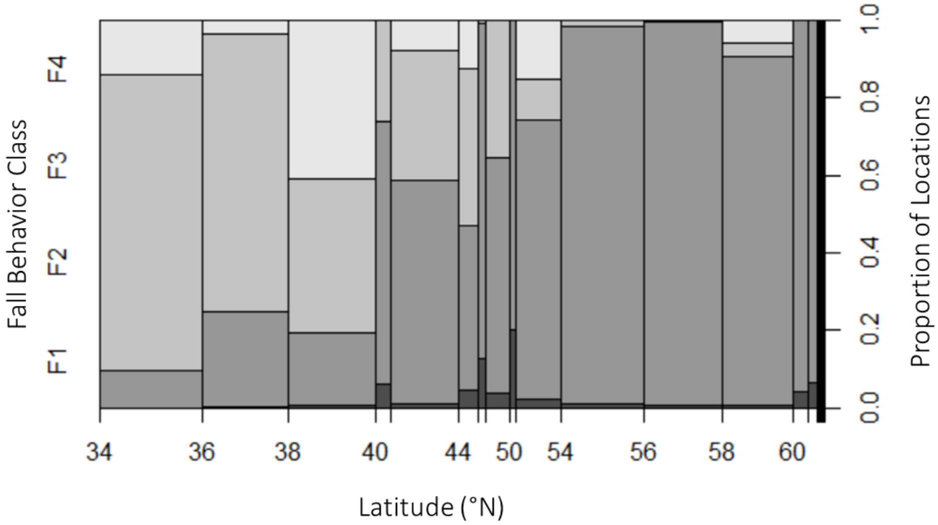


Figure 3.16. Proportion of location points classified as each fall movement behavior type by month. Cluster 1 represents large-scale (> 33 km) ranging and relocation behavior, cluster 2 represents small-scale (< 33 km) ranging and relocation behavior, cluster 3 represents large-scale area-concentrated search behavior, and cluster 4 represents small-scale area-concentrated search behavior. The width of the bars is scaled according to sample size for each month, i.e., months with larger sample sizes have wider bars.

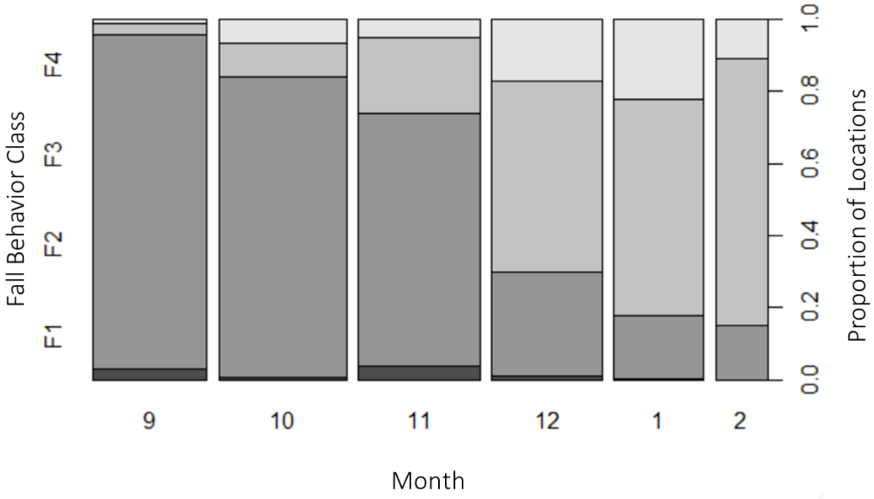


Figure 3.17. Proportion of location points classified as each spring movement behavior type by latitude. Cluster 1 represents small-scale (< 33 km) ranging and relocation behavior, cluster 2 represents large-scale (> 33 km) area-concentrated search behavior, and cluster 3 small-scale area-concentrated search behavior. The width of the bars is scaled according to sample size for each interval of latitude, i.e., latitudes with larger sample sizes have wider bars.

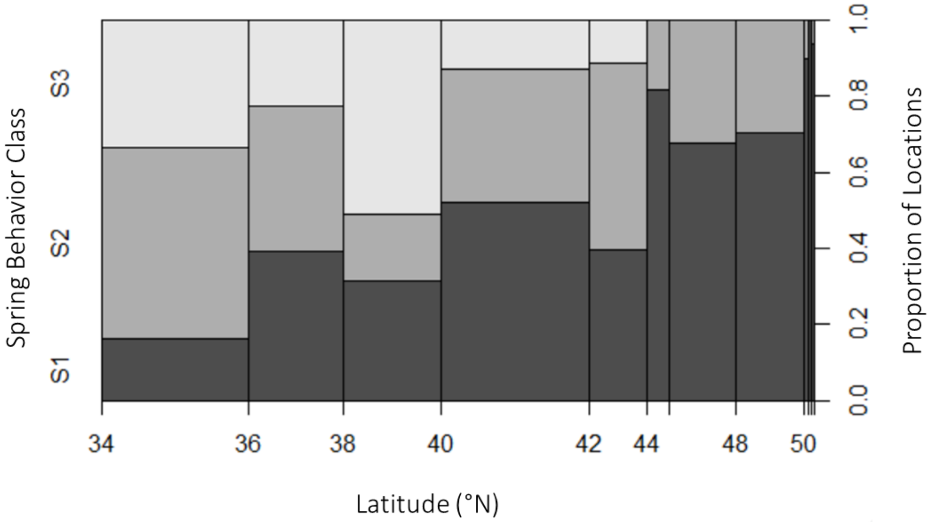
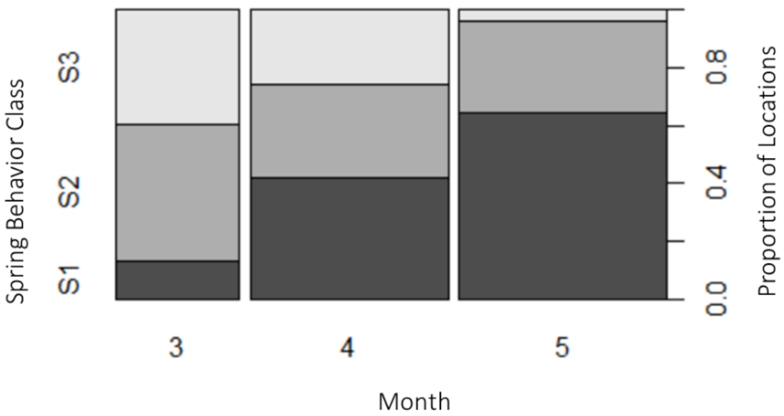


Figure 3.18. Proportion of location points classified as each spring movement behavior type by individual (ID). Cluster 1 represents small-scale (< 33 km) ranging and relocation behavior, cluster 2 represents large-scale (> 33 km) area-concentrated search behavior, and cluster 3 small-scale area-concentrated search behavior. The width of the bars is scaled according to sample size for each month, i.e., months with larger sample sizes have wider bars.



Conversely, the small-scale area-concentrated search modes (S3, F4) did not occur north of 44° N latitude, except for two locations during the fall, and was most prevalent on the wintering grounds and early spring migration in March and April. Large-scale area-concentrated search (S2, F3), on the other hand, was common across all latitudes and occurred with equal frequency in all months of the spring period. Nearly all behavioral modes, however, occurred at some frequency in every month and across most, if not all, latitudes for both the fall and spring analyses.

Much of the variation in behavioral mode, however, was not explained by location or the time of year. Individuals consistently varied in their expression of ranging and relocation (S1, F1, F2) versus area-concentrated search (S2, S3, F3, F4) regardless of month or latitude, and some individuals also independently varied the scale of their area-concentrated search behavior between small- (S3, F4) and large-scale (S2, F3) modes more than others (Figures 3.19 and 3.20). The frequency of area-concentrated search behavioral modes ranged from nearly zero in some individuals to ~70% in others. Similarly, the frequency of small-scale ranging and relocation behaviors (S1, F2) ranged from 16% to 91% among individuals.

Figure 3.19. Proportion of location points classified as each fall movement behavior type by individual (ID). Cluster 1 represents large-scale (> 33 km) ranging and relocation behavior, cluster 2 represents small-scale (< 33 km) ranging and relocation behavior, cluster 3 represents large-scale area-concentrated search behavior, and cluster 4 represents small-scale area-concentrated search behavior. The width of the bars is scaled according to sample size for each individual, i.e., individuals with larger sample sizes are wider bars.

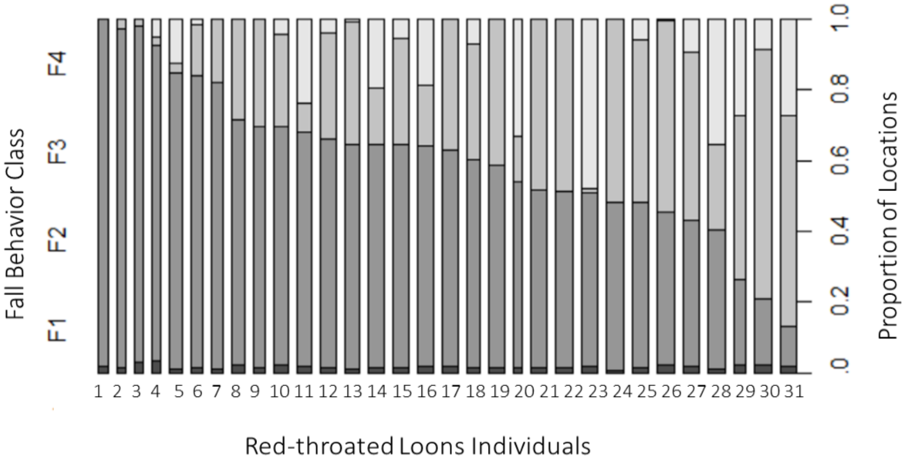
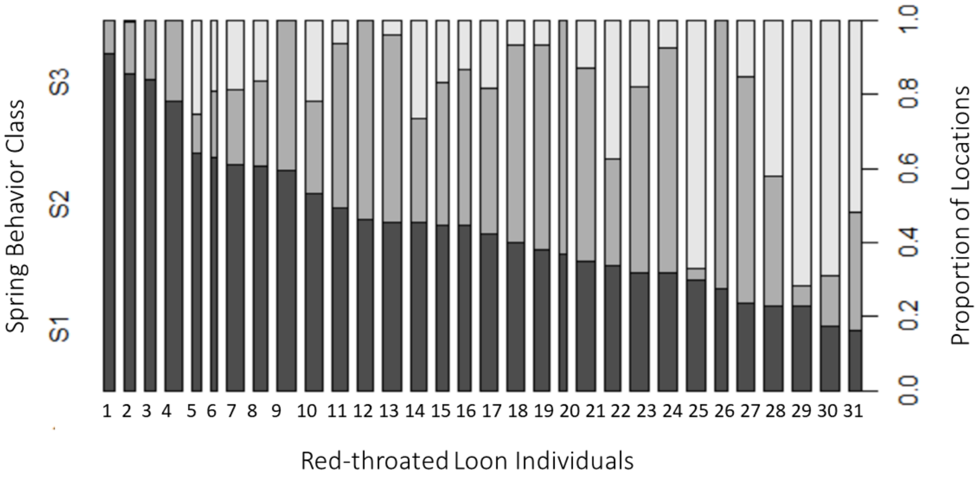


Figure 3.20. Proportion of location points classified as one of three spring movement categories. Each vertical bar represents an individual red-throated loon. Cluster 1 (dark gray) represents small-scale (< 33 km) ranging and relocation behavior, cluster 2 (medium gray) represents large-scale (> 33 km) area-concentrated search behavior, and cluster 3 (light gray) small-scale area-concentrated search behavior. The width of the bars is scaled according to sample size for each individual, i.e., individuals with larger sample sizes are wider bars.



Discussion

Two behaviors, ranging and relocation and area-concentrated search, occurring at both large (> 33 km) and small (< 33 km) scales were distinguished for non-breeding Red-throated Loons in eastern North America. Large-scale ranging and relocation behaviors, which consisted of birds moving several hundreds of kilometers between 6-hr intervals, was exhibited infrequently, but consistently by all birds during some part of their fall migration. Such large-scale movements within well-defined routes among seabirds are thought to correspond with favorable wind conditions that help minimize the cost of flight (Furness and Bryant 1996, Weimerskirch et al. 2000). The absence of this behavior in the spring migration data is at least partially a result of the data ending on May 31, which was necessary due to the switchover to a battery-saving, but less frequent, duty cycle for the summer period. Such large jumps in spring could have occurred in early June, following ice-out of nesting waterbodies, when birds are believed to quickly move north to breeding areas from staging areas in the St. Lawrence River, James Bay, and the lower Great Lakes (Stenhouse et al. 2020). Importantly, however, we have northward movements recorded from 34°N to 52°N, the same area over which many of the large-scale southern migratory jumps were detected during the fall.

The small-scale ranging and relocation behavioral mode, on the other hand, occurred at a much slower pace, where short, directed movements were interspersed with frequent brief stopovers. Birds stayed within one 33-km area for several days and up to two weeks, potentially to rest and renew energy sources while taking advantage of areas with high prey availability. This behavioral mode was detected independently by the cluster analysis in both the fall and spring months. Stopovers play an important ecological role during the migration period, particularly for large migrants, such as loons, with high fuel demands for flapping flight (Alerstam and Hedenstrom 1998, Drent et al. 2007). Larger-bodied birds minimize energy costs by making frequent stops and shorter flights and are expected to utilize sites along the migration route where foraging is most profitable and maximum fuel deposition is attained (Alerstam 2011). This behavioral mode occurred more frequently at higher latitudes during the months when fall and spring migration were well underway; however, while less frequent, this movement type also occurred throughout the winter months. Indeed, it was uncommon for birds in this study to settle into an established home range for the winter, but rather they often remained in a state of slow, yet perpetual ranging and relocation during the entirety of the non-breeding season. As such, while Red-throated Loons exhibit a behavioral state that allows them to successfully complete migration, it is not limited to the migratory period. Indeed, the birds appear to accomplish migration simply by taking a behavior common across the non-breeding period and modifying it slightly: by relocating consistently in a single direction. This pattern suggests how the evolution of a limited number of behaviors might modify movement states to allow for the origin of migration.

Area-concentrated search behavior was commonly displayed at small (< 33 km) and large (> 33 km) scales during the winter months and, in more concentrated occurrences, along both the spring and fall migration routes. Again, the cluster analyses independently identified these two modes in both seasons. Large-scale area-concentrated search was characterized by extended stays of multiple weeks, where birds often moved beyond the 33-km radius but frequently returned and did not leave the larger area.

Seabirds are highly mobile marine predators that utilize a variety of strategies to track prey through a highly heterogenous environment (Weimerskirch 2007, Thiebault et al. 2014). Heterogeneity in prey distributions and abundance likely occurs because of behavioral factors, e.g., shoaling/swarming, and responses to physical forcing processes (Santora et al. 2014). For instance shelf edges, fronts, and upwelling zones may produce conditions that attract or aggregate prey and make them more available for catching more consistently over time (Shealer 2002). High-density aggregations of prey at small scales that are nested within low-density, large-scale patches create a hierarchical system, whereupon predators must adjust their search radius accordingly to increase encounter rates (Fauchald 1999).

Given the ephemeral nature of the spatial distribution of pelagic schooling fish, it is reasonable to hypothesize that movements beyond the 33-km radius while in area-concentrated search mode are responses to declining encounter rates with prey at that scale.

Movements may be random and exploratory when resources lie outside of the perceptual range (Fauchald 1999); however, multiple studies have also indicated the role of memory in seabird foraging activities based on their tendency to return to reliable foraging locations (Davoren et al. 2003, Montevecchi et al. 2009, Pettex et al. 2010, Regular et al. 2013). Furthermore, Goyert et al. (2015) suggested that spatial memory of areas with predictable prey availability may be especially important for foraging specialists, as compared to generalists that tend to feed in flocks and rely more on social cues for information transfer of current prey availability. The tendency for Red-throated Loons in this study to make repeated visits (up to 15) to certain sites supports the role of spatial memory in their foraging strategy. Small, loose flocks of 8 to 10 foraging Red-throated Loons have been observed in winter along the East Coast of the United States, and up to 12 have been reported in one gill net at a time (Rizzolo et al. 2020); however, they are often solitary at sea (pers. obs). Little is known about their winter diet specificity in the western Atlantic Ocean, but they are known to consume largely small forage fish, such as capelin, sand lance, and cod (3 – 25 cm) in Europe. While they may be opportunistic in their selection of small forage fish, it is unlikely they are capable of consuming as wide a range of fish sizes as other larger-bodied seabirds (Montevecchi et al. 2009), and likely must concentrate foraging in areas where these fish are common.

Foraging theory predicts that the detection of aggregations of prey in restricted space should correspond with adjustments in movement behavior, such as increased turning rates and shorter step lengths (Fauchald 1999, Fritz et al. 2003). Longer first passage times arise as a result of such increases in tortuosity, as was observed for the smaller scale area-concentrated search behavior. This behavior was exhibited most often in winter, but also overlapped with some locations along the migration route, interspersed with either of the larger-scale behavioral modes. Birds exhibiting the small-scale area-restricted mode confined all their activities to the 33-km scale for periods lasting up to two months. Transitions from interpatch movements to traditional intrapatch "home-ranging" movements, where the individual confines activities to familiar places that are close together, are likely responses to environmental conditions, but may also be linked to the individual's internal state and condition (Fryxell et al. 2008).

Individual identity and latitude were the most influential variables for both seasons among the intrinsic, spatial, and temporal predictors of movement behavior tested in this study. Individuals varied in the amount of time they allotted to different movement behaviors, particularly in their tendency to engage in small-scale versus large-scale area-concentrated search modes. Differences among individuals also existed, however, in the proportion of time they spent in small-scale ranging and relocation behavior, with some individuals spending far more time continually "on the move" rather than settling into any one area for extended periods. The tendency for some individuals to remain this way throughout the winter months provides evidence for the idea of winter "floaters" in the mid-Atlantic Red-throated Loon population. For some species that winter in areas with patchily distributed resources, one strategy of habitat use may be observed where certain individuals, termed "floaters", use disproportionately larger areas relative to the average winter home range of more sedentary individuals within the population (Brown and Long 2007). Sedentary individuals may possess greater site-specific knowledge allowing them to efficiently exploit resources, thereby depressing available resources, and forcing floater individuals to move on to a new site or return to a previous site where it successfully foraged (Spencer 2012). On the other hand, this behavior may allow floaters to more efficiently exploit seasonal variation in food availability (Brown and Sherry 2008). Regardless of the motivations behind sedentary and floater non-breeding strategies, the notion that migration behavior ends when one arrives at a clearly defined area, whereupon wintering behavior begins, is not supported by this study.

Further, there were not clearly two types of individuals, but a gradient of behavioral types between sedentary and floater endpoints.

There are a number of mechanisms that would result in consistent individual differences like those reported here. Prey selection, for example, may vary across individuals as a result of differences in body condition or energetic needs, thereby resulting in movement differences related to whether selected prey species are clumped or more uniform in their distribution (Austin et al. 2004). Personality differences among individuals, such as boldness, have also been linked to intraspecific variation in movement behaviors within populations; specifically, bolder animals are more willing to take risks and explore unfamiliar environments (Mettke-Hofmann et al. 2005, Cote et al. 2010, Chapman et al. 2011). Furthermore, there is some evidence that behavioral differences in exploratory behavior are linked to heritable genetic variation, and these traits often correlate with other suites of behaviors that ultimately determine how individuals respond to environmental challenges throughout life (Drent et al. 2003, Dingemanse et al. 2004, Patrick et al. 2013). Differences in the tendency for some individuals to show different frequencies in behavioral mode could also be related to age and experience. Life-history theory suggests that individuals with greater future reproductive potential will be more risk-averse than those with lower reproductive potential (Wolf et al. 2007). Therefore, it is plausible that older individuals within the population are more willing to take risks in search of foraging areas with an abundance of high-quality prey, and when that risk turns out to be profitable, it becomes the primary foraging strategy of that individual. Age measurements beyond “after-third year” were not possible in this study and loons have been reported to live as long as 24 years (Rizzolo et al. 2020); however, other studies have indicated a positive relationship between foraging strategy and prey quality with age in seabirds, particularly during periods when foraging conditions are poor (Weimerskirch et al. 2005, Navarro et al. 2010, Haug et al. 2015). These competing hypotheses of intrinsic condition, genetic variation, and developmental or learned age-based changes are not mutually exclusive, and disentangling their relative importance would take more careful study with greater information on individuals.

I should note that variation in capture date among individuals may have contributed to some of the apparent differences in frequency of exhibited behaviors by certain individuals. Specifically, individuals captured later in the season have fewer data points during the early spring, and thus could inflate their individual proportion classified as small-scale ranging and relocation, which is more typical of migration, as they did not have the opportunity to exhibit behaviors more typical of earlier months. Approximately one-third of the loons in the analysis were captured after March 15; however, those birds show similar variability to the remaining two-thirds of birds in terms of the proportion of time allotted to each behavioral category. Therefore, I do not consider these small differences in sample size to be influential in the main findings of this study.

Individual variation was less important in predicting movement behavior type during the fall season, which may indicate less behavioral flexibility during this period compared to the spring, if the decrease in relative predictive power isn't explained by the effect of capture date on spring behavioral variation. In the fall, latitude was the greatest predictor of the amount of time individuals spent within a given area, the size of that area, and the degree to which they moved to new areas. Small-scale ranging and relocation behavior was the predominant behavior exhibited in fall and it occurred across the latitudinal range of the analysis period; however, with the exception of relatively few large-scale ranging and relocation movements, it was the only movement type used north of 54°N latitude.

One potential mechanism that could explain both an increased consistency of all individuals in the fall and smaller scale movements in the northern portion of the fall migration corridor is the fall molt. My data show that most Red-throated Loons move to northern Hudson Bay immediately following the breeding season in late August/early September and then follow both coastlines slowly south to James Bay, at its southern end, sometime in late October/early November. The timing of these movements potentially aligns with the simultaneous molt of flight feathers that leaves individuals flightless for 3 – 4 weeks (Hohman et al. 1992), which Red-throated Loons are thought to undergo during fall migration (Pyle 2008). Molt migration, where birds depart the breeding grounds in late summer or fall and travel to specific areas to molt, is well-documented in waterfowl (Bowman and Brown 1992, Flint et al. 2000, Savard et al. 2007) and to some degree in shorebirds (Jehl 1987, Barbaree et al. 2016). Red-throated Loons, however, are unique among loons in molting during fall migration, as the other *Gavia* species molt in late winter, just prior to the start of spring migration. Individuals in this study, however, did not remain in any one area for the requisite period of time needed to undergo a complete simultaneous flight feather molt until later in migration. Indeed, more stationary behaviors were more common in November, when birds were in James Bay, the lower Great Lakes, and the St. Lawrence River. Most individuals, however, were engaging in large-scale, as opposed to small-scale, area-concentrated search movements in November, which would not be feasible during flightless periods. Furthermore, not all individuals in the sample had an extended stationary period later in migration, which leaves questions unanswered regarding the species' molt strategy and location.

Conclusions

Red-throated Loons exhibited a high degree of individual variation in movement behavior during the non-breeding season. Individuals differed in their tendency to be intensive versus extensive in their movement behaviors, which corresponded with individual differences in the scale of their use of the landscape. Location and time of year were also important factors in determining behavior, with more stationary behavior occurring during the winter months and at lower latitudes. Movement behavior, however, was not discrete in its use according to "season" and few individuals were alike in the proportion of time they spent in any category. I independently identified three behavioral states across two different portions of the year, and these states were observed inside and outside of the migratory period. These results have important consequences for the role of intraspecific behavioral variation in the ecology and evolution of movement.

CHAPTER 4

VARIABLE INFLUENCES OF PRIMARY, SECONDARY, AND INTRINSIC MIGRATORY CUES ON THE SPRING MOVEMENT BEHAVIOR OF A SEABIRD ACROSS ITS MIGRATORY ROUTE

Introduction

Long-distance migratory birds spend much of their annual cycle in migration, and the conditions experienced en route, which can vary dramatically across a given population, have considerable effects on individual survival and population size (Newton 2006). The degree to which intrinsic factors and environmental cues cause variation in migratory movements, however, is still poorly understood (McKinnon et al. 2013). Understanding how individual movements vary in relation to environmental conditions is a key factor both for predicting responses to changing climatic and habitat conditions (Morales and Ellner 2002, Pulido 2007) and for identifying critical habitats or landscapes for conservation or management. Here, I examined how a suite of external cues explained the spring movement behavior of a long-distance migratory seabird. My overall intent was to disentangle the primary effect of increasing daylength from secondary cues associated with environmental conditions, to identify the variables that exerted the greatest effects on behavior. Furthermore, I sought to determine if the magnitude of those effects varied over the course of the migratory period, and the degree of variation that individuals showed in response to those effects.

High levels of variation in migration strategy are evident among the world's bird species as they move between their breeding and non-breeding ranges (Dingle and Drake 2007). All known bird species, however, use external cues to trigger departure both from their residential grounds (i.e., breeding or non-breeding) and to begin or terminate stopover bouts along the migratory route. The nonoptimal timing of migratory arrivals, departures, and stopovers reduces reproductive success or survival (Lerche-Jørgensen et al. 2018). Therefore, to maximize fitness, different species have evolved different mechanisms to regulate the onset, duration, and termination of migratory behavior at appropriate times and places during the annual cycle (Gwinner 1996, Bradshaw and Holzapfel 2007). The precise cues that are used, however, vary among species and within species through time. Internal state can also be a major source of phenological variation during migration (Saino et al. 2017). Stopover and departure decisions may be influenced by multiple intrinsic factors, including: fuel stores (Schaub et al. 2008), sex (Moller 1994), body condition related to both parasite loads (Piersma et al. 2001, Moller et al. 2004) and winter habitat quality (Marra et al. 1998, Saino et al. 2004), and time-constraints related to both total migration distance (Gunnarsson et al. 2006) and breeding latitude (Conklin et al. 2010). And while any combination of these factors may influence migratory decisions, the relative strength of each may change along the route as the season advances (Bauer et al. 2008).

The roles primary, secondary, and intrinsic cues play in modulating migratory behavior, and the balance of their importance relative to each another, across the migratory pathway is not well understood. Yet, the strength of each has important evolutionary and conservation implications, because this variability determines where migratory routes may be most labile in the face of landscape change. Areas where individuals show more variabilty may indicate the potential for adaptation, whereas places where individuals exhibit hard-wired responses may warrant more substantial conservation measures. Among the external cues responsible for eliciting changes in bird behavior, photoperiod is defined as primary because it serves as their most reliable timekeeper, and is the principal driver behind the entrainment of their annual rhythms (Berthold 1996, Gwinner 1996, Coppack and Pulido 2004). Photoreceptors in the pineal gland, hypothalamus, and the eyes allow birds to track seasonal changes in daylength (Yokoyama et al. 1978, Underwood and Groos 1982), and promote the release of hormones that induce profound behavioral changes, such as hyperphagia and migratory restlessness (Gwinner 1987). While endogenous rhythms also trigger migratory behavioral shifts, environmental conditions like photoperiod play an important role in fine-tuning behavior (Saino and Ambrosini 2007, Bauer et al. 2011). Photoperiod may be less reliable for some species, however, in the face of large annual variation in environmental conditions on either stopover sites or residential grounds, which should promote a shift to greater reliance on secondary environmental cues (Marra et al. 2005, Haest et al. 2020).

Progression along the migratory route may be slowed or sped up in accordance with a variety of local conditions. Weather and food availability, in particular, have been found to exert considerable influence on the stopover and departure decisions of migrating birds (Farmer and Wiens 1999, Hüppop and Winkel 2006, Shamoun-Baranes et al. 2017). Atmospheric variables, such as air temperature can create favorable migration conditions; whereas, precipitation and reduced visibility may suppress migration progression (Richardson 1978, Alerstam 1979, Ian Newton 2008). Air temperature is also closely related to advancing spring date and can thereby reinforce the photoperiod cue. Temperature is an important predictor of mass movements of birds during spring migration in the United States and Europe (Tøttrup et al. 2010, Doren and Horton 2018, Haest et al. 2020). Warming spring temperatures are also often associated with favorable south tailwinds (Koistinen 2000), which help to offset fuel demands of flapping flight, thereby extending body reserves and reducing the amount of time necessary for refueling (Alerstam 1979, Weber and Hedenström 2000, McCabe et al. 2018).

The seasonal and geographic patterns of wind conditions (including wind direction, speed, and air pressure) are additional atmospheric characteristics that cue bird movements. Large-scale patterns in wind conditions tend to be consistent from year to year and can explain the evolution of divergent routes for spring and autumn, e.g., loop migrations (Kemp et al. 2010; McCabe et al. 2016). This has been observed repeatedly in marine birds, whose clock-wise migration routes closely follow trade wind patterns associated with oceanic gyres (Felicísimo et al. 2008, Egevang et al. 2010, Stenhouse et al. 2012).

Local environmental cues can also trigger a pause in migration to rest and refuel in both terrestrial songbirds (McCabe and Olsen 2015) and seabirds (Guilford et al. 2009). Optimal bird migration theory suggests these stopovers should occur where foraging is most profitable and maximum fuel deposition is attained (Alerstam and Hedenstrom 1998, Alerstam 2011). It is well-documented that marine birds rely on areas with oceanographic conditions that enhance productivity and create persistent feeding opportunities (Hunt and Schneider 1987, Paiva et al. 2010, Montevecchi et al. 2012); however, disentangling the physical and biological properties that influence seabird habitat choices from those of their prey has proven difficult (Weimerskirch et al. 2005, Weimerskirch 2007). Sea surface temperature, salinity gradients, chlorophyll *a* concentration, water depth, and surface currents have all been linked to seabird distributions and abundance (Ballance et al. 2006), but little information is available regarding how seabirds respond to these environmental cues, and how they affect movement decisions, particularly during migration.

The degree to which migrants rely on climate independent cues, such as photoperiod, versus local environmental conditions as a primary driver of migratory movements is highly species-specific (Bradshaw and Holzapfel 2001, Dawson et al. 2001), and very little is known about how the balance of cues play out across the migratory route. Photoperiod, for instance, may become less reliable than many secondary cues as a predictor of conditions further along the migratory route as individuals get closer to their destination. Further, the relationship between photoperiod and conditions on the destination resident grounds is changing under the effects of climate change (Coppack and Pulido 2004, Pulido 2007). This necessitates a deeper understanding of how environmental cues shape the movement patterns and timing of migratory birds along their migratory routes, so that we can better predict where they rely on canalized primary cues, where they use more labile secondary cues, and how their intrinsic characteristics modify this. Together this will help us understand how they will perceive, respond to, and be impacted by continuing and rapid environmental changes in different areas of their migratory corridor.

Arctic breeding seabirds are an ideal group for such a study because they migrate over long distances, are conspicuous top predators sensitive to changes in food webs, and their movements and behavior are sensitive to a suite of atmospheric and oceanic variables known to be changing with climate (Piatt and Sydeman 2007). Further, seasonal shifts in spring ocean temperatures are advancing in Arctic and mid-latitudes at a rate 30 to 40% faster than on land (Burrows et al. 2011). These temperature shifts can affect salinity, dissolved oxygen, pH, nutrient levels, and surface current direction, which, when combined with shifts in coastal wind patterns, may affect patterns of coastal upwelling intensity and near-shore food webs (Sydeman et al. 2014, Carr et al. 2017). Seabirds are also helpful for the study of migratory cues in a changing environment because they are large enough to carry satellite transmitters. This allows us to measure variability within and among individuals in their responses to environmental conditions across the migratory route.

I examined the relationship between directed migratory movements (measured by movement persistence) and a suite of candidate migration cues during the spring migration of a long-distance migrant seabird, the Red-throated Loon. This species is a High Arctic breeder under strong selection pressure for early spring arrival to reclaim the breeding territory from the previous season (Eberl 1993). Yet, their fuel-loading capacity is limited because of their high body mass to wing surface area ratio, which necessitates a migration strategy that favors frequent stopovers and shorter flights (McCloskey et al. 2018). As such, they likely have a long history of selection for accurate cues to signal migration onset and for migratory stopover frequency and location. Their High Arctic breeding grounds are also some of the fastest changing environments on the planet (Grabowski et al. 2013, Boelman et al. 2015, Prop et al. 2015), and correlations between breeding ground conditions and wintering ground cues are likely changing as well. I tested for relationships between migratory movements and a number of potential cues, including photoperiod, weather, and oceanic habitat characteristics, and attempted to identify variability in how birds responded to cues throughout the migratory period.

Methods

Measuring position and movement

I used Argos telemetry data collected from 40 adult Red-throated Loons, captured on their wintering grounds offshore of the U.S. mid-Atlantic coast, between January and late March in 2012 – 2015. Animal handling and satellite transmitter implantation details can be found in Appendix A. Prior to the analysis, I censored the first 16 days post-release of each bird to minimize the effects of capture, handling, and surgery on behavior (Blomberg et al. 2018) (Appendix A).

I used R package *foieGras* to filter observed locations with a continuous-time state-space model to account for error in the Argos telemetry, estimate true animal locations, and to regularize the filtered locations to a 6-h time interval (Jonsen et al. 2019). These filtered tracks were then used to fit a time-varying move persistence model (mpm) with pooled variance in *foieGras* to estimate movement persistence (g) between consecutive pairs of relocations (steps) for each animal. Movement persistence estimates autocorrelation in speed and direction between a given location and time (x_t) and the two previous locations and times ($x_{(t-1)}$ and $x_{(t-2)}$). It ranges from 0 to 1 and may be used as a behavioral index of movement, with high values reflecting a greater tendency to maintain consistent travel speeds and continue in the same direction (i.e., migratory movements), while low values are indicative of more variable speed and directionality between steps (Jonsen et al. 2019).

Modeling movement persistence

I used a generalized additive mixed model (GAMM) approach to examine how primary and secondary migration cues, as well as intrinsic factors, influenced movement persistence as a proxy for migratory movements during the spring migration of Red-throated Loons along the Atlantic Coast of the U.S. and Canada. I used thin plate regression splines for smooth terms using the *bam* function for large additive models in the R package *mcgv* (Wood 2017). I included an extra penalty for each term so that parameter estimates for weak variables in the model were reduced to zero effect and effectively removed from the results. This allowed me to include all potential variables in the base model, in lieu of multiple models with various terms included or omitted for comparison during model selection. The optimal degree of smoothing was defined using maximum likelihood estimation to allow for ranking of models in a model selection framework. Prior to model construction, multicollinearity among covariates was assessed by calculating variance inflation factors (VIF). All covariates had pairwise correlations of < 0.60 and VIF values of < 3; therefore, all covariates were retained in the modeling process (Zuur et al. 2010).

First, I constructed a base model that compared the relative importance (via parameter estimate magnitudes) of primary and secondary environmental cues and two candidate intrinsic factors. The base model included: (1) a smoothed term for the primary migration cue of photoperiod; (2) smoothed terms for secondary migration cues related to atmospheric conditions and oceanographic characteristics; (3) a smoothed term for latitude and a tensor product smooth for the interaction between latitude and photoperiod, with grouping effect for year which together allowed the effect of photoperiod to vary by location along the migratory route or by year; and (4) and photoperiod with factor smoothed terms for each level of the grouping factors, sex and breeding latitude. Specific definitions of model terms are described below.

Second, I compared the base model with two additional models that included terms to account for individual variation, as described above. Both models allowed me to estimate how much variation in migratory movement was explained by individual variation, which can be thought of as either a static or variable intrinsic migratory cue. One model included all terms in the base model plus a random intercept of id (static individual variation), and the other included all the terms in the base model plus a factor smooth interaction term of photoperiod and id (time-varying individual variation). The three models were ranked and compared using AIC model selection. The models with ΔAIC ≤ 2.0 from the model with the lowest AIC had the most statistical support; those with ΔAIC values between 4 and 7 had considerably less support; and those with ΔAIC > 10.0 had virtually no support relative to the highest ranked model (Burnham and Anderson 2002). The Akaike weight was also considered when determining the relative amount of statistical support for each model. QQ-plots and histograms were used to assess normality, and residuals versus fitted values were used to assess homogeneity (Zuur et al. 2010).

Predictors of migratory movements

Primary and secondary migration cues. The primary migration cue included in the models was photoperiod, which is a measure of daylength, in hours, for a given latitude and day of year. I calculated photoperiod for relocations within each movement track using the R package *meteor* (Hijmans 2019); (Table 4.1). Secondary migration cues included: atmospheric conditions that are predictive of flight conditions or seasonal progression (air temperature [K], air pressure [Pa], north-south wind speed [m/s], east-west wind speed [m/s], precipitation [m], and visibility [m]) and oceanographic characteristics that are tied to foraging conditions during stopover (water depth [m], distance to shore [km], chlorophyll *a* [mg/m^2], salinity [psu], sea surface temperature [K], wave period [s], wave direction [°], wave height [m], charnock parameter, north-south surface current speed [m/s], and east-west surface current speed [m/s]).

Spatiotemporal variation. The effect of the primary cue of photoperiod might be modified not only by the secondary cues listed above, but also by an individual's absolute position along the migratory route (e.g., how much distance is left to travel) or any number of other local environmental cues for spring onset during travel (e.g., how much time is left for travel). To account for these modifying factors, I included latitude, as well as an interactive term between photoperiod and latitude, by year (Table 4.1). The interaction between photoperiod and latitude allows a given day length to cue different movement behaviors depending on where along the roughly north-south migratory route it is experienced. The year grouping term attempts to account for annual variation in the timing of north to south spring advancement.

Intrinsic variation. I examined the potential for variation in the response to primary and secondary migratory cues among the 40 individual Red-throated Loons. Two methods were tested to account for within-group variation among individual birds: (1) using a random effect term to model individual-specific intercepts for each bird; and (2) using a factor smooth interaction term to model individual curves for each bird (Table 4.1). The factor smooth term allowed for variation in the functional response of movement persistence to photoperiod among individuals. Next, I examined the potential for variation in the response to photoperiod between males and females, as well as according to breeding latitude, using factor smooth terms (Table 4.1). Competition among conspecifics for breeding territories appears to result in the selection for earlier arrival on breeding grounds for males compared to females in some bird species (Forstmeier 2002, Drent et al. 2003, Coppack and Pulido 2004, Dierschke et al. 2005). Breeding latitude has been connected to variation in the endogenous programming of migration timing in other long-distance migrants (Conklin et al. 2010, Saino et al. 2015). Breeding latitudes of individual birds in this study ranged from 61.037°N to 82.936°N, a distance of 2421 km. The difference between maximum and minimum breeding latitude was divided by four to create discrete groups covering equal spans of latitude (5.475°, 605 km) into which each bird could be assigned. The resulting groups were: A

(61.036°N to ≤66.511°N); B (>66.511°N to ≤ 71.986°N); C (>71.986°N to ≤77.461°N); and D (>77.461°N to 82.936°N).

Table 4.1. Terms used to model movement persistence of Red-throated Loons during spring migration. Individual smooth terms (s) were included for photoperiod, latitude, and for each oceanographic and atmospheric variable. A tensor product (ti) was used for the interaction between photoperiod and latitude, with a grouping specification (by) for year. Factor smooth terms (bs = “fs”) were included for individual (id), sex, and breeding latitude category to allow each level of each factor its own functional smoothed response to photoperiod.

Term	**Description**
s(ocean)	surface current velocity (N/S & E/W); chlorophyll a; sea surface temperature (SST); sea surface salinity (SSS); water depth; distance from shore; wave height; wave period; wave direction; charnock parameter
s(atmospheric)	wind speed (N/S & E/W); precipitation; visibility; air temperature; air pressure
s (photo)	measure of daylength, in hours, for a given latitude and day of year
s (lat)	latitude
ti (photo, lat, by = year)	Spatiotemporal interaction of photoperiod and latitude with group-specific smoothing term for year (account for annual variation in advancement of spring)
s(photo,sex, bs="fs")	Factor smooth interaction of photoperiod and sex
s(photo,latQ, bs="fs")	Factor smooth interaction of photoperiod and breeding latitude
s(id, bs = “re)	Random intercept for ID
s(id, photo, bs = “fs”)	Factor smooth interaction of photoperiod and ID

Data Sourcing

Daily chlorophyll *a* concentration was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA’s Aqua satellite via Esri’s Living Atlas of the World in ArcMap 10.7.1. All other atmospheric and oceanographic variables were linked to locations for each animal track through the Env-DATA Track Annotation Service on the Movebank website (Dodge et al. 2013). Multiple environmental data products are available to access through the Env-DATA system, and the sources of those data set are noted in the variable descriptions that follow. Distance to nearest coastline is measured in km with a spatial granularity of 0.04 degrees and was sourced from the NASA Ocean Biology Processing Group. Water depth was measured in meters with a spatial granularity of 0.016 degrees and was sourced from the National Oceanic and Atmospheric Administration's ETOPO1 global relief model of ocean bathymetry (Amante and Eakins 2009). Visibility was sourced from the National Centers for Environmental Prediction's (NCEP) North American Regional Reanalysis (NARR) and is a measure of the distance, in meters, at which an object or light can be clearly observed (Mesinger et al. 2006). Ocean surface mixed layer velocity data was sourced from the NASA Ocean Surface Current Analyses Real-Time (OSCAR) project and are calculated using satellite sea surface height, wind, and temperature (Bonjean and Lagerloef 2002). Velocity of the north-south (meridonal or v) and east-west (zonal or u) components of near-surface ocean currents were measured in meters per second with a spatial granularity of 0.33 degrees and temporal granularity of five days

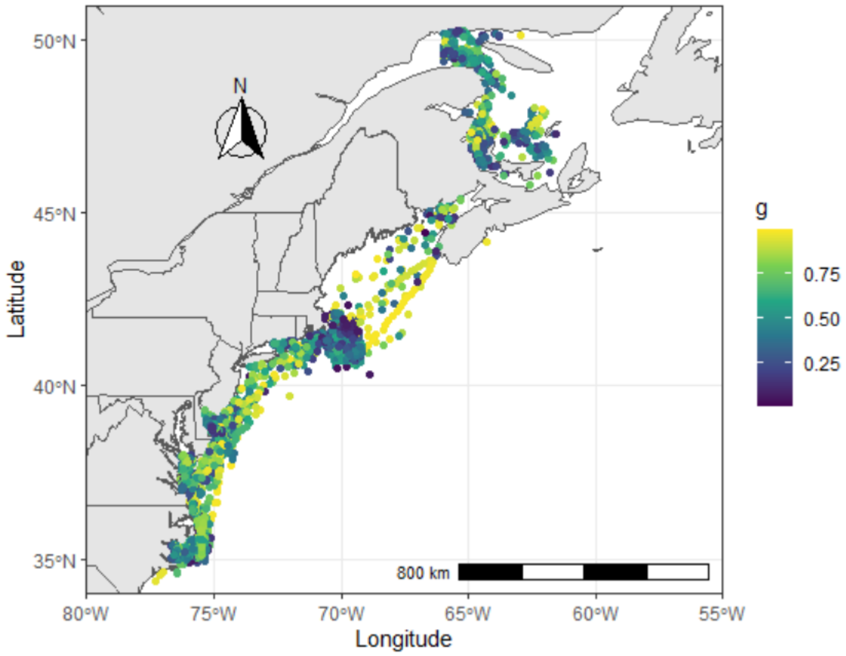
All other atmospheric and oceanographic data were sourced from the European Centre for Medium-Range Weather Forecast (ECMWF) and are measured with a spatial granularity of 0.75 degrees and temporal granularity of 6 hours (Owens and Hewson 2018). Air temperature data are measured in Kelvin (K) at 2 m above the ground or water surface. Atmospheric air pressure is the weight of all the air within a column at sea surface measured in pascals (Pa). Precipitation is an accumulative measure, in meters, of the amount of convective and large-scale rain and snow that falls to the earth's surface. Windspeed measurements are in meters per second for both the north-south (meridional) and east-west (zonal) component of wind at 10 m above the ground or sea, with positive values indicating south to north flow and west to east flow, respectively. Sea surface temperature is measured in Kelvin and is for the uppermost meter of the ocean. Charnock parameter is a unitless value that describes surface roughness length over the ocean surface and can be used to model turbulent wind over the ocean. Mean wave direction is an indicator of what direction waves are propagating, with 0 meaning waves are coming from the north and 90 being from the east. Mean wave period is measured in seconds and is the time it takes for two consecutive wave crests to pass through a fixed point.

Results

Measuring position and movement

Movement persistence (g) estimates for relocation points comprising the 2013, 2014, and 2015 spring migration trajectories of Red-throated Loons (n = 40) had an interquartile range of 0.24 to 0.56 and median value of 0.38. Spring migratory movements among males were associated with greater average persistence estimates ($\bar{x}$ ± SD= 0.47 ± 0.21; n = 14) compared to females ($\bar{x}$ ± SD = 0.39 ± 0.22; n = 26). The birds showed clear geographical patterns, with certain regions associated with slower, area-restricted-search (ARS) type movements typical of stopover behavior and others with fast, directed movements typical of travel corridors (Figure 1).

Figure 4.1. Rates of movement persistence (g) exhibited by migrating Red-throated Loons (n = 40) from March 1 to May 31, in the years 2013, 2014 and 2015. Movement persistence ranges from 0 to 1 and may be used as a behavioral index of movement, with high values reflecting a greater tendency to maintain consistent travel speeds and continue in the same direction, while low values are indicative of more variable speed and directionality between steps



Modeling movement persistence

The top supported model included the factor smoothed term for individual (time-varying random effect; Table 4.2). Using the extra penalty term to remove weak variables from the model resulted in all the atmospheric variables (except for north-south wind speed), wave direction, and charnock parameter being reduced to zero effect in the model results. All other variables were highly significant and accounted for 70% of the variation in movement persistence rates of Red-throated Loons during spring migration. Despite being penalized for having an additional 194 degrees of freedom, the top supported model with the factor smoothed term for individual ranked Δ 3170 AIC units lower than the model with a static random effect for individual. It also accounted for 20% more of the variation in movement persistence that the static random effect model, and 33% more than the base model with no random effect.

Table 4.2. Comparison of generalized additive mixed models examining the influences of primary (photoperiod), secondary (oceanographic and atmospheric conditions), spatiotemporal (latitude and year), and intrinsic (individual, sex, and breeding latitude) effects on movement persistence during the spring migration of red-throated loons (n = 40). Models are ranked according to Akaike Information Criterion (AIC). The table shows the variables included in the model, degrees of freedom (df), differences (delta) between model Akaike Information Criterion (ΔAIC), and adjusted r-square values.

Model	df	AIC	delta	R-sq (adj)
s(ocean)+s(atm)+s(photo)+s(lat)+ti(photo,lat, by = year)+s(photo,sex, bs=”fs)+s(photo, latQ, bs=”fs”)+s(photo, id, bs = “fs”)	389	14527.2	0.00	0.696
s(ocean)+s(atm)+s(photo)+s(lat)+ti(photo,lat, by = year)+s(photo,sex, bs=”fs)+s(photo, latQ, bs=”fs”)+ s(id, bs = “re”)	195	17696.1	3168.93	0.498
s(ocean)+s(atm)+ti(photo)+ti(lat)+ti(photo,lat, by = year)+s(photo,sex, bs=”fs)+s(photo, latQ, bs=”fs”)	146	19189.2	4661.99	0.369

Predictors of migratory movements

Primary and secondary migration cues. The global term for the effect of photoperiod on movement persistence was strongest early on in migration when daylength increased from approximately 11 h to 13 h, after which the strength of the response waned as movement rates slowed (Figure 4.2). Among the atmospheric variables included in the model, all except north-south windspeed reduced to zero effect in the top model, indicating little importance in their effect on movement persistence. North winds were associated with a slight decrease in movement persistence but there was a noticeable increase as winds became stronger and from the south (Figure 4.3). Overall, oceanographic conditions were associated with stronger movement responses compared to atmospheric variables. Slower and more stationary migratory movement behaviors were associated with shallow, nearshore locations with eastward or northward flowing surface currents, shorter wave periods, greater wave heights, and higher SST, salinity, and chlorophyll *a* concentration (Figure 4.4). These slower movements typically occurred within 55 km offshore in water depths of 5 to 20 m, and in wave heights of 1 to 3 m with wave periods of 3 to 5 s. Faster, more directed movements occurred further offshore over cooler (< 7°C), deeper waters with lower chlorophyll *a* concentrations, and when water conditions were calm. The response curve associated with salinity was concave, indicating lower movement persistence in lower saline, brackish locales, as well as in higher saline environments.

Figure 4.2. Movement persistence response curve to photoperiod (h) for Red-throated Loons during spring migration. The curve shows the response to the variable when the responses to all other variables in the model are held constant at their mean values. The solid line represents the smooth function estimate and dashed lines estimate the 95% confidence interval. Zero on the y axis indicates the predictor has no effect of the predictor.

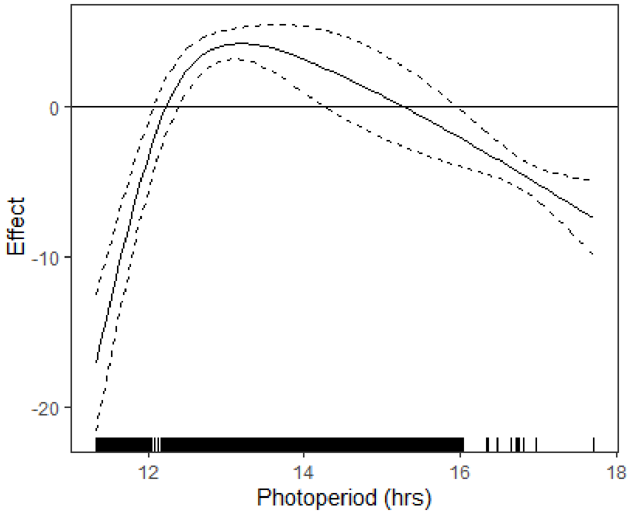


Figure 4.3. Movement persistence response curve to north-south windspeed (m/s) for Red-throated Loons during spring migration. The curve shows the response to the variable when the responses to all other variables in the model are held constant at their mean values. The solid line represents the smooth function estimate and dashed lines estimate the 95% confidence interval. Zero on the y axis indicates the predictor has no effect of the predictor.

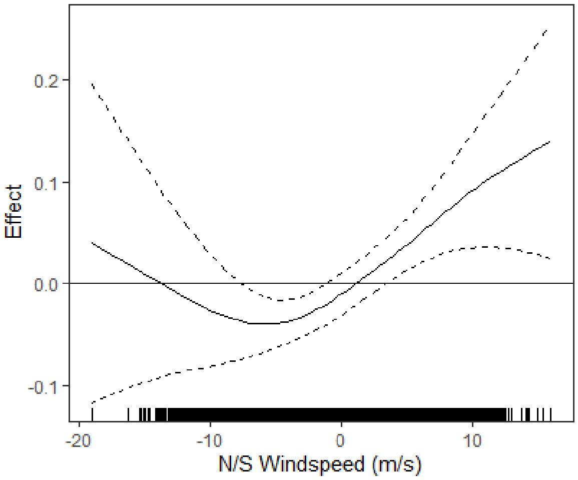
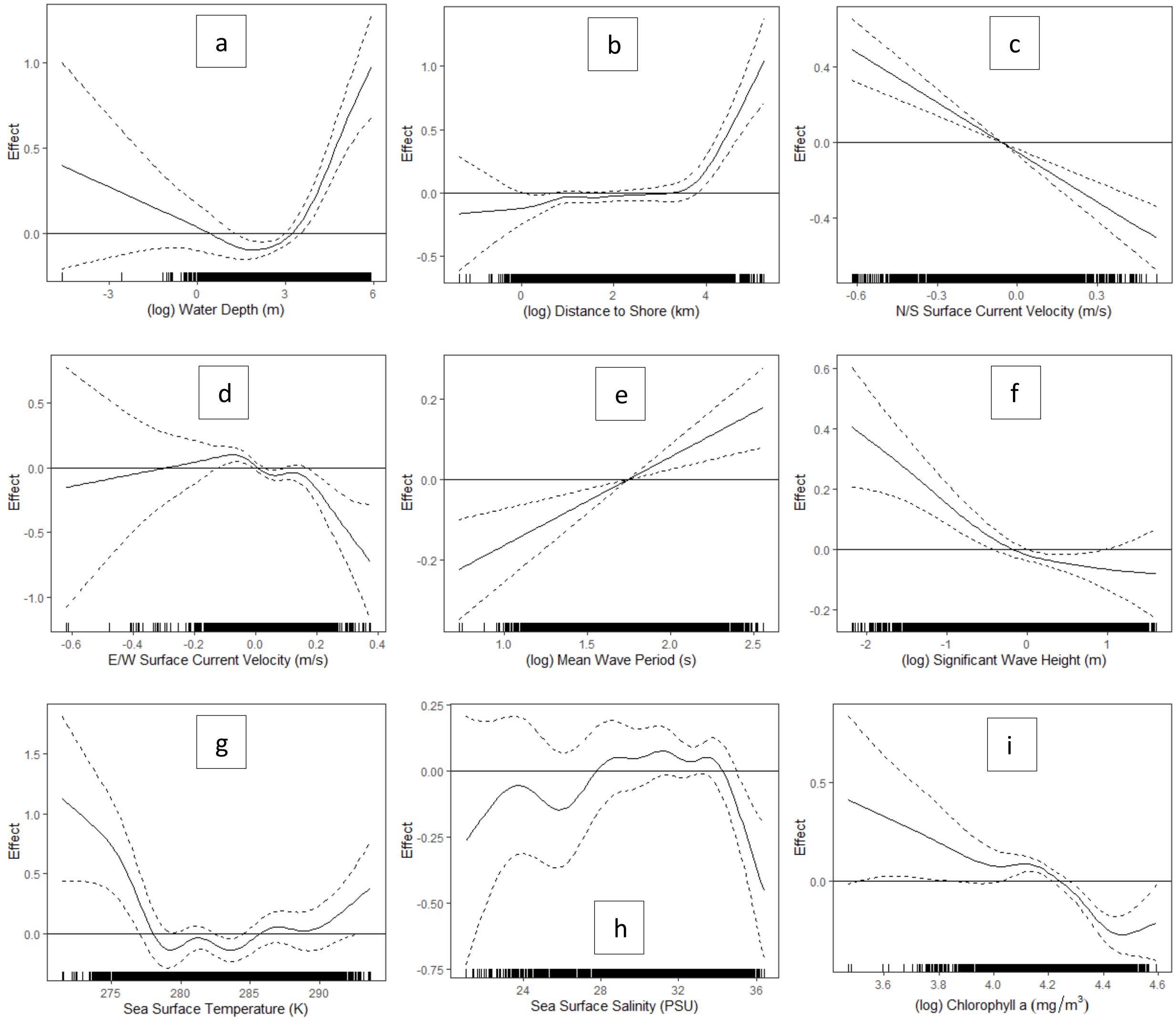
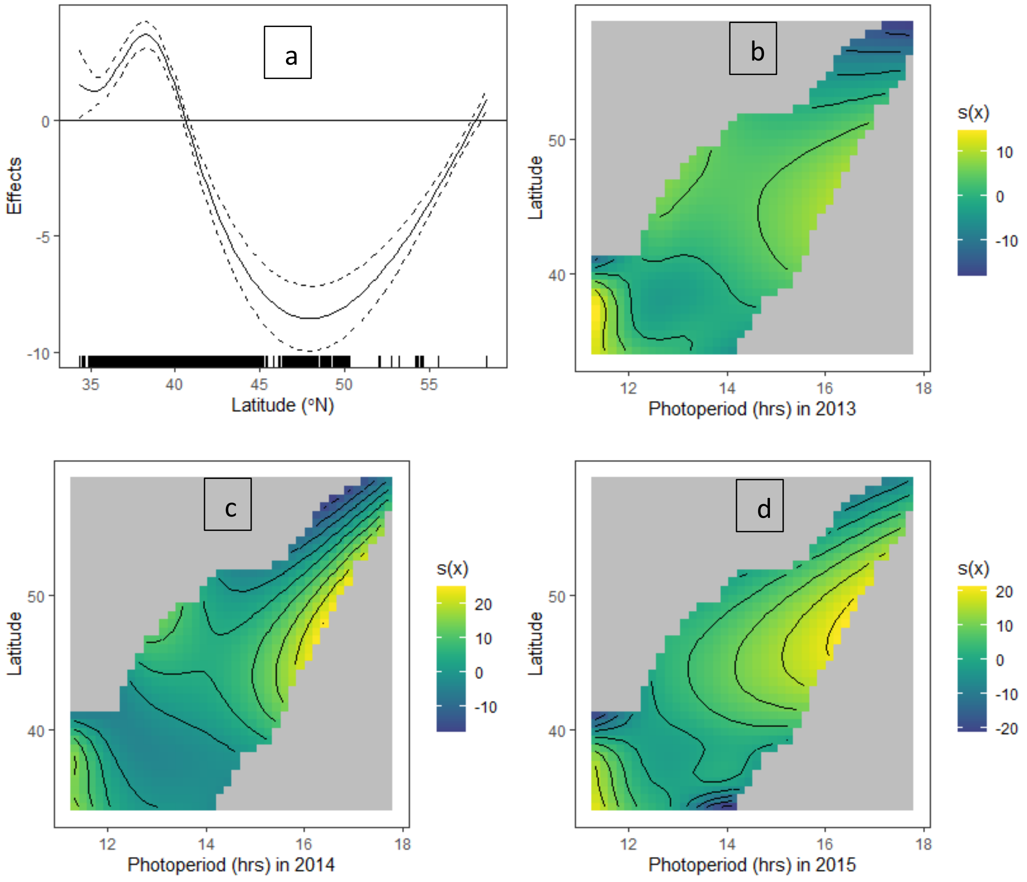


Figure 4.4. Movement persistence response curve among red-throated loons during spring migration to oceanographic secondary migration cues, including: (a) log-transformed water depth (m); (b) log-transformed distance to shoreline (km); (c) east-west surface current velocity (m/s); (d) north-south surface current velocity (m/s); (e) log-transformed wave period (s); (f) log-transformed wave height (m); (g) sea surface temperature (K); (h) sea surface salinity (PSU); and (i) log-transformed chlorophyll a concentration (mg/m^3). The curve shows the response to the variable when the responses to all other variables in the model are held constant at their mean values. The solid line represents the smooth function estimate and dashed lines estimate the 95% confidence interval. Zero on the y axis indicates the predictor has no effect of the predictor.



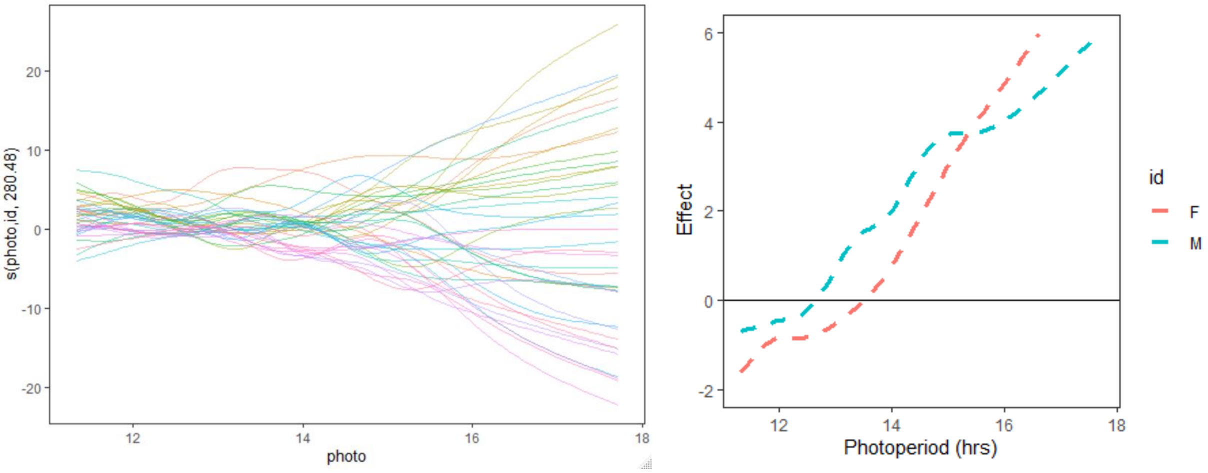
<u>Spatiotemporal variation</u>. The effect of location on movement persistence was strongest between 45° and 50° N latitude, where movement persistence slowed to its lowest rate during the spring migration period (Figure 4.5a). Movements became faster and more directed as birds moved north of 50° N latitude. There was considerable variation in the spatiotemporal pattern of movement behavior among years (Figure 4.5b-d). The highest movement persistence rates were observed later in the season in 2015 and in more northern locations of the migratory route compared to 2013, when these types of movements occurred earlier in the season and further south.

Figure 4.5. Movement persistence response curve among Red-throated Loons during spring migration to spatiotemporal migration cues, including: (a) latitude (°N) and its interaction with photoperiod (hrs) in years (b) 2013, (c) 2014, and (d) 2015.



Intrinsic variation. Among individuals, movement responses to photoperiod were similar early on in spring migration; however, as days grew longer, birds showed high variation in their movement rates (Figure 4.6a). The difference in response to photoperiod between the sexes was minimal, yet highly significant ($P < 0.001$). Movement persistence increased steadily throughout migration as photoperiod increased, although females showed slightly higher rates later in the season compared to males (Figure 4.6b).

Figure 4.6. Intrinsic variation in the response to photoperiod among red-throated loons during spring migration, including: (a) deviations from the global response among individuals (n = 40); and (b) between males (n= 14) and females (n = 26). Zero on the y axis indicates no deviation from the global response.



Discussion

Results from this study demonstrate that the explanatory power of primary, secondary, and intrinsic migratory cues on movement behavior varied across the spring migratory route for Red-throated Loons in eastern North America. The primary cue of photoperiod was the best predictor of movement early in migration, when the first major northward shifts in latitude consistently occurred each year when daylengths approached 11.5 hours in the mid-Atlantic U.S. wintering range and weakened when day lengths exceeded 13 h (Figure 4.2). Correspondingly, the explanatory power of secondary cues increased as the migratory season progressed. While oceanic conditions were better predictors of stopover behavior, atmospheric variables, primarily wind speed, were indicative of whether conditions were conducive to migratory flights (Figure 4.3 & 4.4). Likewise, intrinsic cues and the variability among individuals are strongest later in migration (Figure 4.6).

Birds that breed at High Arctic latitudes should be under significant selection pressure to rely on photoperiod as their primary cue for initiating migration. Yet, it seems logical that they should be flexible in their response to photoperiod once migration is underway, and also rely more on environmental conditions to time their movements (Terrill 1990, Gordo 2007, Saino and Ambrosini 2007). Birds arriving in the Arctic too early may encounter limited resources and harsh climate conditions (Drent et al. 2003); therefore, a switch to secondary environmental cues related to the advancement of spring would explain the loss of response to photoperiod as the season progressed. Considerable spatiotemporal variation was also evident in movement rates from year to year; however, the causes for these differences are not clear. As each year’s migration included a unique set of individual loons in this study, different measures are necessary to disentangle the effect of different interannual environmental conditions from the different intrinsic conditions at play among years.

Minimal variation in the movement behavior of individuals early on suggested that birds were highly entrained to photoperiod, but that as the season progressed, all birds appeared to be on their own schedule due either to encountering different secondary cues or other intrinsic differences among individuals. Such a pattern may be consistent with photoperiod acting as a cue for migration onset and secondary cues being more influential for stopover decisions en route. Departures from the wintering grounds were staggered among individuals, however, with the latest departures occurring when day lengths were as long as 15 h. In general, though, birds showed remarkable annual consistency in the timing of their movements once migration was underway.

Results from this study indicate support for significant differences between the sexes in their movement response to photoperiod. Increased movement rates among males occurred earlier in the season compared to females, whereas females exhibited higher rates of movement persistence as photoperiod increased later in the season (Figure 4.6b). There were greater absolute differences in the response curves to photoperiod among the different breeding latitude categories. Birds breeding in more southern latitudes displayed higher rates of movement persistence late in the season compared to birds breeding at more northern latitudes. This likely reflects the May 31 end date of the sampling period for this study and the latitudinal difference in the length of ice-free conditions. The breeding range of the Red-throated Loon extends over a wide range of latitudes from the northern boreal forests to the high arctic tundra, and spring arrival dates closely follow ice-out of freshwater nesting ponds in early to mid-June (Dickson 1993, Eberl 1993). Therefore, it is probable that the more northern breeding individuals in this study were exhibiting low movement persistence rates late in the season, because their breeding grounds are still frozen, and they must remain at staging grounds longer than their more southern breeding cohorts. Unfortunately, duty cycle differences in our satellite transmitters, which only recorded positions for two hours every five days after May 31, prevent me from testing this hypothesis.

North-south wind speed was the only atmospheric variable with clear influence on movement persistence. Faster, more directed movements were found to occur in association with higher wind speeds that came out of the south. Tailwinds like these help to offset fuel demands of flapping flight, and so, I hypothesize that individuals use wind speed and direction as a modifying cue for stopover departure to take advantage of favorable winds and weigh those benefits versus staying on longer to continue fuel deposition (Weber et al. 1998; McCabe et al. 2018).

Many more oceanographic variables predicted loon movement than did atmospheric variables during spring migration. Slower, more ARS-type movements, typical of stopover behavior, were generally associated with warmer, shallow, coastal waters with higher surface current velocities and chlorophyll *a* concentration. Higher wave heights were also shown to be associated with slower movement persistence rates. This is perhaps indicative of loons selecting sites experiencing wind-driven upwelling events, where foraging conditions are enhanced as prey are pushed closer to the surface (Embling et al. 2013). Movement persistence exhibited a slightly downward concave-shaped response to sea surface salinity. This suggests that, although Red-throated Loons occupied a range of salinity conditions, directed movements occurred at intermediate salinities and ARS-type movement (e.g., foraging behavior) was most prevalent in either low or high salinity environments. This is reflective of their heavy use of river mouths, in the relatively brackish waters of Chesapeake Bay, as well as the high saline waters of Pamlico Sound and the upper Gulf of St. Lawrence. Oceanographic conditions associated with higher movement persistence rates were generally consistent: faster, more directed movements tended to occur over colder, deeper, less productive waters farther offshore, where wave periods were longer. I hypothesize that, together, oceanic conditions act as secondary cues for loons to locate stopover locations where foraging and refueling will be successful.

Significant stopover locations of Red-throated Loons

Oceanographic circulation patterns significantly influence the productivity and distribution of species in marine ecosystems (Puerta et al. 2020). Slow, ARS movement behavior of Red-throated Loons during their spring migration over shelf waters of the northwest Atlantic tended to occur in locations with surface currents that exceeded 20 cm/s and were eastward and northward flowing. Important stopover locations for Red-throated Loons were shallow and subject to intense water column mixing from tidal forces, buoyant water inputs, and wind shear stress on the surface. These conditions support high levels of productivity as nutrients are continually recycled into the broad euphotic zone of shallow environments (Mann and Lazier 2005), which is in keeping with the high levels of chlorophyll *a* observed in these stopover habitats.

Red-throated Loons also made heavy use of estuary systems during stopovers. Their use was most concentrated where freshwater rivers entered the estuary, and where brackish waters exited the estuary into the ocean. Plume fronts are created in these environments when denser saline water is forced below the more buoyant freshwater top layer (Mann and Lazier 2005). Light conditions in this nutrient-rich upper layer promote productivity of phytoplankton that attracts concentrations of zooplankton, forage fish, and piscivores, such as Red-throated Loons (Skov and Prins 2001, Cox et al. 2018). Freshwater input creates a low salinity environment (Drinkwater and Gilbert 2004), which was characteristic of Chesapeake Bay, where loons spent considerable time at the start of the migratory period.

Nantucket Sound and Shoals represented the first major stopover site after leaving the southern mid-Atlantic Bight. Strong, rotating tidal currents in this region keep the water column well-mixed and force prey upward making them more available to foraging birds (Potter and Lough 1987). Tidal pumping of cold nutrient rich water from the Gulf of Maine across the warmer shallow waters of the shoals creates suitable conditions for the production of high phytoplankton biomass (Durbin et al. 1995, Saba et al. 2015). The region is a noted area of biological productivity and provides important habitat for marine birds, particularly during winter and migration (Stenhouse et al. 2020, White and Veit 2020). Red-throated Loons made considerable use of the Muskeget Channel that runs between Nantucket and Martha’s Vineyard while in this area. Strong tidal flows are characteristic of the channel, and narrow passageways in general create favorable foraging conditions through the advection of concentrations of prey from nearby areas (Cox et al. 2018).

The Gulf of St. Lawrence (GSL) and St. Lawrence River Estuary was the next and final major stopover site for Red-throated Loons before they dispersed northward toward their final breeding destinations. This highly productive region supports a diverse array of seabird species that prey upon local forage fish populations, including Atlantic mackerel (*Scomber scombrus*), Atlantic herring (*Clupea* *harengus*), capelin (*Mallotus villosus*), and sand lance (*Ammodytes* sp.; Guse 2013). Surface water circulation in the GSL is cyclonic, with ocean waters flowing west and northward after entering the system via the Strait of Belle Isle and the Laurentian Channel, and freshwater input from the estuary flowing south and eastward toward the ocean (Koutitonsky and Bugden 1991). Movement of water within the system is largely driven by tidal forcing from the Atlantic, buoyancy forcing from freshwater inputs, and wind-stress forcing as continental air masses meet the sea (Koutitonsky and Bugden 1991). Although significant use was observed in the lower estuary, it was not included in the analysis because oceanographic variables were not available for this largely freshwater area. Within the GSL, slow loon movement persistence was evident in the area west of Anticosti Island, where a large gyre circulation system is formed as coastal waters move westward into the estuary along the north shore, and freshwater runoff moves eastward out of the estuary along the south shore with the Gaspe Current (El-Sabh 1976). In May, when loons are using this part of the GSL, chlorophyll *a* concentration associated with phytoplankton biomass can be twice as high in the gyre compared to nearby waters (Le Fouest 2005). Buoyant waters of the Gaspe Current advect south and flow across the Magdalen Shallows (Sheng 2001), which along with the Shediac Valley and Northumberland Strait along the southwestern shore, saw significant use and slow movement persistence rates by Red-throated Loons during their extended stopover in the region. These areas of the GSL, which likely provide critical foraging opportunities prior to the last leg of their migration, have been identified as important for the feeding, refuge, and spawning of pelagic fish (Savenkoff et al. 2007, Nozeres et al. 2015). The regions of the GSL with deeper channels and under more influence by oceanic waters saw relatively little use.

Conclusions

Red-throated Loons relied on a combination of primary, secondary, and intrinsic cues to adjust their movement behavior. Photoperiod was an important indicator of increased speed and direction of movement at the onset of migration; however, its strength waned as the season progressed.

Oceanographic conditions were important factors in switching to stopover behavior, which consisted of slower, more area-restricted search movements. Physical processes, such as tidal mixing, buoyancy-driven circulation, and wind-induced coastal upwelling, create highly productive stopover sites necessary for sustaining migrating seabirds. Red-throated Loons relied on relatively few stopover sites, but stays were extended, and their use was consistent among individuals. Resumption of directed movements away from these stopover locations was predicted by atmospheric conditions related to flight efficiency, mainly wind speed and direction. Similar to migrating landbirds, favorable tail winds were an important driver of faster, more directed movement behavior in a migratory seabird.

I hypothesize that photoperiod serves as the primary migratory cue and a migratory onset trigger, while secondary environmental cues signal stopover onset (foraging ground conditions as indicated by oceanographic characteristics) and cessation (flight conditions as indicated by atmospheric characteristics). This hypothesized mechanism is consistent with a high degree of interannual consistency in migratory onset and stopover location, which also made latitude a reliable indicator of movement persistence. Annual variation in spatiotemporal pattern of movement, however, was also apparent among years in ways left unexplained by the environmental conditions I investigated here. It is clear that individuals react differently to some of the same environmental cues, and interestingly this variation was more pronounced during the latter portion of the spring migration when secondary environmental cues were more predictive of migratory movements.

I wonder whether individual variability in movement, either through plasticity or genetic diversity, is less early in migration, when movement is driven more by photoperiod, due to the greater canalization of migratory onset behaviors relative to stopover behaviors. Certainly, stopover habitats possess greater variability than photoperiod across a migratory route, across years, and through loon generations. Of course, this increase in individual variability in movement during the latter stages of migration could be explained equally well by (1) the influence of additional secondary environmental cues that I did not capture, (2) the increased importance of individual condition in determining movement decisions as time spent in migration increases, or (3) higher environmental variability in higher latitude environments during the onset of spring, among other causes. Regardless, I show here how the importance of primary, secondary, and intrinsic migratory cues vary across the migratory route of a long-distance migrating seabird. These results have consequences for the ability of migrant bird populations to adequately adjust the timing of their movements in accordance with changing climatic conditions. Increases in spring temperatures have advanced the phenology of certain plant and insect species in certain parts of the globe, thus creating the potential for trophic mismatches between migratory birds and their food sources (Amano et al. 2010, Thackeray et al. 2010, Everall et al. 2014). Mounting evidence suggests many species in the northern hemisphere are advancing their migration and breeding dates in response to these climatic shifts (Lehikoinen et al. 2004, Rubolini et al. 2007, Møller et al. 2008). Species that rely more on endogenous cues to time these events, or who are constrained in their timing due to other life cycle events, e.g., molt, may require more time to adjust. Those that fail to do so may face population level consequences (Møller et al. 2008), and our ability to detect these trends, will depend on coordinated long-term monitoring programs along migration corridors and within the breeding range.

CHAPTER 5

VARIABILITY IN DIRECTION AND MAGNITUDE OF SELECTION RESPONSES TO OCEANOGRAPHIC CHARACTERISTICS OF HOME RANGES AMONG INDIVIDUAL RED-THROATED LOONS IN WINTER

Introduction

Understanding how habitat characteristics shape species distribution patterns is a necessary component of effective wildlife management. Our ability to identify suitable sites for targeted conservation initiatives will be hampered when we are unable to characterize the physical and biological requirements of our focal species. For seabirds, limited information is available on their offshore distribution, foraging movements, and habitat requirements during the nonbreeding season (Schreiber and Burger 2001). Yet, evidence suggests that habitat quality during that part of the annual cycle may cause carryover effects that influence individual performance during subsequent seasons (Marra et al. 1998, Studds and Marra 2005). As seabird populations experience rapid declines in many parts of the world (Paleczny et al. 2015), identifying important habitats for conservation, such as marine protected areas, has become a critical tool in seabird conservation (Thaxter et al. 2012, Lascelles et al. 2016). Seabirds are highly mobile marine predators that utilize a variety of strategies to track prey, such as schooling fish, through a highly heterogenous environment (Weimerskirch 2007, Thiebault et al. 2014). Strong spatiotemporal variability in the oceanographic processes that create favorable foraging conditions presumably makes food availability the biggest constraint affecting seabird habitat use during the nonbreeding season (Hutto 1985, Fauchald 1999). This has made efforts to quantify spatial temporal overlap with prey distributions a priority area of research with important implications for management of seabird and fisheries populations. But making direct correlations between seabird and prey distributions has been challenging due to the difficulty of detecting patchily distributed prey at sea (Fauchald 1999, Tremblay et al. 2009).

Prior to the 1990s, obtaining distribution data on marine birds while at sea was limited to ship-based surveys that were restricted in the spatiotemporal extent of their observations; however, the advent of satellite tracking technology has made it possible to track the movements of individual seabirds. Indeed, the use of tracking technology on seabirds has proven an effective alternative in the identification of core use areas that provide important habitat at sea (Wakefield et al. 2009, Lascelles et al. 2016). Remote collection of relocation data also provides us with the means to examine how seabirds interact with their environment. For example, higher quality habitat is generally associated with longer periods of occupancy and more consistent use over time in comparison to lower quality habitats (Johnson 2007, Faaborg et al. 2010). Once these spatial areas are determined, resource selection analyses (RSAs) can be used to differentiate characteristics that comprise high-quality versus low-quality habitats by relating spatially explicit patterns of use to the distribution of resources within the landscape (Boyce and McDonald 1999, Manly et al. 2002).

Reliability of selection estimates from RSA models may be limited, however, when availability of habitat varies among individuals occupying different parts of the landscape (Beyer et al. 2010). The ability of individuals to obtain necessary resources from their environment also varies within a population and may be associated with social status, population density, and/or habitat quality (Harrison et al. 2011). Identifying intra-specific variation in the behavioral responses to local conditions can be a key factor in increasing our understanding of animal space use (Morales and Ellner 2002, Dingemanse and Dochtermann 2013, Muff et al. 2020). We can identify variation among individuals, and produce more reliable selection coefficients, by incorporating random slopes in RSAs (Gillies et al. 2006, Leclerc et al. 2016, Muff et al. 2020). From there, we can test whether differences in selection coefficients is due to true individual variation or if there is evidence of a functional response. Functional responses occur when differences in the availability of a resource exist between individual home ranges and it corresponds with the strength of the selection response (Mysterud and Ims 1998, Hebblewhite and Merrill 2007).

I sought to further this field of research by exploring how oceanographic and intrinsic factors influence variation in resource selection of Red-throated Loons wintering offshore of the mid-Atlantic U.S. Red-throated Loons are piscivorous seabirds and are considered opportunistic feeders whose diet composition likely reflects availability more than food specialization (Guse et al. 2009). This makes them an excellent species to test for evidence of functional responses in selection behavior because spatial heterogeneity in prey distributions should result in, at least some individuals within the population, making extensive movements during the winter period in response to shifts in food availability. Furthermore, quantifying the variability of seabird responses to physical and biological conditions can help to foster our understanding of the physical processes and trophic transfer that promote optimal foraging conditions in the marine environment. Our objectives were threefold: (1) estimate individual home ranges to better describe important winter habitat for the species within the Mid-Atlantic Bight; (2) use individual home ranges and mixed effect models to estimate resource selection of habitat characteristics known to influence seabird and prey distributions; and (3) identify individual variation in resource selection and test for evidence of functional responses related to differences in home range characteristics.

Methods

Data Collection and Management

I used Argos telemetry data (location classes 1, 2 and 3) collected from 23 adult Red-throated Loons during December, January, and February on their wintering grounds offshore of the U.S. mid-Atlantic coast. Loons were captured and implanted with platform terminal transmitters (PTTs) during in late winter and early spring of 2012 to 2015 in three primary sampling areas of the mid-Atlantic:

Delaware Bay, Chesapeake Bay, and Pamlico Sound. Battery life associated with the PTTs provided approximately one year of relocation data for each loon. I opted not to use data from the winter of capture because of potential behavior effects associated with the post-surgery period after PTTs were implanted (Mulcahy and Esler 1999, Esler et al. 2000). To obtain accurate winter home range information, only loons that provided at least 60 days of relocation data the following winter were included in the analysis. Animal handling and satellite transmitter implantation details can be found in Appendix A. Prior to the analysis, I censored the first 16 days post-release of each bird to minimize the effects of capture, handling, and surgery on behavior (Blomberg et al. 2018) (Appendix A). I used R package *foieGras* to filter observed locations with a continuous-time state-space model to account for error in the Argos telemetry, estimate true animal locations, and to regularize the filtered locations to a 6-h time interval (Jonsen et al. 2019).

Estimating Winter Home Ranges

Winter home ranges and core use areas used by each loon were estimated from utilization distributions (UDs) calculated using the autocorrelated kernel density (AKDE) method in R packages *amt* and *ctmm* (Calabrese et al. 2016, Signer et al. 2019). Kernel methods are a standard method used to examine the variation in intensity of spatial point patterns, e.g., animal relocation data, and the UD describes the probability of an animal's occurrence at any location within the AKDE (Van Winkle 1975, Worton 1987). The home range and core use areas correspond with the area that encompasses 95% and 50% of the volume of the UD, respectively (Anderson 1982, Samuel et al. 1985). I measured total area of each home range (95% isopleth) using R package *amt* and tested for significant differences in home range size between sexes using the Wilcoxon sign-rank test.

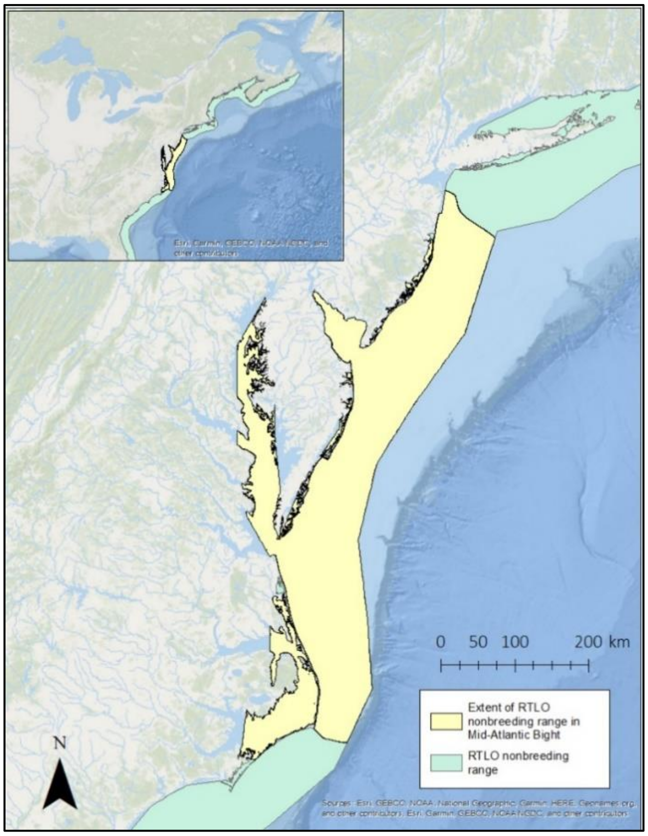
Modeling Resource Selection

Background. Animals are expected to select resources at four hierarchical scales: (1) first order – the geographic range of the species; (2) second order – the home range of an individual; (3) third order – the habitats used by an individual within its home range; and (4) the individuals resources selected within each habitat (Johnson 1980). My objectives were to identify: (1) second order resource selection of individual home ranges relative to the nonbreeding geographic range of the species; and (2) third order resource selection of core use areas within individual home ranges (Johnson 1980). The evaluation of resource selection pertains to the measurement of habitat components an animal "uses" in its environment compared to what is "available" (Johnson 1980). Usage of a resource is defined as the proportion of a resource used by an animal or population over a fixed period, while availability refers to the amount that was accessible during that same period (Manly et al. 2002). Therefore, used resources are a subset of available resources, and a key factor in resource selection studies will be in determining the extent of the area that will be included for sampling available resources (Buskirk and Millspaugh 2006).

Habitat characteristics for differentiating used versus available locations for second and third order resource selection among Red-throated Loons were chosen based on *a priori* knowledge of marine habitat and availability of spatial data within the study area. Habitat covariates included: water depth (m), distance to shore (km), monthly mean sea surface temperature (°C), monthly mean chlorophyll *a* (mg/m^3) concentration, mean monthly sea surface salinity (practical salinity units, PSU), tidal current velocity (m/s), mean wave period (s), and significant wave height (m). Covariates were log-transformed when necessary to improve normality. Multicollinearity among covariates was assessed by calculating pairwise correlations and variance inflation factors (VIF). All covariates had pairwise correlations < 0.60 and VIF values < 2.3 and were retained as variables in the modeling process.

Second Order Resource Selection. To understand predictors for the selection of home ranges within the species winter range (second order selection), I defined used points as the telemetry locations that fell within the 0.95 isopleth of an individual's home range. Available points were randomly generated throughout the extent of the nonbreeding range that occurs within the Mid-Atlantic Bight (Figure 5.1). I constrained the extent of the available habitat to this region to ensure available habitat was indeed reachable at any given point during the period of study. Ten available points were generated for each used point following guidelines by Signer and Fieberg (2020). Second order resource selection was estimated using generalized linear mixed models with the R package, *glmmTMB* (Brooks et al. 2017). I modeled each covariate as a singular term and included a random intercept in each model to accommodate nonindependence between repeated locations on the same individuals. I built upon the singular term with random intercept models for the next series of models by adding random slopes to allow for individual variation in selection responses to habitat characteristics. Next, I constructed a global model with all eight covariates with a random intercept and another global model with random intercepts and random slopes for each individual. Each covariate was scaled so that effect sizes were comparable among habitat characteristics with different units of measurement. Models were ranked with Akaike Information Criterion. The model with the lowest AIC, and those having $\Delta AIC \leq 2$ had the most statistical support, values between 4 and 7 had considerably less support, and those > 10 had virtually no support (Burnham and Anderson 2002).

Figure 5.1. Extent of available habitat for second order resource selection among satellite-tracked Red-throated Loons (n = 23). Light green represents the east coast winter range of the species and the yellow represents the portion of the range that fall within the U.S. Mid-Atlantic Bight. The yellow area was chosen to represent available habitat for resource selection analysis to ensure we were modeling only the part of the range that was truly available to each loon.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors. Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Third Order Resource Selection and Functional Responses. To understand predictors for the selection of core use areas within home ranges (third order selection), I defined used points as telemetry locations that fell within core use areas (the 0.50 isopleth of the UD) and the extent of available habitat was the individual's home range (0.95 isopleth) (Manly et al. 2002). Ten available points were generated for each used point following guidelines by Signer and Fieberg (2020). I used the same suite of mixed models and AIC model selection framework for the third order resource selection analysis. I then tested to see if differences in the strength of regression coefficients among individuals (i.e., random slopes) were related to differences in availability of the resources between individual home ranges

(Hebblewhite and Merrill 2007). To test for this type of functional response to availability, I used linear models to explore the relationship between individual selection coefficients (random slopes) for a given habitat characteristic and the mean value of that covariate within the individual's home range. Variation in habitat selection among individuals that is independent of changes in resource availability are expected to exhibit a slope of zero; I thus considered evidence of a functional response to occur whenever slopes assumed negative or positive values. Because heterogeneity among individuals in the strength of resource selection coefficients can arise because of other intrinsic factors, I also included sex, body mass, breeding latitude, and home range size in the functional response models as other sources of potential variation.

Data Sourcing

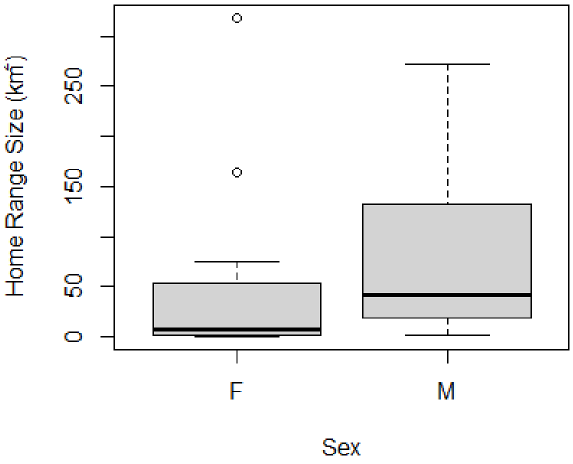
Daily chlorophyll *a* concentration was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua satellite via Esri's Living Atlas of the World in ArcMap 10.7.1. All other atmospheric and oceanographic variables were linked to locations for each animal track through the Env-DATA Track Annotation Service on the Movebank website (Dodge et al. 2013). Multiple environmental data products are available to access through the Env-DATA system, and the sources of those data set are noted in the variable descriptions that follow. Distance to nearest coastline is measured in km with a spatial granularity of 0.04 degrees and was sourced from the NASA Ocean Biology Processing Group. Water depth was measured in meters with a spatial granularity of 0.016 degrees and was sourced from the National Oceanic and Atmospheric Administration's ETOPO1 global relief model of ocean bathymetry (Amante and Eakins 2009). Ocean surface mixed layer velocity data was sourced from the NASA Ocean Surface Current Analyses Real-Time (OSCAR) project and are calculated using satellite sea surface height, wind, and temperature (Bonjean and Lagerloef 2002).

Results

Estimating Winter Home Ranges

Home ranges were primarily concentrated in southern Delaware Bay, middle to lower Chesapeake Bay, and Pamlico Sound. Red-throated Loons made extensive use of tidal tributaries, particularly in Chesapeake Bay and Pamlico Sound. The mouth of Delaware Bay near Cape Henlopen, and the mouth of Chesapeake Bay were also heavily used. Winter home range size ranged widely from <1 km^2 to 318.9 km^2; however, the median winter home range size was 21.3 km^2 ($\bar{x}$ = 67.3 km^2). Median home range size for males (n = 11) was 42 km^2, compared to only 7 km^2 for females (n=12; Figure 5.2); however, the difference was not significant (W = 39, p = 0.10).

Figure 5.2. Boxplots comparing home range size sizes of male (n = 11) and female (n = 12) Red-throated Loons while wintering in the U.S. Mid-Atlantic Bight. The gray shaded area of the box represents the interquartile range, the black line represents the median, the lower horizontal line represents the minimum of the first quartile and the second horizontal line represents the end of the fourth quartile (not including outliers, which are represented by circles).



Modeling Resource Selection

Second Order Resource Selection. The top supported model of resource selection for winter home range included random slopes to allow for individual variation in response to the effects of chlorophyll *a*, distance to shore, current velocity, sea surface temperature, water depth, and significant wave height (Table 5.1). Population-averaged coefficients for fixed effects indicated that the oceanographic variables with the strongest effects were chlorophyll *a*, sea surface temperature, water depth, mean wave period, and significant wave height (Table 5.2). The oceanographic characteristics associated with the strongest selection were water depth and distance to shore, but there was considerable variation among individuals (Table 5.2 and Figure 5.3). Red-throated loons selected for smaller measurements of distance to shore, water depth, significant wave height, and mean wave period. Conversely, they selected for increasing values of chlorophyll a, current velocity, sea surface salinity and temperature in the home range; however, confidence intervals are wide, and we cannot exclude no selection *for* or selection *against* any of those covariates. Random slopes also revealed considerable variation among individuals for selection of chlorophyll *a* and sea surface salinity, with some individuals selecting for higher concentrations of chlorophyll *a* and lower salinity levels (Figure 5.3). Minimal to no variability in selection was detected for sea surface temperature, current velocity, wave period, or wave height.

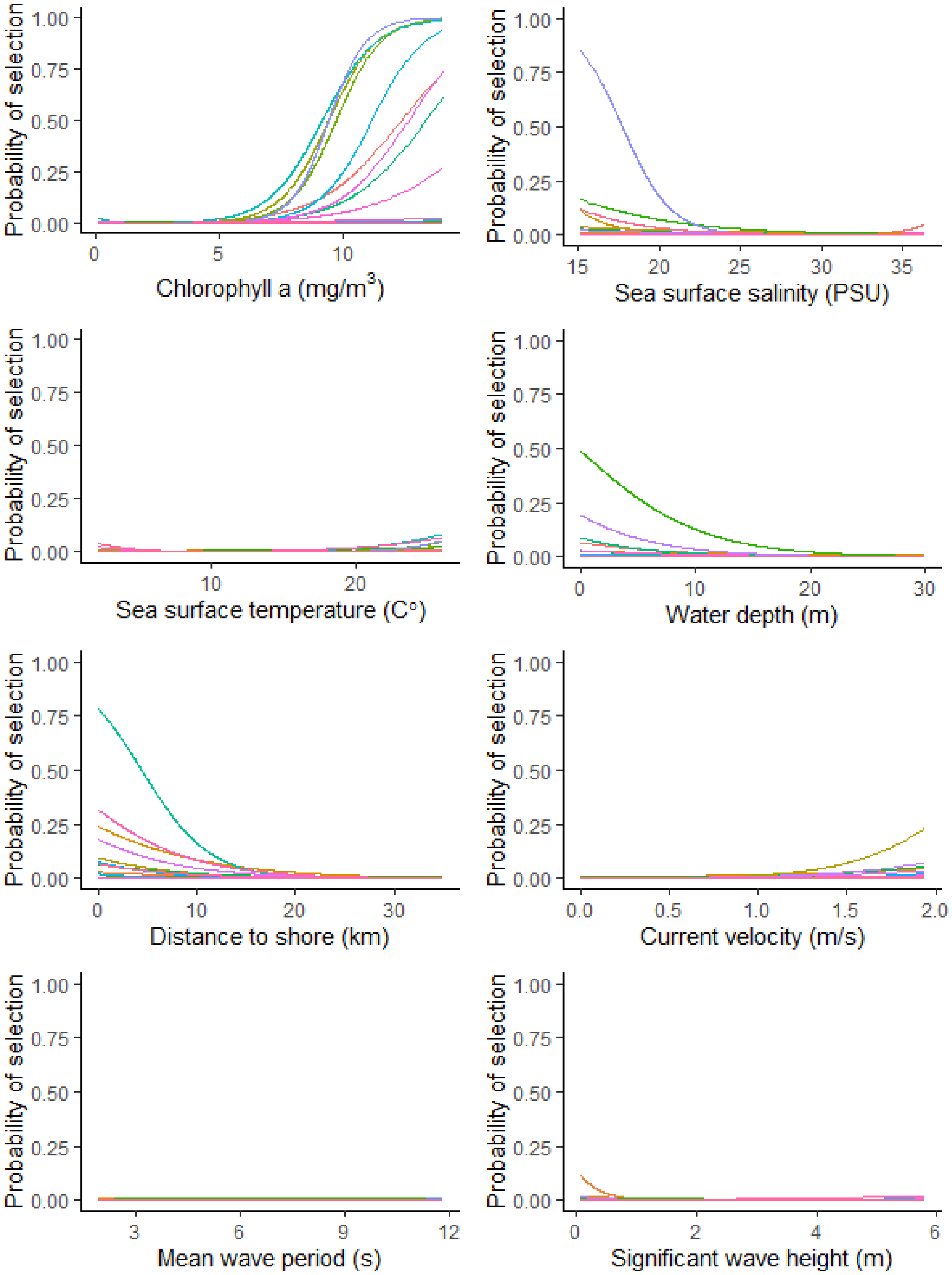
Table 5.1. Comparison of generalized linear mixed models of second order resource selection for home range habitat among Red-throated Loons (n = 23) wintering in the U.S. Middle Atlantic Bight. Models are ranked according to Akaike Information Criterion (AIC). Rankings are for null model, single term fixed effect models, global model including all fixed effects and random effect to allow intercept to vary for individual loons, and global model including all fixed effect terms and random effects to allow slopes of each term to vary for individual loons. Fixed effects included the oceanographic variables: distance to shore (dist); mean monthly chlorophyll a (chl); mean monthly sea surface temperature (SST); 6-hr mean wave period (wavper); 6-hr significant wave height (wavht), surface current velocity (curr); water depth (dep); and sea surface salinity (SSS). The table shows the variables included in the model, number of estimated parameters (K), and differences between model Akaike Information Criterion (ΔAIC).

Model Terms	K	AIC	ΔAIC
Global model + random intercept + random slopes	18	7878.6	0.0
Water depth (m) + random intercept + random slopes	4	10991.0	3112.36
Global model + random intercept	10	11012.4	3133.82
Chlorophyll a concentration (mg/m^3) + random intercept + random slopes	4	11092.7	3214.10
Water depth (m) + random intercept	3	11810.3	3931.73
Chlorophyll a concentration (mg/m^3) + random intercept	3	11971.0	4092.38
Distance to shore (km) + random intercept + random slopes	4	13074.2	5195.66
Distance to shore (km) + random intercept	3	13131.1	5252.51
Sea surface salinity (psu) + random intercept + random slopes	4	14708.7	6830.15
Significant wave height (m) + random intercept + random slopes	4	16152.4	8273.79
Mean wave period (s) + random intercept + random slopes	4	16777.6	8899.04
Sea surface temperature (°C) + random intercept + random slopes	4	16946.5	9067.88
Sea surface salinity (psu) + random intercept	3	17161.3	9282.68
Current velocity + random intercept + random slopes	4	17173.9	9295.31
Current velocity + random intercept	3	17458.0	9579.40
Significant wave height (m) + random intercept	3	17540.7	9662.11
Mean wave period (s) + random intercept	3	17564.2	9685.59
Sea surface temperature (°C) + random intercept	3	17772.9	9894.35
null (~1)	1	18638.6	10759.98

Table 5.2. Second order resource selection coefficients (β) for habitat characteristics of home ranges of Red-throated Loons (n = 23) within the U.S. Mid-Atlantic winter range. The 95% confidence intervals (CI) of the coefficient estimates and the standard deviation around each estimate that is associated with the random effect of individual are also included.

Term	β	95% CI	Random Effect SD
Intercept	-7.50	(-8.36 – -6.64)	1.76
Sea surface temperature	0.05	(-0.33 – 0.44)	0.87
Distance from shore	-1.50	(-2.37 – -0.63)	1.95
Current velocity	0.19	(0.01 – 0.36)	0.28
Sea surface salinity	0.36	(-0.3 – 1.01)	1.54
Chlorophyl a	0.37	(-0.36 – 1.09)	1.70
Water depth	-1.26	(-1.93 – -0.58)	1.32
Mean wave period	-0.07	(-0.23 – 0.09)	0.34
Significant wave height	-0.38	(-0.7 – -0.05)	0.74

Figure 5.3. Random effect slopes for individual selection of home range habitat characteristics within the winter range among Red-throated Loons (n = 23) in the U.S. Mid-Atlantic Bight. Variables were scaled for comparison purposes and each line represents the selection response of an individual loon that was estimated using a second order resource selection analysis framework with mixed effect models.



Third order resource selection. The top supported model of resource selection for winter home range included random slopes to allow for individual variation in response to the effects of chlorophyll a, distance to shore, current velocity, sea surface temperature, water depth, mean wave period and significant wave height (Table 5.3). The habitat characteristics with the greatest effect was chlorophyll a; although, selection was against higher levels in the third order RSA, whereas selection was for higher levels in the second order RSA (Table 5.4). It is important to note that some of the available points for the third order RSA were associated with higher concentrations compared to available points in the second order RSA. In general, effect sizes of all the variables I tested were much smaller in the third order RSA compared to the second order RSA. In fact, all the other terms besides chlorophyll *a* overlapped zero; therefore, I cannot rule out no selection for any of these habitat characteristics at the core use level. The greatest variation in selection among individuals I identified was for sea surface salinity and current velocity, with some individuals exhibiting slightly stronger selection for lower saline waters and higher tidal current velocities (Figure 5.4). But, generally, limited individual variation was evident at the third order selection scale for the covariates I tested. Of the limited variation I did detect in the strength of individual selection, mean habitat availability in the individual's home range was not a significant predictor for any of the covariates we tested (Figure 5.5). i did find that males selected for colder sea surface temperatures compared to females (Figure 5.6); however, sex, breeding latitude, body mass, and home range size were not significant predictors of individual differences in any other selection responses.

Table 5.3. Comparison of generalized linear mixed models of third order resource selection for core use area habitat in the winter home ranges of Red-throated Loons in the U.S. Middle Atlantic Bight. Models are ranked according to Akaike Information Criterion (AIC). Rankings are for null model, single term fixed effect models, global model including all fixed effects and random effect to allow intercept tto vary for individual loons, and global model including all fixed effect terms and random effects to allow slopes of each term to vary for individual loons. Fixed effects included the oceanographic variables: distance to shore (dist); mean monthly chlorophyll a (chl); mean monthly sea surface temperature (SST); 6-hr mean wave period (wavper); 6-hr significant wave height (wavht), surface current velocity (curr); water depth (dep); and sea surface salinity (SSS). The table shows the variables included in the model, number of estimated parameters (K), differences between model Akaike Information Criterion (ΔAIC).

Model	df	logLik	AIC	Δ AIC
Global model + random intercept + random slopes	18	-8289.02	16614.05	0.00
Distance to shore + random intercept +random slopes	4	-8339.11	16686.23	72.18
Current velocity + random intercept + random slopes	4	-8347.77	16703.55	89.49
Sea surface salinity + random intercept + random slope	4	-8367.98	16743.95	129.90
Global model + random intercept	10	-8364.04	16748.08	134.03
Wave height + random intercept + random slope	4	-8370.19	16748.38	134.32
Water depth + random intercept + random slope	4	-8372.50	16753.01	138.95
Water depth + random intercept	3	-8373.59	16753.17	139.12
Distance to shore + random intercept	3	-8374.57	16755.14	141.09
Current velocity + random intercept	3	-8375.81	16757.63	143.58
Chlorophyll a + random intercept + random slope	4	-8375.41	16758.81	144.76
Wave period + random intercept + random slope	4	-8377.05	16762.11	148.06
Wave height + random intercept	3	-8378.09	16762.19	148.13
Chlorophyll a + random intercept	3	-8379.86	16765.72	151.67
Sea surface salinity + random intercept	3	-8380.06	16766.11	152.06
Wave period + random intercept	3	-8380.28	16766.56	152.50
Sea surface temperature + random intercept	3	-8380.39	16766.78	152.73
Sea surface temperature + random intercept + random slope	4	-8380.29	16768.58	154.52
null model	1	-8454.54	16911.08	297.02

Table 5.4. Third order resource selection coefficients (β) for habitat characteristics of core use areas of Red-throated Loon (n = 23) winter home ranges within the U.S. Mid-Atlantic Bight. The 95% confidence intervals (CI) of the coefficient estimates and the standard deviation around each estimate that is associated with the random effect of individual are also included.

Term	β	95% CI	Random Effect SD
Intercept	-3.86	(-4.02 – -3.70)	< 0.001
Sea surface temperature	-0.04	(-0.11 – 0.03)	<0.001
Distance from shore	-0.08	(-0.24 – 0.08)	0.35
Current velocity	-0.06	(-0.29 – 0.17)	0.43
Sea surface salinity	-0.04	(-0.29 – 0.21)	1.54
Chlorophyl a	-0.33	(-0.52 – -0.13)	0.29
Water depth	-0.08	(-0.17 – 0.02)	0.07
Mean wave period	-0.01	(-0.07 – 0.04)	<0.001
Significant wave height	-0.06	(-0.13 – 0.01)	<0.001

Figure 5.4. Random effect slopes for individual selection of core use area habitat characteristics within the home range among wintering Red-throated Loons (n = 23) in the U.S. Mid-Atlantic Bight. Variables were scaled for comparison purposes and each line represents the selection response of an individual loon that was estimated using a resource selection analysis framework with mixed effect models.

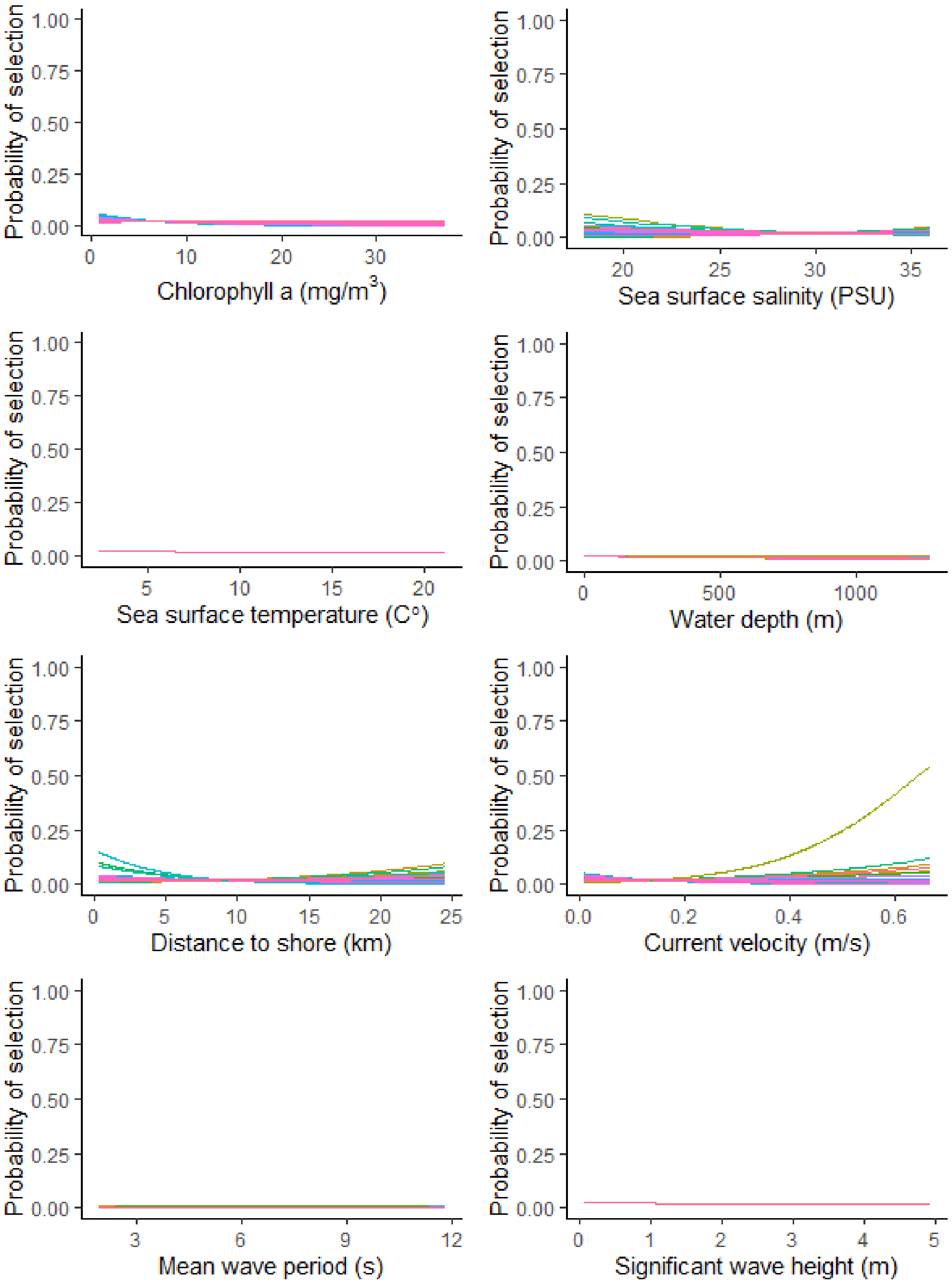


Figure 5.5. Functional response of third order resource selection regression coefficients for Red-throated Loons in relation to the log-transformed mean of that habitat covariate within an individual's winter home range.

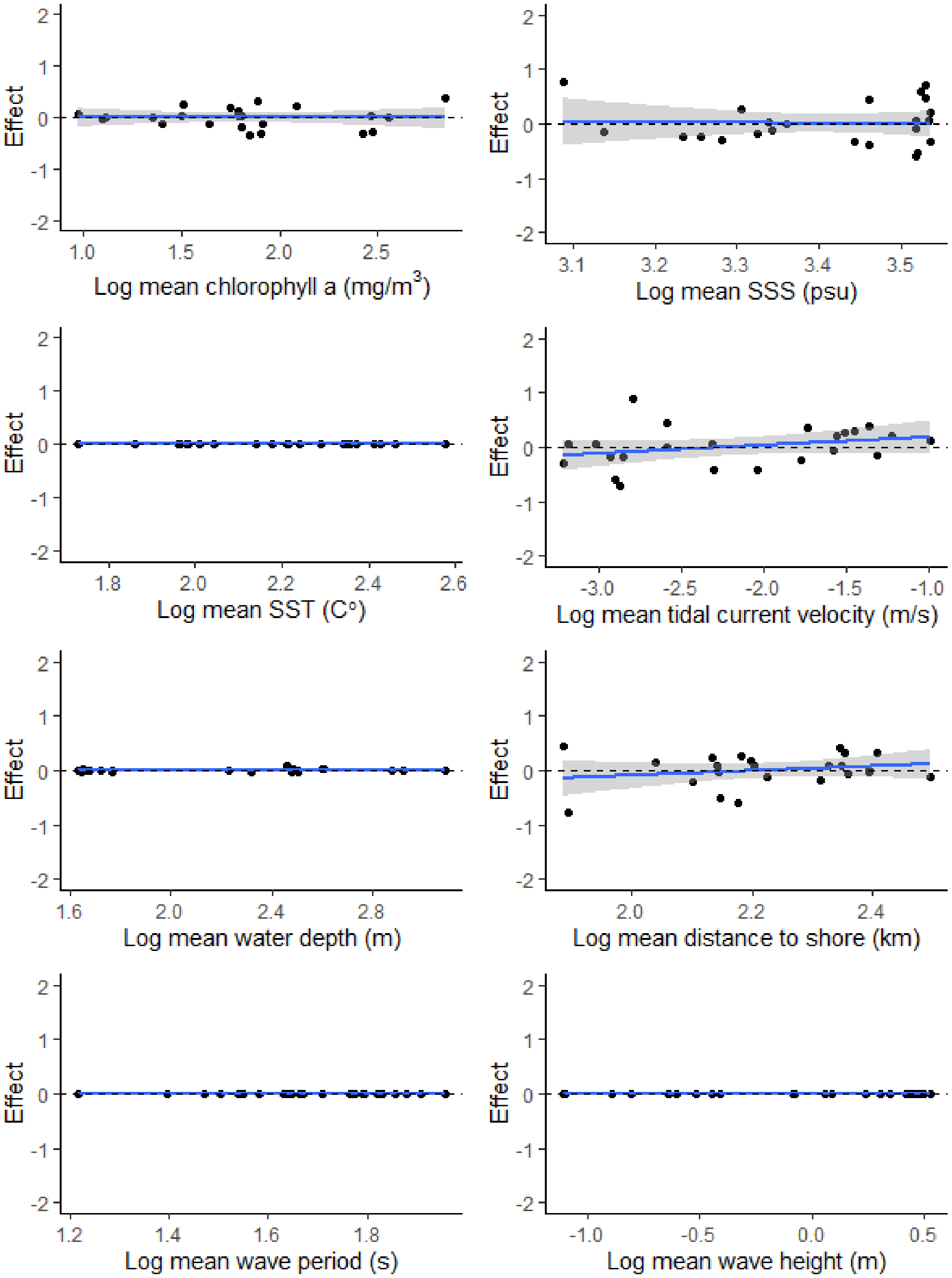
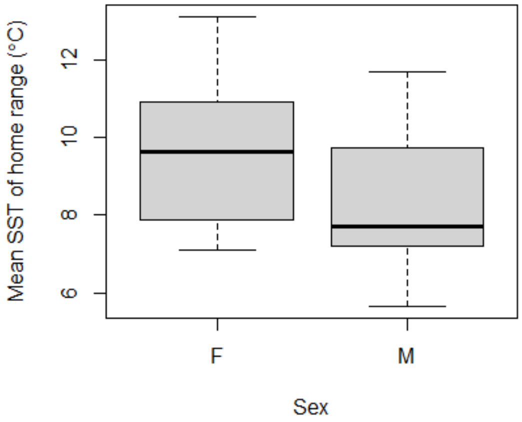


Figure 5.6. Boxplots comparing mean sea surface temperatures (°C) in winter home ranges of male (n = 11) and female (n = 12) red-throated loons in the U.S. Mid-Atlantic Bight. The gray shaded area of the box represents the interquartile range, the black line represents the median, the lower horizontal line represents the minimum of the first quartile and the second horizontal line represents the end of the fourth quartile (not including outliers, which are represented by circles).



Discussion

This study highlights individual variation in the selection of home range habitat characteristics. Incorporating individual-specific variation into my modeling framework allowed me to identify how Red-throated Loons differed in their response to oceanographic characteristics when selecting winter home ranges and core use areas along the mid-Atlantic U.S. coast. Using the more traditional approach of modeling resource selection at the population level would have obscured the variable responses to habitat I detected among individual loons within my sample. Likewise, estimating population-averaged response coefficients would not have shown that while certain individuals may respond strongly to certain habitat characteristics, others used resources in proportion to their availability.

Most birds occupied an area of 75 km^2 or less; yet, several apparently utilized areas up to 4 times larger. Multiple factors in the environment can influence the size of an individual's home range, including food availability, patchiness in the environment, population density, and predation, as well as intrinsic factors, such as body mass and sex (McLoughlin and Ferguson 2000). Males occupied considerably larger home ranges than females in our study, but a larger sample size is likely necessary to determine if this pattern is significant and holds at the population level. For some species that winter in areas with patchily distributed resources, one strategy of habitat use may be observed where certain individuals, termed “floaters”, use disproportionately larger areas relative to the average winter home range of more sedentary individuals within the population (Brown and Long 2007). It is unclear, however, if that pattern is beneficial or not. Sedentary individuals may possess greater site-specific knowledge allowing them to efficiently exploit resources, thereby depressing available resources, and forcing floater individuals to move on to a new site or return to a previous site where they successfully foraged (Spencer 2012). On the other hand, such behavior may allow floaters to more efficiently exploit seasonal variation in food availability (Brown and Sherry 2008). Habitat conditions during the non-breeding season have been linked with differential probabilities of nesting success during the following breeding season in other species (Lehikoinen et al. 2006, Morrissette et al. 2010, Sedinger et al. 2011). However, understanding how winter home range size relates to home range quality and fitness is currently unknown in Red-throated Loons.

Home ranges of Red-throated Loons wintering in the U.S. Mid-Atlantic Bight encompassed a wide range of oceanographic conditions. Relative to each covariate’s availability within this region, however, I found selection for cold, nearshore, shallow, brackish waters with higher current velocity and chlorophyll *a* concentration for home ranges. Among the covariates I tested, selection of winter home ranges was most influenced by water depth and distance to shore. Indeed, winter home ranges were consistently in relatively shallow areas of the winter range, with 75% of used locations occurring in water depths less than 12 m and within 10 km of shore. Surveys of bycatch mortality of seabirds indicated that most Red-throated Loons were killed in mid-Atlantic waters less than 8 m deep (84%), 16% occurred at depths of 8 – 12 m, and none were observed in water ≥ 12 m (Warden 2010). Red-throated Loons in Europe were also found to winter in nearshore, sandy, shallow marine waters (O’Brien et al. 2008, Guse et al. 2009, Busch et al. 2013). Population-level estimates of chlorophyll *a* and sea surface salinity were not considered significant; however, I observed considerable individual variation in selection for these habitat characteristics in the home range. Approximately half the birds I modeled exhibited strong selection for increasing concentrations of chlorophyll *a*, while the remainder showed little to no response. Marine bird distributions are often correlated with high levels of chlorophyll, which leads to the presumption that these locations support high biomasses of forage fish as a result of enhanced net primary productivity (Winiarski et al. 2013). While higher levels of chlorophyll *a* certainly create the *potential* for increased productivity levels, Friedland et al. (2012) noted that using it as a proxy for greater phytoplankton biomass or net primary productivity can be problematic, and direct correlations between higher levels of net primary productivity and fisheries yields are not always consistent (Stock et al. 2017). For the loons in this study, selection for higher levels of chlorophyll *a* is likely a reflection of their affinity for the mouths of tidal rivers and bays, where a suite of physical and biological conditions collectively create enhanced foraging opportunities. For example, plume and estuarine fronts form in these zones when reduced saline waters from freshwater influences meets denser, more saline coastal water. Here, frontal upwelling and tidal mixing force nutrients into the photic zone creating suitable conditions for phytoplankton production. Phytoplankton subsequently provides a food source for zooplankton, and when these organisms are maintained in the upper level of the water column through physical forcing, profitable foraging conditions for fish and seabirds may result.

Spatial use within the home range may vary dramatically, with certain core use areas being used more frequently, more consistently, or for longer periods of time than others (Samuel et al. 1985, Johnson 2007). Core use areas tended to have slightly lower chlorophyll *a* concentration relative to the rest of the home range, but otherwise, we were unable to identify strong selection for the habitat characteristics we tested. Selection for lower chlorophyll *a* levels in core use areas reflects the exceptionally high levels of chlorophyll *a* that were associated with some available points within the home range. While I documented selection *for* higher levels of chlorophyll *a* in the second order resource selection, the scale of chlorophyll *a* concentration was considerably lower for that analysis. It appears that at the finer spatial scale of core use selection, red-throated loons avoided areas with chlorophyll *a* concentrations exceeding 25 mg/m^3, which may be associated with low dissolved oxygen concentrations and water clarity in the study area (Harding et al. 2019). One potential reason for this avoidance may be related to their pursuit diving foraging strategy. Successful underwater foraging for such visual predators relies on visual acuity and decreasing water clarity is likely associated with decreased prey detectability (Haney and Stone 1988).

Because individual home ranges varied in location, I also tested for evidence that individual variation in selection of core use habitat characteristics were related to differences in the extent of available resources within each home range. However, I found no evidence for this type of functional response among any of the covariates I tested. Nor did they appear to be related to the other intrinsic variables I tested; although, I did note that males tended to select for colder sea surface temperatures than females. This could be related to their tendency to maintain larger winter home ranges if it results in their exposure to a wider range of water temperatures. For example, greater use of waters in the northern part of the study area or greater use of areas with cold freshwater influence, such as the tidal rivers of Upper Chesapeake Bay.

Conclusions

Home ranges of wintering red-throated loons in the U.S. Mid-Atlantic Bight occurred in a range of habitats, including tidal rivers, bays, and coastal locations. The loons I tracked occupied a wide range of home range areas, which may be reflective of the hierarchical patch structure of their prey base. Males tended to occupy larger home ranges and select for colder sea surface temperature compared to females in my study; although, a larger sample size is necessary to determine if this pattern holds at the population level. It is unclear why some individuals remained relatively stationary, while others covered much greater areas, during the nonbreeding season. Individual variation in resource use is common in seabirds and likely promotes the foraging success of populations by reducing competition between individuals (Ceia and Ramos 2015). Efforts to quantify the potential fitness consequences each strategy incurs would be beneficial to developing our understanding of the dynamics of predator-prey relationships that occur across multiple scales within the marine environment.

Selection response for oceanographic characteristics in the winter home range was scale-dependent and varied in both direction and magnitude among the individuals I tracked. I noted stronger selection ratios for home range habitat characteristics within the species range (second order RSA) compared to those for core use areas within the home range (third order RSA). This pattern reflects the evenly distributed quality of these resources within the species winter home range, which precluded me from differentiating core use areas using the habitat measures I examined. Obtaining data related to small pelagic fisheries abundance in winter for the study area would be beneficial to understanding why core use areas occur where they do and how oceanographic characteristics can be used to predict seabird foraging hotspots in space and time. For example, the birds I tracked showed an affinity for higher chlorophyll *a* concentration at the home range scale, but selected against levels exceeding 25 mg/m^3 in core use areas. It would be valuable to know if an easily measured proxy for primary productivity, such as chlorophyll *a*, can be used to predict forage fish abundance, and if so, what time lag exists with that response? That information, combined with any other physical and biological conditions that must be present to create favorable foraging conditions for seabirds, would provide vital information for seabird and fisheries management, and marine spatial planning.

CHAPTER 6

SUMMARY

This study presents the first complete description of the annual space use and migration routes of Red-throated Loons as they move between wintering areas along the U.S. Atlantic coast and their breeding grounds. This study revealed considerable sympatry of wintering Red-throated Loons from a wide swath of the breeding range and used a network approach to identify a number of migration bottlenecks in important movement corridors, despite multiple, clearly discrete, migration strategies. The major sites identified as core use areas included lower Hudson Bay and James Bay, the lower Great Lakes, the Gulf of St Lawrence, Nantucket Shoals, and the major bays of the mid-Atlantic region, where birds were captured in winter, including Delaware Bay, Chesapeake Bay, and Pamlico Sound. Prominent movement corridors were evident along the New York Bight and the Gulf of Maine, as well as from southern Hudson Bay and James Bay to points south and southeast, primarily the lower Great Lakes and the Gulf of St. Lawrence.

Red-throated Loons exhibited a high degree of individual variation in movement behavior during the non-breeding season. Individuals differed in their tendency to be intensive versus extensive in their movement behaviors, which corresponded with individual differences in the scale of their use of the landscape. Location and time of year were also important factors in determining behavior, with more stationary behavior occurring during the winter months and at lower latitudes. Home ranges of wintering red-throated loons in the U.S. Mid-Atlantic Bight occurred in a range of habitats, including tidal rivers, bays, and coastal locations. The loons I tracked occupied a wide range of home range areas;

although, it is unclear why some individuals remain relatively stationary, while others cover much greater areas, during the nonbreeding season.

In migration, Red-throated Loons relied on a combination of primary, secondary, and intrinsic cues to adjust their movement behavior. Photoperiod was an important indicator of increased speed and direction of movement at the onset of migration; however, its strength waned as the season progressed. Oceanographic conditions were important factors in switching to stopover behavior, which consisted of slower, more area-restricted search movements. Red-throated loons relied on relatively few stopover sites, but stays were extended, and their use was consistent among individuals. Resumption of directed movements away from these stopover locations was predicted by atmospheric conditions related to flight efficiency, mainly wind speed and direction. Similar to migrating landbirds, favorable tail winds were an important driver of faster, more directed movement behavior for this migratory seabird.

Characterizing spatial distributions during the breeding, migration, and winter periods is an important first step to understanding the full annual cycle of a species. This study provides considerable information for filling data gaps about habitat use of the Red-throated Loon population in eastern North America. By identifying where and when individuals and populations are located throughout the year, we can identify the most important parts of the network that can be used to focus species conservation initiatives. The importance of a site may be based on how intensively it is used, the proportion of the population it supports, the demographic function it serves, and/or its role in maintaining overall connectivity of the network, particularly when alternate sites are not available. My hope is that this body of research will serve to advance conservation of the species, as well as encourage further innovation in the study of the movement ecology of migratory birds.

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APPENDIX A: DATA COLLECTION AND MANAGEMENT

Background

Data used in this dissertation were obtained secondarily from a satellite-tracking study of Red-throated Loons while on their wintering grounds offshore of the U.S. Mid-Atlantic Coast (Spiegel et al. 2017). The study was funded primarily by the U.S. Bureau of Ocean Energy Management (BOEM) and was a collaborative project among research partners, including the U.S. Fish and Wildlife Service (Hadley, MA), USGS Patuxent Wildlife Research Center (Laurel, MD), Biodiversity Research Institute (Portland, ME), and Memorial University (St. Johns, Newfoundland, Canada). The primary objective of the study was to identify local and migratory movement patterns of diving birds in relation to proposed offshore wind energy development areas within Federal waters of the U.S. Mid-Atlantic region. Therefore, the sampling design of the data used for this dissertation was established according to the research priorities of the BOEM study and is reflected in the location of field-related capture efforts and in the selection of the satellite transmitter's duty cycle settings, i.e., frequency of satellite data transmissions. These factors were carefully considered when developing the research questions and analytical methods included in this dissertation to ensure appropriate post hoc use of the data set and to minimize sampling bias in the results.

Field Efforts

Red-throated Loons were captured January to March (2012 – 2015) while on their wintering grounds in waters off the U.S. mid-Atlantic coast from Delaware to the southern border of North Carolina. Capture efforts in 2012 were attempted on the following waterbodies: Pamlico Sound, NC; Chesapeake Bay, MD and VA; Chincoteague Bay, MD and VA; Assawoman Bay and Isle of Wight Bay, MD; Indian River Bay, DE; Delaware Bay, DE and NJ, and the coastal Atlantic Ocean in DE and VA. These pilot year efforts identified areas with high concentrations of Red-throated Loons, where captured efforts were then focused the following three winters (2013–2015), including: Pamlico Sound, offshore of Hatteras, NC; Chesapeake Bay, offshore of Cape Charles, VA; Delaware Bay, offshore of Lewes, DE; and the Atlantic Ocean, offshore of Cape Henlopen, DE, and Chesapeake Bay Bridge area, VA.

Birds were captured using night-lighting techniques, i.e., birds were approached at night by boat with a spotlight and captured with a dip net. All captured birds were fitted with a USFWS aluminum band and aged according to criteria established by (Pyle 2008). Individuals determined to be “after third year” (ATY) and “after second year” (ASY) were considered primary candidates for PTT implantation; all others were banded and released. To minimize stress related to capture and handling, individuals were administered 2 mg/kg of a mild sedative, midazolam hydrochloride IM, prior to being transported to land-based surgery locations. Surgical implantations of intra-abdominal PTTs with external antenna were conducted by qualified veterinarians following techniques described elsewhere (Chapter 5, Spiegel et al. 2017).

Over four winters, 111 Red-throated Loons were captured, of which 86 were released with PTTs (2012: *n* = 17; 2013: *n* = 26; 2014: *n* = 23; and 2015: *n* = 20) (Table A.1). Of the 86 birds released with PTTs, there were 51 females, 28 males, and 7 of unknown sex. Body mass of females ranged from 1,400-2,150 g and 1,700-2,600 g for males. In total, 24 died within the immediate 14-day post-release period, which is the time period in which mortality can confidently be attributed to surgery (Mulcahy and Esler 1999). This corresponds with surgery-related mortality rates of 41% (*n* = 7) for 2012, 31% (*n* = 8) for 2013, 17% (*n* = 4) for 2014, and 25% (*n* = 5) for the 2015 season.

Table A.1. Details of capture and platform terminal transmitter (PTT) deployment of all Red-throated Loons captured in this study, 2012 – 2015. Duration days indicates the number of days the satellite transmitter collected location data.

Loon PTT ID	USFWS Leg Band #	Sex	Age	Body Mass (g)	Capture Location	Duration Days
113899_1	1367-19516	F	ASY	1950	Pamlico Sound, NC	12
113900_1	1367-19517	M	ASY	1950	Pamlico Sound, NC	439
113901_1	2017-14940	U	ASY	2160	Chesapeake Bay, Tangier Sound	341
113902_1	2017-14939	F	ASY	1400	Chesapeake Bay, Tangier Sound	306
113903_1	1367-19520	U	ASY	2200	Indian River Bay, DE	406
115193_1	1367-19521	U	ATY	1472	Chesapeake Bay, Deal Island	4
115194_1	1367-19523	F	ATY	1472	Chesapeake Bay, Deal Island	365
115195_1	1367-73516	F	ATY	1723	Delaware Bay	12
115195_2	1367-19555	M	ASY	NA	Chesapeake Bay, Kiptopeke, VA	405
115196_1	2017-14938	F	ATY	1600	Chesapeake Bay, Tangier Sound	107
115197_1	1367-19524	M	ATY	2200	Chesapeake Bay, Deal Island	411
115198_1	2017-14937	M	ATY	2000	Chesapeake Bay, Tangier Sound	378
115199_1	1367-19527	F	SY	1500	Chesapeake Bay, Tangier Sound	58
115200_1	1367-19531	M	SY	1640	Chesapeake Bay, Tangier Sound	3
115201_1	2017-14931	M	ATY	1900	Chesapeake Bay, Broad Creek	2
115202_1	2017-14933	U	ATY	1900	Chesapeake Bay, Broad Creek	4
115203_1	2017-14932	U	SY	1900	Chesapeake Bay, Broad Creek	1
115204_1	2017-14934	F	ATY	1900	Chesapeake Bay, Broad Creek	268
115205_1	1367-19553	F	ATY	1900	Pamlico Sound, NC	382
115206_1	1367-19552	F	ASY	1950	Pamlico Sound, NC	359
115207_1	1367-19554	F	ASY	1600	Pamlico Sound, NC	332
123467_1	1367-19534	F	ATY	2000	Atlantic Ocean, Cape Henlopen	461
123468_1	1367-19533	F	ATY	1900	Atlantic Ocean, Cape Henlopen	7

Table A.1 Continued

Loon PTT ID	USFWS Leg Band #	Sex	Age	Body Mass (g)	Capture Location	Duration Days
123468_2	1367-19543	F	ASY	1600	Chesapeake Bay, Bay-bridge, VA	406
123469_1	1367-19537	F	ATY	1900	Atlantic Ocean, N of Bay-bridge	11
123469_2	1367-19557	F	ATY	1500	Delaware Bay, Cape Henlopen	27
123470_1	1367-19538	F	ASY	1550	Pamlico Sound, NC	9
123471_1	1367-19541	M	ATY	2100	Chesapeake Bay, Bay-bridge, VA	4
123471_2	1587-50834	F	ASY	1550	Chesapeake Bay, Cape Charles	381
123472_1	1367-19536	F	ATY	1700	Atlantic Ocean, N of Bay-bridge	100
123473_1	1367-19545	M	ATY	2075	Chesapeake Bay, Bay-bridge, VA	30
123474_1	1367-19544	F	ATY	1800	Pamlico Sound, NC	195
123475_1	1367-19546	F	ATY	1800	Pamlico Sound, NC	544
123476_1	1367-19547	F	ASY	1600	Pamlico Sound, NC	328
123477_1	1367-19556	M	ATY	1900	Delaware Bay, Cape Henlopen	5
123478_1	1367-19558	F	ASY	1800	Delaware Bay, Cape Henlopen	15
123479_1	1367-19548	F	ATY	1750	Pamlico Sound, NC	55
123480_1	1367-19549	M	ATY	2200	Pamlico Sound, NC	141
123481_1	1367-19550	M	ASY	1950	Pamlico Sound, NC	7
123482_1	1367-19551	M	ATY	2100	Pamlico Sound, NC	397
123483_1	1367-19559	F	ATY	1500	Delaware Bay, Cape Henlopen	3
123483_2	1587-50829	F	TY	2150	Delaware Bay, Cape Henlopen	448
123484_1	1367-19561	F	ATY	1525	Cape Henlopen, DE	339
123485_1	1367-19562	F	ATY	1650	Delaware Bay, Cape Henlopen	21
123486_1	1367-19563	M	ATY	2050	Delaware Bay, DE	12
132840_1	2017-14904	F	ASY	1900	Cedar Island ferry boat ramp, NC	13
132841_1	2017-14905	F	ASY	2000	Cedar Island ferry boat ramp, NC	386
132842_1	2017-14908	F	ASY	1700	Cedar Island ferry boat ramp, NC	280

Table A.1 Continued

Loon PTT ID	USFWS Leg Band #	Sex	Age	Body Mass (g)	Capture Location	Duration Days
132843_1	2017-14910	M	ASY	2300	Cedar Island ferry boat ramp, NC	415
132844_1	2017-14911	M	ASY	1800	Cedar Island ferry boat ramp, NC	7
132845_1	2017-14912	F	ASY	1700	Cedar Island ferry boat ramp, NC	353
132846_1	1587-50823	F	ASY	1800	Delaware Bay, DE	343
132847_1	1587-50833	M	ASY	2150	Delaware Bay, DE	334
132848_1	1587-50828	M	ASY	2250	Delaware Bay, DE	41
132849_1	1587-50818	F	ASY	1900	Delaware Bay, DE	6
132849_2	1587-50831	F	ASY	1600	Delaware Bay, DE	313
132850_1	1587-50820	F	ASY	1850	Delaware Bay, DE	414
132851_1	1587-50826	F	ASY	1600	Delaware Bay, DE	373
132852_1	1587-50824	M	ASY	1750	Delaware Bay, DE	406
132853_1	1587-50817	F	ASY	1750	Delaware Bay, DE	387
132854_1	1587-50816	M	ASY	2300	Delaware Bay, DE	369
132855_1	1587-50821	F	ASY	1750	Delaware Bay, DE	357
132856_1	1587-50825	F	ASY	1800	Delaware Bay, DE	19
132857_1	1587-50819	M	ASY	2100	Delaware Bay, DE	16
132858_1	1587-50822	M	ASY	2300	Delaware Bay, DE	438
132859_1	1587-50827	F	ASY	1600	Delaware Bay, DE	11
146508_1	0767-05213	F	ASY	1825	Hatteras NC	176
146509_1	1587-59718	M	ASY	2500	Cape Charles, VA	450
146510_1	0767-05216	F	ASY	1650	Hatteras NC	150
146511_1	0767-05215	U	ASY	1900	Hatteras NC	314
146512_1	0767-05214	F	ASY	2125	Hatteras NC	182
146513_1	0767-05219	M	ASY	2150	Hatteras NC	323
146514_1	0767-05221	F	ASY	1600	Hatteras NC	340

Table A.1 Continued

Loon PTT ID	USFWS Leg Band #	Sex	Age	Body Mass (g)	Capture Location	Duration Days
146515_1	0767-05218	F	ASY	1700	Hatteras NC	359
146516_1	0767-05222	M	ASY	2000	Hatteras NC	8
146517_1	0767-05224	F	ASY	1700	Hatteras NC	309
146518_1	0767-05233	F	ASY	1500	Hatteras NC	9
146519_1	0767-05232	F	ASY	1600	Hatteras NC	55
146520_1	0767-05229	F	ASY	1800	Hatteras NC	439
146521_1	0767-05234	F	ASY	1700	Hatteras NC	7
146522_1	0767-05235	F	ASY	1700	Hatteras NC	7
146523_1	0767-05236	F	ASY	1600	Hatteras NC	310
146524_1	0767-05239	M	ASY	2300	Cape Charles, VA	43
146525_1	0767-05237	M	TY/ATY	2000	Hatteras NC	386
146526_1	0767-05240	M	ASY	2600	Cape Charles, VA	373
146527_1	0767-05241	F	ATY	1700	Cape Charles, VA	7

Satellite Transmitters

Satellite transmitters weighed approximately 49 g and comprised < 4% of the average body mass of birds deployed. The Argos system of satellites (http://www.argos-system.org/) receive location data from PTTs and retransmit those data back to regional stations on Earth in real time. The number of hours per day that PTTs communicate with transmitters, i.e., duty cycle, determines the battery life of the PTT. Transmitters used in this study were programmed with three distinct duty cycles that extended battery life to approximately one year to ensure coverage over multiple stages of the annual cycle. As noted previously, duty cycles were selected in accordance with the BOEM study objectives; therefore, sampling intensity was prioritized during the periods when birds were expected to occur in the offshore areas of the mid-Atlantic region. As such, a duty cycle of 4 hours on and 13 hours off was used for the period of 1 November to 31 May. Longer duty cycles were employed for the remainder of the year, when birds were expected to be outside of the mid-Atlantic region: 2 hours on and 5 days off from 31 May to 31 August, and 4 hours on and 24 hours off from 31 August to 01 November. Satellite transmitters had an average duration of 370 ± 74 days, with a maximum duration of 544 days and minimum of 100 days.

Data Management

Location data for all active PTTs was downloaded from Argos servers every five days during the BOEM study and archived at several locations including MoveBank (www.movebank.org) and servers at the USGS Patuxent Wildlife Research Center Data. Data was also filtered with the Douglas Argos Filter (DAF, http://alaska.usgs.gov/science/biology/spatial/douglas.html) prior to being received for the analyses in this dissertation. The DAF is used to filter out improbable locations in satellite tracking data that do not pass a spatial redundancy test and a movement rate and turning angle test (Douglas et al. 2012).

Animal movement behavior may be affected during the period immediately following the implant procedure and it is recommended that data collected during the post-surgery period be culled from data sets to limit surgery-related bias (Mulcahy and Esler 1999, Sexson et al. 2014). To determine the number of days to censor from the Red-throated Loon data set, I calculated daily survival probabilities for the 30-day post-surgery period using nest survival models in RMark (Laake 2013) as described in Blomberg et al. 2018. I first investigated the influence of potential group effects on daily survival, such as sex, capture year, and capture location. Each single term model was compared against each other and the null model using AIC model selection. The model with the lowest AIC_c, and those having $\Delta AIC_c \leq 2$ had the most statistical support, values between 4 and 7 had considerably less support, and those > 10 had virtually no support (Burnham and Anderson 2002). Results indicated considerable support for the capture location effect on daily survival; however, there was similar support for the null model and so the simpler model was retained for the next stage of the analysis (Table A.2).

Table A.2. Comparison of the null model (S(~1)) with models containing group effects (capture location, year, and sex) on daily survival probability of red-throated loons (n = 88) for the first 30 days following abdominal implant surgery of satellite transmitters. Models are ranked according to Akaike Information Criterion (AIC). The table shows the variables included in the model, number of estimated parameters (K), differences between model Akaike Information Criterion (ΔAIC), and AIC weights (w_i).

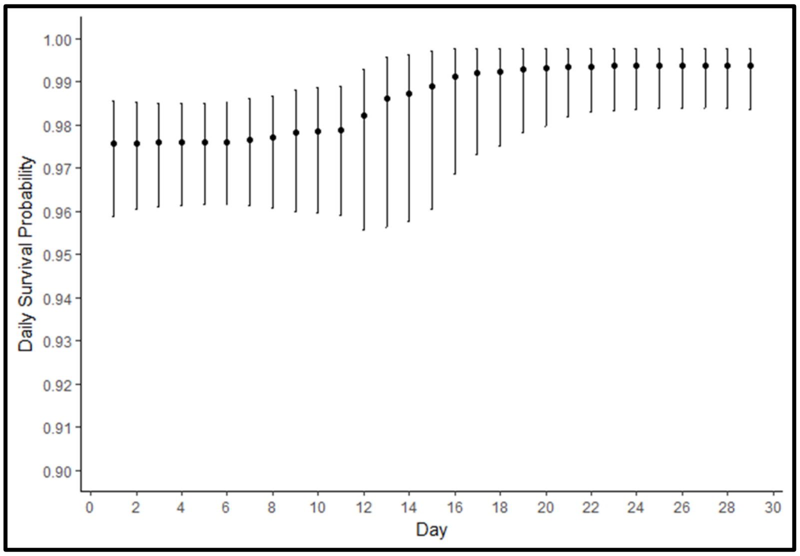
Model	K	AIC	ΔAIC	w_i
S(~1)	1	292.955	0.000	0.564
S(~CapLoc)	3	294.732	1.777	0.232
S(~year)	4	296.163	3.208	0.113
S(~sex)	3	296.623	3.668	0.090

The next stage examined a series of potential temporal effects on survival that included a fully independent effect for each post-release day (days 2 to 30), linear and quadratic trends on number of days post-release, as well as a logarithmic transformation of day that was similar to the quadratic effect but did not force the non-linear shape on the ends of the data. Threshold models were also explored for each day to determine if there was a point, where survival probability showed a marked increase, which would indicate the appropriate day to left-censor the data. For example, for day 13 after surgery, days 2 to 11 and days 15 to 29 were allowed to vary independently in survival probability but survival for the interval of day 12 to 13 and 13 to 14 were held constant. This was repeated for days 2 to 29 and each model was compared with each other, as well as the other time effect models, using AIC model selection. The top supported models included the threshold models for days 12, 13, 15, and 16 (Table A.3 and Figure A.1). I chose the most conservative option among those models and censored days ≤ 16 post-release for each Red-throated Loon prior to all analyses in this dissertation. The probability of surviving the first 30 days was 0.66 and a total of 28 individuals were ultimately left-censored due to surgery-related mortality within the first 16 days after release.

Table A.3. Comparison of the top ten models containing time effects (quadratic trend and threshold models for days 7, 9, 12 – 17, and 19 shown) on daily survival probability of Red-throated Loons (n = 88) for the first 30 days following abdominal implant surgery of satellite transmitters. Models are ranked according to Akaike Information Criterion (AIC). The table shows the variables included in the model, number of estimated parameters (K), differences between model Akaike Information Criterion (ΔAIC), and AIC weights (w_i).

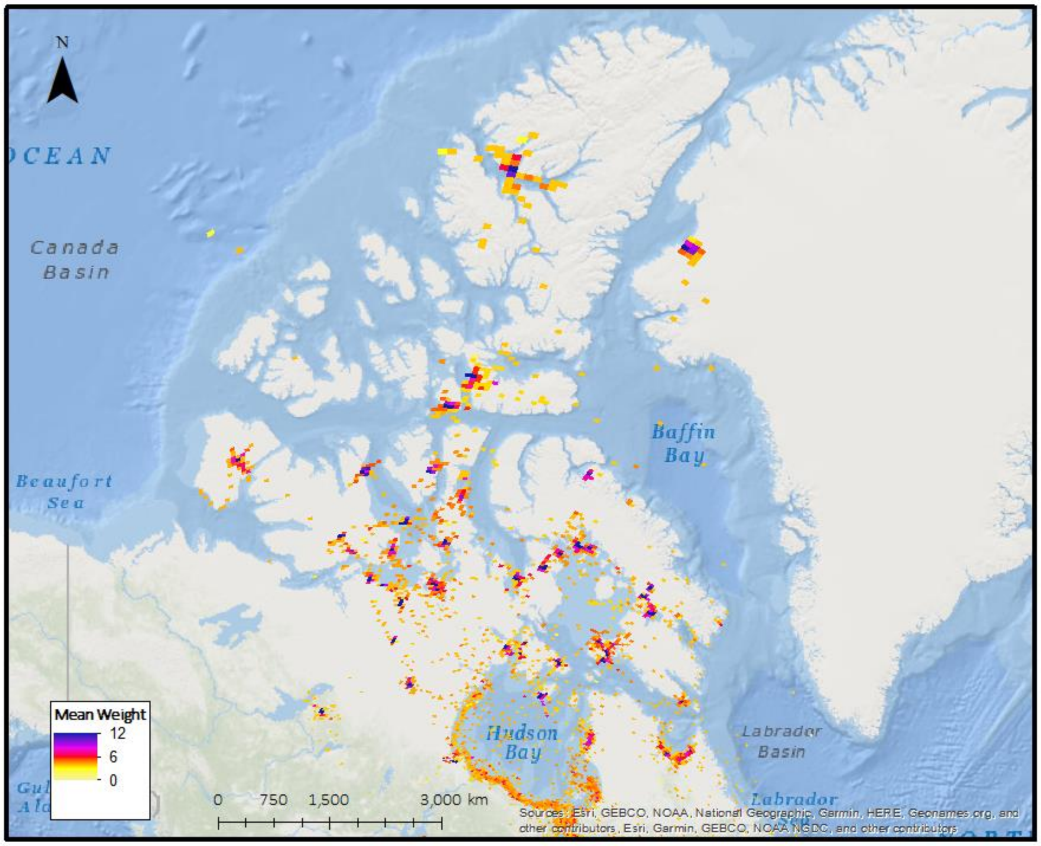
Model	K	AIC	ΔAIC	w_i
S(~day13)	2	282.762	0	0.211
S(~day12)	2	283.138	0.375	0.175
S(~day16)	2	283.705	0.943	0.132
S(~day15)	2	284.488	1.725	0.089
S(~day14)	2	285.048	2.286	0.067
S(~day9)	2	285.514	2.752	0.053
S(~day17)	2	285.769	3.007	0.046
S(~Time+I(Time^2))	3	286.670	3.908	0.030
S(~day19)	2	286.732	3.970	0.029
S(~day7)	2	286.873	4.110	0.027

Figure A.1. Model-averaged daily survival estimates of Red-throated Loons (n = 88) during the 30-day period following abdominal implant surgery of satellite transmitters. Daily survival is lowest during the first 10 days after the procedure, increases each day from day 12 to 16, and levels off for the remainder of the period.



APPENDIX B: SUPPLEMENTAL FIGURES FOR CHAPTER 1

Figure B.1. Node-level metric of weight calculated on satellite-tagged Red-throated Loon (n =38) movements in northern part of the annual range. Nodes with higher weights are indicative of locations with greater levels of use in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.2. Node-level metric of weight calculated on satellite-tagged Red-throated Loon (n =38) movements in central part of the annual range. Nodes with higher weights are indicative of locations with greater levels of use in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.

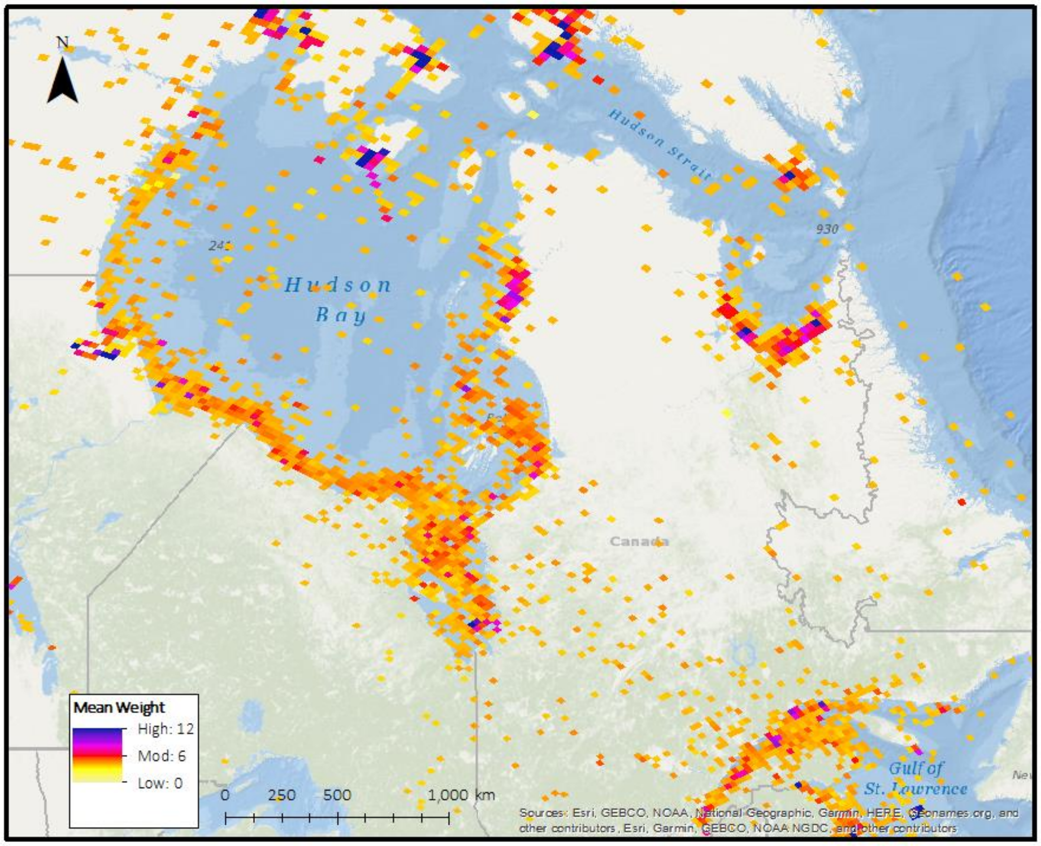
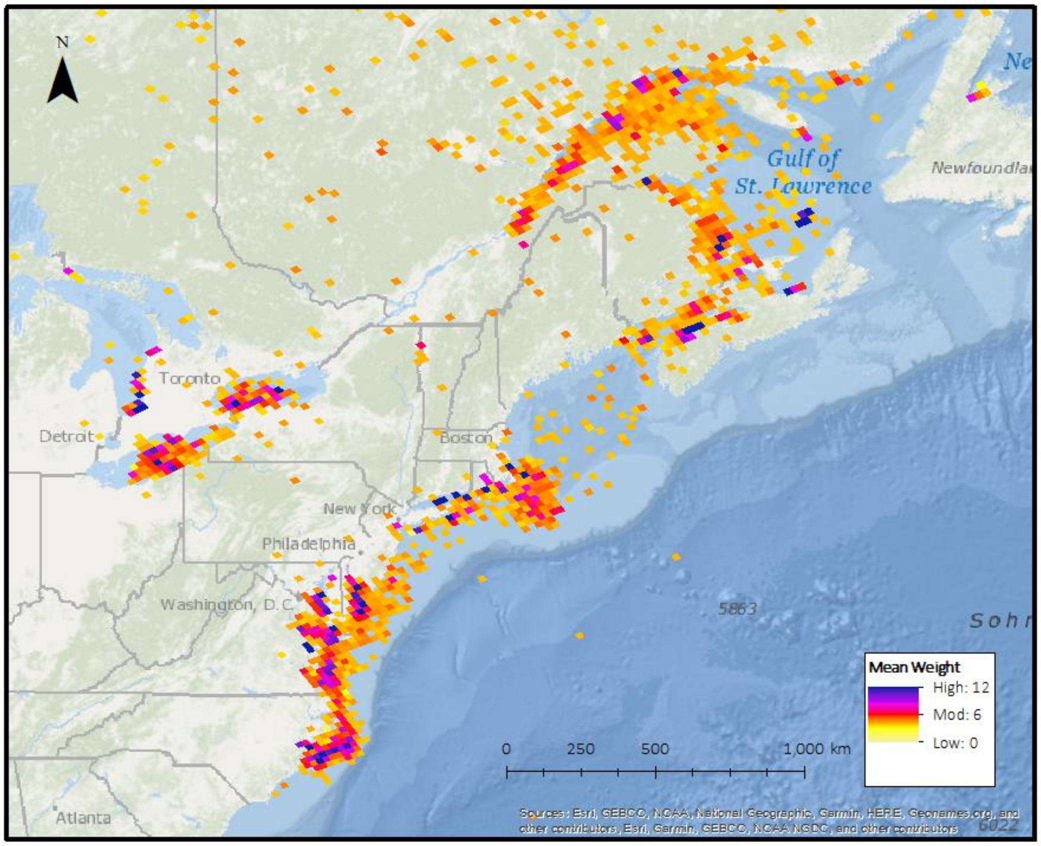
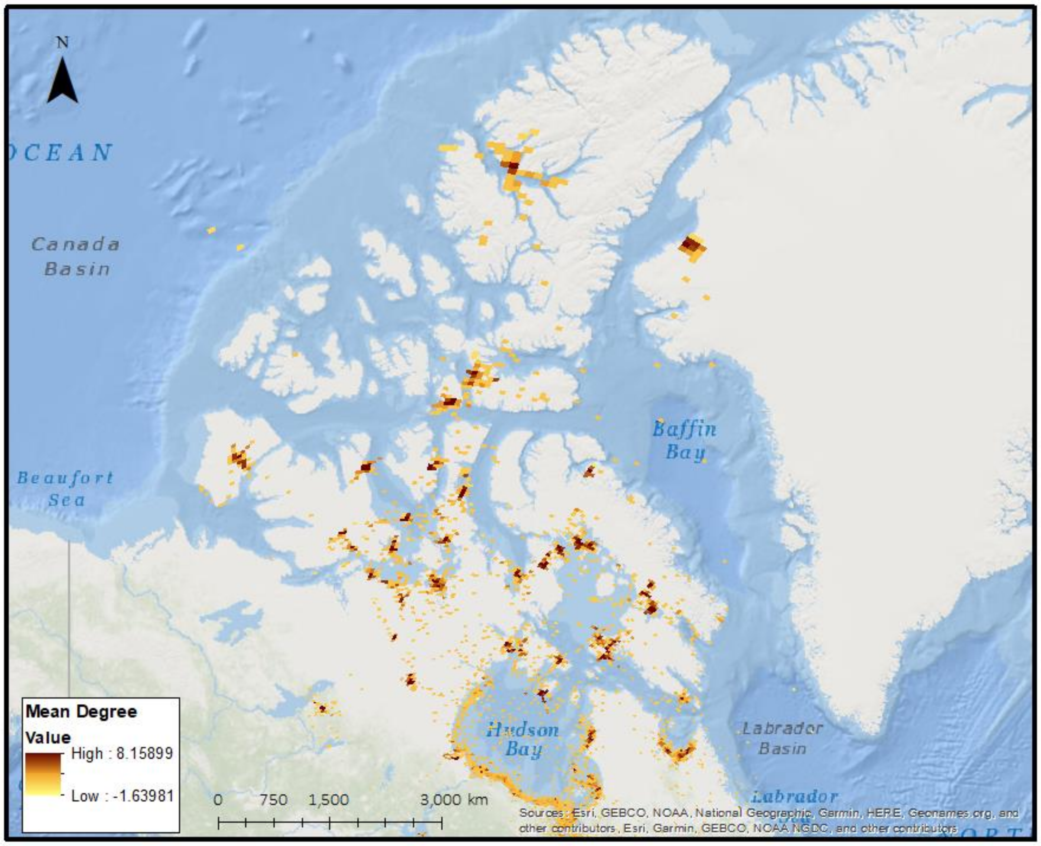


Figure B.3. Node-level metric of weight calculated on satellite-tagged Red-throated Loon (n =38) movements in southern part of the annual range. Nodes with higher weights are indicative of locations with greater levels of use in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.



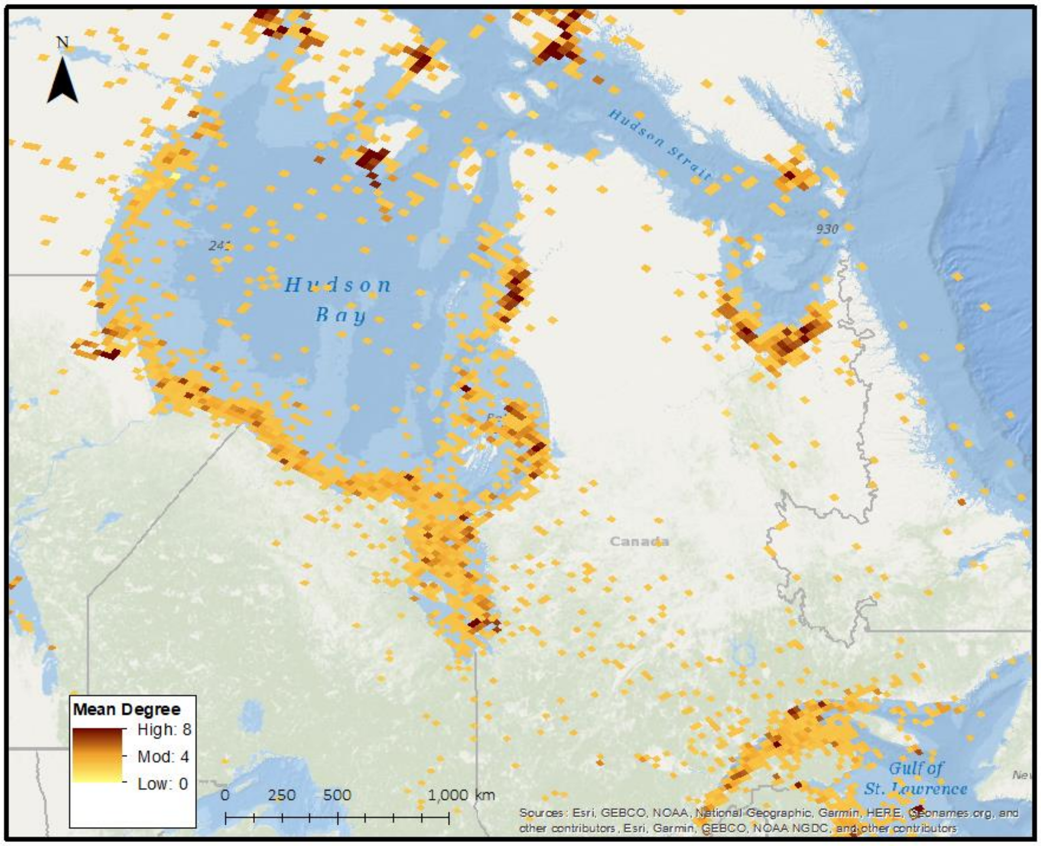
Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.4. Node-level metric of degree calculated on satellite-tagged Red-throated Loon (n =38) movements in northern part of the annual range. Nodes with higher mean degree values are indicative of locations with more connections to other used nodes in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.5. Node-level metric of degree calculated on satellite-tagged Red-throated Loon (n =38) movements in central part of the annual range. Nodes with higher mean degree values are indicative of locations with more connections to other used nodes in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.6. Node-level metric of degree calculated on satellite-tagged Red-throated Loon (n =38) movements in southern part of the annual range. Nodes with higher mean degree values are indicative of locations with more connections to other used nodes in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.

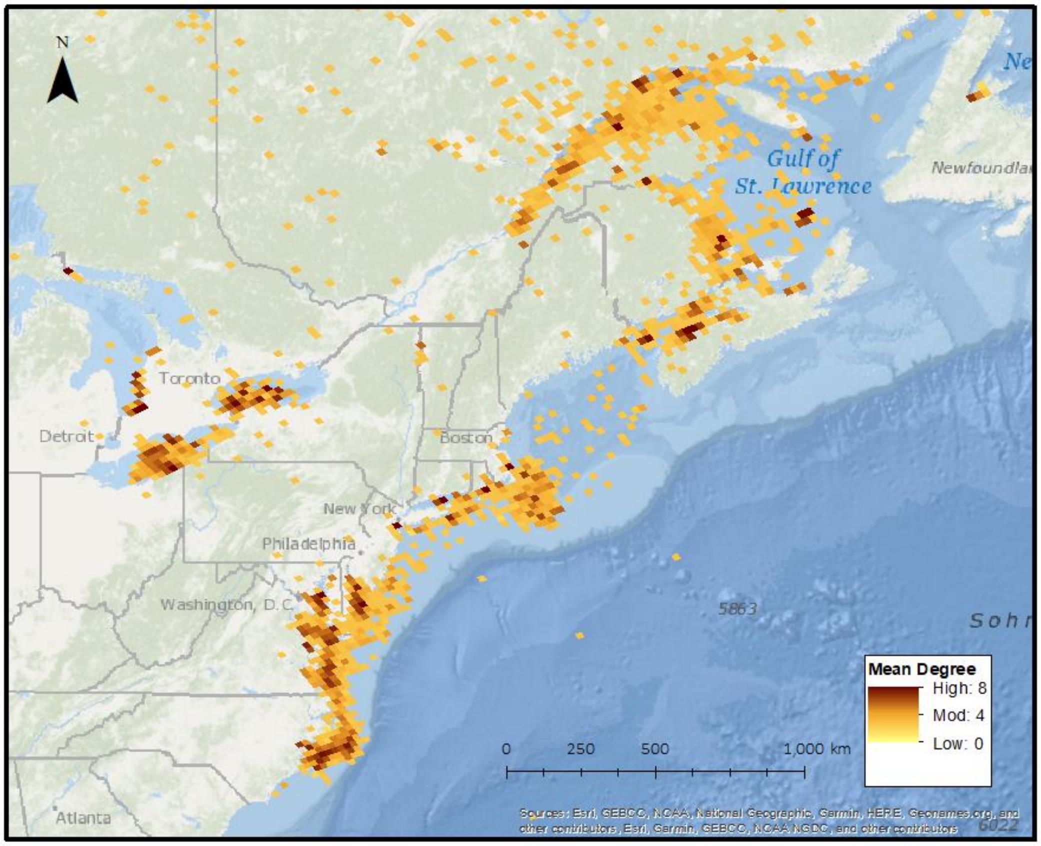
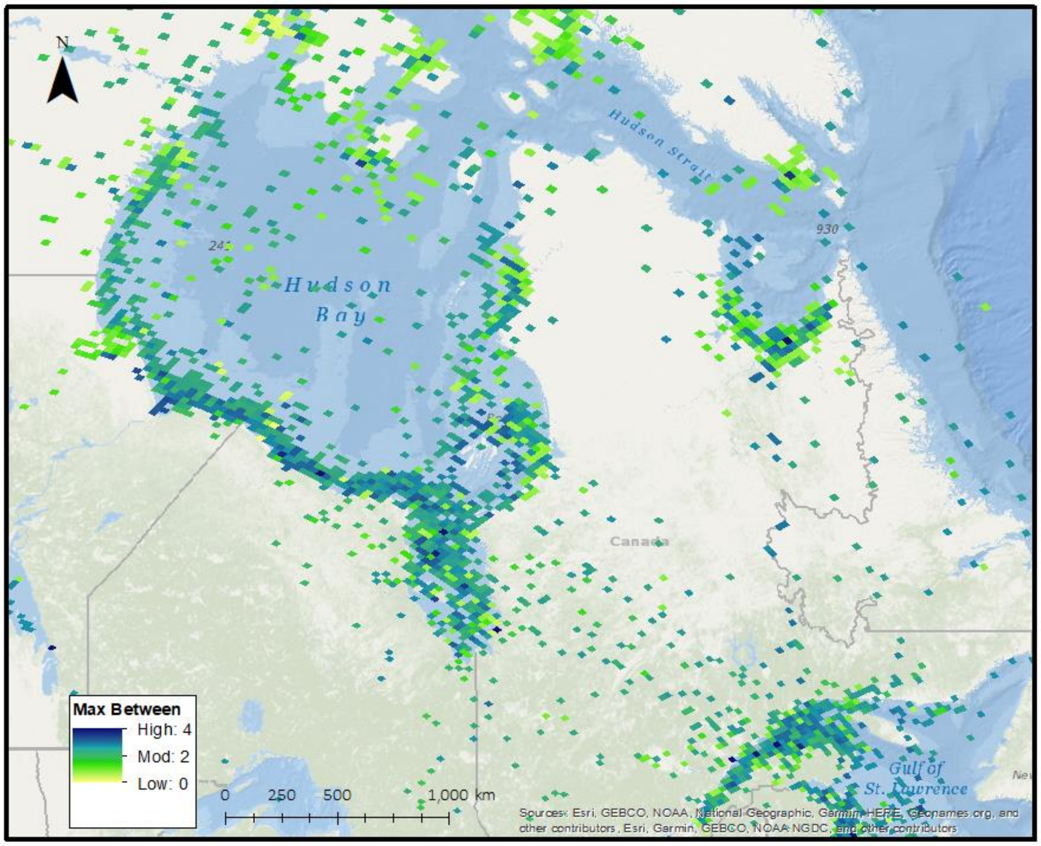


Figure B.7. Node-level metric of betweenness calculated on satellite-tagged Red-throated Loon (n =38) movements in central part of the annual range. Nodes with higher maximum betweenness values are indicative of locations important for maintaining connections between other used nodes in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.8. Node-level metric of betweenness calculated on satellite-tagged Red-throated Loon (n =38) movements in southern part of the annual range. Nodes with higher maximum betweenness values are indicative of locations important for maintaining connections between other used nodes in the network. Pixel size of individual nodes (19.6 km) is based on the median step length of all individuals.

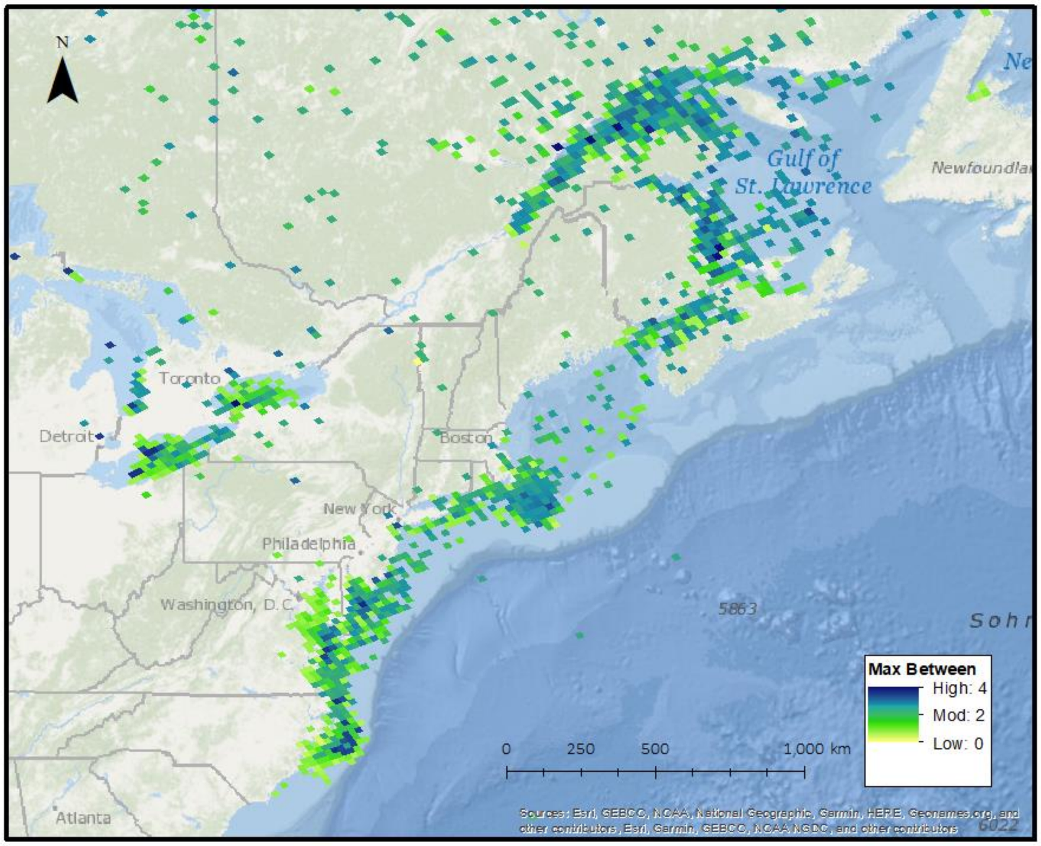


Figure B.9. Annual cycle movement trajectory of Red-throated Loon id# 113900.

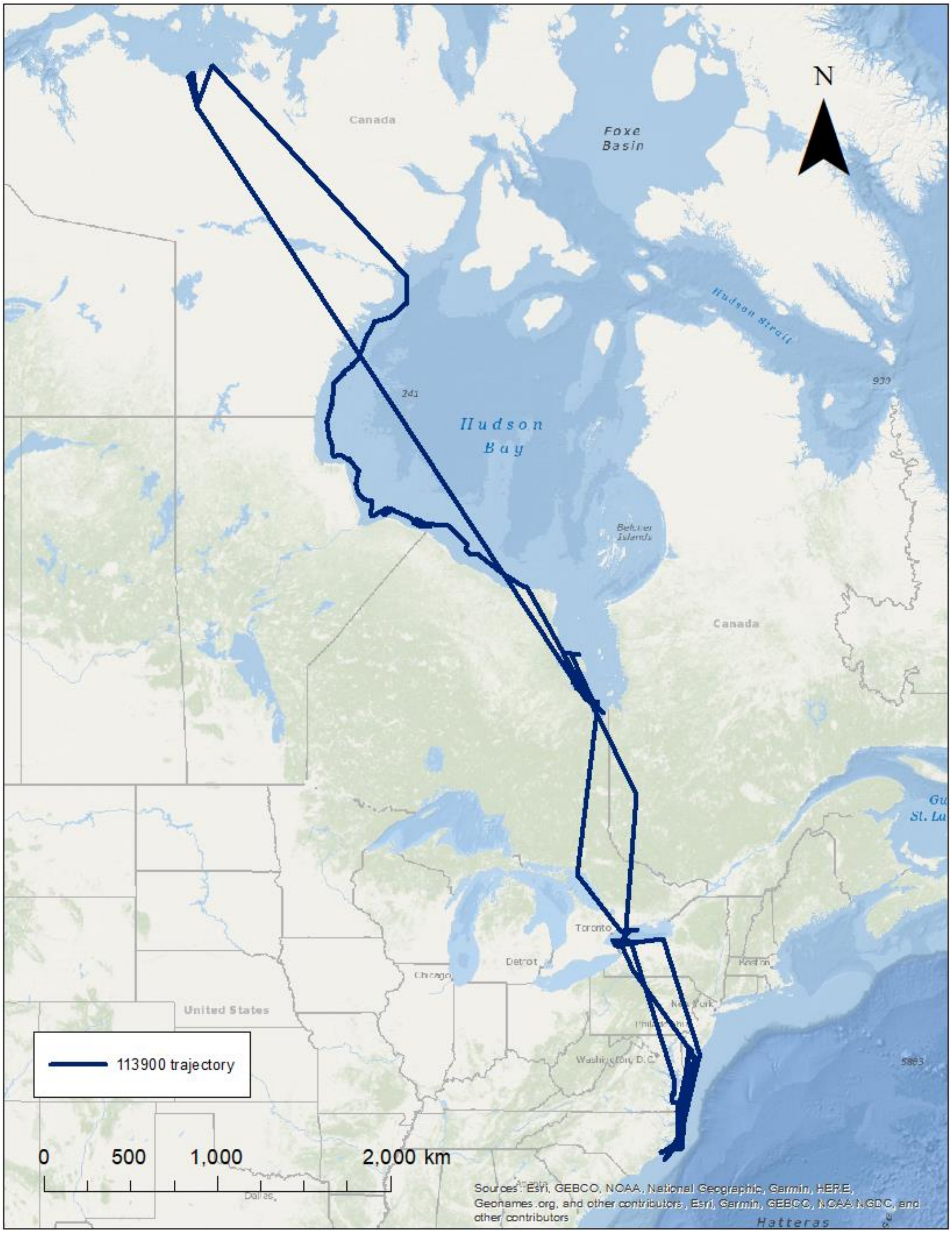


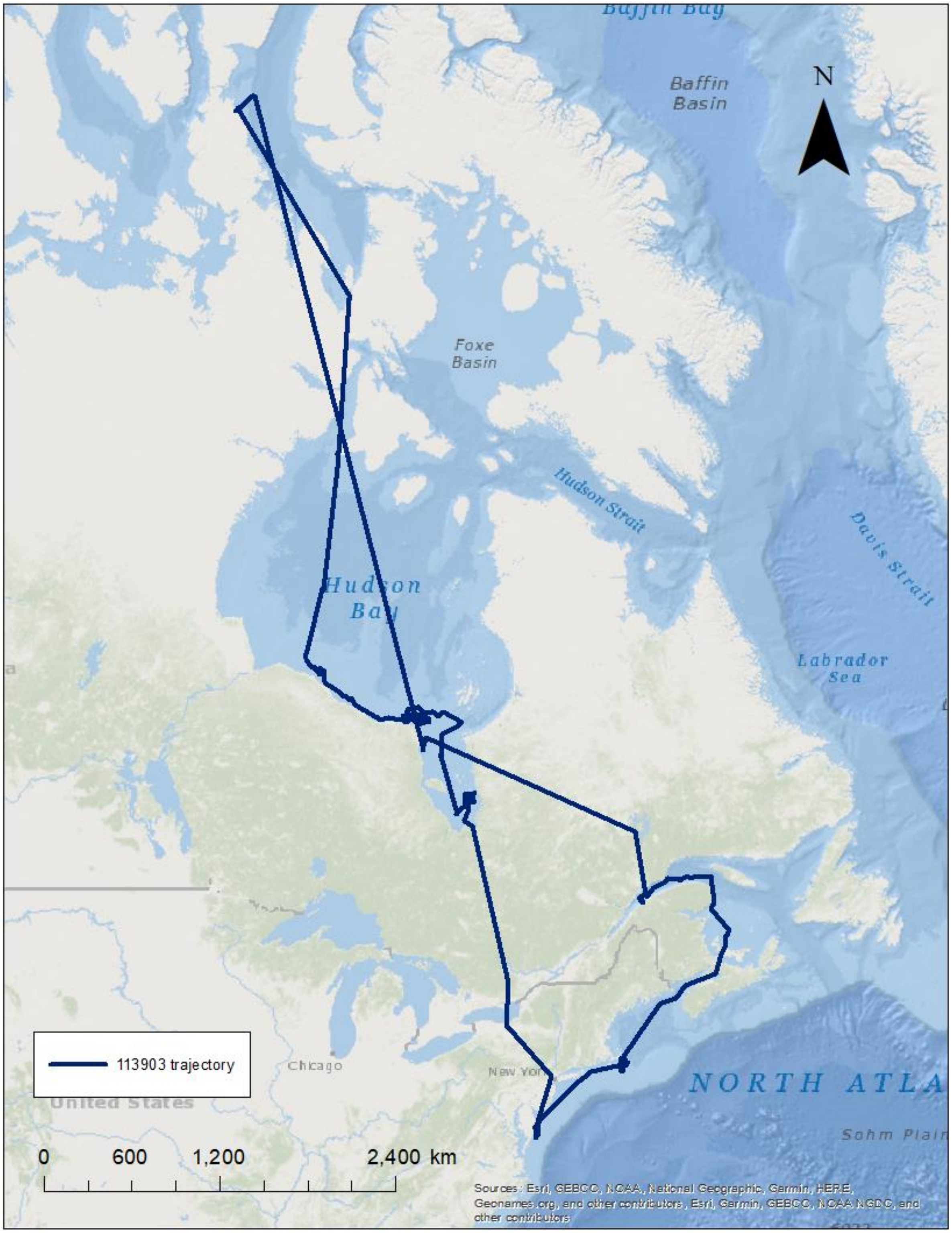
Figure B.10. Annual cycle movement trajectory of Red-throated Loon id# 113901.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.11. Annual cycle movement trajectory of Red-throated Loon id# 113902.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.12. Annual cycle movement trajectory of Red-throated Loon id# 113903.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.13. Annual cycle movement trajectory of Red-throated Loon id# 115194.

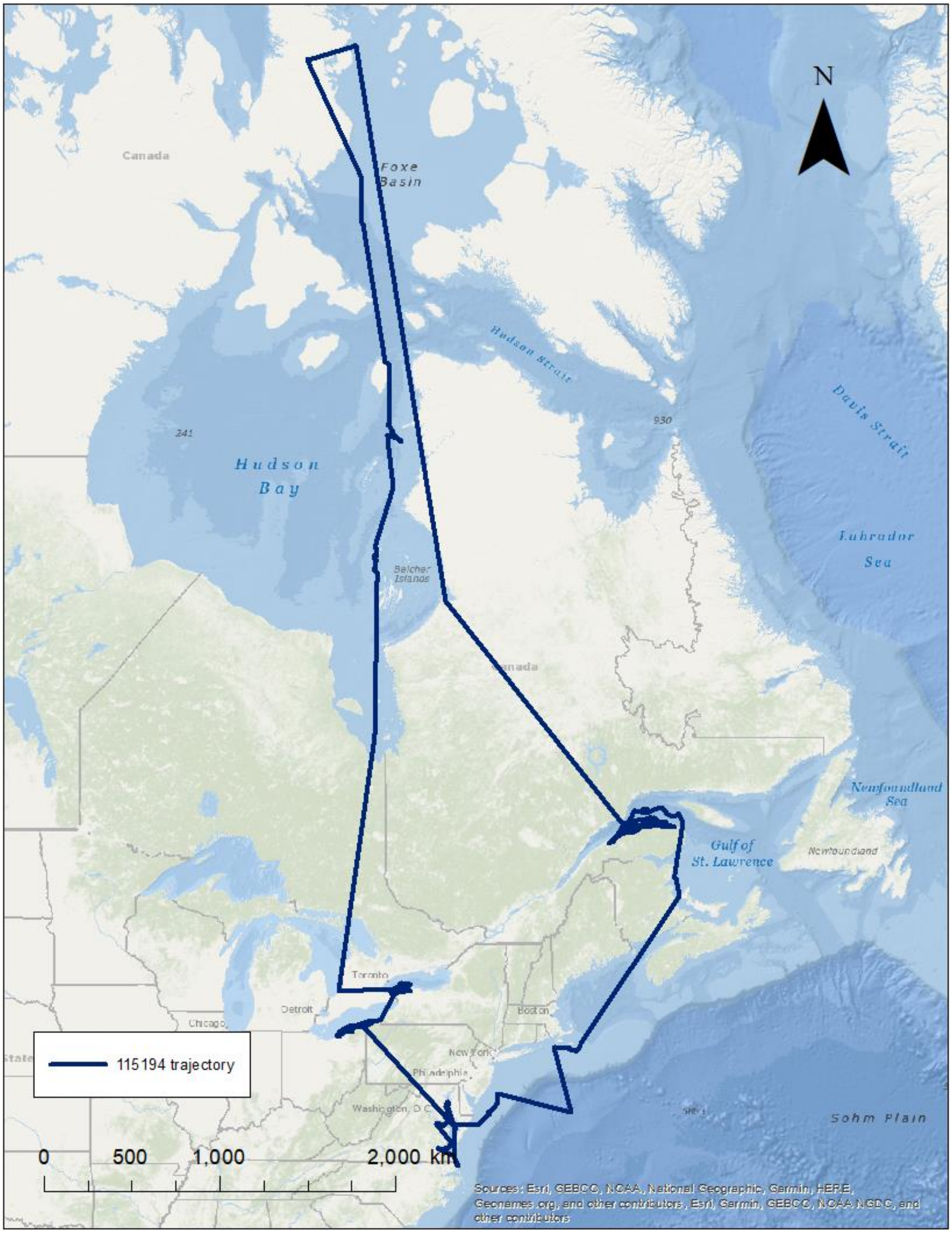


Figure B.14. Annual cycle movement trajectory of Red-throated Loon id# 115195.

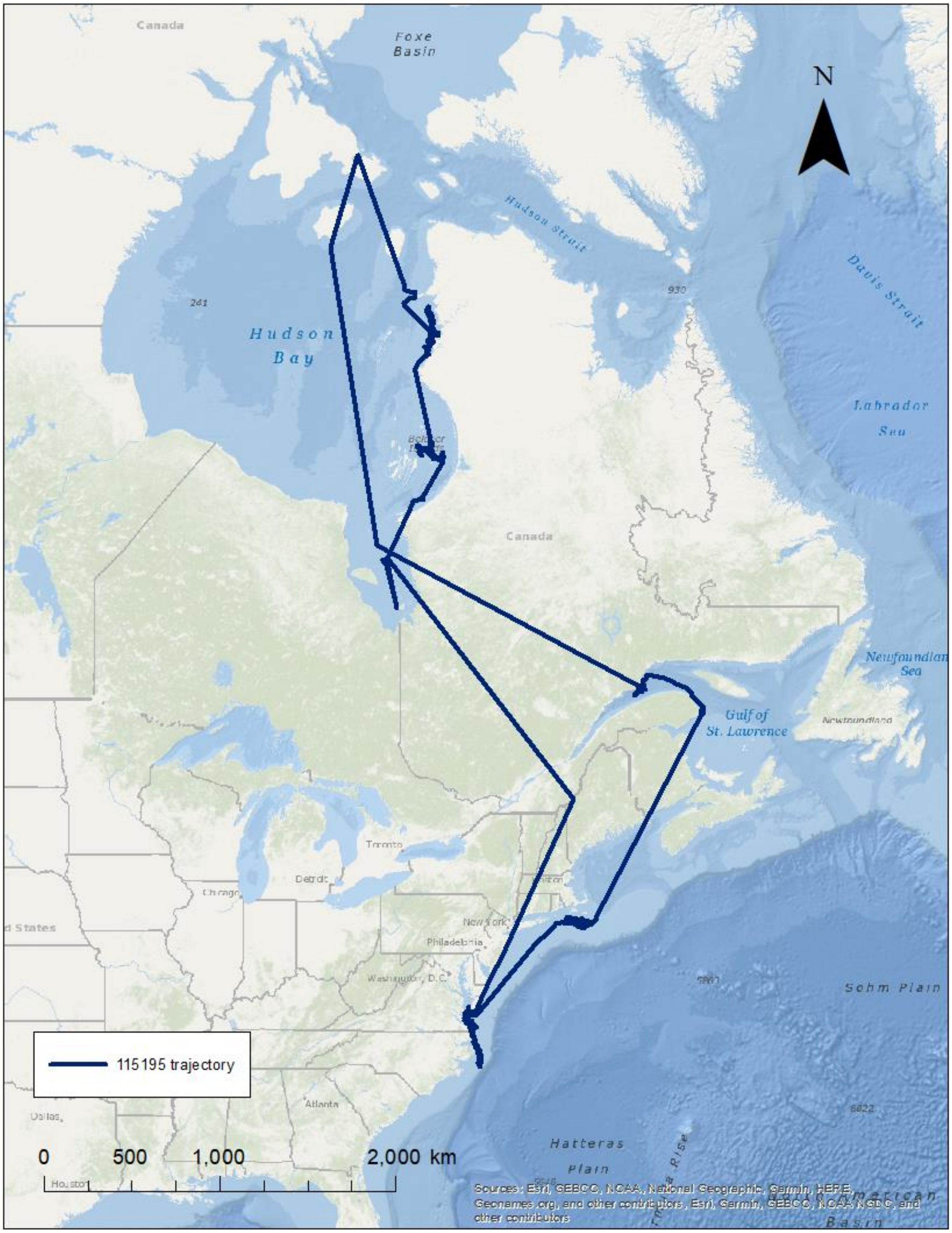
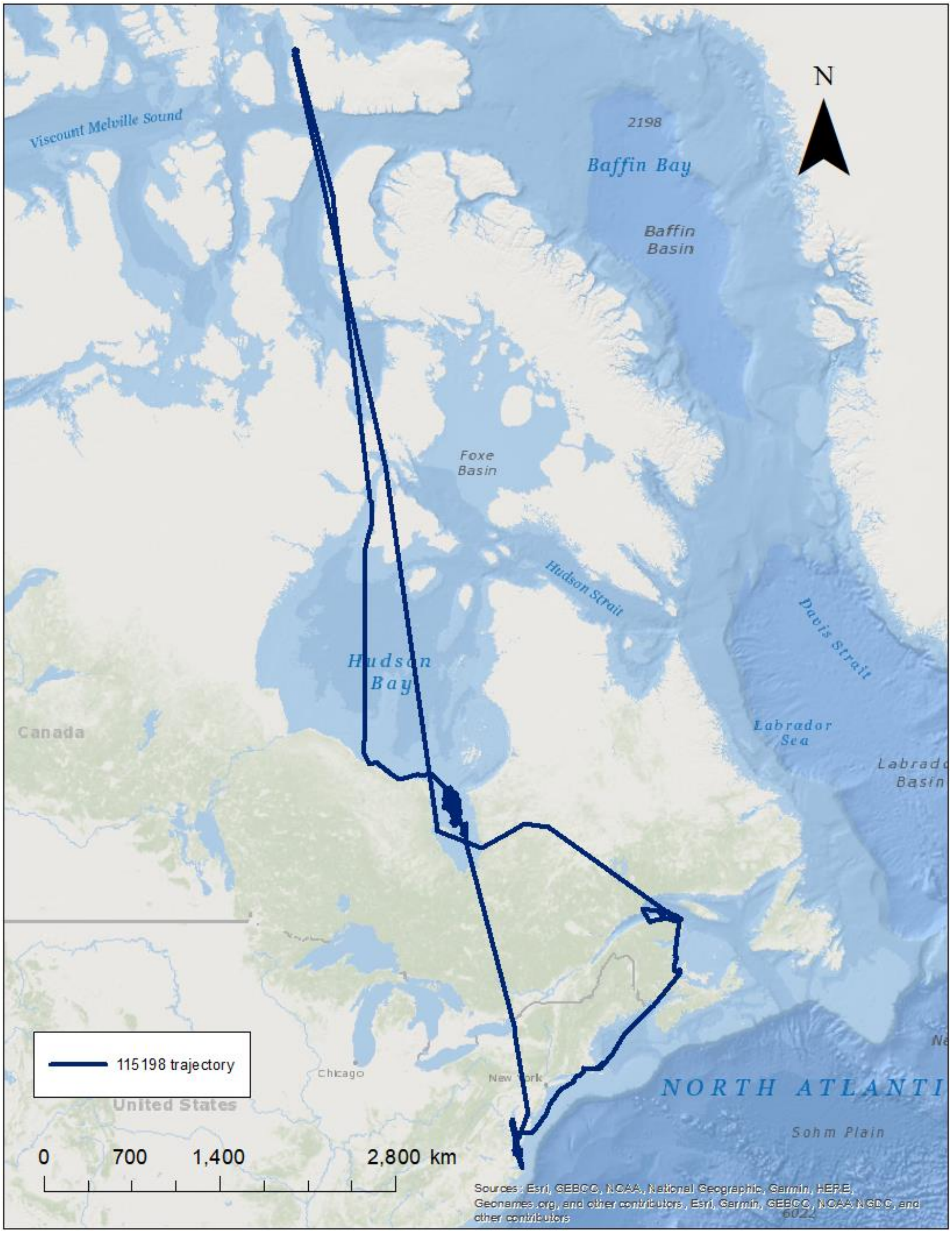


Figure B.15. Annual cycle movement trajectory of Red-throated Loon id# 115197.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.16. Annual cycle movement trajectory of Red-throated Loon id# 115198.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.17. Annual cycle movement trajectory of Red-throated Loon id# 115204.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.18. Annual cycle movement trajectory of Red-throated Loon id# 115205.

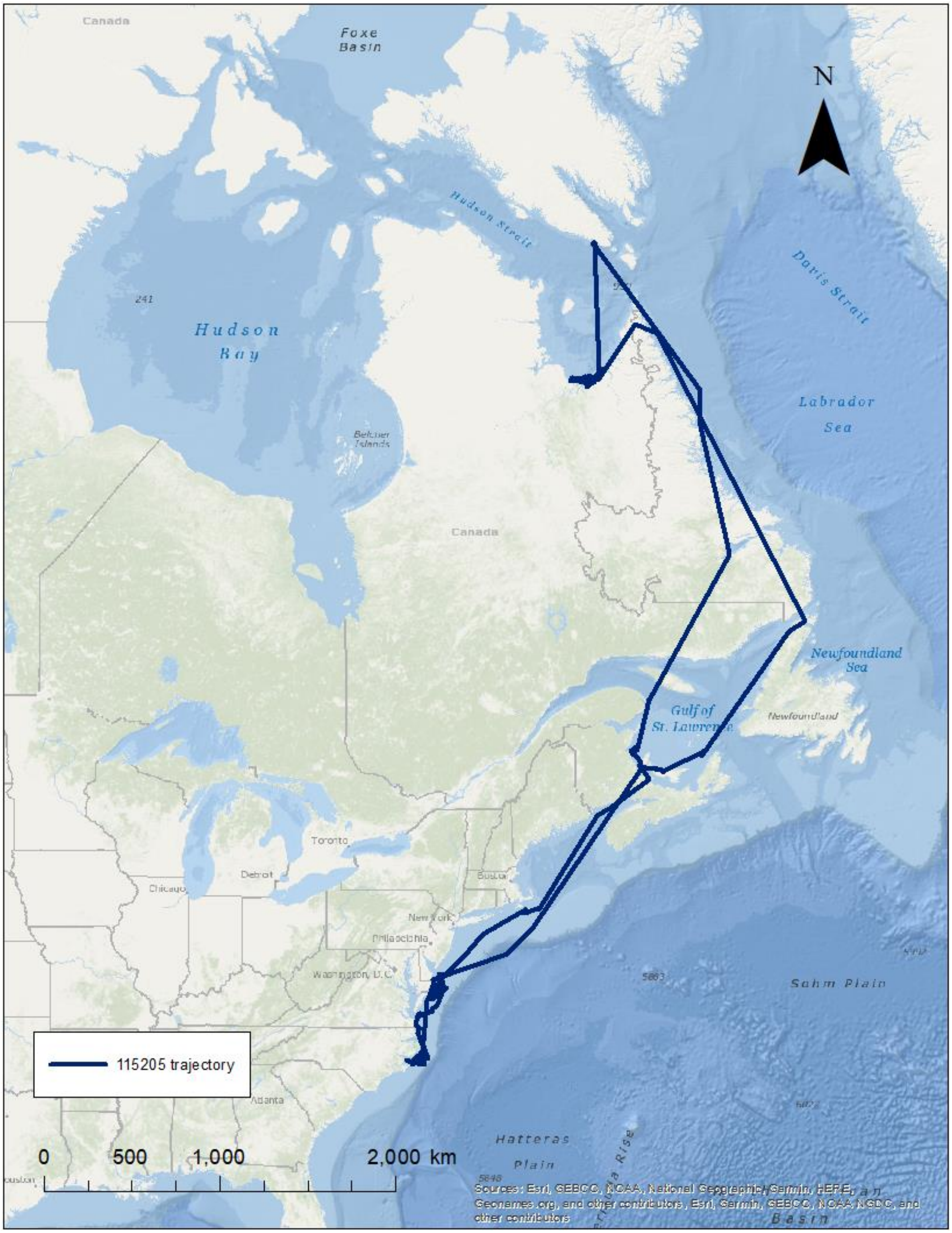


Figure B.19. Annual cycle movement trajectory of Red-throated Loon id# 115206.

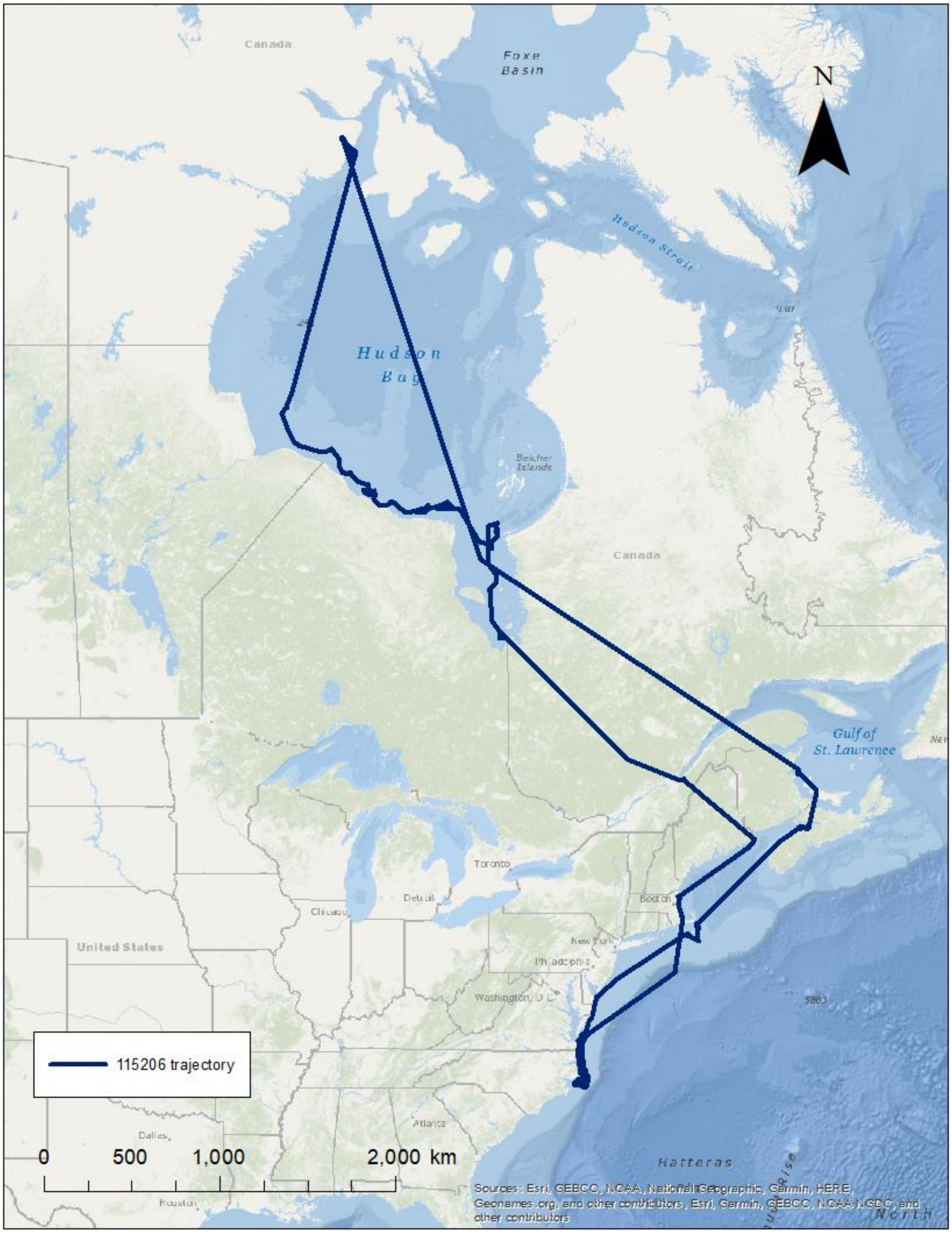


Figure B.20. Annual cycle movement trajectory of Red-throated Loon id# 115207.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.21. Annual cycle movement trajectory of Red-throated Loon id# 123468.

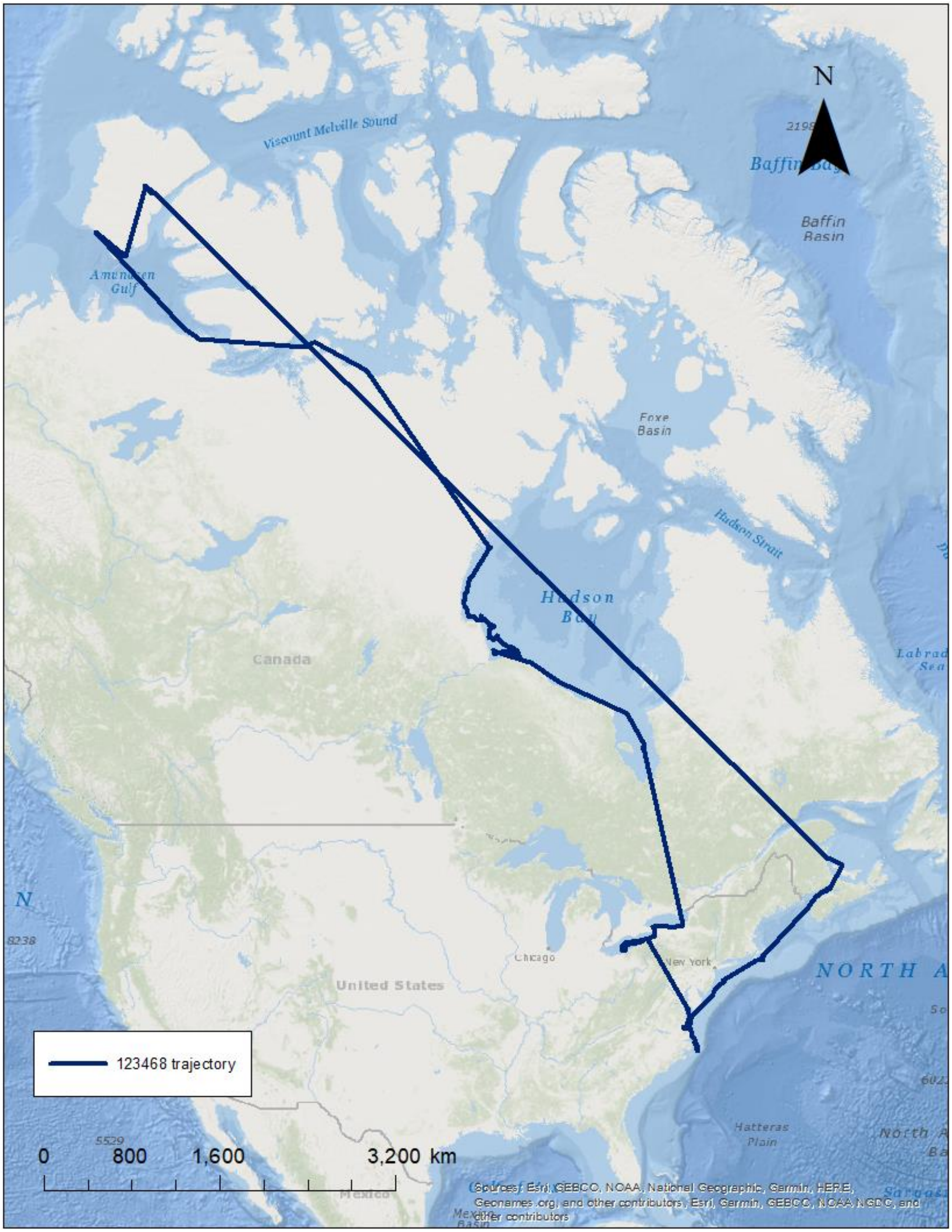


Figure B.22. Annual cycle movement trajectory of Red-throated Loon id# 123476.

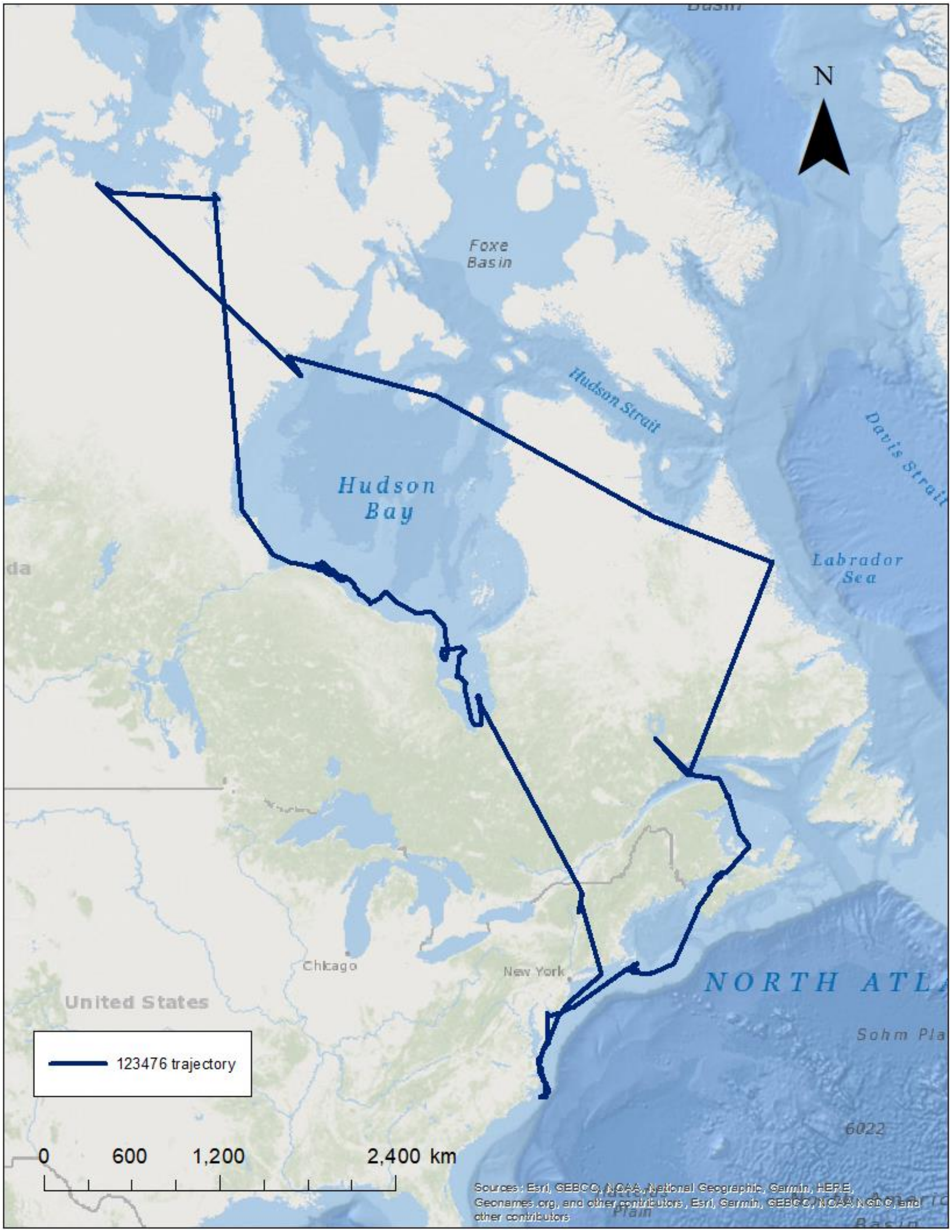


Figure B.23. Annual cycle movement trajectory of Red-throated Loon id# 123482.

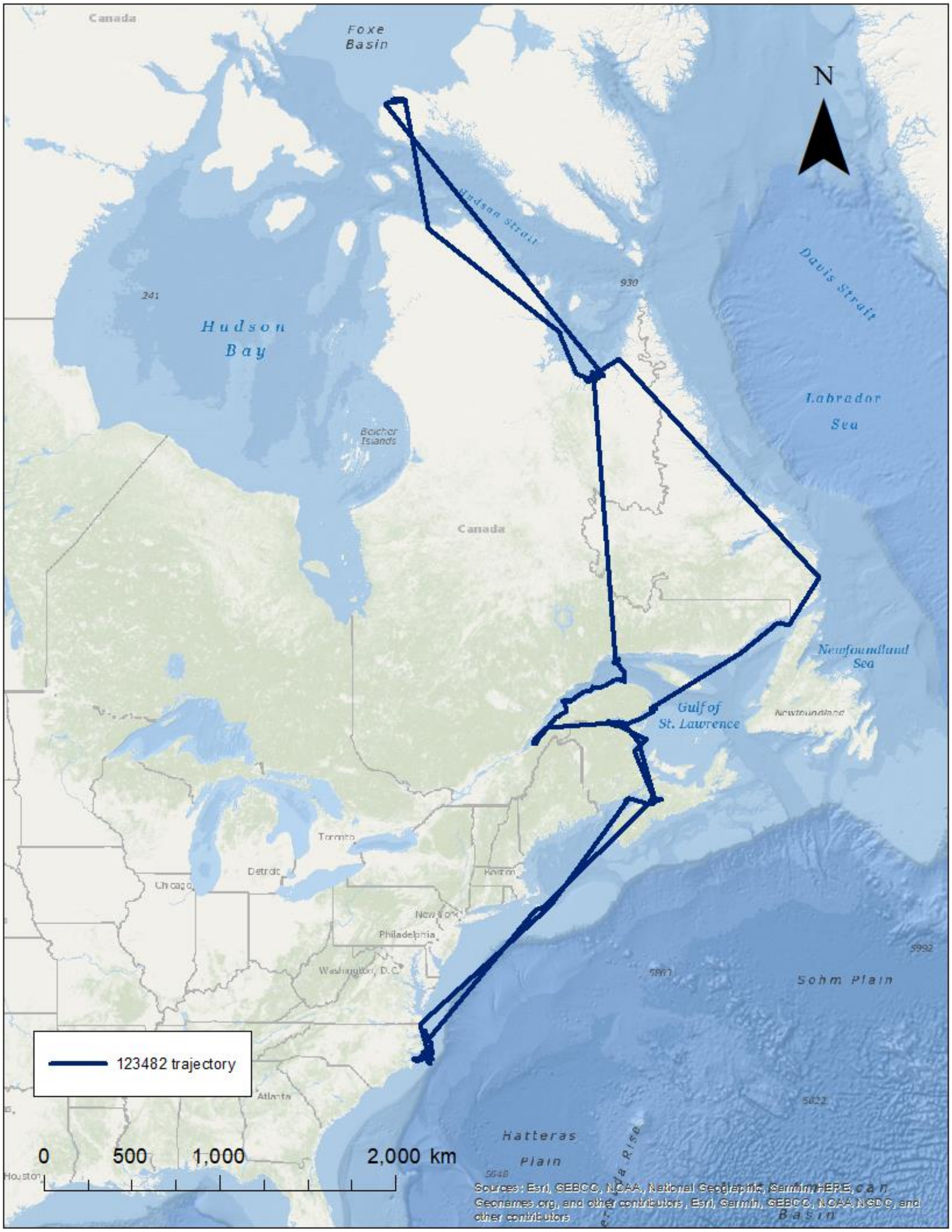
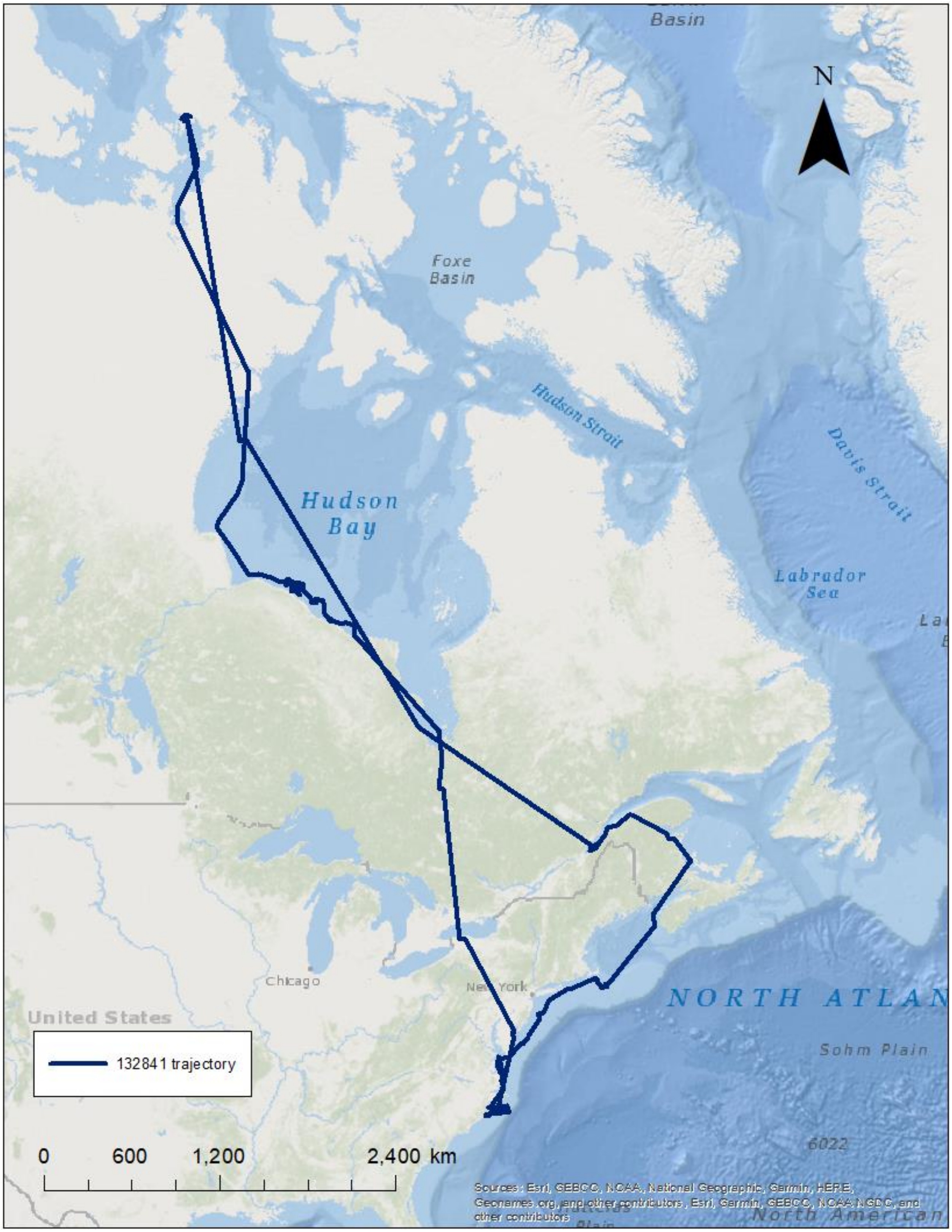


Figure B.24. Annual cycle movement trajectory of Red-throated Loon id# 123484.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.25. Annual cycle movement trajectory of Red-throated Loon id# 132841.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.26. Annual cycle movement trajectory of Red-throated Loon id# 132845.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.27. Annual cycle movement trajectory of Red-throated Loon id# 132847.

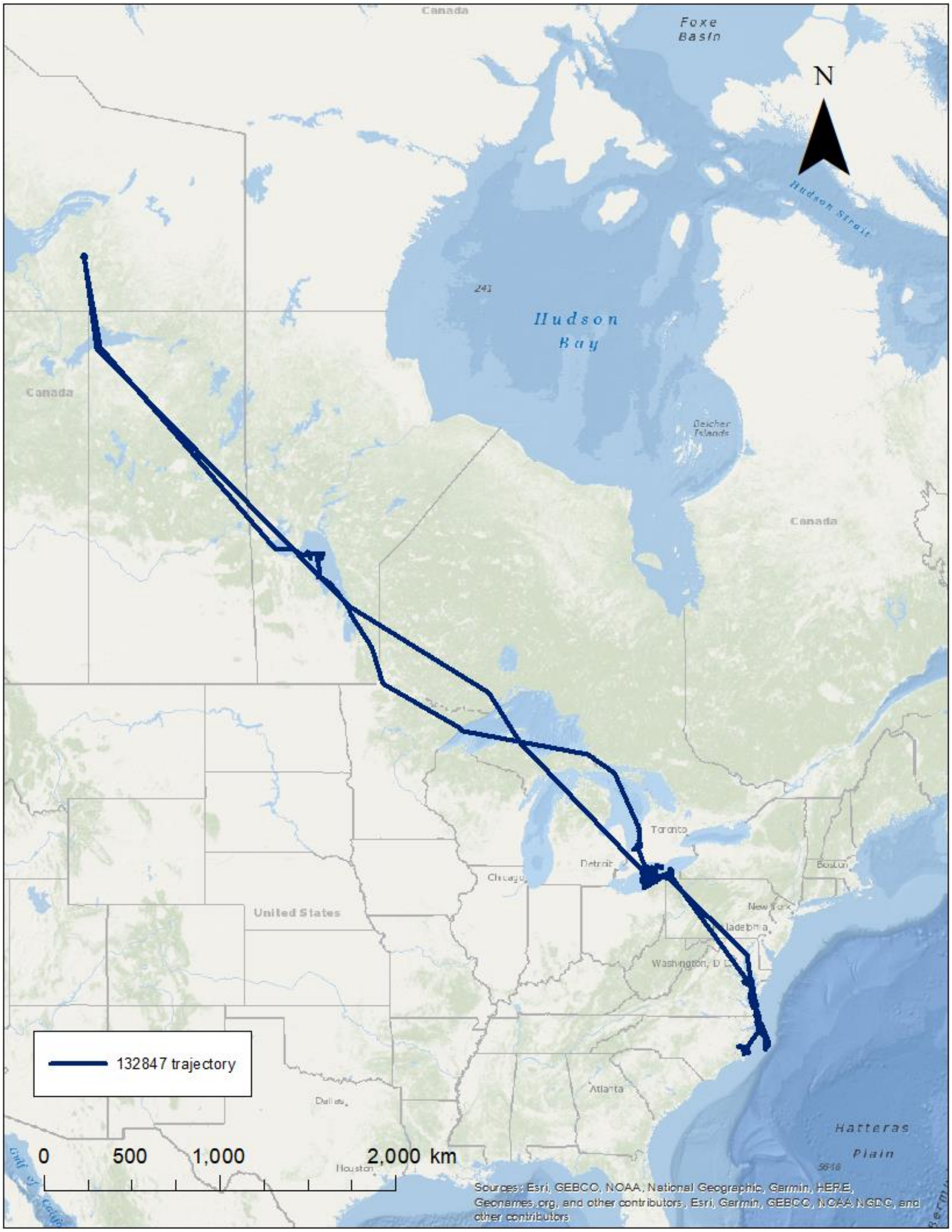


Figure B.28. Annual cycle movement trajectory of Red-throated Loon id# 132850.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.29. Annual cycle movement trajectory of Red-throated Loon id# 132851.

Figure B.30. Annual cycle movement trajectory of Red-throated Loon id# 132852.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.31. Annual cycle movement trajectory of Red-throated Loon id# 132853.

Figure B.32. Annual cycle movement trajectory of Red-throated Loon id# 132854.

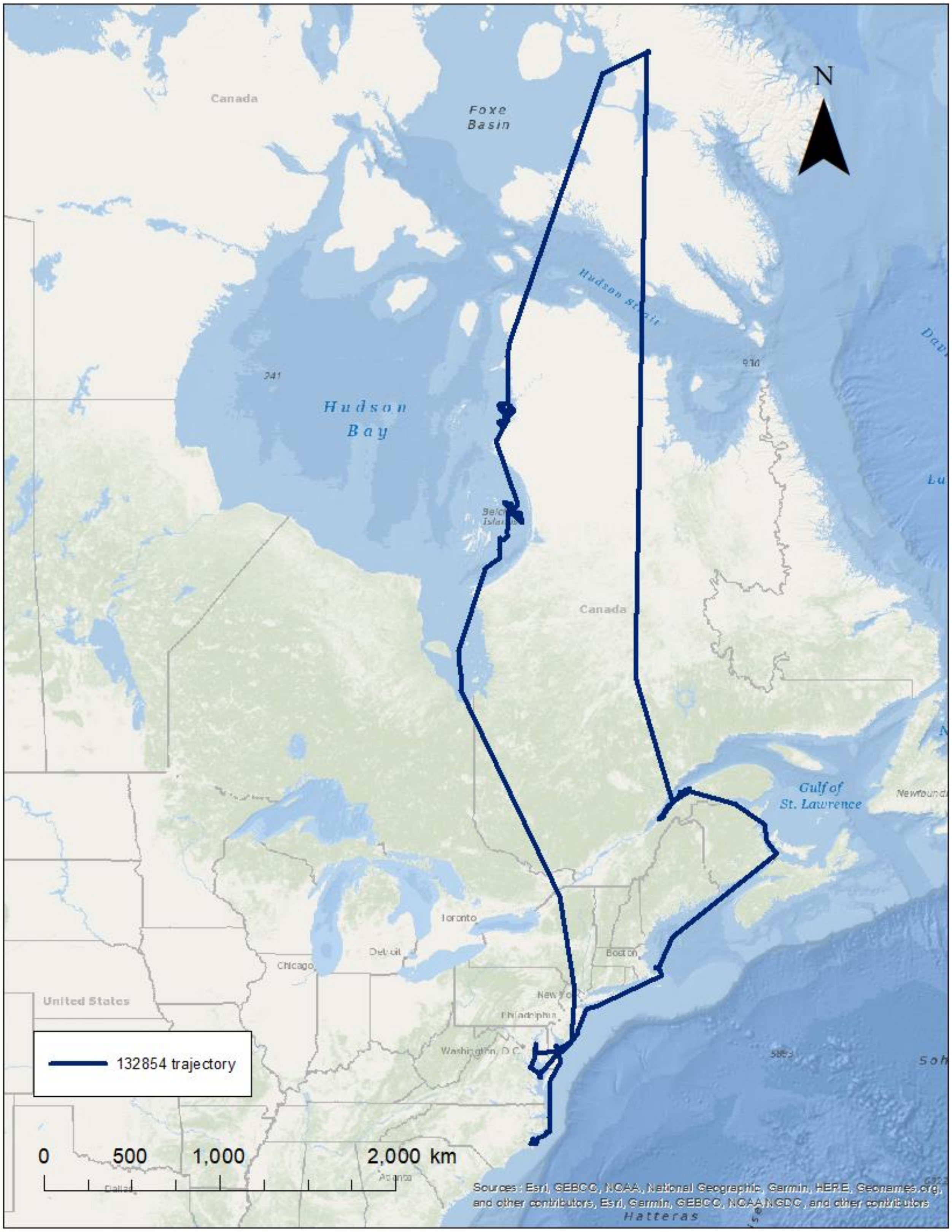


Figure B.33. Annual cycle movement trajectory of Red-throated Loon id# 132855.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.34. Annual cycle movement trajectory of Red-throated Loon id# 132858.

Figure B.35. Annual cycle movement trajectory of Red-throated Loon id# 146513.

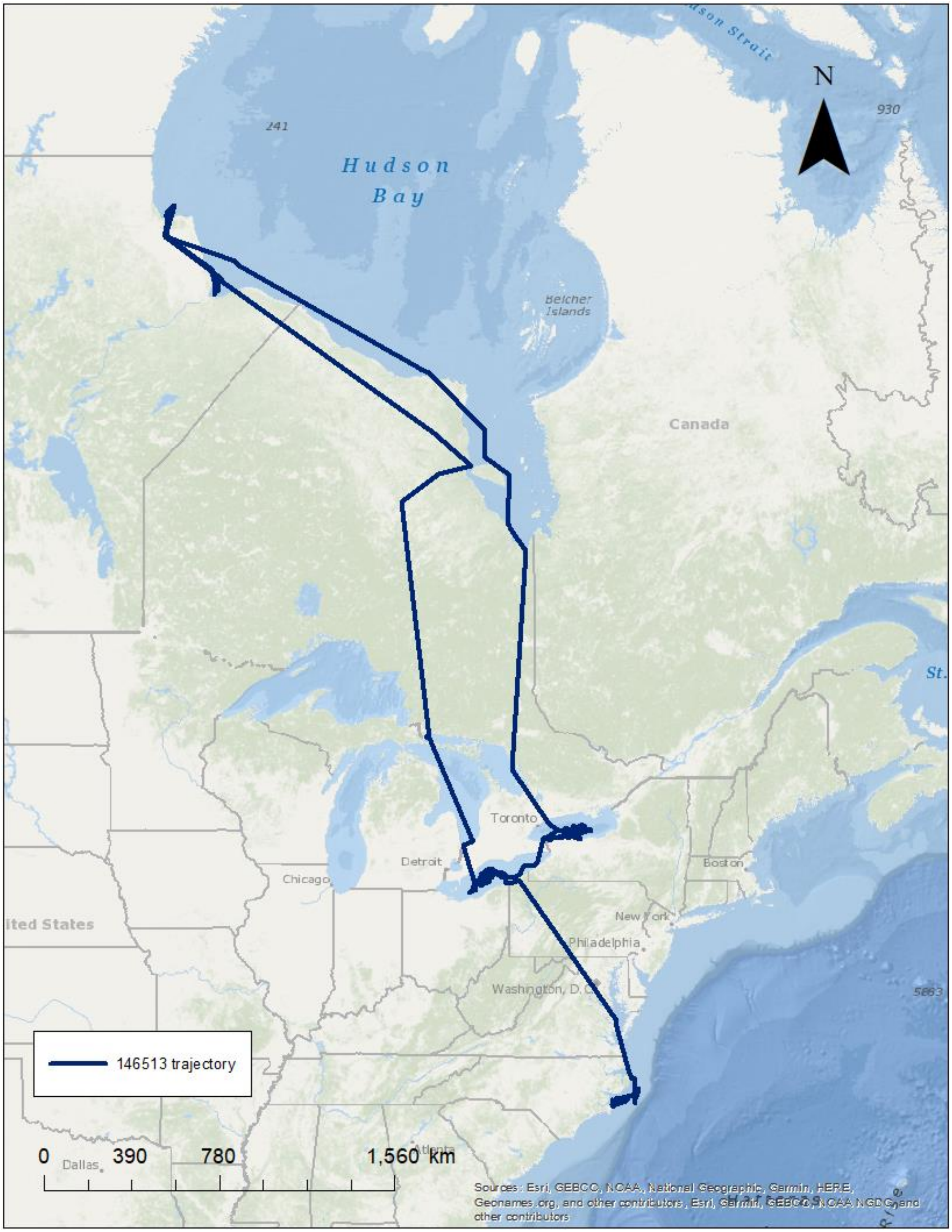
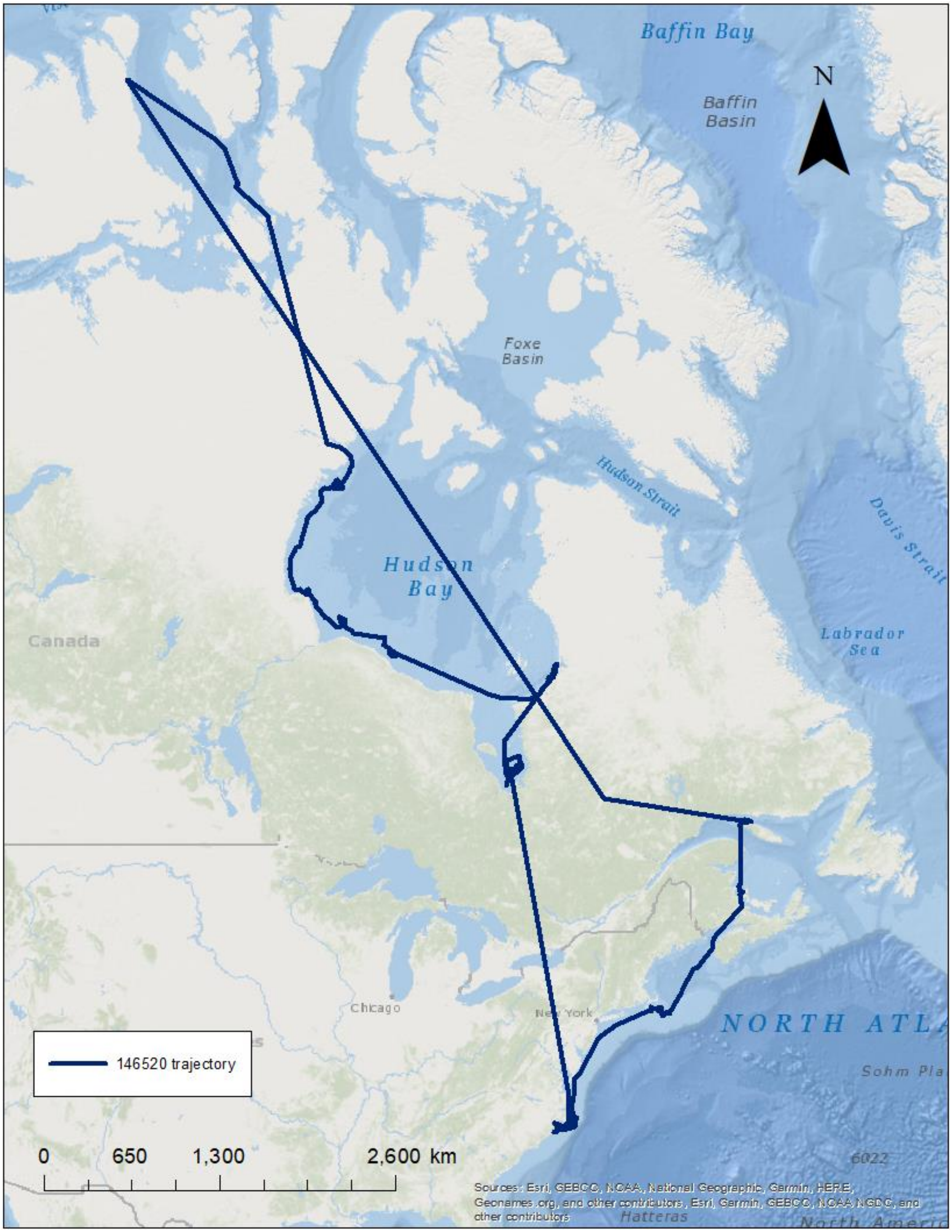


Figure B.36. Annual cycle movement trajectory of Red-throated Loon id# 146514.

Figure B.37. Annual cycle movement trajectory of Red-throated Loon id# 146515.

Figure B.38. Annual cycle movement trajectory of Red-throated Loon id# 146517.

Figure B.39. Annual cycle movement trajectory of Red-throated Loon id# 146520.



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.40. Annual cycle movement trajectory of Red-throated Loon id# 146525.

Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure B.41. Annual cycle movement trajectory of Red-throated Loon id# 146526.

BIOGRAPHY OF THE AUTHOR

Carrie Gray was born in Dover, Delaware on September 3, 1975. She was raised in upstate New York and graduated from Berne-Knox-Westerlo High School in 1993. After several years of working and traveling in the United States and Europe, she began part-time study at Hudson Valley Community College, where she earned an Associate's degree in Environmental Science. She then attended the State University of New York at Cobleskill and graduated in 2005 with a Bachelor's degree in Wildlife Management. In 2008, she earned a Master of Science degree in Wildlife Biology and Management from the State University of New York College of Environmental Science and Forestry, where her research focused on the survival and harvest of waterfowl in eastern Long Island, NY. She spent five years working in the waterbird conservation program for the New York State Department of Environmental Conservation in Albany, NY and seven years as a wildlife research biologist in the loon conservation program at Biodiversity Research Institute in Portland, Maine. In 2016, she began further graduate study at the University of Maine, where Carrie is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences in May 2021.