

NON-BREEDING ECOLOGY OF SEABIRDS IN THE FAMILY ALCIDAE
IN THE NORTHWEST ATLANTIC

by
Emily S. Runnells

A Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
of the University of Manitoba
in partial fulfilment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences
University of Manitoba
Winnipeg

Copyright © 2026 by Emily S. Runnells

Preface

This thesis was written using a grouped manuscript style following the guidelines outlined by the University of Manitoba Faculty of Graduate and Postdoctoral Studies. I confirm that the research described in this thesis was conducted in adherence with guidelines of the Canadian Council of Animal Care (Protocol numbers: F16-017, F20-017, F24-006). I, Emily Runnells, declare that this thesis contains my original research for which I performed the majority of the work. The roles and contribution of all authors are described below for each chapter.

Chapter 1: Comparison of light-level geolocator data processing methods

Emily Runnells: Conceptualization, Investigation, Project administration, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing

Mark Baran: Data curation, Formal analysis, Writing – review & editing

Vegard Sandøy Bråthen: Project administration, Data curation, Formal analysis, Writing – review & editing

Mark Dodds: Data curation, Formal analysis, Writing – review & editing

David Fifield: Investigation, Data curation, Formal analysis, Software, Writing – review & editing, Supervision

April Hedd: Project administration, Funding acquisition, Resources, Writing – review & editing, Supervision

Matthew Legard: Investigation, Data curation, Writing – review & editing

Ariel Lenske: Data curation, Formal analysis, Writing – review & editing

Kristina McOmber: Investigation, Formal analysis, Data curation

Gail Davoren: Conceptualization, Project administration, Funding acquisition, Resources, Writing – review & editing, Supervision

Chapter 2: Spatiotemporal and isotopic niche overlap among Atlantic Puffins, Razorbills, and Common Murres during the non-breeding season in the Northwest Atlantic

Emily Runnells: Conceptualization, Investigation, Project administration, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing

William Montevecchi: Investigation, Project administration, Resources, Funding acquisition, Writing-Review & Editing

Gail Davoren: Conceptualization, Resources, Funding acquisition, Writing-Review & Editing, Supervision

Chapter 3: Seasonal variability in migratory connectivity for Atlantic Puffins in eastern Canada

Emily Runnells: Conceptualization, Investigation, Project administration, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing

Mark Baran: Investigation, Data curation, Writing – review & editing

Joshua Cunningham: Investigation, Writing – review & editing

Antony Diamond: Project administration, Funding acquisition, Writing – review & editing, Supervision

David Fifield: Investigation, Project administration, Data curation, Resources, Writing – review & editing, Supervision

Michelle Fitzsimmons: Investigation, Writing – review & editing

April Hedd: Project administration, Data curation, Funding acquisition, Resources, Writing – review & editing, Supervision

Heather Major: Project administration, Funding acquisition, Resources, Writing – review & editing, Supervision

Raphael Lavoie: Project administration, Data curation, Funding acquisition, Resources, Writing – review & editing, Supervision

Lauren Lescure: Investigation, Data curation, Writing – review & editing

Gail Davoren: Conceptualization, Project administration, Funding acquisition, Resources, Writing – review & editing, Supervision

Chapter 4: Influence of breeding season energy expenditure on razorbill fall and winter foraging and energy

Emily Runnells: Conceptualization, Investigation, Project administration, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing

Gail Davoren: Conceptualization, Project administration, Funding acquisition, Resources, Writing – review & editing, Supervision

Abstract

There is increasing recognition of the energetic challenges faced by high-latitude seabirds outside the breeding season, due to the harsh winter ocean environment. Pursuit-diving species, such as alcids (family Alcidae), may be especially vulnerable due to their high energetic costs of flight to locate areas of higher productivity. For these long-lived species, high winter mortality risks can have demographic consequences, underscoring the importance of elucidating their non-breeding ecology. Recent technological advances provide the opportunity to investigate alcid distributions, interactions, and energetic trade-offs during their 9-10 months at sea, a formerly understudied phase of the annual cycle.

The aims of this thesis were to:

1. Determine whether researchers and managers can combine or compare location estimates and resulting spatial analyses using GLS data that have been processed with different methods
2. Determine the spatiotemporal and isotopic niche overlap during the non-breeding season among Atlantic puffins (*Fratercula arctica*), razorbills (*Alca torda*), and common murrelets (*Uria aalge*) that breed sympatrically in the northwest Atlantic
3. Determine the migratory connectivity of Atlantic puffins from four breeding colonies in the northwest Atlantic during different months throughout the non-breeding period
4. Investigate how energy expenditure during the breeding season affects fall and early winter foraging activity and energy expenditure of razorbills

In Chapter 1, I determined that most GLS data processing methods produced comparable results when tracking Atlantic puffins, if data inputs were standardized, and with caveats for certain tag models. In Chapter 2, I found mostly low spatiotemporal and isotopic niche overlap among three alcid species during the non-breeding season. In Chapter 3, I found strong migratory connectivity among Atlantic Puffins at the bookends of the breeding period, and otherwise gradual weakening of migratory connectivity, culminating in shared key winter foraging areas. Lastly, in Chapter 4, I found supporting evidence that foraging conditions and parental care during breeding and non-breeding may mediate the strength and direction of carry-over effects. Overall, these new insights inform effective species management and marine spatial planning in the northwest Atlantic, an ocean region undergoing major change.

Acknowledgements

I would like to acknowledge the stewards of the lands that I have called home during my program. The University of Manitoba campuses are located on the original lands of the Anishinaabeg, Cree, Oji-Cree, Dakota and Dene peoples and on the homeland of the Metis Nation. I now reside in N'dakinna, the unceded Wabenaki homeland. Newfoundland, where my research was conducted, is the unceded ancestral homeland of the Beothuk.

Gail Davoren, you deserve the 'best advisor in the world' award. Thank you for seeing and stating the underlying challenges, making it clear that I wasn't alone. You always treated me as a worthy and admirable scientist, and this brought out my best. My sincere gratitude to my committee members for their enthusiasm about my project. Kevin Fraser, I always looked forward to your comments on my written work. The interest and insight in your feedback fueled my own curiosity and motivation. Cory Matthews, thank you for taking the time to tutor me in stable isotope analysis. Your explanations made complex concepts incredibly clear, and I feel so fortunate to have had the chance to learn from you. Thank you also to J. Treberg for asking about sharks in my candidacy exam, & C. Garroway for Bayesian analysis chats on the bus.

This research could not have happened without the field expertise of L. Lescure & M. Fahmy in 2020. My sincere appreciation to J. Gulka, E. Jenkins, & L. Maynard, for feather collections, along with M. Athayde & M. Berard for feather processing. Thanks to M. Legard & G. Rieger for learning fast despite 2 AM training, K. McOmber & M. Dalton for having my back on James, and M. Athayde, C. Currie, K. Vonderbank, & O. Roy for sharing the joy and keeping me organized. A. Tripp, M. Epp, & K. Wilcox, you made the field house a home. Thank you, L. Easton, B. Abbott, J. Chaulk, & A. Chaulk for getting us safely there and back again, with the best detours. The kindness of the Musgrave Harbour community was the foundation of everything. Geolocators for murrelets and many of the puffins were provided by SEATRACK, and M. Haggie's bands saved the day. My gratitude to the alcids who carried small burdens for my science.

I was fortunate to have support from far and wide. SEATRACK Fledglings, the World Seabird Union (Seabird Sessions), and Pacific Seabird Group stepped up and provided a science community when we were all stuck at our screens. J. Lech, thank you for organizing virtual card nights. D. Fifield, A. Patterson, & M. Schrimpf generously helped improve my analysis skills. My Davoren Lab colleagues were a core pillar of intellectual support, besides a source of lifelong friendships (looking at you, American girls). A. Korpach, E. de Greef, M. Stoetz, E. Thomas, & A. Bell complemented my lab friendships and made me feel at home in Winnipeg. Z. Kuriyama, thank you for the Phoebe time, and J. Lech, thanks for the games. J. Dolliver, you are the best sounding board, for whatever, whenever. E. DeBold & J. Spiegelman, I am so grateful we walked the PhD path together; you are always there in the ways that really matter. To my entire family, thank you for your love, for always having confidence in me, and for stepping up in my absence. None of you should underestimate your profound impact on my project and quality of life.

Finally, I would like to acknowledge the support and infrastructure provided by the University of Manitoba through Field Work Support Grants, as well as the Graduate Fellowship program and Department of Biological Sciences. This work was principally funded by Natural Sciences and Engineering Research Council Discovery Grants to Dr. Gail Davoren, as well as financial contributions that supported the field work, data management, and time of our collaborators.

Dedication

To Mike, whose love and support has been with me every step of the way

In memorium, Betsy Brooks (1935 – 2024) and Helen Hays (1931 – 2025).
Thank you for lighting the path.

Table of contents

Preface.....	ii
Abstract	iv
Acknowledgements	v
Dedication.....	vi
Table of contents.....	vii
List of tables	x
List of figures	xi
General Introduction	1
Figure I:.....	5
References	5
Chapter 1: Comparison of light-level geolocator data processing methods	12
Background	14
Methods.....	16
Table 1.1:	19
Results	3
Figure 1.1:	4
Figure 1.2:	5
Figure 1.3:	6
Figure 1.4:	8
Figure 1.5:	9
Discussion	9
Conclusion.....	12
References	13
Supplementary figures:	18
Figure 1.S1:.....	18
Figure 1.S2:	19
Figure 1.S3:	20
Figure 1.S4:	21
Figure 1.S5:	22
Link between Chapters 1 & 2	23
Chapter 2: Spatiotemporal and isotopic niche overlap among Atlantic Puffins, Razorbills, and Common Murres during the non-breeding season in the Northwest Atlantic.....	24

Abstract	25
Introduction	26
Methods.....	28
Figure 2.1:	28
Table 2.1:	30
Results	33
Figure 2.2:	34
Table 2.2:	36
Figure 2.4:	37
Discussion	38
References	41
Supplementary Tables and Figures.....	51
Table 2.A1:	51
Table 2.A2:	52
Figure 2.S1:	53
Link between Chapters 2 & 3	54
Chapter 3: Seasonal variability in migratory connectivity for Atlantic Puffins in eastern Canada	
.....	55
Abstract	56
Introduction	57
Methods.....	59
Figure 3.1:	60
Table 3.1:	60
Results	62
Figure 3.2:	64
Figure 3.3:	65
Figure 3.4:	66
Figure 3.5:	67
Discussion	68
References	71
Supplementary Figures	81
Figure 3.S1:	81
Figure 3.S2:	82

Link between Chapters 3 & 4.....	83
Chapter 4: Influence of breeding season energy expenditure on Razorbill fall and winter foraging and energy.....	84
Abstract	85
Introduction	86
Methods.....	87
Figure 4.1:	88
Figure 4.2:	89
Results.....	91
Figure 4.3:	92
Figure 4.5:	94
Discussion	95
References	98
Supplemental Figures	102
Fig 4.S1:.....	102
Fig 4.S2:..	103
Table 4.S1:	104
Table 4.S2:	104
General Discussion & Conclusions	105
References	109

List of tables

Table 1.1: Summary of input parameters and processing time for each GLS processing method. White boxes = required parameters, light blue = optional parameters, and dark blue = not applicable. Text describes parameters used in this study. ‘Equinox delineation’ refers to how each method incorporated information on equinox timing into estimating locations. ‘Known locations’ refers to how each method incorporates colony attendance into estimating locations. ‘Run times’ are based on the processing capabilities of a standard business laptop. *Standardized parameters. ^a More details in main text.	19
Table 2.1: Summary of deployments of light-level geolocators on Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) during 2019 and 2020, including the number of Migrate Technology C330 and C65+ and Biotrack MK3006 model geolocators used in each year for each species, the number of geolocators retrieved in each year (2020 and 2021), the overall retrieval rate during this project, and summarized arrival and departure dates.	30
Table 2.2: Mean ($\pm$ SE) stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) along with estimates of isotopic niche breadth, including SEA_c , the standard ellipse area corrected for small sample sizes, and SEA_b , the MAP of the Bayesian standard ellipse area posterior and associated 90% credible intervals from Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) head, belly, and first secondary (S1) feathers collected during July-August, 2017-2020 on the northeast coast of Newfoundland.	36
Table 2.A1: ‘ProbGLS’ model input parameters for estimating locations using geocator data from Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU).	51
Table 2.A2: Utilization distribution overlap index (UDOI) values of pairwise 50% kernel density distribution overlap between Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) during successive 2-month periods in the non-breeding season, calculated with two different underlying grid sizes (25 km and 150 km). The degree of green shading ranges from the smallest value (white) to the largest in each column (darkest green).	52
Table 3.1: Geocator (GLS) retrieval summary for Atlantic Puffin breeding colonies in this study, with abbreviated colony names, the years included in the tracked migratory periods of puffins from each colony (including both older and recent periods for GI and MSI), the number of GLS tags retrieved in each period, and the colony abundance as estimated number of puffin breeding pairs at each colony (Carvey et al. 2024).	60
Table 4.S1: Probability that the relationship between breeding and non-breeding DEE has a positive slope (<i>i.e.</i> , $p[\beta_1 > 0]$) or a negative slope, and the maximum a posteriori (MAP) and 95% credible interval (95% CrI) of the slope for each non-breeding month of 2021 and 2022.	104
Table 4.S2: Probability that the relationship between breeding DEE and non-breeding time diving has a positive slope (<i>i.e.</i> , $p[\beta_1 > 0]$), and the maximum a posteriori and 95% credible interval of the slope for each non-breeding month of 2021 and 2022	104

List of figures

Figure I: Estimated timeframe during which wing feather, body feather, and head feather molt occurs in Atlantic Puffins, Common Murres, and Razorbills, based on studies from across their range. The timing of flight feather molt is uncertain among individual puffins.	5
Figure 1.1: Median pairwise distances (MPD, in km) among iterations of stochastic methods for locations during non-equinox periods (A) and during equinox periods (B). Note the different y-axis scale on graphs. The shaded area indicates 200-400 km, typical geolocator accuracy range, shown to emphasize the difference in scale. Violin widths are scaled to maximum weight within each comparison. The map (C) shows non-equinox location estimates from two different iterations (different colors) of the same bird from ‘FlightR’.	4
Figure 1.2: Median pairwise distances (MPD, in km) for each method comparison for locations during non-equinox periods (top panel) and during the equinox periods (bottom panel). Note the different y-axis scale on graphs. The shaded area indicates 200-400 km, typical geolocator accuracy range, shown to emphasize the difference in scale. Violin widths are scaled to maximum weight within each comparison.	5
Figure 1.3: Matrices of the proportions of distance differences over 400 km for each method comparison for non-equinox (left panel) and equinox (right panel) locations, with color shading darker for larger proportions. The lower half of the matrices are the number of distances between location estimates included in each comparison outside of the equinox (out of a maximum of $n = 10182$, except $n = 4554$ for ‘probGLS with SST’ as it could only be run on tags with SST data) and during equinox (out of a maximum of $n = 4884$, except $n = 2489$ for ‘probGLS with SST’).	6
Figure 1.4: BA for each method comparison for locations during non-equinox periods (top panel) and during equinox periods (bottom panel). Note the different y-axis scale on graphs. The shaded area indicates BA values in the range of 0.80-0.90 , shown to emphasize the difference in scale. Violin widths are scaled to maximum weight within each comparison.	8
Figure 1.5: Median pairwise distances (MPD, in km) for each method comparison for BioTrack tags from Gull Island (red boxplots) and Migrate Technology tags from James Island (blue boxplots) during non-equinox periods. The BioTrack tags from Gull Island had lower resolution, clipped light values and no SST data were recorded, while the Migrate Technology tags from James Island had full resolution light values and SST data. Hence, the ‘probGLS’ method with SST could not be used on the BioTrack tag data from Gull Island.	9
Figure 1.S1: Median pairwise distances (MPD, in km) of great-circle distance and latitudinal distance, for each method comparison for locations during non-equinox periods (A) and during equinox periods (B). Note different y-axis scales. The shaded area indicates 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.	18
Figure 1.S2: Median pairwise distances (MPD, in km) of great-circle distance and latitudinal distance, for each method comparison for locations during non-equinox periods. The shaded area indicates 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.	19

Figure 1.S3: Bhattacharyya's Affinity (BA) among iterations of stochastic methods for locations during non-equinox periods (A) and during equinox periods (B). The shaded area indicates BA values of 0.80-0.90. Note the different y-axis scale on graphs.	20
Figure 1.S4: Earth Mover's Distance (EMD, in km) for each method comparison for locations during non-equinox periods (A) and during equinox periods (B). The large distances to 'seatrackGLS' during equinox are because positions outside the boundary box were included. Note different y-axis scales. The shaded area indicates 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.	21
Figure 1.S5: Median pairwise distances (MPD, in km) among iterations of stochastic methods for BioTrack tags from Gull Island (red boxplots) and Migrate Technology tags from James Island (blue boxplots) during non-equinox periods. The BioTrack tags from Gull Island had a reduced range of light values and no SST data were recorded, while the Migrate Technology tags from James Island had full range light values and SST data. Hence, the 'probGLS' method with SST could not be used on the BioTrack tag data from Gull Island. The shaded area indicates the lower end of 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.	22
Figure 2.1: Bathymetric map of the study area in the northwest Atlantic, indicating the breeding colonies of Funk Island (FI, blue diamond) and James Island (JI, purple diamond) off the northeastern Newfoundland coast, along with other referenced oceanographic and political locations: The New York Bight (NYB), Gulf of Maine (GOM), Labrador Coast (LC), Grand Banks (GB), Orphan Basin (OB), Flemish Cap (FC), and North Atlantic Current and Evlanov Sea OSPAR MPA (NACES MPA). Depth information is from Blue Earth Bathymetry, a GEBCO (https://www.gebco.net) derived product, the MPA boundaries are provided by OSPAR (https://www.ospar.org), and the land boundaries are from Natural Earth (https://www.naturalearthdata.com).....	28
Figure 2.2: 50% Kernel density estimates and Utilization Distribution Overlap Indices (UDOI) during successive two-month periods of the non-breeding season for Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) tracked with light-level geolocators.....	34
Figure 2.4: Isotopic niche breadth (SEA_c) and isotopic niche overlap (% overlap of SEA_b MAP, 90% CrI) of Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) first secondary (S1), belly, and head feathers. Calculated SEA_c ellipses are plotted for visualization of overlap. The matching calculations of overlap are based on SEA_b , to provide an indication of variability. The MAP is the most probable value for the % overlap (i.e., the mode of the posterior distribution), and credible intervals provide a 90% probability that the overlap is within the proscribed range. SEA and overlap calculations were based on feathers collected in 2017-2020 and included untagged birds (open circles) and geolocator tagged birds (filled circles). Feathers collected from geolocator tracked birds in 2021 (filled triangles) are presented but were not included in SEA or overlap calculations.	37
Figure 2.S1: Head feather $\delta^{13}C$ of individual geolocator-tagged Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) at their estimated geographic median locations during March – May, the time of year when head feathers are molted. Solid error bars represent the 25 th -75 th quantiles of latitude and longitude estimates, and dotted lines indicate the entire range of latitude and longitude estimates during this period.	53

Figure 3.1: Study area in the northwest Atlantic, indicating the breeding colonies of Gull Island (GI), James Island (JI), Machias Seal Island (MSI), and the Mingan Archipelago (MA), along with referenced areas: The New York Bight (NYB), Gulf of Maine (GOM), Labrador Sea, Hudson Bay, Mid- Atlantic, North Atlantic Current and Evlanov Sea basin Marine Protected Area (NACES MPA), Stellwagen Bank National Marine Sanctuary (SBNMS), and Northeast Canyons and Seamounts Marine National Monument (NCS MNM). The MPA boundaries are provided by OSPAR (ospar.org), NOAA (sanctuaries.noaa.gov) and the Northeast Regional Ocean Council (northeastoceandata.org), and the land boundaries are from Natural Earth (naturalearthdata.com).

..... 60

Figure 3.2: Geographic median locations of puffin tracks for select months from the recent period (2017-2021) from four colonies: GI = Gull Is., JI = James Is., MA = Mingan Archipelago, MSI = Machias Seal Is. Shape and color indicate the birds from each breeding colony. Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth (naturalearthdata.com). 64

Figure 3.3: Mantel correlation by month for birds from James Is., Gull Is., the Mingan Archipelago, and Machias Seal Is., A) including all years in the recent dataset (2017-2021) and B) only including birds from one year, 2019-2020. Means are represented by a dot, medians by an x, and error bars denote 95% confidence intervals. 65

Figure 3.4: Mantel correlation by month for birds only from Gull Island and Machias Seal Island during A) 2013-2015 and B) 2017-2021. Means are represented by a dot, medians by an x, and error bars denote 95% confidence intervals. 66

Figure 3.5: Geographic median locations of puffin tracks for select months from recent (teal and purple) and older (pink and yellow) years from two colonies: GI = Gull Is. (circles), MSI = Machias Seal Is. (triangles). Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth (naturalearthdata.com). 67

Figure 3.S1: Monthly geographic median locations of puffin tracks from the recent period (2017-2021) from four colonies: GI = Gull Is., JI = James Is., MA = Mingan Archipelago, MSI = Machias Seal Is. Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth (naturalearthdata.com).81

Figure 3.S2: Maps of monthly geographic median locations from recent (teal and purple) and older (pink and yellow) years of puffin tracks from two colonies: GI = Gull Is. (circles), MSI = Machias Seal Is. (triangles). Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth (naturalearthdata.com). 82

Figure 4.1: Location of James Island, where GLS-TDR loggers were deployed and retrieved. Background from services.arcgisonline.com, map produced in QGIS 3.16.1 (qgis.osgeo.org). 88

Figure 4.2: Flow chart of activity category classification based on immersion, pressure, and temperature data from GLS-TDR loggers. 89

Figure 4.3: Modeled relationships between breeding and non-breeding DEE in 2021 (purple) and 2022 (green) with their associated 95% credible intervals (gray shading). Monthly modes of each tag are included as points.	92
Figure 4.5: Posterior distributions of the slope parameter from Bayesian generalized linear mixed models of non-breeding DEE (A) and time diving (B). Maximum a posteriori (MAP) estimates (points), and 50% (thick line) and 95% (thin line) credible intervals for slope values from 2021 and 2022. MAP is the most probable value for the slope (i.e. the mode of the posterior distribution), and credible intervals provide a 95% or 50% probability that the slope value is within the given range.	94
Fig 4.S1: Probability density of daily time spent diving for each tag deployment during breeding and 4 nonbreeding months. Colors represent individuals. The vertical line is at the median, and the mode is at the highest peak. During breeding, sample sizes range between 6-24 days of data.	102
Fig 4.S2: Probability density of daily energy expenditure (DEE) for each tag deployment during breeding and 4 nonbreeding months. Colors represent individuals. The vertical line is at the median, and the mode is at the highest peak. During breeding, sample sizes range between 6-24 days of data.	103

General Introduction

Theoretical Background

Species have evolved to occupy a defined range of both abiotic and biotic environmental conditions, their ecological niche (Grinnell 1917, Elton 1927), quantitatively visualized as an n-dimensional hypervolume (Hutchinson 1978). There are multiple factors that lead to niche differentiation, one of which is competition for limited resources (Schluter and Grant 1984), but the degree of competition depends on how much shared resources are limited (Wiens 1977). The competitive exclusion principle states that species occupying the same niche cannot coexist (Volterra 1928, Gause 1934), and sympatric species are therefore only possible when their niches differ along one or more axes (Schoener 1974). This may happen as species evolve to use a unique set of abiotic and biotic resources, termed the fundamental niche, which can further be constrained to the realized niche as interspecific competition leads to niche partitioning (MacArthur 1958, Schoener 1974, Hutchinson 1978, Tilman 1987).

Intraspecific competition can also constrain the amount of resources an individual can acquire. Individuals have limited energy to invest in survival, relative to reproduction, the main life history trade-off (Stearns 1992). Accordingly, species have evolved life history strategies to maximize fitness, given selection pressures experienced in the past. For example, long-lived species are more likely to abandon an annual breeding attempt to ensure their own survival and offspring production in future breeding attempts. These trade-offs are seen when comparing life history traits among species (e.g., Ricklefs 1977) and within species (e.g., Reznick and Endler 1982), but the same energy allocation trade-off is also repeatedly occurring within the lifetime of an individual as resource availability varies (e.g., Boyce and Perrins 1987, Barringer et al. 2013). Although periods of an animal's life can be divided temporally and sometimes spatially, those seasons or stages are not independent, and energy expenditure in one period can influence an individual's ability to survive or reproduce in the following periods, referred to as 'carry-over effects' (Fretwell 1972, Norris and Taylor 2006, Norris and Marra 2007, Harrison et al. 2011). Although the concept of seasonal interactions is not new (Fretwell 1972), most research on vertebrates has been conducted during only one season, primarily the breeding season, and only 5.5% of studies considered seasonal interactions (Marra et al. 2015). It is important to understand these carry-over effects because they can have impacts on fitness and ultimately population dynamics (Norris and Taylor 2006, Norris and Marra 2007, Harrison et al. 2011). If less resources are available and more energy is used in one season, then less will be available for the next season, or vice versa, and we would expect individuals to show associated changes in behavior.

For many animals, including birds, regular seasonal movements link breeding locations to non-breeding locations, and understanding these migrations is an important part of understanding species ecology and planning effective conservation (Faaborg et al. 2010, Costa et al. 2012, Lascelles et al. 2014, Allen and Singh 2016, Fraser et al. 2018). Environmental conditions and anthropogenic threats at non-breeding locations, including along migratory routes, have been shown to affect individuals during the breeding season and vice versa (e.g.,

Marra et al. 1998, Szostek and Becker 2015, Desprez et al. 2018, Wojczulanis-Jakubas et al. 2020). Carry-over effects like these within breeding populations can ultimately influence abundances of species in broader regions, but these seasonal interactions are often poorly understood (Fretwell 1972, Norris and Marra 2007). Therefore, management of threatened migratory species first requires information on how breeding populations are connected throughout the annual cycle (Taylor and Norris 2010). One approach to determining how breeding populations are linked across seasons is studying migratory connectivity, which describes the spatial and temporal structure of a migration network by linking individuals, as members of breeding populations, between breeding and non-breeding seasons (Marra et al. 2019). As localized anthropogenic threats during non-breeding would have a greater influence on breeding population dynamics if breeding populations also winter together (Marra et al. 2019), migratory connectivity is key to understanding how breeding populations will be affected by changes in survival and reproduction rates due to conditions during non-breeding.

Methodological Background

The isotopic ratios of different elements within an individual's tissues provide a chemical record of the processes involved in building that tissue, hence stable isotope analysis provides insight into the ecological niche of the organism at the time of tissue growth (Fry 2006, Newsome et al. 2007). Paralleling Hutchinson's (1978) niche concept of a multi-dimensional hypervolume, an area or volume with isotopic ratios as coordinates delineates the isotopic niche of a species (Newsome et al. 2007, Shipley and Matich 2020). Stable isotopic ratios are often expressed as δ -values, which are the ratio of the heavy to light isotopes for each element relative to international standards, expressed in parts per thousand (Fry 2006). The most commonly used elements as a proxy of the trophic niche are carbon and nitrogen, because consumer tissue is enriched in ^{15}N relative to prey, indicating trophic position, while consumer tissue is only slightly enriched in ^{13}C relative to their prey, so can represent the location where prey are consumed (e.g., inshore vs offshore, benthic vs pelagic) due to baseline shifts in carbon sources (DeNiro and Epstein 1978, Minagawa and Wada 1984, Peterson and Fry 1987). By accounting for factors such as isotopic baseline shifts and trophic fractionation (Bearhop et al. 2002, Vanderklift and Ponsard 2003), we can compare isotopic niches among consumers (Post 2002). There have long been attempts to calculate niche breadth and niche overlap (Vandermeer 1972), and the quantifiable isotopic niche can be used as a proxy of trophic/dietary resource differentiation among community members (Bearhop et al. 2004, Layman et al. 2007, Rader et al. 2017). The metric for isotopic niche breadth is the standard ellipse area (SEA), calculated as the standard deviation around the bivariate mean and often visualized on a biplot of δ -values. Additionally, a suite of geostatistical calculations based on the SEA or the biplot have become standard measures of niche overlap, trophic diversity, and trophic redundancy in a community (Bearhop et al. 2004, Layman et al. 2007, Sargeant 2007, Inger and Bearhop 2008, Jackson et al. 2011, Jenkins and Davoren 2021).

Integrating feather stable isotope analysis and bird-borne data logging devices has increased our understanding of seabird ecology during non-breeding. Because feathers are metabolically inert once grown, they represent an individual's isotopic niche at the time and place they were

grown (Hobson 1993, 2011, Bearhop et al. 2002, Inger and Bearhop 2008). For example, razorbills annually molt secondary feathers in the fall, body feathers during the late-winter, and head feathers in the spring (Fig. 1) and, thus, collecting each feather type at the breeding colony provides information on the isotopic niche during those three periods over the previous year. Geolocators (GLS) measure light levels to estimate bird location, and versions designed for seabirds often include immersion and temperature sensors to provide further information on behavior (e.g., flying or on land versus on water) and refine spatial accuracy. Processing light data from GLS tags involves twilight annotation, calibration, estimating and refining locations, and sometimes movement pattern extraction (Lisovski et al. 2020). Location estimates could be used to help interpret whether any variation measured in feather $\delta^{13}\text{C}$ is caused by differences in location or prey source. Temperature-depth recorders (TDRs) record seabird foraging behavior (Wilson et al. 1995), which is particularly important for pursuit diving birds that capture prey underwater (Wilson et al. 1989, Elliott et al. 2008). These data also allow estimates of time-activity budgets (e.g., time spent foraging, resting, flying) during the non-breeding season (e.g., Patterson et al. 2022). These archival data loggers collect data for a year or more, but must be retrieved, at which time feather samples can be taken. Recent studies have combined stable isotope analysis and these biologging methods to study spatial and trophic niche differentiation, compare behavior patterns, and determine molting strategies (e.g., Burke et al. 2015, Orben et al. 2015, Cherel et al. 2016, St. John Glew et al. 2019, Delord et al. 2020, Quillfeldt et al. 2020).

Despite the importance of GLS devices in advancing our understanding of seabird distribution and behavior during non-breeding, they have a number of limitations. First, geolocators provide a relatively coarse resolution of spatial information, as error is introduced through any effect on light measurement, such as the amount of refraction, the weather, shading from the environment, and behavior of the bird (Lisovski et al. 2012). Second, it is especially difficult to estimate latitude for periods around the equinoxes and for animals near the equator or the poles because of equal daylengths at all latitudes and long periods without sunrises or sunsets, respectively (Wilson et al. 1992, Hill 1994). Due to these limitations, spatial accuracy of GLS tags deployed on birds is highly variable depending on species, habitat, and data processing methods, but mostly is in the range of 200-400 km (Phillips et al. 2004, Shaffer et al. 2005, Lisovski et al. 2012, Merkel et al. 2016, Halpin et al. 2021) and 2-3x greater during equinox periods (Halpin et al. 2021). Although a variety of GLS data processing methods (many incorporated into R packages) have been developed to estimate bird locations while minimizing the effect of error in location estimates (Sumner et al. 2009, Lisovski and Hahn 2012, Merkel et al. 2016, Rakhimberdiev et al. 2017, Bindoff et al. 2018, Bråthen et al. 2021), it is unclear whether location estimates from different packages can be combined. The latter is a key unknown for managers as it represents an important step toward interpretation and comparison of spatial information from geolocators across studies for protected area planning.

Study species

Members of the seabird family Alcidae (hereafter ‘alcids’) are characterized by a stout body shape, high wing loading (body mass/wing area), and wing-propelled pursuit diving. Atlantic puffins (*Fratercula arctica*), razorbills (*Alca torda*), and common murrelets (*Uria aalge*), are

three alcids that breed sympatrically across the North Atlantic during the boreal summer, where they forage predominantly on locally abundant small fish. Common murres are the largest and heaviest of the three and can dive the deepest (maximum 180 m) and longest (41-71 s). Razorbills are in the middle in terms of size and dive capabilities (140 m, 19-49 s), while Atlantic puffins are the smallest of the three with the shallowest maximum dive depths (68 m) and shortest dive duration (20-30 s) (Wanless et al. 1988, Ainley et al. 2020, Lavers et al. 2020, Lowther et al. 2020). Studies have shown that allometric relationships between body size and dive depth lead to spatial partitioning of prey resources during the breeding season, perhaps because larger body size might make a species more competitive and, thus, more likely to exploit the highest quality prey patches and exclude similar smaller bodied birds (Piatt 1990, Wanless et al. 1990). During breeding, all three species are central place foragers, making round trips to and from the breeding colony where they care for a single egg or chick each year. Because flight is very energetically demanding for these species due to high wing loading (Elliott et al. 2013), the time spent flying to locate prey directly influences energy expenditure during the breeding season, which may affect energy reserves available for subsequent seasons. These carry-over effects, however, have yet to be studied in these three species.

During non-breeding, alcids disperse from colonies and remain at sea. Therefore, we are just beginning to learn about niche differentiation among these similar species during this period (St. John Glew et al. 2018, Dunn et al. 2019, St. John Glew et al. 2019). Razorbill and common murre chicks fledge after ~21 days at 25% of adult body mass and the male parent continues to care for their chick at sea for ~2 months, during which the chick reaches adult body mass, grows flight feathers and learns to forage for themselves (Ainley et al. 2020, Lavers et al. 2020). In contrast, puffin chicks are raised at the colony for an extended period (38-44 days) until they reach adult body mass and, thus, are independent upon fledging (Lowther et al. 2020). Also during non-breeding, alcids molt all feathers in a complex alternate strategy (Fig. 1), including a rapid, sequential flight feather molt which renders them flightless for 2-3 months (Taverner 1929, Birkhead and Taylor 1977, Harris and Yule 1977, Gaston and Jones 1998, Thompson et al. 1998, Pyle 2009).

Study Area

On the Northeastern Newfoundland coast, common murres, razorbills, and Atlantic puffins breed sympatrically in multi-species colonies on offshore islands. Alcids time the energetically demanding chick rearing period to take advantage of the annual spawning migration of a highly abundant forage fish species, capelin (*Mallotus villosus*), from offshore areas into coastal regions (Davoren and Montevecchi 2003). Nearby coastal spawning sites of capelin are important seabird foraging locations (Davoren et al. 2007, Davoren 2013) and, thus, variability in capelin spawning biomass and the timing of spawning affects seabird diet and foraging effort during breeding (Gulka and Davoren 2019, Gulka et al. 2020, Jenkins and Davoren 2021, Lescure et al. 2023). Although most male capelin die during spawning, a proportion of spawning females are known to recover and move back offshore (Flynn et al. 2001, Magnaye et al. 2019). Therefore, a summer with low spawning capelin biomass may also indicate lower prey biomass in offshore overwintering areas. In general, the winter ocean environment is typically low productivity with patchy prey distribution (Haury et al. 1978).

The objectives of my thesis are to:

1. Determine whether we can combine or compare location estimates and resulting spatial analyses using GLS data that have been processed with different methods
2. Determine the spatiotemporal and isotopic niche overlap during the non-breeding season among Atlantic puffins, razorbills, and common murres that breed sympatrically in the Northwest Atlantic
3. Determine the migratory connectivity of Atlantic puffins from four breeding colonies in the Northwest Atlantic during different months throughout the non-breeding period
4. Investigate how energy expenditure during the breeding season affects fall and early winter foraging activity and energy expenditure of razorbills

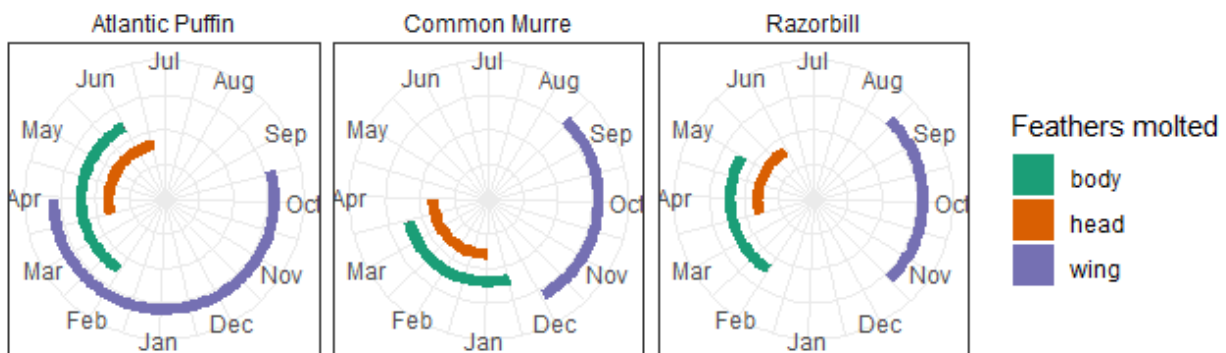


Figure I: Estimated timeframe during which wing feather, body feather, and head feather molt occurs in Atlantic Puffins, Common Murres, and Razorbills, based on studies from across their range. The timing of flight feather molt is uncertain among individual puffins.

References

- Ainley, D. G., D. N. Nettleship, H. R. Carter, and A. E. Storey. 2020. Common Murre (*Uria aalge*). Page <https://doi.org/10.2173/bow.commur.01> in S. M. Billerman, editor. *Birds of the World*. version 1. Cornell Lab of Ornithology, Ithaca, NY.
- Allen, A. M., and N. J. Singh. 2016. Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution* 3:1–13.
- Barringer, B. C., W. D. Koenig, and J. M. H. Knops. 2013. Interrelationships among life-history traits in three California oaks. *Oecologia* 171:129–139.
- Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology* 73:1007–1012.
- Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* 75:451–458.

- Bindoff, A. D., S. J. Wotherspoon, C. Guinet, and M. A. Hindell. 2018. Twilight-free geolocation from noisy light data. *Methods in Ecology and Evolution* 9:1190–1198.
- Birkhead, T. R., and A. M. Taylor. 1977. Moulting of the guillemot *Uria aalge*. *Ibis* 119:80–85.
- Boyce, M. S., and C. M. Perrins. 1987. Optimizing great tit clutch size in a fluctuating environment. *Ecology* 68:142–153.
- Bråthen, V. S., B. Moe, F. Amélineau, S. Descamps, M. Ekker, P. Fauchald, H. H. Helgason, M. K. Johanson, B. Merkel, A. Tarroux, J. Åstrøm, and H. Strøm. 2021. An automated procedure (v2.0) to obtain positions from light-level geolocators in large-scale tracking of seabirds - a method description for the SEATRACK project.
- Burke, C. M., W. A. Montevecchi, and P. M. Regular. 2015. Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. *PLoS ONE* 10:e0141190.
- Cherel, Y., P. Quillfeldt, K. Delord, and H. Weimerskirch. 2016. Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. *Frontiers in Ecology and Evolution* 4.
- Costa, D. P., G. a. Breed, and P. W. Robinson. 2012. New Insights into Pelagic Migrations: Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and Systematics* 43:73–96.
- Davoren, G. K. 2013. Distribution of marine predator hotspots explained by persistent areas of prey. *Marine Biology* 160:3043–3058.
- Davoren, G. K., C. May, P. Penton, B. Reinfort, A. D. Buren, C. Burke, D. Andrews, W. A. Montevecchi, N. Record, B. DeYoun, C. Rose-Taylor, T. Bell, J. T. Anderson, M. Koen-Alonso, and S. Garthe. 2007. An ecosystem-based research program for capelin (*Mallotus villosus*) in the northwest Atlantic: overview and results. *Journal of Northwest Atlantic Fishery Science* 39:35–48.
- Davoren, G. K., and W. A. Montevecchi. 2003. Signals from seabirds indicate changing biology of capelin stocks. *Marine Ecology Progress Series* 258:253–261.
- Delord, K., A. Kato, A. Tarroux, F. Orgeret, C. Cotté, Y. Ropert-Coudert, Y. Cherel, and S. Descamps. 2020. Antarctic petrels ‘on the ice rocks’: wintering strategy of an Antarctic seabird. *Royal Society Open Science* 7:191429.
- DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42:495–506.
- Desprez, M., S. Jenouvrier, C. Barbraud, K. Delord, and H. Weimerskirch. 2018. Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. *Functional Ecology* 32:2040–2053.
- Dunn, R. E., S. Wanless, J. A. Green, M. P. Harris, and F. Daunt. 2019. Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season. *Journal of Avian Biology* 50:1–14.
- Elliott, K. H., K. Woo, A. J. Gaston, S. Benvenuti, L. Dall’Antonia, and G. K. Davoren. 2008. Seabird foraging behaviour indicates prey type. *Marine Ecology Progress Series* 354:289–

- Elton, C. 1927. *Animal ecology*. Sidgwick & Jackson, London.
- Faaborg, R. T., J. Holmes, A. Anders, K. L. Bildstein, K. Dugger, S. Gauthreaux, P. Heglund, K. Hobson, D. H. Johnson, S. Latta, D. J. Levey, P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. S. Sillett, T. W. Sherry, F. R. Thompson, and N. Warnoc. 2010. Managing migratory landbirds in the New World: do we know enough? *Ecological Applications* 20:398–418.
- Flynn, S. R., B. S. Nakashima, and M. P. M. Burton. 2001. Direct assessment of post-spawning survival of female capelin, *Mallotus villosus*. *Journal of the Marine Biological Association of the United Kingdom* 81:307–312.
- Fraser, K. C., K. T. A. Davies, C. M. Davy, A. T. Ford, D. T. T. Flockhart, and E. G. Martins. 2018. Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution* 6:1–8.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton University Press.
- Fry, B. 2006. *Stable Isotope Ecology*. Page (Springer, Ed.). New York, New York.
- Gaston, A. J., and I. L. Jones. 1998. *The Auks: Alcidae*. illustrate. Oxford University Press, Oxford, UK.
- Gause, G. F. 1934. *The Struggle for Existence*. Page Baltimore, Maryland.
- Grinnell, J. 1917. The Niche-Relationships of the California Thrasher. *The Auk* 34:427–433.
- Gulka, J., and G. K. Davoren. 2019. High individual flexibility in the foraging behavior of a marine predator, the common murre. *Marine Biology* 166:1–16.
- Gulka, J., E. Jenkins, L. D. Maynard, W. A. Montevecchi, P. M. Regular, and G. K. Davoren. 2020. Inter-colony foraging dynamics and breeding success relate to prey availability in a pursuit-diving seabird. *Marine Ecology Progress Series* 651:183–198.
- Halpin, L. R., J. D. Ross, R. Ramos, R. Mott, N. Carlile, N. Golding, J. M. Reyes-González, T. Militão, F. De Felipe, Z. Zajková, M. Cruz-Flores, S. Saldanha, V. Morera-Pujol, L. Navarro-Herrero, L. Zango, J. González-Solís, and R. H. Clarke. 2021. Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution* 12:2243–2255.
- Harris, M. P., and R. F. Yule. 1977. The moult of the Puffin *Fratercula arctica*. *Ibis* 119:535–541.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277–327 in J. H. Steele, editor. *Spatial Pattern in Plankton Communities*. Springer, New York.
- Hill, R. D. 1994. Theory of geolocation by light levels. Pages 227–236 *Elephant Seals: Population Ecology, Behavior, and Physiology*.
- Hobson, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-

- dependent stable-isotope models. *Marine Ecology Progress Series* 95:7–18.
- Hobson, K. A. 2011. Isotopic ornithology: A perspective. *Journal of Ornithology* 152.
- Hutchinson, G. E. 1978. *An Introduction to Population Biology*. Yale University Press, New Haven.
- Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. *Ibis* 150:447–461.
- Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80:595–602.
- Jenkins, E. J., and G. K. Davoren. 2021. Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. *Ibis* 163:183–196.
- St. John Glew, K., S. Wanless, M. P. Harris, F. Daunt, K. E. Erikstad, H. Strøm, J. R. Speakman, B. Kürten, and C. N. Trueman. 2019. Sympatric Atlantic puffins and razorbills show contrasting responses to adverse marine conditions during winter foraging within the North Sea. *Movement Ecology* 7:1–14.
- St. John Glew, K., S. Wanless, M. P. Harris, F. Daunt, K. E. Erikstad, H. Strøm, and C. N. Trueman. 2018. Moults location and diet of auks in the North Sea inferred from coupled light-based and isotope-based geolocation. *Marine Ecology Progress Series* 599:239–251.
- Lascelles, B., G. Notarbartolo Di Sciara, T. Agardy, A. Cuttelod, S. Eckert, L. Glowka, E. Hoyt, F. Llewellyn, M. Louzao, V. Ridoux, and M. J. Tetley. 2014. Migratory marine species: Their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24:111–127.
- Lavers, J., J. M. Hipfner, and G. Chapdelaine. 2020. Razorbill (*Alca torda*). Page <https://doi.org/10.2173/bow.razorb.01> in S. M. Billerman, editor. *Birds of the World*. version 1. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Layman, C. A., D. A. Arrington, G. Montana, Carmen, and D. M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48.
- Lescure, L., J. Gulka, and G. K. Davoren. 2023. Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Marine Ecology Progress Series* 709:109–123.
- Lisovski, S., S. Bauer, M. Briedis, S. C. Davidson, K. L. Dhanjal-Adams, M. T. Hallworth, J. Karagicheva, C. M. Meier, B. Merkel, J. Ouwehand, L. Pedersen, E. Rakhimberdiev, A. Roberto-Charron, N. E. Seavy, M. D. Sumner, C. M. Taylor, S. J. Wotherspoon, and E. S. Bridge. 2020. Light-level geolocator analyses: A user's guide. *Journal of Animal Ecology* 89:221–236.
- Lisovski, S., and S. Hahn. 2012. GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution* 3:1055–1059.
- Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn. 2012. Geolocation by light: Accuracy and precision affected by environmental

- factors. *Methods in Ecology and Evolution* 3:603–612.
- Lowther, P. E., A. W. Diamond, S. W. Kress, G. J. Robertson, K. Russell, D. N. Nettleship, G. M. Kirwan, D. Christie, C. Sharpe, E. Garcia, and P. F. D. Boesman. 2020. Atlantic Puffin (*Fratercula arctica*). Page <https://doi.org/10.2173/bow.atlpuf.01> in S. M. Billerman, editor. *Birds of the World*. version 1. Cornell Lab of Ornithology, Ithaca, NY, USA.
- MacArthur, R. H. 1958. Population Ecology of Some Warblers of Northeastern Coniferous Forests. *Ecology* 39:599–619.
- Magnaye, M., R. M. Rideout, and G. K. Davoren. 2019. Irregular growth patterns in the otoliths of a short-lived forage fish do not reliably indicate reproductive history. *Fisheries Research* 218:120–126.
- Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* 11.
- Marra, P. P., E. Cohen, A. L. Harrison, C. E. Studds, and M. Webster. 2019. Migratory Connectivity. *Encyclopedia of Animal Behavior, Second Edition: Volume 1-5* 3:V3-643-V3-654.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable- carbon isotopes. *Science* 282:1884–1886.
- Merkel, B., R. A. Phillips, S. Descamps, N. G. Yoccoz, B. Moe, and H. Strøm. 2016. A probabilistic algorithm to process geolocation data. *Movement Ecology* 4:26–37.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48:1135–1140.
- Newsome, S. D., C. Martinez del Rio, S. Bearhop, and D. L. Phillips. 2007. A Niche for Isotope Ecology. *Frontiers in Ecology and the Environment* 5:429–436.
- Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- Norris, D. R., and C. M. Taylor. 2006. Predicting the consequences of carry-over effects for migratory populations. *Biology Letters* 2:148–151.
- Orben, R. A., D. B. Irons, R. Paredes, D. D. Roby, R. A. Phillips, and S. A. Shaffer. 2015. North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. *Journal of Biogeography* 42:401–412.
- Patterson, A., H. G. Gilchrist, G. J. Robertson, A. Hedd, D. A. Fifield, and K. H. Elliott. 2022. Behavioural flexibility in an Arctic seabird using two distinct marine habitats to survive the energetic constraints of winter. *Movement Ecology* 10:1–16.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual review of ecology and systematics*. Vol. 18:293–320.
- Phillips, R. A., J. R. D. Silk, J. P. Croxall, V. Afanasyev, and D. R. Briggs. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266:265–272.
- Piatt, J. F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of

- capelin. *Studies in Avian Biology* 14:36–51.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83:703–718.
- Pyle, P. 2009. Age determination and molt strategies in North American alcids. *Marine Ornithology* 37:219–226.
- Quillfeldt, P., H. Weimerskirch, K. Delord, and Y. Cherel. 2020. Niche switching and leapfrog foraging: Movement ecology of sympatric petrels during the early breeding season. *Movement Ecology* 8:1–14.
- Rader, J. A., S. D. Newsome, P. Sabat, R. T. Chesser, M. E. Dillon, and C. Martínez del Río. 2017. Isotopic niches support the resource breadth hypothesis. *Journal of Animal Ecology* 86:405–413.
- Rakhimberdiev, E., A. Saveliev, T. Piersma, and J. Karagicheva. 2017. FLIGHTR: an R package for reconstructing animal paths from solar geolocation loggers. *Methods in Ecology and Evolution* 8:1482–1487.
- Reznick, D., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies. *Evolution* 36:160–177.
- Ricklefs, R. E. 1977. On the Evolution of Reproductive Strategies in Birds: Reproductive Effort. *The American Naturalist* 111:453–478.
- Sargeant, B. L. 2007. Individual foraging specialization: niche width versus niche overlap. *Oikos* 116:1431–1437.
- Schluter, D., and P. R. Grant. 1984. Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist* 123:175–196.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Shaffer, S. A., Y. Tremblay, J. A. Awkerman, R. W. Henry, S. L. H. Teo, D. J. Anderson, D. A. Croll, B. A. Block, and D. P. Costa. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147:833–843.
- Shipley, O. N., and P. Matich. 2020. Studying animal niches using bulk stable isotope ratios: an updated synthesis. *Oecologia* 193:27–51.
- Stearns, S. C. 1992. The evolution of life histories.
- Sumner, M. D., S. J. Wotherspoon, and M. A. Hindell. 2009. Bayesian Estimation of Animal Movement from Archival and Satellite Tags. *PLoS ONE* 4:19–22.
- Szostek, K. L., and P. H. Becker. 2015. Survival and local recruitment are driven by environmental carry-over effects from the wintering area in a migratory seabird. *Oecologia* 178:643–657.
- Taverner, P. A. 1929. The Summer Molt of the Razor-Billed Auk (*Alca torda*). *The Auk* 46:223–224.
- Taylor, C. M., and D. R. Norris. 2010. Population dynamics in migratory networks. *Theoretical Ecology* 3:65–73.

- Thompson, C. W., M. L. Wilson, E. F. Melvin, and D. J. Pierce. 1998. An unusual sequence of flight-feather molt in Common Murres and its evolutionary implications. *The Auk* 115:653–669.
- Tilman, D. 1987. The Importance of the Mechanisms of Interspecific Competition. *The American Naturalist* 129:769–774.
- Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: A meta-analysis. *Oecologia* 136:169–182.
- Vandermeer, J. H. 1972. Niche Theory. *Annual Review of Ecology and Systematics* 3:107–132.
- Volterra, V. 1928. Variazione e fluttuazione del numero d'individui in specie animali conviventi. *Journal du Conseil international pour l'exploration de la mer* III 1:409–448 in Chapman, R. N. 1931. *Animal ecology*. Ne.
- Wanless, S., J. A. Harris, and M. P. Morris. 1988. Diving behaviour of guillemot *Uria aalge*, puffin *Fratercula arctica* and razorbill *Alca torda* as shown by radio-telemetry. *Journal of Zoology* 216:73–81.
- Wanless, S., M. P. Harris, and J. A. Morris. 1990. A comparison of feeding areas used by individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the breeding season. *Colonial Waterbirds* 13:16–24.
- Wiens, J. A. 1977. On Competition and Variable Environments: Populations may experience “ecological crunches” in variable climates, nullifying the assumptions of competition theory and limiting the usefulness of short-term studies of population patterns. *American Scientist* 65:590–597.
- Wilson, R. P., A. E. Burger, B. L. H. Wilson, M. P. T. Wilson, and C. Nöldeke. 1989. An inexpensive depth gauge for marine animals. *Marine Biology* 103:275–283.
- Wilson, R. P., J.-J. Ducamp, G. Rees, B. M. Culik, and K. B. Niedersachsen. 1992. Estimation of location: global coverage using light intensity. Pages 90–98 in I. M. Priede and S. M. Swift, editors. *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horwood, Chichester.
- Wilson, R. P., H. Weimerskirch, and P. Lys. 1995. A Device for Measuring Seabird Activity at Sea. *Journal of Avian Biology* 26:172–175.
- Wojczulanis-Jakubas, K., M. Jiménez-Muñoz, D. Jakubas, D. Kidawa, N. Karnovsky, D. Cole, and E. Matechou. 2020. Duration of female parental care and their survival in the little auk *Alle alle* - are these two traits linked? *Behavioral Ecology and Sociobiology* 74.

Chapter 1: Comparison of light-level geolocator data processing methods

Emily S. Runnells¹, Mark A. Baran², Vegard Sandøy Bråthen³, Mark Dodds⁴, David A. Fifield⁵, April Hedd⁵, Matthew Legard¹, Ariel K. Lenske⁶, Kristina R. McOmber¹, Gail K. Davoren¹

¹University of Manitoba, Winnipeg, MB, Canada

²SUNY Plattsburgh, Plattsburgh, NY, USA

³Norwegian Institute for Nature Research (NINA), Trondheim, Norway

⁴University of New Brunswick, St. John, NB, Canada

⁵Wildlife Research Division, Environment and Climate Change Canada, Mount Pearl, NL, Canada

⁶Canadian Wildlife Service, Environment and Climate Change Canada, Delta, British Columbia, Canada

This chapter is prepared for publication in Animal Biotelemetry

[*Return to table of contents*](#)

Abstract

Multiple methods are available for obtaining location estimates from light-level geolocator data, and a growing body of ecology literature is based on this tracking technique. Currently, it is unclear what factors to consider when choosing a processing method or whether all geolocator-based location estimates are directly comparable. Our objective was to show how position estimates differ depending on the GLS processing method and the GLS tag model and settings used (i.e., with temperature data and without, different light intensity resolution). We processed Atlantic puffin (*Fratercula arctica*) data from BioTrack tags (no SST, low resolution light intensity) and Migrate Technology tags (with SST, full range light intensity), using the methods implemented in six R packages: 'Geolight', 'ProbGLS', 'TwilightFree', 'FlightR', 'SGAT', and 'seatrackGLS'. Location estimates were compared with simple geostatistics and measures of similarity. Most of the processing methods produced location estimates within the known error range for geolocators (i.e. mostly < 400 km apart) outside of equinox periods, but tag type mattered for some of the methods. We recommend certain tag types (i.e., sensors) for certain processing methods and address how methodology choices might impact analyses for different research questions (e.g., differences between repeat tracks vs. spatial overlap, marine spatial planning). By also highlighting the degree of analysis complexity compared to the results obtained, this study provides a resource for researchers seeking to use geolocators for ecology research.

Background

Recent advances in technology have allowed an increase in vertebrate tracking studies (Wilmers et al. 2015, Joo et al. 2022). There is proportionally far less vertebrate research outside of the breeding season, and a need for studies of non-breeding ecology and interactions between seasons (Marra et al. 2015). Tracking data provide key information on distribution and movements (Nathan et al. 2008, Joo et al. 2020), but year-round deployments of loggers on smaller species require light-weight devices. Light level geolocators (global location sensors, or GLS) are well suited for this purpose. GLS devices record time and light levels, from which the timing of sunrise and sunset determine longitude and the length of the day or night determine latitude (Wilson et al. 1992, Hill 1994, Ekstrom 2004). First used in 1992 (Delong et al. 1992), further miniaturization around 2002 and their relatively low cost compared to other tracking technology (e.g., PTT, GPS) increased their use in answering a wide range of ecological questions (Lisovski et al. 2020). Although light-level geolocators are used on a variety of taxa, such as marine mammals (e.g., Thums et al. 2025) and marine fish (e.g., Walli et al. 2009), they have particularly been used on birds (McKinnon et al. 2013). For seabirds, geolocators are commonly employed to study non-breeding and migration ecology, and now underlie a large body of seabird ecology literature (Strøm et al. 2021).

The relatively coarse resolution of spatial information from geolocators is their main limitation. Error is introduced through any effect on light measurement, such as the amount of refraction, the weather, shading from the environment, and behavior of the bird (Lisovski et al. 2012). Calibration is required to relate observed and expected light levels, but all calibration methods are imperfect, as they require data that are difficult or impossible to collect and generally assume that light measurements vary linearly over time (Hill and Braun 2001, Lisovski et al. 2020). It is especially difficult to estimate latitude for periods around the equinoxes and for animals near the Equator or the poles because of equal daylengths at all latitudes and long periods without sunrises or sunsets, respectively (Wilson et al. 1992, Hill 1994). Spatial accuracy of GLS tags deployed on birds is highly variable depending on species, habitat, and data processing methods, with mean/median errors between 17 - 713 km reported, although most are in the range of 200-400 km, and an error range from 0-17,516 km (Phillips et al. 2004, Shaffer et al. 2005, Lisovski et al. 2012, Merkel et al. 2016, Halpin et al. 2021). Error during equinox has been shown to be 2-3x greater than in non-equinox periods (Halpin et al. 2021). Most studies report lower error on birds that spend considerable time in flight (e.g., albatross, shearwaters, petrels, tropic birds), with higher measurement error reported for penguins (e.g., 383 km, 352 km, Phillips et al. 2004). Even among albatross of the same species from the same colony, the mean error of geolocators compared to PTT (platform transmitting terminal) tags ranged between 145 ± 84 km – 251 ± 132 km (Phillips et al. 2004), showing the variation among tags and individual birds. Based on these studies, the accuracy of geolocators is generally considered to range between 200-400 km.

A number of GLS data processing methods (many incorporated into R packages) have been developed to estimate bird locations while minimizing the effect of error in location estimates. The R package ‘GeoLight’ was developed to provide a standardized procedure for analyzing geocator data using astronomical formulas (Lisovski and Hahn 2012). Other methods build on

this basic, deterministic package with filtering and smoothing techniques intended to reduce the error introduced by environmental variability and animal behavior. One such method, ‘seatrackGLS’, was developed by the SEATRACK project, and is particularly tailored towards arctic seabirds (Bråthen et al. 2021). Several stochastic modeling methods have also been developed to address issues with geolocator data and refine location estimates with additional information, particularly by using neighboring location estimates. One approach, the ‘probGLS’ method, employs a probabilistic model to reduce reliance on the assumption of constant or linearly varying solar angles and allow the easy incorporation of behavior and environmental data (e.g., sea surface temperature (SST), Merkel et al. 2016). To estimate locations when data are too noisy to reliably estimate the time of dawn or dusk, a twilight-free method employs a hidden Markov model, easily run in the ‘TwilightFree’ package (Bindoff et al. 2018). Another method, now contained in the ‘SGAT’ R package, is a Bayesian model, which can incorporate additional information (such as existing knowledge of a species range and movement patterns) as priors (Sumner et al. 2009). Finally, ‘FlightR’ is one of the few commonly used R packages that is based on a template fit method, which uses the rate of change in light level during the twilight period to determine latitude, rather than simply the length of day/night (threshold method). This method builds the template fit algorithm (Ekstrom 2004) into a hidden Markov chain movement model (Rakhimberdiev et al. 2017). These four stochastic methods and two deterministic methods are the predominant packages used recently for processing seabird geolocator data.

Our objective was to determine whether we can combine or compare location estimates and resulting spatial analyses from GLS data that have been processed with different methods. Specifically, we aimed to show how much positions differ depending on the GLS processing method and the GLS tag type and settings used (specifically differences in the light range recorded and the addition of SST sensors). For stochastic methods, we also examined consistency of the spatial location estimates across multiple model runs of the same data. We used data from two different types of GLS tags attached to Atlantic puffins (*Fratercula arctica*) from colonies in coastal Newfoundland, Canada, processed with 6 main methods: ‘GeoLight’, ‘seatrackGLS’, ‘TwilightFree’, ‘probGLS’, ‘FlightR’, and ‘SGAT’. We focused on a species within the family Alcidae because there is a large body of research based on geolocators on alcids (e.g., Harris et al. 2010, Jessopp et al. 2013, Frederiksen et al. 2016, St. John Glew et al. 2018, Shoji et al. 2023). Atlantic Puffins were specifically chosen because they reliably stay in open ocean habitat during the non-breeding period, so the effect of shading is minimized (Lisovski et al. 2012), and their distribution is concentrated at latitudes high enough that day length strongly varies with latitude, but not so high that dawn and dusk are indistinguishable (Hill 1994, Lisovski et al. 2012). As there are known species and spatiotemporal effects on geolocation accuracy, we focused this method comparison on one species with limited geographic range, movement types, and behaviors, to limit confounding effects. This study will aid researchers in choosing among available GLS data processing packages and tag types and is an important step toward interpretation and comparison of spatial information from geolocators across studies.

Methods

Study area and timing

Geolocators were deployed on Atlantic Puffins at two Newfoundland colonies. We used 14 loggers from Gull Island, in Witless Bay (47.26° N, 52.77° W), all deployed in 2019, and 14 from James Island, off the northeast coast (49.58° N, 53.78° W), 6 deployed in 2019 and 8 deployed in 2020. Puffins were hand captured in their nesting burrows, and tags were attached to plastic leg bands with cable ties and retrieved the next breeding season. The tags used on James Island were Migrate Technology models C330 (3.4 g; 2019) and C65+ (1.0 g; 2020). These loggers sense and record the full range of light intensity and were set to additionally measure immersion status every 30 s and record counts of ‘wet’ status every 10 min. When these tags were immersed continuously for 20 min, temperature was measured once, and the maximum, minimum, and mean temperature every 8 h were recorded. The tags used on Gull Island were BioTrack model MK4083 (1.9 g), which have a 6-bit light sensor and record a truncated range (0 - 64 units) of light intensity. They do not have a temperature sensor, but were set to measure immersion status every 3 s and record counts of ‘wet’ status every 10 min. Both tag models measured light intensity every 60 s and recorded maximum values every 5 min.

Only locations after calculated colony departure dates and before colony arrival dates were included in our analysis. To estimate colony presence, light levels from Migrate Technology tags were logged, then daily patterns in light levels from both tag types were inspected. Colony departure dates were calculated as the last day between August 30th to September 12th when light intensity was less than 0.9 during daylight hours, conditions indicative of burrow attendance. The colony arrival dates on James Island were the first date after May 15th where light intensity was less than 0.9 during daylight hours. For Gull Island tags, the recorded range of light was much narrower, so arrival dates were calculated as the first dates after May 1st where a 6-hour rolling mean of light intensity was less than 0.9 during daylight hours. After processing, we adjusted the arrival dates for 3 birds from Gull Island to be earlier, based on the first day without clear twilights, another indication of burrow attendance.

Data standardization

For all methods except ‘FlightR’, we worked with a standard set of twilights and/or solar angles/zeniths produced using SEATRACK methodology. FlightR was an exception because twilight delineation is part of the unique template fit calibration process, and TwilightFree only used zeniths, as this method does not use twilights. In R, twilights and solar angles were derived from light data using ‘GeoLight::twilightCalc’ (Lisovski and Hahn 2012) and the ‘Filter-’ and ‘Edit twilights’ functions described in Bräthen et al. (2021). We selected a threshold of 11 lux for loggers produced by Migrate Technology and 1 arbitrary unit of light for loggers produced by BioTrack to separate night (below) from day (above). As light sensitivity varies between loggers, such that using the same threshold of light will not produce the exact same timing of twilights from loggers recording the same ambient changes in light, all GLS processing methods require the data to be calibrated. For all methods except ‘FlightR’, we obtained solar angle/zenith values

following Bråthen et al. (2021), based on 3 characteristics of a series of latitude versus time plots for a range of solar angles: minimizing latitudinal error close to the equinoxes, similar latitudes on both sides of the equinox, and positions that fit the latitude of the colony at the beginning and end of the track. Different solar angles were assigned to the start and finish of a track, allowing a linear interpolation between these two values which captures tag aging effects. The twilight error distribution used for ‘SGAT’ and ‘probGLS’ was based on the average shape and scale parameters calculated in ‘GeoLight::getElevation’ in R, using data from calibration periods of the Migrate Technology loggers (see Runnells et al. 2024 for details).

‘FlightR’ did not use this standardized twilight information because it uses a template-fit calibration (Ekstrom 2004, Rakhimberdiev et al. 2017). Instead, ‘FlightR’ includes a built-in *make.calibration* function, which was used to estimate the relationship between observed and theoretical light levels (based on Ekstrom 2004) for each tag, using light level data recorded while the puffin was at the breeding colony. For tags deployed on James Island, light level data were available for a pre- and post-deployment calibration period (i.e. from the date of tag deployment to the calculated date of colony departure, and from the calculated date of colony arrival to the date of tag retrieval, respectively). MK tags were deployed on Gull Island late in the breeding season, so light level data were only available for a post-deployment calibration period. As such, tag aging was accounted for in the ‘FlightR’ calibration of James Island tags and not accounted for when calibrating Gull Island tags.

We differentiate between equinox periods, when latitudes may be unreliable due to the similarity in daylength across the globe (the equinox effect, Hill and Braun 2001) and non-equinox periods in subsequent analysis. We delineated equinox periods as 15 days before fall equinox and after spring equinox, and 28 days after fall equinox and before spring equinox, to later classify location estimates as equinox or non-equinox. This was done by using the ‘aut_equinox_periods’ function in ‘seatrackGLS’ using the average estimated latitude of the puffins in this study on the day of fall or spring equinox. In brief, ‘seatrackGLS’, decides the length and timing of an equinox based on the approximate location of an individual before and after the equinox. For length, the closer an individual is towards the Equator, the longer the equinox period will be. For timing, the date of equinox will be moved according to where the sun is to the horizon at the time the light cross the threshold for defining dusk and dawn. In this study, a low threshold of light means the sun will be below the horizon at any defined dusk and dawn, and the apparent equinox will be shifted towards winter solstice (Hill and Braun 2001).

For all methods, we also used a standard geographic bounding box, a land mask, consistent colony arrival and departure dates, comparable equinox delineation, and daily movement limits. The bounding box was based on previous geolocator research on puffins from these colonies (Table 1.1, Fayet et al. 2017a, Runnells et al. 2024), and the land mask (plus SST data, if used) was from the National Oceanic and Atmospheric Administration Physical Science Laboratory (Reynolds et al. 2007). The boundary box and land mask were firm limits on estimated locations for most methods, with the exceptions of ‘SGAT’, which incorporated both as a prior, and ‘seatrackGLS’, which did not apply latitudinal boundaries during equinox periods. Locations associated with successive twilights were limited to being less than 550 km apart or less than

700 km apart within 24 hours either in the method's movement parameters ('FlightR'), as a prior ('SGAT'), or by removal in post-processing (for 'GeoLight', 'probGLS', 'seatrackGLS', and 'TwilightFree'). See Appendix 1 for standard method parameters.

Table 1.1: Summary of input parameters and processing time for each GLS processing method. White boxes = required parameters, light blue = optional parameters, and dark blue = not applicable. Text describes parameters used in this study. ‘Equinox delineation’ refers to how each method incorporated information on equinox timing into estimating locations. ‘Known locations’ refers to how each method incorporates colony attendance into estimating locations. ‘Run times’ are based on the processing capabilities of a standard business laptop. *Standardized parameters. ^aMore details in main text.

	GeoLight	seatrackGLS	SGAT	probGLS	FlightR	TwilightFree
solar angle/zenith	tag specific calculation*	tag specific calculation*	tag specific calculation*	Range for all tags ± 1	'make.calibration' function ^a	tag specific calculation*
twilight error distribution			log-normal (location:2, scale: 1)	log-normal (location:2, scale: 1)	"make.calibration" function ^a	$\alpha = 0.25$ (shading hyperparameter)
known location	colony locations*	colony locations* tag specific deployment/retrieval		colony locations* tag specific deployment/retrieval	colony locations*	colony locations* tag specific departure/arrival*
twilight times	'preprocessLight' twilight annotation*	'preprocessLight' twilight annotation*	'preprocessLight' twilight annotation*	'preprocessLight' twilight annotation*	'preprocessLight' twilight annotation*	tag specific thresholds ^a
geographic bounding box	Longitude = [-85, -1], Latitude = [25, 70]	Longitude = [-85, -1], Latitude = [25, 70] ^a	Longitude = [-85, -1], Latitude = [25, 70] ^a	Longitude = [-85, -1], Latitude = [25, 70]	Longitude = [-85, -1], Latitude = [25, 70]	Longitude = [-85, -1], Latitude = [25, 70]
spatial grid size					50 km	0.5°
equinox delineation		tag specific calculation ^a		tolerance = 0.08		
land mask	From NOAA PSL*	From NOAA PSL*	NOAA PSL*	From NOAA PSL*	From NOAA PSL* max 300 km overland flights	From NOAA PSL*
auxiliary data				SST & ice cover, proportion time wet		
flight speeds		maximum 45 km/h, if positions are missing then speed is reduced	gamma distribution (shape: 1, rate: 0.14)	flight: max 17.6, SD 0.2, max allowed 18.6; swim: max 1, SD 1.3, max allowed 5 m/s		$\beta = 0.45$ (likelihood of daily positional shift)
model iterations			75,000 burn in, 120,000 tuning, 15,000 final sample	2000 locations per twilight, 100 track iterations	1,000,000 particles	
run time per track	< 5 s	< 5 s	~ 2 h	10-30 min	~ 2 h	5-10 min

Location estimation

‘GeoLight’ and ‘seatrackGLS’ use deterministic methodology for estimating locations directly from twilights. Both are based on ‘GeoLight::coord()’ (Lisovski and Hahn 2012), which uses solar angles and two successive twilight times to calculate locations, based on Meeus’s Astronomical Algorithms (1998). This computes longitude based on the apparent time of local noon and midnight, and latitude from the average of the times of sunrise and sunset (Lisovski and Hahn 2012). The only additional steps taken using ‘GeoLight’ were to remove failed location estimates, where the algorithm cannot provide a latitude or longitude, and to remove locations outside of the geographic boundary box or on land. ‘SeatrackGLS’ methodology includes additional adjustment steps beyond the ‘GeoLight’ method, including twilight filtering and smoothing, equinox filtering, a speed filter, and an angle and distance filter (Table 1.1, Bråthen et al. 2021).

The remaining four methods that we explored all use some form of stochastic modeling to estimate locations. We tried to provide all models with similar inputs, even when parameters were defined differently. For the details about the parameters used in these models, see Table 1.1. ‘TwilightFree’ and ‘FlightR’ are spatially discretized methods that estimate positions in a defined grid (Rakhimberdiev et al. 2017, Bindoff et al. 2018). We based grid cell size on GLS accuracy (Phillips et al. 2004), using 0.5° for ‘TwilightFree’ and the unchangeable default is 50 km for ‘FlightR’ (Table 1.1). ‘TwilightFree’ runs a forward-backward Hidden Markov Model, using maximum likelihood, and estimates one location every 24 h directly from the pattern of light-levels over that period, based on inputs including light-level threshold, zenith, the probabilities of light sensor shading, and the likelihood of daily positional shifts (Bindoff et al. 2018). The output is a single, most likely, location estimate for each day (24 h period), rather than two location estimates. ‘FlightR’ employs a Hidden Markov Model computed via a Bayesian particle filter algorithm to estimate locations based on change in light during twilight, solar angle, and starting location (Rakhimberdiev et al. 2017). We ran ‘FlightR’ with 1 million particles. It also incorporates and estimates parameters on the probability of moving, the likely direction of movement, and the distance traveled. ‘FlightR’ outputs median location estimates for each twilight (2 location estimates per day) at the center of squares on a grid, along with uncertainty estimates in the form of the posterior distribution.

The final two stochastic modeling approaches, ‘SGAT’ and ‘probGLS’, are spatially continuous methods. The ‘probGLS’ algorithm is based on a random walk, using iterative forward step selection, where the model repeatedly “walks” through point clouds of possible location estimates computed for each twilight with a range of probable solar angles (and associated twilight error distribution), weighted by additional data such as the interaction of tag immersion and movement speeds, and SST (Merkel et al. 2016). We set ‘probGLS’ to generate 2000 possible locations for each twilight event, both with and without incorporating SST data (available for tags from James Island) to examine the impact on daily location estimates. The output is the geographic median of a chosen number of track iterations (we chose 100 iterations) for each twilight. ‘SGAT’ employs a Markov chain Monte Carlo (MCMC) sampler that uses initial location estimates based on twilight times and then simulates tracks based on the initial location estimates and priors, which included a land mask, twilight error distribution, and distribution of

expected movement speeds in our analysis (Sumner et al. 2009). We ran SGAT with 75,000 iterations for model burn in, and an additional 120,000 iterations for tuning of the proposal distribution, then drew a final 15,000 samples, run across 3 chains and thinned by a factor of 15, for a resulting 1000 samples. A full posterior distribution is produced for each location estimate for each twilight, from which we chose to report the medians.

For six birds, three from James Island and three from Gull Island, five iterations of models were run in ‘SGAT’, ‘FlightR’, and ‘probGLS’ to determine the baseline variation within each of these stochastic methods. Each of the 28 total birds (14 per tag type) were then processed once using each of the six processing methods, and the birds with tags that measured SST (14 from James Island), were processed once incorporating SST data and once without SST data using ‘probGLS’. The resulting dataset was the foundation of the inter-method comparison and also allowed for quantifying the differences between tag types, specifically looking at the effect of different light ranges and the inclusion of SST sensors.

Comparisons

Output location estimates for each track were then compared. The comparison analyses in the following paragraphs were completed for location estimates from three different datasets: 1) among the five iterations within each of the three stochastic methods (‘SGAT’, ‘probGLS’ – both with and without SST, and ‘FlightR’) that ran iterations for the subset of 6 birds, 2) among the six methods including all 28 birds, and adding ‘probGLS’ with SST as a method for the 14 tags that measured SST and 3) among the six methods within the two different tag types (different light ranges). Each of those datasets were further split into equinox and non-equinox periods (as defined above) before comparisons were calculated.

We assigned each location estimate to the first of the two twilight times it was derived from, to match up corresponding location estimates among methods or iterations. Then we measured the geographic (great circle) distance between each available location estimate for the same twilight from different processing methods or iterations. For ‘TwilightFree’, with only one location estimate per day, the distance between this single location and the (up to) two location estimates of each of the other methods were computed. With the distances from the pairwise comparisons, we calculated the proportion of location estimates that were below or above 400 km apart. We chose 400 km as it is towards the upper end of the error range expected from GLS tags and, thus, comparisons exceeding this distance would likely indicate that processing methods do not produce comparable location estimates. Within each comparison, the median and standard deviation of those distances for each track were computed, outside of and during the equinox. We refer to these medians as the Median Pairwise Distance (MPD). These same calculations were performed for latitudinal distance only, assuming 1° latitude equals 111 km. Because distances were only measured when there were location estimates available for a given twilight for both methods or iterations, there were different sample sizes for each MPD.

Earth Mover’s distance (EMD) and Bhattacharyya’s Affinity (BA), both of which represent the similarity of two distributions, were computed as well. EMD is based on computer vision analysis but functionally calculates the minimum distances (in km) between two distributions

(Kranstauber et al. 2017, Franklin et al. 2022). This measure was calculated in the same pairwise fashion as MPD, comparing tracks of each bird among methods or iterations during and outside of equinox periods, but location estimates missing from one track did not have to be dropped from the other track because distances are calculated by comparing to the closest location estimates regardless of date. As temporal proximity is not accounted for in EMD computation, we addressed concerns about fall and spring positions near the colony being inappropriately compared to each other by calculating EMD without any location estimates before the autumn equinox. BA is a commonly used overlap index, designed as a statistical measure of the similarity of two kernel density estimates (Bhattacharyya 1943, Fieberg and Kochanny 2005). Values of the BA index range from 0, indicating that distributions do not overlap, to 1, indicating identical distributions. We calculated BA of the 95% kernel density estimates for all possible pairs of methods using ‘adehabitatHR::kerneloverlap’ (Callenge 2006) on a 200 x 200 cell grid with bandwidth chosen via the ‘reference bandwidth’ method, incorporating all the location estimates of all the puffins from each method, separated into equinox and non-equinox periods.

Results

As Earth Mover’s Distance (EMD) showed the same patterns and similar values to the Median Pairwise Distances (MPD), we focus on the MPD and Bhattacharyya’s Affinity (BA), with EMD results provided in supplementary material. The majority of the distance between location estimates from different methods calculated in the MPDs was latitudinal (Fig. 1.S1), so latitudinal distances are also provided in supplementary material.

Variation among iterations within each stochastic method was well under typical geolocator accuracy (200-400 km) outside of the equinox (Fig. 1.1A). The MPDs between ‘FlightR’ iterations were most commonly zero, though when location estimates were not in the same grid cell, jumps of multiples of 50 or $50\sqrt{2}$ km were introduced (Fig. 1.1C), increasing the MPD. ‘ProbGLS’ occasionally had large MPDs between iterations, usually when locations ended up on opposite sides of a land mass, or when a rapid-long distance movement was estimated to occur on a different day. Including sea-surface temperature data in ‘probGLS’ made location estimates among iterations more similar (Fig. 1.1). Comparatively, the variation among SGAT iterations was consistently much less, with only rare long distances between concurrent locations. Most of the variation within methods was from latitudinal differences, though not all, and less so for ‘probGLS’ than the others (Fig. 1.S2). BA values were very close to 1.0 when comparing iterations for ‘probGLS’ (with SST) and ‘SGAT’, and comparisons within all methods produced BA values mostly above 0.97 (Fig 1.S3). For ‘probGLS’ without SST outside of the equinox periods, 4 (out of 15) of the iteration comparisons were around BA = 0.90, but during the equinox some iterations had similarity indexes as low as 0.55 (Fig 1.S3). During the equinox, comparisons among iterations showed the same patterns as outside of the equinox, but MPDs roughly doubled (Fig. 1.1B).

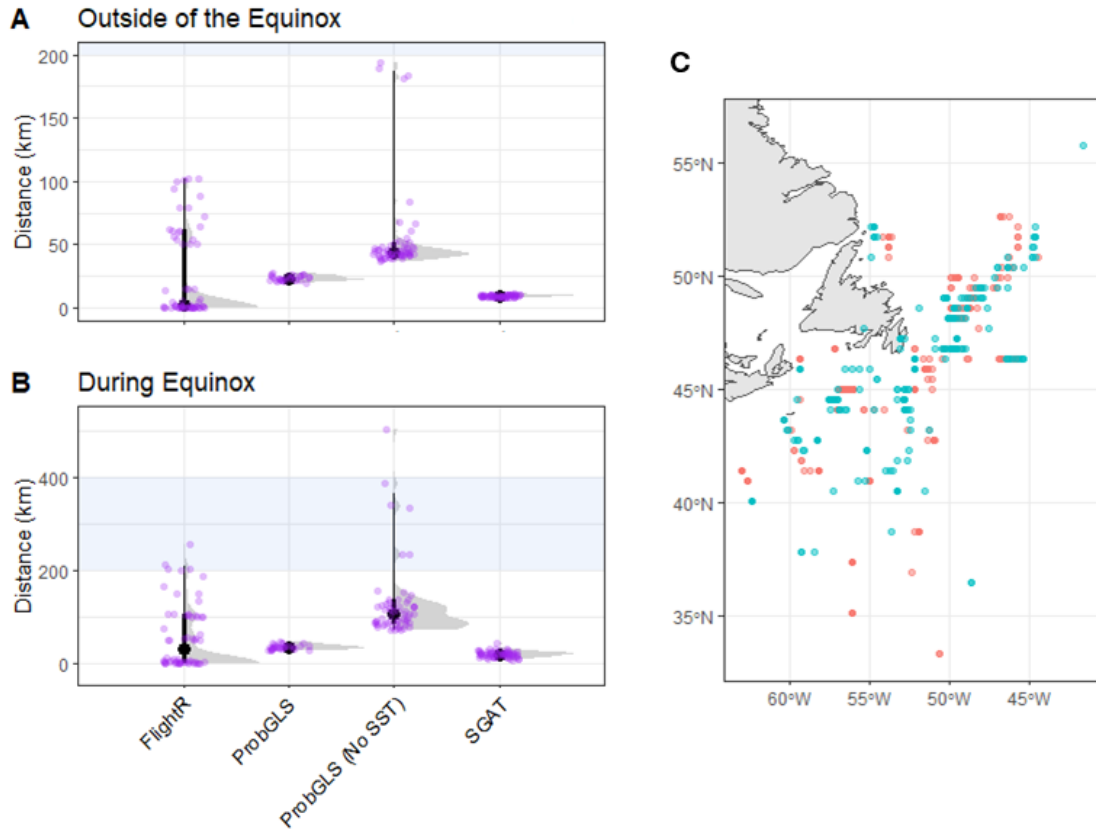


Figure 1.1: Median pairwise distances (MPD, in km) among iterations of stochastic methods for locations during non-equinox periods (A) and during equinox periods (B). Note the different y-axis scale on graphs. The shaded area indicates 200–400 km, typical geolocator accuracy range, shown to emphasize the difference in scale. Violin widths are scaled to maximum weight within each comparison. The map (C) shows non-equinox location estimates from two different iterations (different colors) of the same bird from ‘FlightR’.

The two deterministic methods (‘GeoLight’ and ‘seatrackGLS’) produced similar location estimates (Fig. 1.2, Fig. 1.S4). Outside of equinox periods, some positions from both methods were either not estimated or removed through post-processing or filtering (GeoLight 11%, seatrackGLS 14%), but only 2% of the 8486 compared location estimates were more than 200 km apart. MPDs between these two methods were all less than 63 km (Fig. 1.2), and none of the distances were more than 400 km (Fig. 1.3). The BA for all the birds was very close to 1.0, indicating essentially the same distribution was produced by both methods (Fig. 1.4). During the equinox, the MPDs were all less than 194 km (Fig. 1.2), although 12% of the distances were over 400 km (Fig. 1.3). Many positions were dropped from both methods during the equinox, but a higher proportion of the possible equinox locations were estimated using ‘seatrackGLS’ (87%), partly because the bounding box was not applied, compared to ‘GeoLight’ (69%).

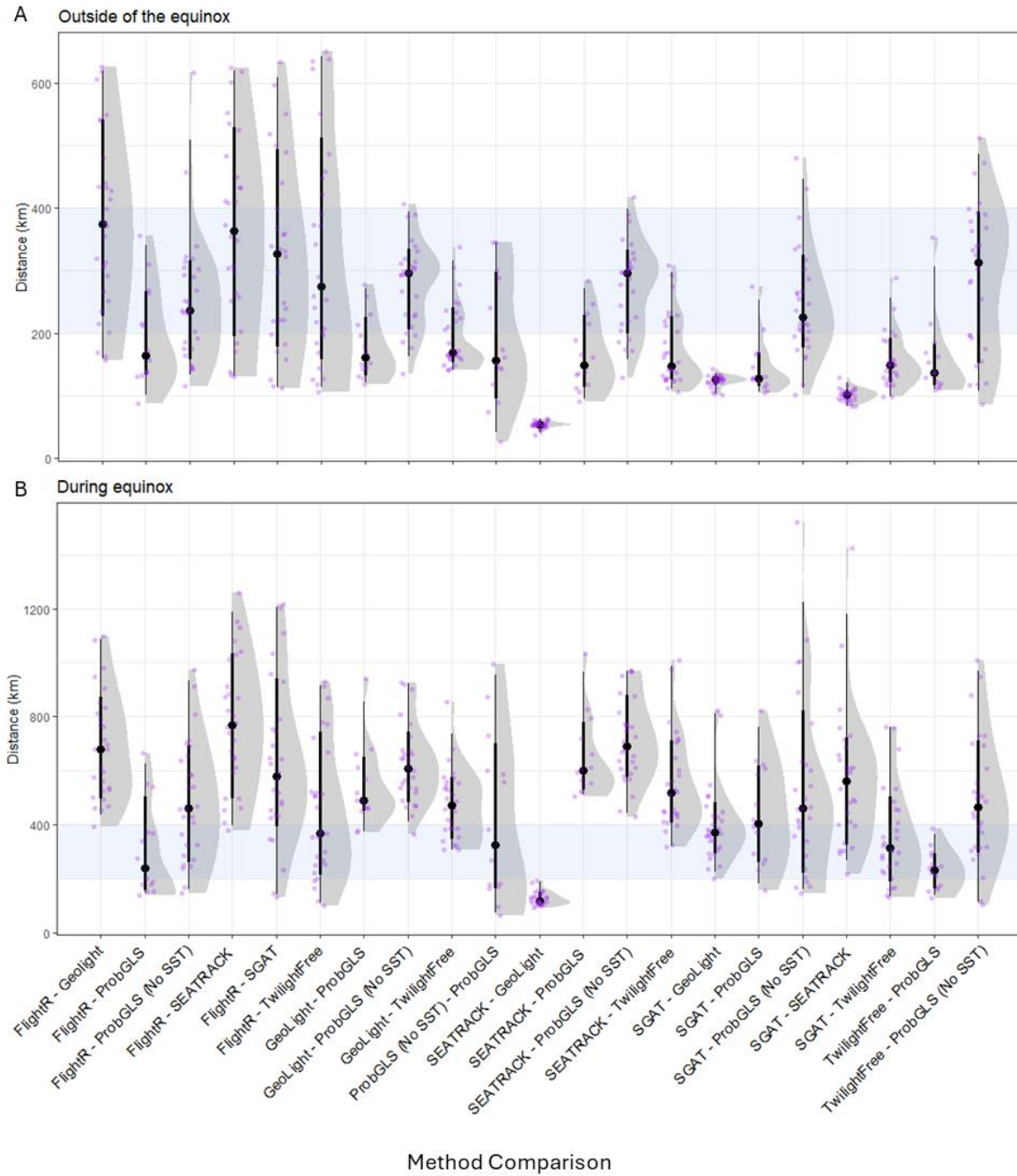


Figure 1.2: Median pairwise distances (MPD, in km) for each method comparison for locations during non-equinox periods (top panel) and during the equinox periods (bottom panel). Note the different y-axis scale on graphs. The shaded area indicates 200-400 km, typical geolocator accuracy range, shown to emphasize the difference in scale. Violin widths are scaled to maximum weight within each comparison.

Outside of the equinox periods, some, but not all, of the stochastic methods produced location estimates within typical geolocator accuracy distance (~200-400 km) of those from other methods (Fig. 1.2, Fig. 1.S4A). ‘FlightR’ location estimates were the farthest from all other methods, with proportionally more distances above 400 km for most comparisons (Fig. 1.3). The closest location estimates to ‘FlightR’ were the ‘probGLS’ estimates (Fig. 1.2, Fig. 1.3, Fig. 1.S4A). ‘ProbGLS’ run without SST data also produced divergent location estimates, with MPD interquartile ranges (IQRs) extending past 300 km for all comparisons except with SGAT (Fig. 1.2). As with the iterations, including SST data in ‘probGLS’ brought location estimates closer to the other methods (Fig. 1.2, Fig. 1.S4A). For all other method comparisons, the MPD IQRs were under 226 km (Fig. 1.2), although between 9 – 14% of the measured distances were over 400 km for the rest of the comparisons including ‘TwilightFree’, ‘probGLS’, ‘seatrackGLS’ and ‘GeoLight’ (Fig. 1.3). ‘SGAT’ had the closest location estimates to most other methods (Fig. 1.2, Fig. 1.S4A), particularly the two deterministic methods (median MPDs = 125 km, 101 km). There was more variation in MPDs when comparing ‘SGAT’ with ‘probGLS’, although the median of the MPDs was still 127 km. All these same patterns were observed in BA calculations, with values mostly above 0.90, except for ‘FlightR’ and ‘probGLS’ without SST (Fig. 1.4).

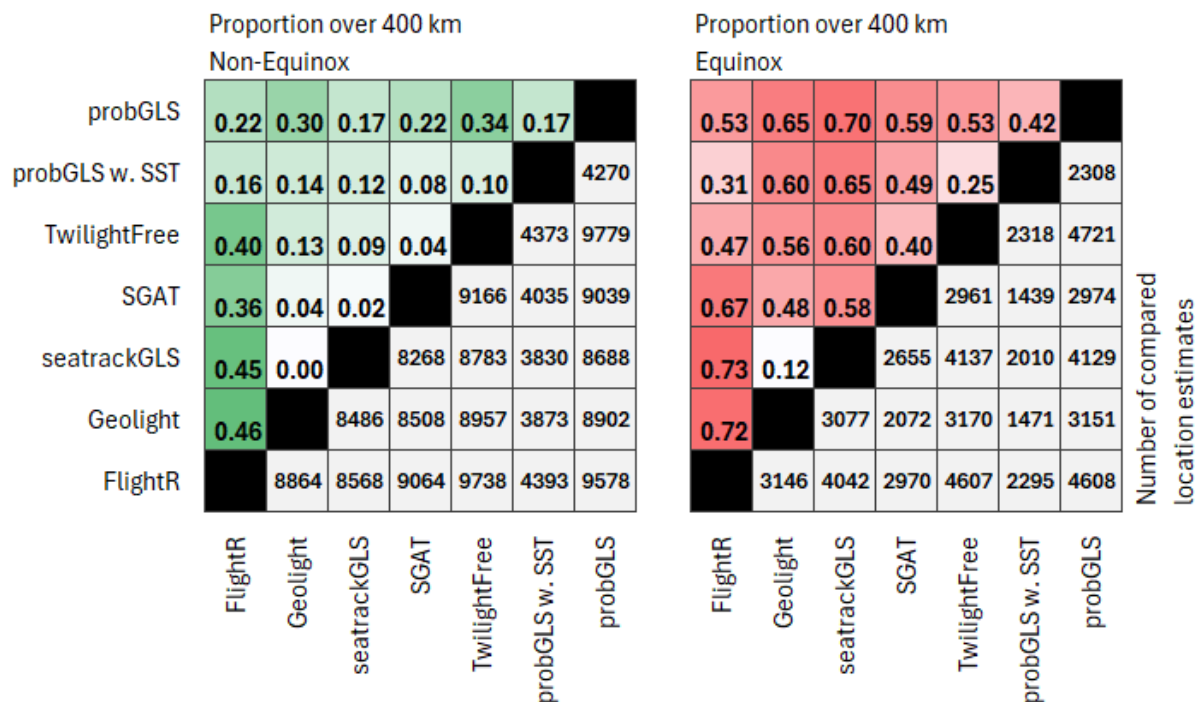


Figure 1.3: Matrices of the proportions of distance differences over 400 km for each method comparison for non-equinox (left panel) and equinox (right panel) locations, with color shading darker for larger proportions. The lower half of the matrices are the number of distances between location estimates included in each comparison outside of the equinox (out of a maximum of $n = 10182$, except $n = 4554$ for ‘probGLS with SST’ as it could only be run on tags with SST data) and during equinox (out of a maximum of $n = 4884$, except $n = 2489$ for ‘probGLS with SST’).

During equinox periods, location estimates were more dissimilar, compared to non-equinox periods (Fig. 1.2, Fig. 1.S4B). Even more than non-equinox, all MPDs for method comparisons during the equinox were driven by latitude differences (Fig. 1.S1B). The deterministic methods, ‘Geolight’ and ‘seatrackGLS’, were not expected to produce accurate equinox period location estimates, but this comparison still had the smallest MPDs because of their basis on the same algorithm (Fig. 1.2). Very few of the other comparisons were 200 km. Only 25% of the distances in the ‘TwilightFree’ – ‘probGLS’ comparison were over 400 km (Fig. 1.3), with the next most similar comparisons being ‘FlightR’ – ‘probGLS’, and then ‘SGAT’ – ‘TwilightFree’ in the same range (Fig. 1.2). The majority of the comparisons during equinox had MPDs between 400 – 800 km. BA values also indicated increased dissimilarity during the equinox, ranging as low as 0.11 (Fig. 1.4). The median BA of all except for two comparisons (‘seatrackGLS’-‘TwilightFree’ and ‘seatrackGLS’-‘Geolight’) was under 0.85, and 6 comparisons (mostly with ‘seatrackGLS’) had median BA values under 0.64 (Fig. 1.4).

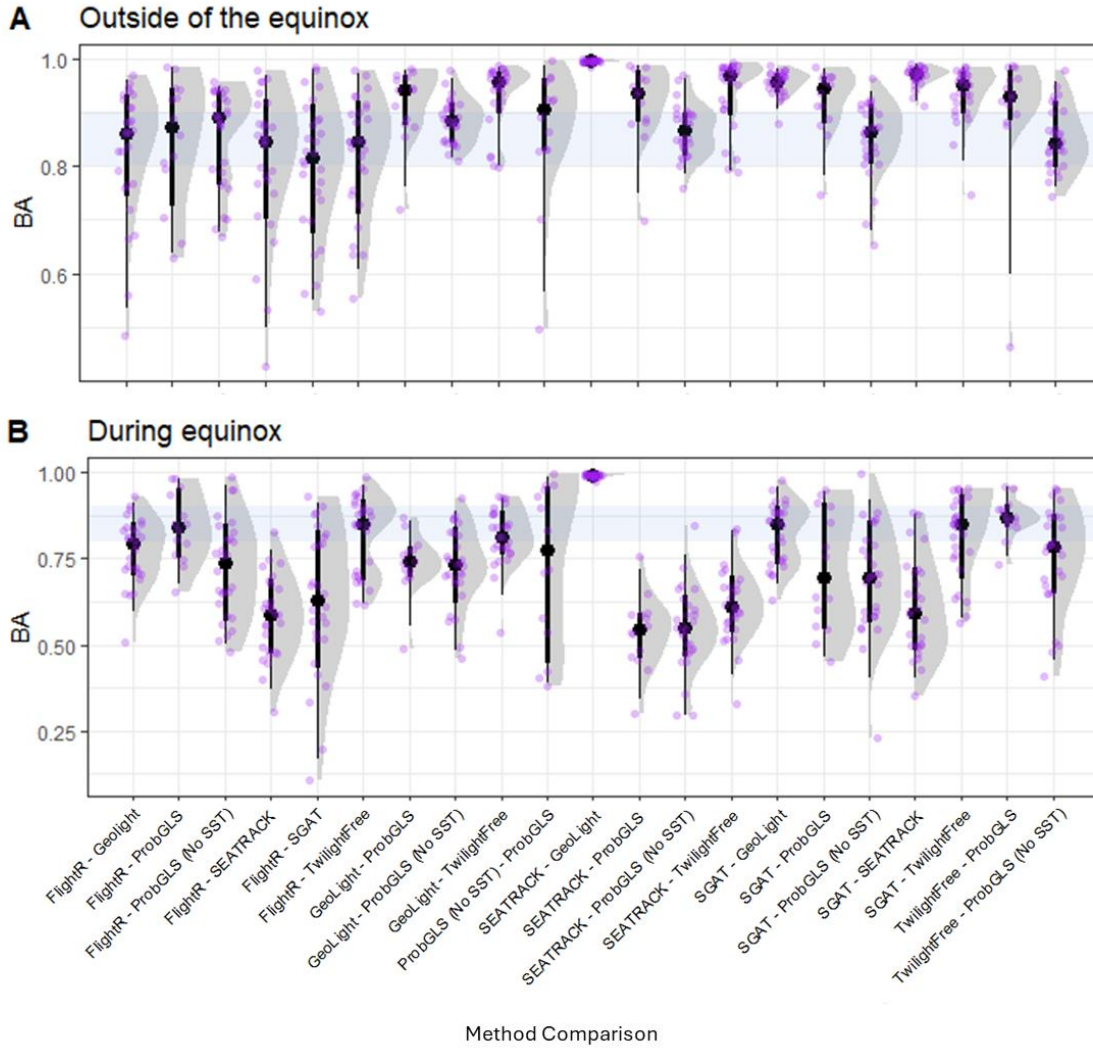


Figure 1.4: BA for each method comparison for locations during non-equinox periods (top panel) and during equinox periods (bottom panel). Note the different y-axis scale on graphs. The shaded area indicates BA values in the range of 0.80-0.90, shown to emphasize the difference in scale. Violin widths are scaled to maximum weight within each comparison.

Tag type impacted location estimates of non-equinox periods, more for some processing methods than others (Fig. 1.5). All except for 3 twilights were successfully detected during non-breeding, and about 93% of locations were estimated across methods for both tag types. ‘FlightR’ showed dramatically different within-method variation, indicated by comparing iterations, depending on tag type (Fig. 1.S5). Outside of the equinox, the median MPD from the Migrate Technology tags was 0 km, while the median MPD of the BioTrack tags was 55 km. This difference held during the equinox as well, with the Migrate Technology tag median MPD at 2 km, and a BioTrack tag median MPD of 102 km. When ‘FlightR’ was compared to other methods, all the largest MPD values were from BioTrack tags, and MPDs from Migrate Technology tags were mostly under 400 km (Fig. 1.5). As previously mentioned, including SST

data in ‘probGLS’ brought location estimates closer to the other methods (Fig. 1.2). This effect was less during equinox, when comparing to all methods except for ‘TwilightFree’ (Fig. 1.2B).

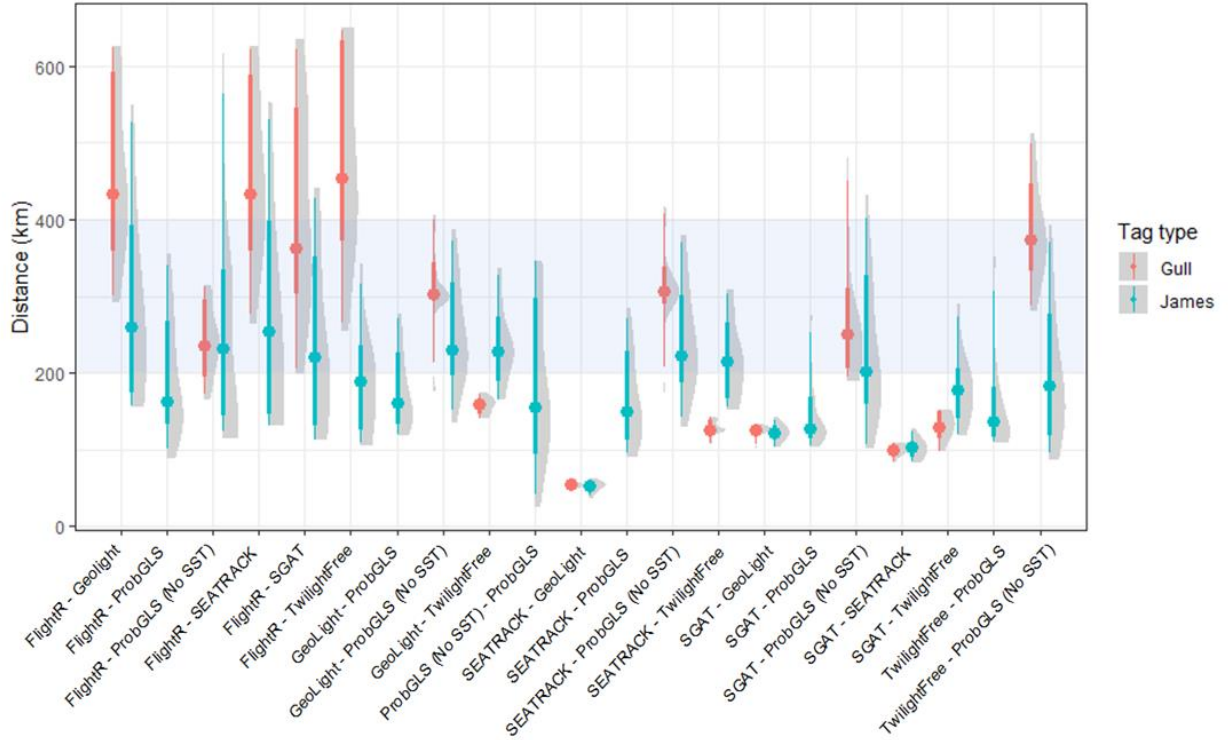


Figure 1.5: Median pairwise distances (MPD, in km) for each method comparison for BioTrack tags from Gull Island (red boxplots) and Migrate Technology tags from James Island (blue boxplots) during non-equinox periods. The BioTrack tags from Gull Island had lower resolution, clipped light values and no SST data were recorded, while the Migrate Technology tags from James Island had full resolution light values and SST data. Hence, the ‘probGLS’ method with SST could not be used on the BioTrack tag data from Gull Island.

Discussion

This study illustrated the difference in location estimates resulting from different GLS processing methods and GLS tag types on non-breeding Atlantic puffins, along with the baseline variation in location estimates across multiple model runs of the same data from stochastic GLS processing methods. We found low baseline variation within stochastic processing methods, and, although there were exceptions, most of the processing methods produced comparable location estimates (i.e., under the GLS error range) during non-equinox periods. ‘Geolight’ and ‘seatrackGLS’ produced nearly the same results for puffins at these latitudes. Although ‘seatrackGLS’ included additional filtering steps to remove or smooth outlier locations, EMD values were comparable to MPD values, suggesting that this filtering did not cause the two deterministic methods to give different results. This similarity is partly a result of our

standardization process, which led to both methods using the same twilights and solar angles in the same astronomical formula (Lisovski and Hahn 2012, Bråthen et al. 2021). Relatedly, the larger differences in location estimates from 'FlightR' relative to other methods were likely because the template-fit algorithm required different calibration information than the other methods (Rakhimberdiev et al. 2017). Location estimates from 'FlightR', however, were much more comparable to other methods when run on the un-clipped, high-resolution light data collected by the Migrate Technology tags relative to the truncated light data collected by the BioTrack tags. Similarly, location estimates produced from 'probGLS' were much more comparable to other methods when SST was incorporated. Unsurprisingly, location estimates were less consistent during equinox periods, suggesting that researchers should be cautious when comparing estimates of latitude from those times of the year (longitude similarities are expected to match non-equinox period results, Hill and Braun 2001). Based on these findings, we focus on outlining the advantages (e.g., lower differences in spatial location estimates between processing packages) and disadvantages (e.g., longer model run times) to help recommend processing packages for different research questions.

For researchers trying to choose which processing method to use, it is worth considering the data inputs and the time and effort commitments for each package (Table 1.1). 'Geolight' requires minimal upfront effort, and the run time (assuming the processing power of a standard business laptop) is very short (seconds/track). The effort to achieve biologically reasonable positions from this package occurs in pre- or post-processing, where filtering and smoothing can be as minimal or complex as the user chooses. Variation in post-processing decisions and effort, however, could make it more difficult to standardize among researchers and, thus, produce comparable location estimates. By standardizing the pre- and post-processing decisions, 'seatrackGLS' ensures that location estimates are comparable among researchers, and shares the rapid run time of 'Geolight'. Although 'TwilightFree' requires confidence in the solar angles used, its mid-range run times (5-10 min/track) allow the option of including an iterative process, where the model is run with increasingly smaller data sets, with potentially erroneous light data removed, until the results best match user-defined, biologically reasonable expectations. Thus, this method is a good option if a relatively quick run time is preferred, but it is also important to minimize discarding data. A possible disadvantage to 'TwilightFree' is the alpha (tag shading) and beta (movement probability) parameters (Bindoff et al. 2018), which are difficult to conceptualize and therefore determine whether they are being used in a biologically appropriate way. 'ProbGLS' does not require precise solar angle estimates (Merkel et al. 2016), and allows relatively easy incorporation of auxiliary data, such as immersion and temperature records (Lisovski et al. 2020). Setting movement parameters is also simple, although less straightforward for alcid, for whom flight speeds need to be reduced to compensate for times when the tag is dry but the bird is not in flight (e.g., leg-tucking, Buckingham et al. 2022, Runnells et al. 2024). Run time of 'probGLS' was around 20-30 minutes/track. The run times for 'FlightR' and 'SGAT' were much longer (~2 h/track), and parameters for these models are more difficult to conceptualize and require comfort with more advanced R scripting (Sumner et al. 2009, Rakhimberdiev et al. 2017, Lisovski et al. 2020).

Output from each of the methods also varies, thus processing method choice may depend on the information needed for specific research goals. Some of the methods produce latitude estimates during the equinox that are unreliable ('GeoLight', 'seatrackGLS'), although confidence in the estimates during equinox from the other methods may be unwarranted. If analyzing year-round migratory paths (e.g., Fayet et al. 2017b, Schaefer et al. 2022, Wong et al. 2022), researchers will want to use a method that provides equinox estimates but should acknowledge the increased uncertainty during that period (Lisovski et al. 2018), as birds more than 400 km apart could be in the same location, or the opposite. Environmental data, such as SST, can be integrated with 'probGLS', 'TwilightFree', and 'SGAT' or can be added in post-processing for any method, using the approach given in Teo et al. (2004) (e.g., Fifield et al. 2014). Including SST can help refine position estimates both during and outside of equinox periods (Sumner et al. 2009, Merkel et al. 2016, Bindoff et al. 2018) and, thus, choosing these methods would require careful selection among available tag types. Another consideration is the additional information available with some methods, which may be necessary or beneficial for addressing certain research questions. For instance, 'FlightR', 'probGLS', and 'SGAT' all provide some estimate of uncertainty around each position, which can be incorporated into subsequent analyses (e.g., as a buffer when mapping). 'SGAT' also provides information on model convergence, which can be used to filter by location estimate quality, as it was in this study (Table 1.1). For researchers interested in behavioral states (as in Matsuoka et al. 2025, Pavlinec et al. 2025), 'FlightR' provides estimates of migration status parameters (i.e., stationary/moving), as can 'GeoLight' with easy, additional post-processing, while 'probGLS' output includes summaries of any included auxiliary data (e.g., SST) associated with each time point, facilitating their inclusion in downstream modeling (e.g., habitat selection models). Overall, there are tradeoffs between time and effort versus output richness.

Given the above, our findings affect the interpretation of previous analyses and inform the appropriateness of combining previously processed data, allowing the proper use of existing data by managers. If researchers plan to use already processed data, the tag data used to produce the location estimates needs to be considered, as the geolocator tag type and settings selected determine what data were available and therefore impact appropriate processing method choice. Although most of the GLS processing methods produced comparable spatial location estimates in our analysis, archived, processed GLS data may not be comparable if the calibration and other parameters were not known, similar and/or standardized. Location estimates produced using 'probGLS' may only be reliably compared with location estimates from other methods if SST was included, although reduced solar angle variation could increase the similarity. 'FlightR', and location estimates produced using 'FlightR', are only a good option to use for tags which record the full light range, as the template-fit method is not effective otherwise (Rakhimberdiev et al. 2016, Lisovski et al. 2020). Our results also inform decisions about subsequent analyses. For instance, our Bhattacharyya's Affinity (BA) analysis indicated very similar kernel density estimates among methods outside of the equinox, but even the small observed differences in BA suggest that the same method should be used for all location estimates when comparing distributions with this type of analysis. When considering similarity of migratory paths (e.g., repeatability, consistency), if locations estimated on a grid (e.g., 'TwilightFree', 'FlightR') are compared with spatially continuous estimates (e.g., 'probGLS'), grid size must be factored into the calculations. Because large databases of archived, processed

GLS data exist (Strøm et al. 2021, Kays et al. 2022), our results facilitate the appropriate compilation and comparison of data from multiple sources for conservation and management purposes.

This study focused on a subset of data from one species with movement characteristics and distribution patterns that would limit the impact of confounding effects on our comparison, which leaves open many opportunities for building on this research. It would be interesting to determine how comparably different methods perform under conditions that make light-level geolocation more challenging. For instance, in areas where birds spend time in embayments or areas of the ocean that are surrounded by large land masses (e.g., North Sea: Harris et al. 2010, Gulf of St. Lawrence: Baran et al. 2022), the use of land masks can lead to obviously erroneous location estimates with many of the stochastic processing methods, when positions originally on land are forced to the nearest open water by the model. Additionally, no cases of very short or non-existent periods of daylight were experienced by these birds, nor did they travel close enough to the Equator for our location estimates to be based on nearly equal day and night length regardless of latitude for most of the non-breeding period. For researchers working in polar regions, ‘seatrackGLS’ includes an option for automatically generating position estimates under conditions when twilight periods are long and begin to merge, so this method would provide more positions in the Arctic or Antarctic close to the solstices. Finally, because of their high wing-loading, alcids generally move gradually instead of with rapid, long-distance movements (Dunn et al. 2020), so the issue of changes to apparent day/night duration resulting from longitudinal travel (i.e., zig-zagging latitude estimates) could not be considered in this study, and would likely decrease the similarity of ‘GeoLight’ and ‘seatrackGLS’ (Hill and Braun 2001, Bråthen et al. 2021). It is also possible that positions from the various methods would be more comparable if we had allowed adjustments to input parameters or extra polishing steps, but it would be difficult to standardize these extra steps across studies. For example, perhaps running additional iterations of ‘TwilightFree’ without subsets of bad data increases its’ similarity to other methods or maybe incorporating SST data into ‘TwilightFree’ and ‘SGAT’ models would pull their location estimates closer to those from ‘probGLS’. Future research could consider adding processing steps and information to understand how much they would influence location estimates.

Conclusion

Scientists who are just beginning geolocator projects need to carefully consider their choice of tag type and processing method to successfully meet their research objectives. Those undertaking conservation and management efforts (e.g., spatial planning) should be wary of combining already processed GLS data without considering calibration parameters, tag type, and processing method, along with how the data will be used in subsequent spatial analyses. Based on our findings, efforts might need to begin with reprocessing raw light data, which is in line with other recent studies that indicate how seemingly small differences in choices made by analysts can introduce impactful variation in results (Gould et al. 2024). Overall, we hope our findings aid researchers in deciding among available GLS data processing packages and will help appropriately combine location estimates from geolocators across studies to address a variety of ecological research questions and meet important conservation and management targets.

References

- Baran, M. A., S. W. Kress, P. Shannon, D. E. Lyons, H. L. Major, and A. W. Diamond. 2022. Overwinter movement of Atlantic puffins (*Fratercula arctica*) breeding in the Gulf of Maine: Inter- and intra-colony effects. *Waterbirds* 45:1–16.
- Bhattacharyya, A. 1943. On a measure of divergence between two statistical populations defined by their probability distribution. *Bulletin of the Calcutta Mathematical Society* 35:99–110.
- Bindoff, A. D., S. J. Wotherspoon, C. Guinet, and M. A. Hindell. 2018. Twilight-free geolocation from noisy light data. *Methods in Ecology and Evolution* 9:1190–1198.
- Bråthen, V. S., B. Moe, F. Amélineau, S. Descamps, M. Ekker, P. Fauchald, H. H. Helgason, M. K. Johanson, B. Merkel, A. Tarroux, J. Åstrøm, and H. Strøm. 2021. An automated procedure (v2.0) to obtain positions from light-level geolocators in large-scale tracking of seabirds - a method description for the SEATRACK project.
- Buckingham, L., M. Bogdanova, J. Green, R. Dunn, S. Wanless, S. Bennett, R. Bevan, A. Call, M. Canham, C. Corse, M. Harris, C. Heward, D. Jardine, J. Lennon, D. Parnaby, C. Redfern, L. Scott, R. Swann, R. Ward, E. Weston, R. Furness, and F. Daunt. 2022. Interspecific variation in non-breeding aggregation: A multi-colony tracking study of two sympatric seabirds. *Marine Ecology Progress Series* 684:181–197.
- Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.
<https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Delong, R. L., B. S. Stewart, and R. D. Hill. 1992. Documenting migrations of northern elephant seals using day length. *Marine Mammal Science* 8:155–159.
- Dunn, R. E., S. Wanless, F. Daunt, M. P. Harris, and J. A. Green. 2020. A year in the life of a North Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Scientific Reports* 10:5993.
- Ekstrom, P. A. 2004. An advance in geolocation by light. *Memoirs of the National Institute of Polar Research* 58:210–226.
- Fayet, A. L., R. Freeman, T. Anker-Nilssen, A. Diamond, K. E. Erikstad, D. Fifield, M. G. Fitzsimmons, E. S. Hansen, M. P. Harris, M. Jessopp, A. L. Kouwenberg, S. Kress, S. Mowat, C. M. Perrins, A. Petersen, I. K. Petersen, T. K. Reiertsen, G. J. Robertson, P. Shannon, I. A. Sigurðsson, A. Shoji, S. Wanless, and T. Guilford. 2017a. Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Current Biology* 27:3871–3878.e3.
- Fayet, A. L., A. Shoji, R. Freeman, C. M. Perrins, and T. Guilford. 2017b. Within-pair similarity in migration route and female winter foraging effort predict pair breeding performance in a monogamous seabird. *Marine Ecology Progress Series* 569:243–252.
- Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management* 69:1346–1359.
- Fifield, D. A., Montevecchi, W. A., Garthe, S., Robertson, G. J., Kubetzki, U., and Rail, J.-F.

2014. Migratory tactics and wintering areas of Northern Gannets (*Morus bassanus*) breeding in North America. *Ornith Monog* 79:1-63.)
- Franklin, K. A., K. Norris, J. A. Gill, N. Ratcliffe, A. S. Bonnet-Lebrun, S. J. Butler, N. C. Cole, C. G. Jones, S. Lisovski, K. Ruhomaun, V. Tatayah, and M. A. C. Nicoll. 2022. Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Movement Ecology* 10:1–14.
- Frederiksen, M., S. Descamps, K. E. Erikstad, A. J. Gaston, H. G. Gilchrist, D. Grémillet, K. L. Johansen, Y. Kolbeinsson, J. F. Linnebjerg, M. L. Mallory, L. A. McFarlane Tranquilla, F. R. Merkel, W. A. Montevecchi, A. Mosbech, T. K. Reiertsen, G. J. Robertson, H. Steen, H. Strøm, and T. L. Thórarinnsson. 2016. Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: Conservation implications. *Biological Conservation* 200:26–35.
- Gould, E., E. Sciences, H. S. Fraser, T. H. Parker, S. Nakagawa, P. A. Vesk, E. Sciences, F. Fidler, D. G. Hamilton, R. N. Abbey-lee, J. K. Abbo, L. A. Aguirre, C. Alcaraz, I. Aloni, D. Altschul, K. Arekar, J. Atkinson, C. M. Baker, M. Barre, S. K. Bello, S. Arabia, B. J. Berauer, and M. G. Bertram. 2024. Same data, different analysts : variation in effect sizes due to analytical decisions in ecology and evolutionary biology. *EcoEvoRxiv*:1–76.
- Halpin, L. R., J. D. Ross, R. Ramos, R. Mott, N. Carlile, N. Golding, J. M. Reyes-González, T. Militão, F. De Felipe, Z. Zajková, M. Cruz-Flores, S. Saldanha, V. Morera-Pujol, L. Navarro-Herrero, L. Zango, J. González-Solís, and R. H. Clarke. 2021. Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution* 12:2243–2255.
- Harris, M. P., F. Daunt, M. Newell, R. A. Phillips, and S. Wanless. 2010. Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Marine Biology* 157:827–836.
- Hill, R. D. 1994. Theory of geolocation by light levels. Pages 227–236 *Elephant Seals: Population Ecology, Behavior, and Physiology*.
- Hill, R.D. & Braun, M.J. (2001) Geolocation by light level – the next step: latitude. *Electronic Tagging and Tracking in Marine Fisheries* (ed. by J.R. Sibert and J. Nielsen), pp. 315–330. Kluwer Academic Publishers, Dordrecht, The Netherlands.)
- Jessopp, M. J., M. Cronin, T. K. Doyle, M. Wilson, A. McQuatters-Gollop, S. Newton, and R. A. Phillips. 2013. Transatlantic migration by post-breeding puffins: A strategy to exploit a temporarily abundant food resource? *Marine Biology* 160:2755–2762.
- St. John Glew, K., S. Wanless, M. P. Harris, F. Daunt, K. E. Erikstad, H. Strøm, and C. N. Trueman. 2018. Moulting location and diet of auks in the North Sea inferred from coupled light-based and isotope-based geolocation. *Marine Ecology Progress Series* 599:239–251.
- Joo, R., S. Picardi, M. E. Boone, T. A. Clay, S. C. Patrick, V. S. Romero-Romero, and M. Basille. 2020. A decade of movement ecology:1–17.
- Joo, R., S. Picardi, M. E. Boone, T. A. Clay, S. C. Patrick, V. S. Romero-Romero, and M. Basille. 2022. Recent trends in movement ecology of animals and human mobility. *Movement Ecology* 10:1–20.
- Kays, R., S. C. Davidson, M. Berger, G. Bohrer, W. Fiedler, A. Flack, J. Hirt, C. Hahn, D.

- Guggel, B. Russell, A. Kölzsch, A. Lohr, J. Partecke, M. Quetting, K. Safi, A. Scharf, G. Schneider, I. Lang, F. Schaeuffelhut, M. Landwehr, M. Storhas, L. van Schalkwyk, C. Vinciguerra, R. Weinzierl, and M. Wikelski. 2022. The Movebank system for studying global animal movement and demography. *Methods in Ecology and Evolution* 13:419–431.
- Kranstauber, B., M. Smolla, and K. Safi. 2017. Similarity in spatial utilization distributions measured by the earth mover's distance. *Methods in Ecology and Evolution* 8:155–160.
- Lisovski, S., S. Bauer, M. Briedis, S. C. Davidson, K. L. Dhanjal-Adams, M. T. Hallworth, J. Karagicheva, C. M. Meier, B. Merkel, J. Ouwehand, L. Pedersen, E. Rakhimberdiev, A. Roberto-Charron, N. E. Seavy, M. D. Sumner, C. M. Taylor, S. J. Wotherspoon, and E. S. Bridge. 2020. Light-level geolocator analyses: A user's guide. *Journal of Animal Ecology* 89:221–236.
- Lisovski, S., and S. Hahn. 2012. GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution* 3:1055–1059.
- Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn. 2012. Geolocation by light: Accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution* 3:603–612.
- Lisovski, S., H. Schmaljohann, E. S. Bridge, S. Bauer, A. Farnsworth, S. A. Gauthreaux, S. Hahn, M. T. Hallworth, C. M. Hewson, J. F. Kelly, F. Liechti, P. P. Marra, E. Rakhimberdiev, J. D. Ross, N. E. Seavy, M. D. Sumner, C. M. Taylor, D. W. Winkler, S. J. Wotherspoon, and M. B. Wunder. 2018. Inherent limits of light-level geolocation may lead to over-interpretation. *Current Biology* 28:R99–R100.
- Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* 11.
- Matsuoka, T. D., V. P. Patil, J. W. Hupp, A. G. Leach, J. A. Reed, J. S. Sedinger, and D. H. Ward. 2025. Shortening migration by 4500 km does not affect nesting phenology or increase nest success for black brant (*Branta bernicla nigricans*) breeding in Arctic and subarctic Alaska. *Movement Ecology* 13.
- McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* 130:211–222.
- Meeus, J. 1998. *Astronomical algorithms* by J. Meeus. Meeus. Richmond, VA: Willmann-Bell.
- Merkel, B., R. A. Phillips, S. Descamps, N. G. Yoccoz, B. Moe, and H. Strøm. 2016. A probabilistic algorithm to process geolocation data. *Movement Ecology* 4:26–37.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105:19052–19059.
- Pavlinec, Ž., S. Piro, A. Schmitz Ornés, L. Jurinović, D. Ćiković, V. Tutiš, and J. Kralj. 2025. Influence of ocean primary production on the activity pattern of wintering Common Terns. *Journal of Ornithology*.
- Phillips, R. A., J. R. D. Silk, J. P. Croxall, V. Afanasyev, and D. R. Briggs. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266:265–272.

- Rakhimberdiev, E., A. Saveliev, T. Piersma, and J. Karagicheva. 2017. FLIGHTR: an R package for reconstructing animal paths from solar geolocation loggers. *Methods in Ecology and Evolution* 8:1482–1487.
- Rakhimberdiev, E., N. R. Senner, M. A. Verhoeven, D. W. Winkler, W. Bouten, and T. Piersma. 2016. Comparing inferences of solar geolocation data against high-precision GPS data: annual movements of a double-tagged black-tailed godwit. *Journal of Avian Biology* 47:589–596.
- Reynolds, R. W., T. M. Smith, C. Liu, D. B. Chelton, K. S. Casey, and M. G. Schlax. 2007. Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate* 20:5473–5496.
- Runnells, E. S., W. A. Montevecchi, and G. K. Davoren. 2024. Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murrelets during the non-breeding season in the Northwest Atlantic. *Marine Ecology Progress Series* 739:241–256.
- Schaefer, A. L., K. B. Gorman, and M. A. Bishop. 2022. Light-level geolocation reveals the short-distance non-breeding movements and distribution of tufted puffins throughout the Northeast Pacific Ocean. *Frontiers in Marine Science* 9.
- Shaffer, S. A., Y. Tremblay, J. A. Awkerman, R. W. Henry, S. L. H. Teo, D. J. Anderson, D. A. Croll, B. A. Block, and D. P. Costa. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147:833–843.
- Shoji, A., S. Whelan, J. Cunningham, S. Hatch, Y. Niizuma, C. Nakajima, and K. Elliott. 2023. Ecological niche partitioning in two Pacific puffins. *Marine Ecology Progress Series* 709:125–139.
- Strøm, H., S. Descamps, M. Ekker, P. Fauchald, and B. Moe. 2021. Tracking the movements of North Atlantic seabirds: Steps towards a better understanding of population dynamics and marine ecosystem conservation. *Marine Ecology Progress Series* 676:97–116.
- Sumner, M. D., S. J. Wotherspoon, and M. A. Hindell. 2009. Bayesian Estimation of Animal Movement from Archival and Satellite Tags. *PLoS ONE* 4:19–22.
- Teo, S. L. H., A. Boustany, S. Blackwell, A. Walli, K. C. Weng, and B. A. Block. 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Marine Ecology Progress Series* 283:81–98.
- Thums, M., L. C. Ferreira, A. Davenport, M. Jenner, L. Möller, G. Russell, R. D. McCauley, and C. Jenner. 2025. Tracking pygmy blue whale diving behaviour and validation of foraging areas defined from horizontal movement data. *Global Ecology and Conservation* 57.
- Walli, A., S. L. H. Teo, A. Boustany, C. J. Farwell, T. Williams, H. Dewar, E. Prince, and B. A. Block. 2009. Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS ONE* 4.
- Wilmers, C. C., B. Nickel, C. M. Bryce, J. A. Smith, R. E. Wheat, and V. Yovovich. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96:1741–1753.
- Wilson, R. P., K. Hustler, P. G. Ryan, A. E. Burger, and E. C. Noldeke. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *American Naturalist* 140:179–

200.

- Wilson R.P., J-J. Ducamp, G. Rees, B.M. Culik & K. Ber. Niedersachsen 23 : 90-98. Niekamp 1992. Estimation of location: Global coverage using light intensity. In: Priede, I.M. & S.M. Swift (eds) Wildlife Telemetry : 131-134 . Ellis Horwood, Chichester.
- Wong, J. B., S. Lisovski, R. T. Alisauskas, W. English, A. L. Harrison, D. K. Kellett, M. Maftai, A. Nagy-MacArthur, R. A. Ronconi, P. A. Smith, M. L. Mallory, and M. Auger-Méthé. 2022. Variation in migration behaviors used by Arctic Terns (*Sterna paradisaea*) breeding across a wide latitudinal gradient. *Polar Biology* 45:909–922.

Supplementary figures:

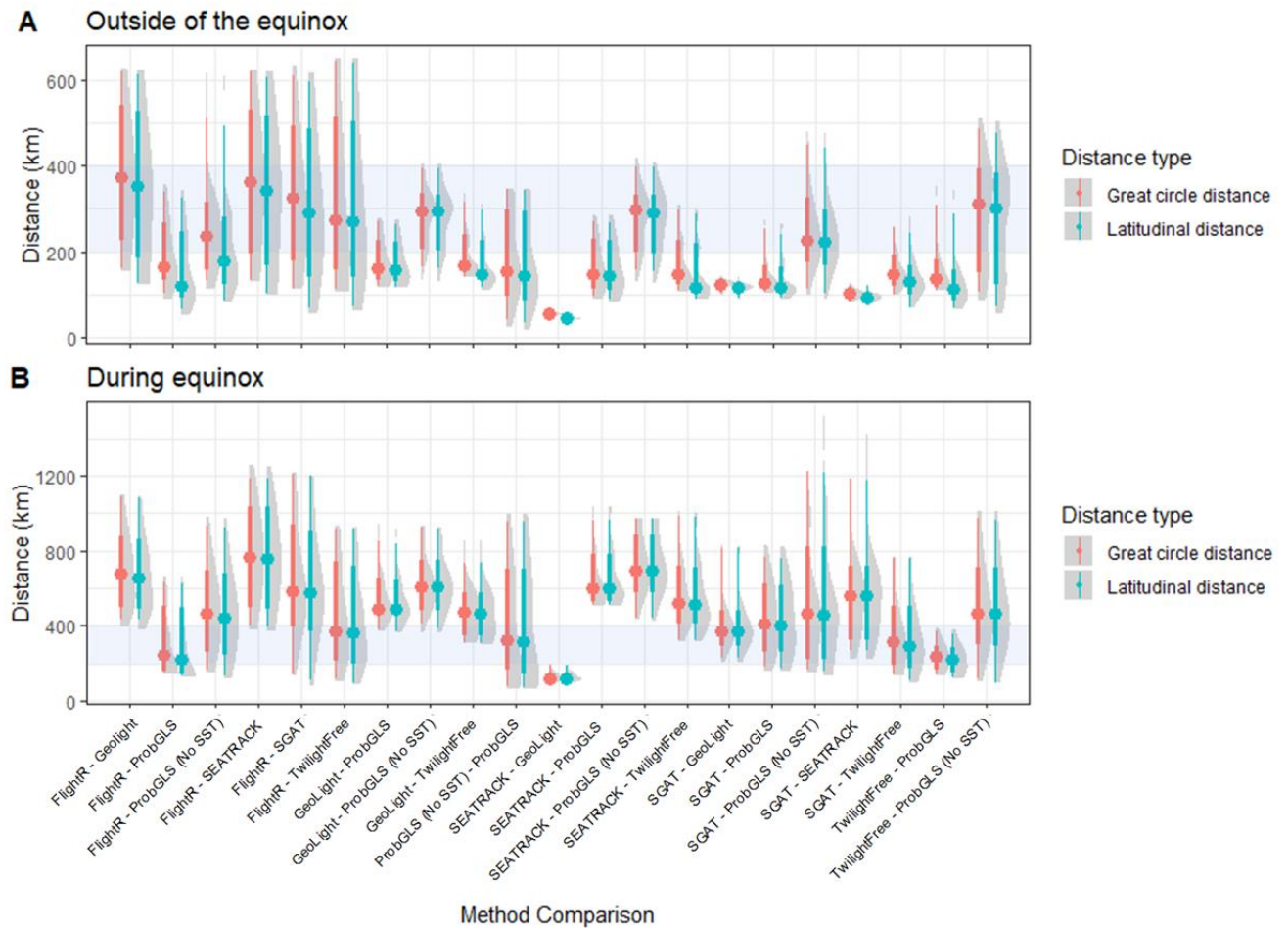


Figure 1.S1: Median pairwise distances (MPD, in km) of great-circle distance and latitudinal distance, for each method comparison for locations during non-equinox periods (A) and during equinox periods (B). Note different y-axis scales. The shaded area indicates 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.

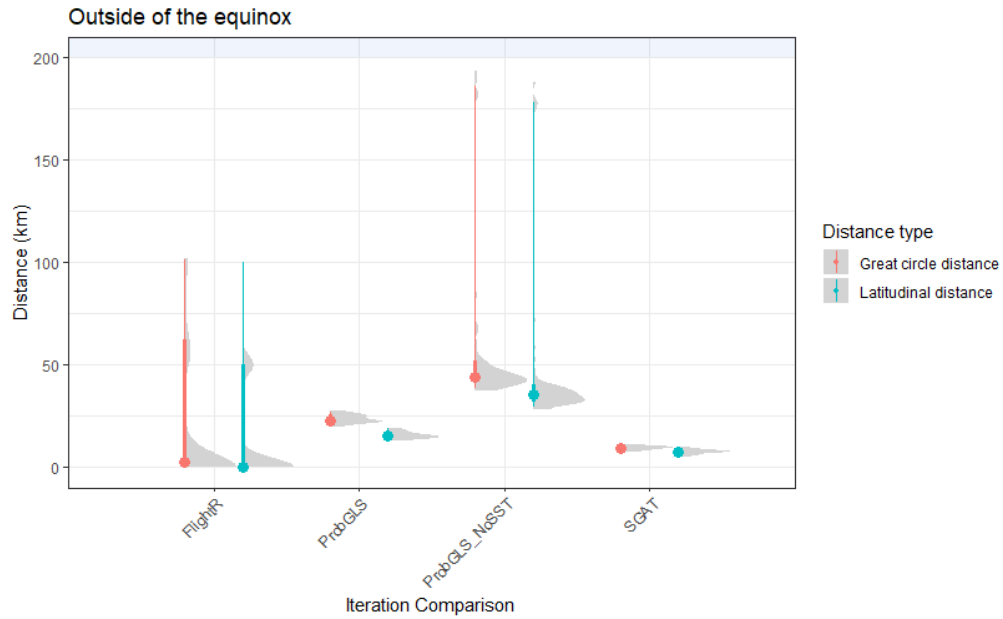


Figure 1.S2: Median pairwise distances (MPD, in km) of great-circle distance and latitudinal distance, for each method comparison for locations during non-equinox periods. The shaded area indicates 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.

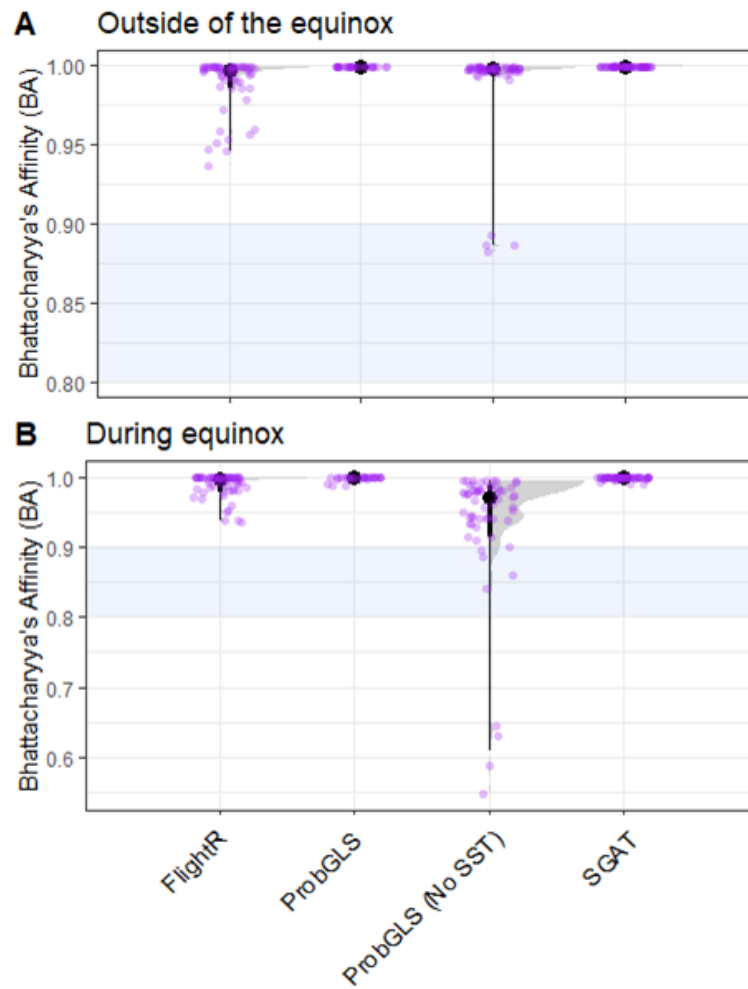


Figure 1.S3: Bhattacharyya's Affinity (BA) among iterations of stochastic methods for locations during non-equinox periods (A) and during equinox periods (B). The shaded area indicates BA values of 0.80-0.90. Note the different y-axis scale on graphs.

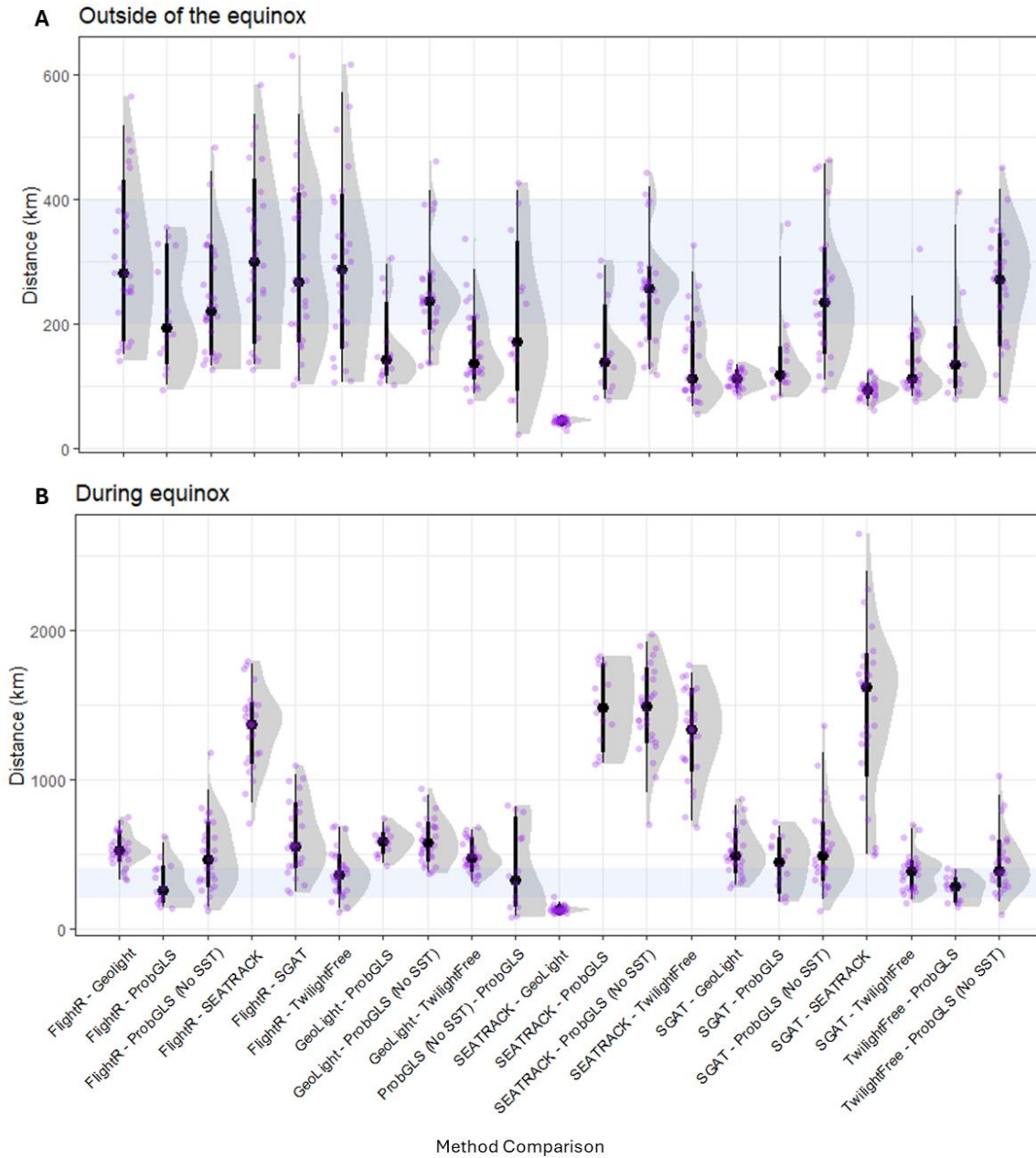


Figure 1.S4: Earth Mover's Distance (EMD, in km) for each method comparison for locations during non-equinox periods (A) and during equinox periods (B). The large distances to 'seatrackGLS' during equinox are because positions outside the boundary box were included. Note different y-axis scales. The shaded area indicates 200-400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.

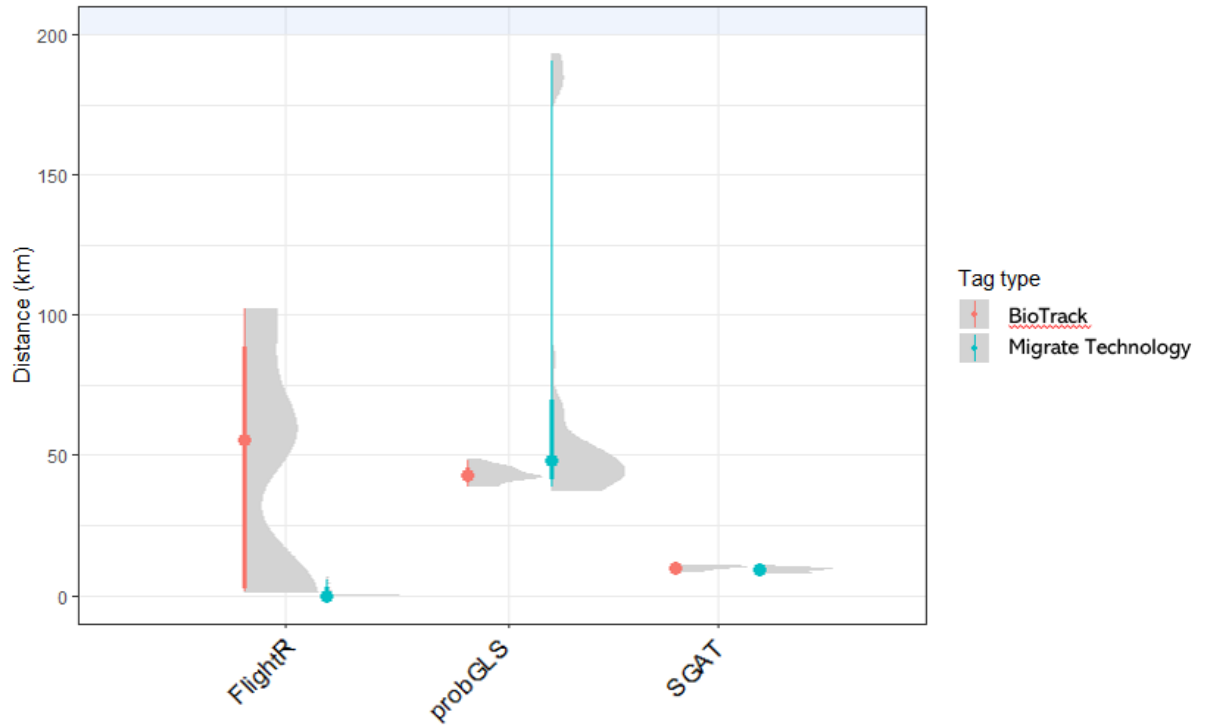


Figure 1.S5: Median pairwise distances (MPD, in km) among iterations of stochastic methods for BioTrack tags from Gull Island (red boxplots) and Migrate Technology tags from James Island (blue boxplots) during non-equinox periods. The BioTrack tags from Gull Island had a reduced range of light values and no SST data were recorded, while the Migrate Technology tags from James Island had full range light values and SST data. Hence, the ‘probGLS’ method with SST could not be used on the BioTrack tag data from Gull Island. The shaded area indicates the lower end of 200–400 km, typical geolocator accuracy range. Half-violin widths are scaled to maximum weight within each comparison.

Link between Chapters 1 & 2

Our understanding of the non-breeding distributions of north Atlantic seabirds has greatly expanded following the development of small geolocators (GLS) in the 21st century. GLS data have limitations, and a variety of processing methods have been developed for maximizing the accuracy of location estimates from these loggers. As GLS-based movement ecology continues to advance, it is important to evaluate the impact of processing method choices on our research results.

In Chapter 1, I determined that most GLS data processing methods produced comparable results when tracking Atlantic puffins, if data inputs were standardized. I also found extremely low baseline variation within stochastic processing methods, such as ‘probGLS’. Interestingly, even comparable location estimates affected the interpretation of an analysis of kernel density distribution similarity. Therefore, in Chapter 2, my kernel density overlap analysis was based on positions all estimated by the same GLS processing method, ‘probGLS’. Additionally, to ensure data input standardization, I re-processed Atlantic puffin GLS data from four colonies using ‘probGLS’ for the location estimates underlying the migratory connectivity analysis in Chapter 3.

Chapter 2: Spatiotemporal and isotopic niche overlap among Atlantic Puffins, Razorbills, and Common Murres during the non-breeding season in the Northwest Atlantic

Emily S. Runnells¹, William A. Montevecchi², and Gail K. Davoren¹

¹Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

²Memorial University of Newfoundland and Labrador, St. John's, NL, A1C 5S7, Canada

Published in Marine Ecology Progress Series:

Runnells, E. S., W. A. Montevecchi, and G. K. Davoren. 2024. Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murres during the non-breeding season in the Northwest Atlantic. Marine Ecology Progress Series 739:241–256.
<https://doi.org/10.3354/meps14614>

[*Return to table of contents*](#)

Abstract

Little is known about the spatial and dietary overlap of seabird species during the non-breeding season, when scarce and patchy marine food resources could lead to interspecific competition. We aimed to quantify spatiotemporal and isotopic niche overlap among common murres (*Uria aalge*), razorbills (*Alca torda*), and Atlantic puffins (*Fratercula arctica*) outside the breeding season by combining data from geolocators and stable isotope ratios ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) of belly, secondary, and head feathers collected in 2017-2020 from birds breeding in coastal northeastern Newfoundland, Canada. Seasonal utilization distributions of each species indicated generally low spatial overlap during most of the non-breeding period, with exceptions immediately post-breeding and with variability in movement paths among puffins. Stable isotope analysis revealed a broader isotopic niche (1.5-3 $\times$) for puffins than other species, matching their greater spatial variation. There was no isotopic niche overlap among the three species, except during flight feather molt of razorbills and murres. Individual puffins located in the same area as razorbills or murres had lower $\delta^{15}\text{N}$ values, suggesting a lower trophic position. The minimal overlap of these three alcid species during an understudied phase of their annual cycle suggests that they segregate spatially and partition resources, implying that different spatial planning and ecosystem conservation strategies should be applied to each of these three species.

Key words: Seabird – Interspecific Competition – Distribution – Stable Isotope – Geocator – North Atlantic – Alcid

Introduction

The patchy prey distribution in the ocean brings foraging seabirds together in areas of higher prey density (Hunt et al. 1999). If prey resources are not limited in these patches, species could co-occur without detriment to foraging success, and facilitative interactions could even enhance prey capture rates (e.g., Harrison et al. 1991, Silverman et al. 2004). Alternately, co-occurring species may compete if shared prey resources are limited at these patches when foraging tactics overlap in space and time (Lack 1944). These circumstances create the opportunity for interspecific interactions and the evolution of niche partitioning. Sympatric seabird species have many ways to minimize competition for limited prey resources through niche differentiation, including spatial segregation (McFarlane Tranquilla et al. 2015), foraging depth differences (Ballance et al. 1997), prey specialization (Mancini et al. 2014), and phenological differences (Navarro et al. 2013).

When breeding seabirds are concentrated in space and time at multi-species colonies there is ample opportunity for competition (Ashmole 1963), but species interactions are also possible during low productivity winter periods in the patchy ocean environment (May & MacArthur 1972, Hutchinson 1978; see also Haury et al. 1978). There is a higher potential for competition among seabird species if they forage in the same prey-limited patches on similar prey types during the winter than if seabird species are not in the same location and foraging on dissimilar prey types.

Niche overlap may be more likely between closely related species that obtain prey in a similar manner, as their shared ancestor evolved while relying on a comparable pool of resources (Wiens and Graham 2005). Atlantic puffins (*Fratercula arctica*), razorbills (*Alca torda*), and common murres (*Uria aalge*) are wing-propelled pursuit diving Alcidae that are characterized by stout body shape and high wing loading (body mass/wing area; Gaston & Jones 1998). All three species breed sympatrically across the North Atlantic during the boreal summer, where they forage predominantly on locally abundant, small forage fish (e.g., Barrett & Furness 1990, Scopel et al. 2019, Jenkins & Davoren 2020). Common murres (hereafter, sometimes, “murres”) are the largest and heaviest of the three and can dive the deepest (maximum 180 m; Piatt & Nettleship 1985) and longest (41–212 s; Wanless et al. 1988, Hedd et al. 2009, Ainley et al. 2020). Razorbills are of intermediate size and dive capabilities (140 m, 19–49 s; Wanless et al. 1988, Lavers et al. 2020), while Atlantic puffins (hereafter, sometimes, “puffins”) are the smallest of the three with the shallowest maximum dive depths (68 m) and shortest dive duration (20–30 s; Wanless et al. 1988, Lowther et al. 2020). This size variation can lead to spatial partitioning of prey resources during the breeding season, perhaps because larger body size might impart a competitive advantage and ability to exploit the highest quality prey patches while excluding similar smaller bodied birds (Piatt 1990, Wanless et al. 1990, Linnebjerg et al. 2013). Spatial and diet segregation among the three alcids has been observed within foraging ranges of colonies during breeding, but both spatial and dietary overlap increase when and where prey is abundant (Wanless et al. 1990, Pratte et al. 2017, Jenkins & Davoren 2020, Lescure 2021, Petalas et al. 2021). Pre- and post-breeding, sympatric alcids are more spatially dispersed; however, there is evidence of high dietary similarity (Linnebjerg et al. 2013). Increased spatial segregation during non-breeding may allow these alcids to feed on similar prey types, but it is also possible that both spatial and dietary overlap remain high.

Tracking technology has increased understanding of the non-breeding movement patterns of Northwest Atlantic alcids (e.g., McFarlane Tranquilla et al. 2013, Burke et al. 2015, Baran et al. 2022). During non-breeding, Atlantic puffins are thought to disperse widely and gradually move off the continental shelf (Hedd et al. 2010, Fayet et al. 2017, Lowther et al. 2020).

Newfoundland common murres do not appear to disperse far from breeding colonies (McFarlane Tranquilla et al. 2013, Burke & Montevecchi 2018, Ainley et al. 2020), while Newfoundland razorbills stay near the coast or in shallow areas (Lavers et al. 2020). Male razorbills and murres are limited to areas near swimming-distance from colonies during the fall molt, when they are flightless and attending flightless, post-fledging offspring. The distribution and movements of all three species may depend strongly on environmental conditions (Oedekoven et al. 2001, Veit & Manne 2015, Diamond et al. 2020), and prey predictability (Skov et al. 2000), and may also be influenced by other species' density and distribution patterns. As only a few studies have examined species-specific seasonal variation in distributional patterns in a multi-species context (e.g., Buckingham et al. 2022), spatial overlap among species during the non-breeding season remains unclear.

Although overlap in alcid diet is difficult to assess during non-breeding, when they are not accessible at colonies, Atlantic puffin, razorbill, and common murre winter diets have been studied in a few parts of their range. Winter stomach contents from all three species include both fish (e.g., capelin, herring) and invertebrates (e.g., euphausiids, squid) of various types and proportions depending on location. Most studies found that common murres consume a higher proportion of fish in the winter than the other two species (Ainley et al. 1996, Rowe et al. 2000), and Atlantic puffins often consume a higher proportion of invertebrates (Falk et al. 1992, Hedd et al. 2010, Harris et al. 2015) although species-specific diets vary among regions (Blake 1984, Huettman et al. 2005). Stable isotope analysis of feathers can provide insight into non-breeding diet (Karnovsky et al. 2012), with $\delta^{15}\text{N}$ generally indicating prey trophic levels and $\delta^{13}\text{C}$ generally indicating spatially varying ecosystem baselines (Hobson et al. 1994, Bond & Jones 2009, Shipley & Matich 2020). Although there are shared prey species among the three alcids, different proportions of higher and lower trophic level prey consumed during feather growth will be reflected in the isotopic niche. Recent research using feather stable isotope analysis in the North Sea showed that the three alcids have different diets during fall, winter, and spring, suggesting that trophic segregation coupled with spatiotemporal differences could reduce interspecific competition (St. John Glew et al. 2018).

Our objective was to determine the spatiotemporal and isotopic niche overlap during the non-breeding season among Atlantic puffins, razorbills, and common murres that breed sympatrically in the Northwest Atlantic. Based on previous single-species studies in this region (e.g., Hedd et al. 2012, Burke & Montevecchi 2018), we hypothesize that non-breeding alcid species will vary in their spatial and isotopic niche during different seasonal stages of the non-breeding season. We predict some shared space-use among the three species occurring during initial dispersal in the fall and return to the breeding colony during spring, but generally low spatial overlap of species-specific core use areas during the remainder of the non-breeding period. Specifically, we predict razorbills will be distributed closer to the coast, puffins mostly off the continental shelf and murres on the Grand Banks. Isotopic niche overlap among the species is expected to be minimal, especially when spatial overlap is high.

Methods

2.1 Tag deployment and feather sampling

Logger deployment and feather sampling took place during the breeding season on two colonies on the northeastern Newfoundland coast (Fig. 2.1): James Island (49.58° , -53.78°), where razorbills ($\sim 3,000$ pairs) and Atlantic puffins ($\sim 16,000$ pairs) breed sympatrically (Jenkins et al. 2018), and, 47 km to the east-northeast, Funk Island (49.76° , -53.18°), the largest breeding colony of common murres in the Atlantic ($\sim 470,000$ pairs; Wilhelm et al. 2015, Ainley et al. 2020). On James Island, puffins and razorbills were hand captured from burrows or nest crevices after hatching and predominantly between midnight and sunrise to reduce disturbance. On Funk Island, breeding murres were captured with telescopic noose poles at breeding sites or nets on long poles while returning to breeding sites during daylight. We measured tarsus length (mm), wing chord (mm), and body mass (g) of each individual. Fieldwork was conducted in accordance with the Canadian Council on Animal Care (University of Manitoba Protocol F16-017/1/2/3, F20-017/1; Memorial University of Newfoundland 19-01-WM) and Canadian Bird Banding Office (Banding Permits 10873 and 10332).

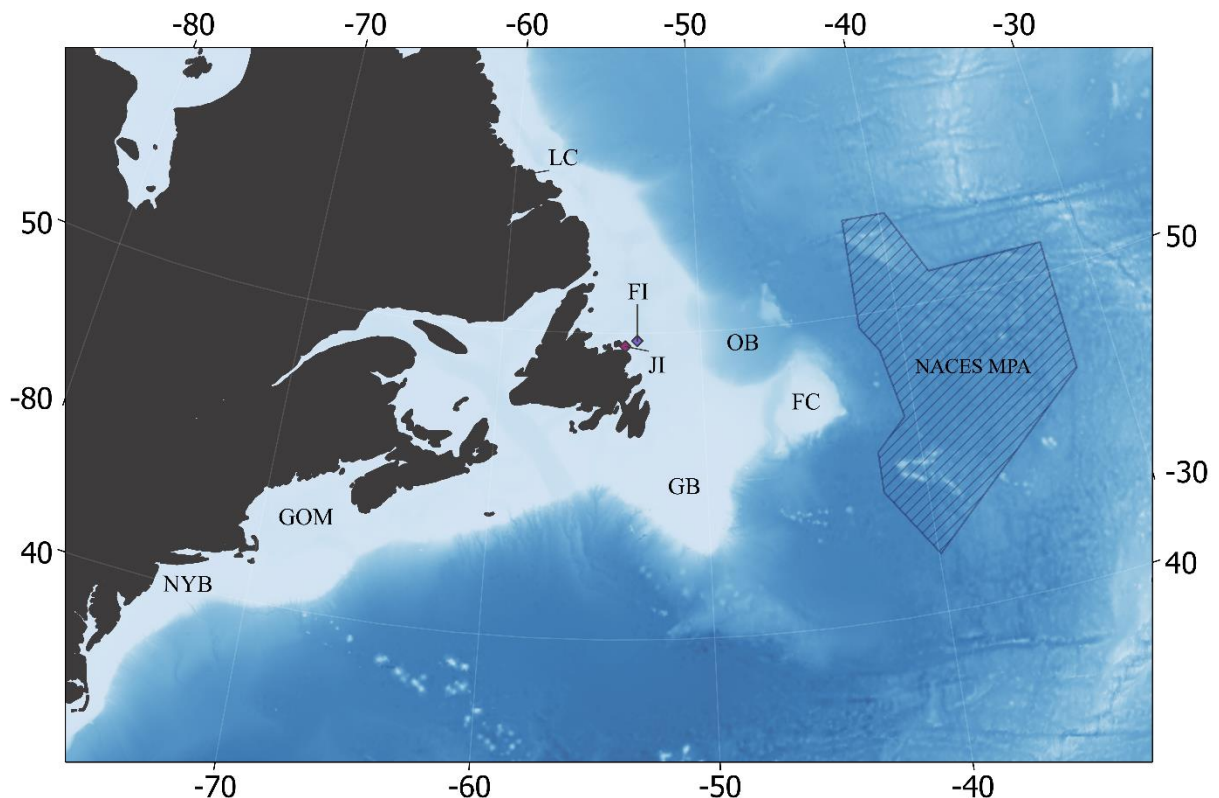


Figure 2.1: Bathymetric map of the study area in the northwest Atlantic, indicating the breeding colonies of Funk Island (FI, blue diamond) and James Island (JI, purple diamond) off the

northeastern Newfoundland coast, along with other referenced oceanographic and political locations: The New York Bight (NYB), Gulf of Maine (GOM), Labrador Coast (LC), Grand Banks (GB), Orphan Basin (OB), Flemish Cap (FC), and North Atlantic Current and Evlanov Sea OSPAR MPA (NACES MPA). Depth information is from Blue Earth Bathymetry, a GEBCO (<https://www.gebco.net>) derived product, the MPA boundaries are provided by OSPAR (<https://www.ospar.org>), and the land boundaries are from Natural Earth (<https://www.naturalearthdata.com>).

During 2019 and 2020, we deployed 10–25 light-level geolocators per species per year with immersion switches and temperature loggers (Migrate Technology C330 and C65+ on razorbills and puffins, Biotrack MK3006 on murres; see Table 2.1). The geolocators were attached to plastic leg bands with cable ties for year-round deployments and retrieval the following breeding season. Most loggers and bands were < 1% of birds' weight at the time of attachment (except 4 puffins were < 1.25%), minimizing potential for device effects during long-term deployment (Bodey et al. 2018, Geen et al. 2019). To examine possible device effects, we compared the mass:wing chord ratios of birds upon deployment and upon retrieval (as in Baran et al. 2022) and found individual body condition did not differ (Paired t-test: $t = 2.04$, $df = 30$, $p = 0.56$). Low recapture rates of common murres (Table 2.1) were primarily due to murres breeding on flat rock (in contrast with the crevice- and burrow-nesting puffin and razorbill) and, thus, flushing upon researcher approach. Slightly different data were collected and recorded by the two brands of geolocators. The Biotrack MK 3006 loggers, deployed as part of the SEATRACK project (Strøm et al. 2021), measured light intensity every 60 s and recorded the maximum of these light intensity values every 10 min, along with salt water immersion status every 3 s and recorded counts of 'wet' samples every 10 min. Temperature (°C) also was measured every 4 h, when two samples were taken and recorded 20 min apart, after the logger has been continually immersed for 20 min. Both Migrate Technology models measured light intensity every 60 s and recorded the maximum of these light intensity values every 5 min, along with immersion status every 30 s and recorded counts of 'wet' status every 10 min. When the tags were immersed continuously for 20 min, temperature (°C) was measured once, and the maximum, minimum, and mean temperature every 8 h were recorded. Before deployment of the Migrate Technology geolocators, we performed a 3–8-day rooftop light-level calibration. Upon retrieval, we also conducted a simulated in situ light-level calibration where the geolocators were suspended below a plastic common murre decoy at the depth of the foot and moored at known coordinates for 5–8 days.

Table 2.1: Summary of deployments of light-level geolocators on Atlantic puffins (ATPU), razorbills (RAZO), and common murres (COMU) during 2019 and 2020, including the number of Migrate Technology C330 and C65+ and Biotrack MK3006 model geolocators used in each year for each species, the number of geolocators retrieved in each year (2020 and 2021), the overall retrieval rate during this project, and summarized arrival and departure dates.

Species	Quantity and models deployed		Quantity retrieved		Retrieval rate	Median (range) dates of non-breeding period boundaries	
	2019	2020	2020	2021		Departure	Arrival
ATPU	10 C330	15 C65+	3	11	0.56	9/6 (8/28 – 9/13)	5/13 (5/8 – 5/26)
RAZO	10 C330	15 C330	5	8	0.52	8/13 (8/2 – 9/14)	5/12 (5/5 – 5/31)
COMU	25 MK3006	25 MK3006	3	5	0.16	8/12*	5/6 (5/3 – 7/02)

*The geolocators deployed on murres were programmed to start recording between late July – mid August, so all murre departure dates were set to August 12, a reasonable estimate for when many individuals have left the colony based on the typical breeding schedule.

Samples of head (3–5 feathers) and first secondary (2 cm² snips) feathers were collected to quantify stable isotope ratios of carbon and nitrogen from 20 untagged chick-rearing individuals per species per year during 2017–2019. In 2020, fewer birds were sampled (17 puffins and murres, 14 razorbills) and belly feathers (3–5 feathers) were also collected. These birds were captured on the colony typically on one day each year. Head, first secondary, and belly feather samples were also collected from birds with geolocators upon recapture, with the exception of a secondary from one puffin in 2020 and head feathers from another in 2021. Reported molt schedules of these alcid species vary (Harris and Yule 1977, Thompson et al. 1998, Pyle 2009, Glew et al. 2018, Lowther et al. 2020), though a commonality is that they are timed relative to the regional breeding season. Adjusting that relative annual molt timing based on the breeding schedule on the northeastern Newfoundland coast, we estimated murre and razorbill secondaries were molted during September–November and all three species molt head feathers during March–May. The timing of puffin secondary feather molt, however, may be highly variable (Harris & Yule 1977, Howell & Pyle 2005, Darby et al. 2022). Belly feather molt timing of all three species is also uncertain, with a fall molt potentially supplemented by additional body feather replacement later in the non-breeding season.

2.2 Spatial analysis

Arrival and departure dates from the colony for puffins and razorbills were determined based on the first or last day during an appropriate seasonal window (razorbills: Jun 15–Sep 1 & May 15–Jun 15; puffins: Aug 30–Sep 12 & Apr 15–Jun 15) when daytime light measurements dropped below a species-specific threshold, indicating burrow or nest crevice attendance. As the geolocators deployed on murres were programmed to start recording between late July – mid August, all murre departure dates were set to August 12. This date is a reasonable estimate for when many individuals have left the colony based on the typical breeding schedule. Murre

arrival dates were set as the first time during an appropriate seasonal window (May 1–Jun 15) that the immersion sensor was dry for 6 h continuously during daylight, suggesting dedicated colony attendance, as long flights are unlikely in this and other alcid species (Elliott & Gaston 2014, Dunn et al. 2020). Murres in Newfoundland are not known to visit the colony during non-breeding, as they do in other regions (e.g., Bennett et al. 2022), thus this 6 h “dry” threshold for murres avoids excluding data before the likely onset of incubation.

Geolocator data processing followed commonly used methods (Lisovski et al. 2012) in R version 4.0.3 (R Core Team 2020). Twilights were detected and extracted from the non-breeding, logged light data with ‘TwGeos’ (Lisovski et al. 2016) using a visually confirmed light threshold of 0.9. Location estimates were determined using ‘ProbGLS’ (Merkel et al. 2016), by incorporating light, immersion, and temperature data into a probabilistic model, which estimated 2000 possible locations based on each twilight time, and weighted those locations by possible flight distances, based on the immersion data, species-specific flight speeds and environmental characteristics. Combining these data, 100 iterations were then computed of the most likely movement paths, and the geographic median track for each individual was reported. The flight speeds used were based on estimates by Pennycuick (1987), adjusted to be more conservative (Buckingham et al. 2022), given that the activity data are based on immersion sensors, which register as dry when alcids sitting on the water’s surface are leg tucking, a more common occurrence than long flights in alcids (Dunn et al. 2020). Environmental variables included land cover, ice cover, and sea surface temperature (SST) obtained from the NOAA High-resolution Blended Analysis of Daily SST and Ice, a 0.25 degree resolution interpolation of observations from different platforms (Reynolds et al. 2007). We set a range of solar angles as input parameters (-6 to -3) based on values calculated with ‘GeoLight’ (Lisovski & Hahn 2012) using data from the two calibration methods. A list of all input parameters is in Table 2.A1 in the Appendix.

Spatial data (i.e., GLS location estimates) were projected in a Lambert Azimuthal Equal Area centered on James Island. Bivariate normal kernel density of core (50%) utilization distributions were calculated for each species in successive 2-month periods (Aug–Sep, Oct–Nov, Dec–Jan, Feb–Mar, Apr–May) with ‘adehabitatHR’ 0.4.19 (Calenge 2006). Smoothing factors for all periods and all species were set to a bandwidth of 150 km, based on reasonable assumptions about geolocator spatial precision (186 ± 114 km: Phillips et al. 2004; 304 ± 413 km: Halpin et al. 2021), with an extent of 1 and grid cell size of 25 km, approximately the same resolution as the environmental data supporting the location estimates. Pairwise comparisons of the spatial overlap between species within each 2-month period were quantified with the utilization distribution overlap index (UDOI) of the 50% kernels (Fieberg & Kochanny 2005). The UDOI represents niche overlap and shared space use because the concentration of occurrences within the kernels is considered together with the overlap of the kernels. For 50% kernel density estimates, a UDOI of 0 indicates no overlap, while a UDOI of 0.25 indicates a complete overlap and uniform distribution of occurrences throughout. UDOI values are often between 0 and 0.25, indicating that even where kernels overlap, species occurrences are not concentrated in the same places; however, UDOI values > 0.25 could result from varying overlap of kernels but high overlap of concentrated occurrences of two species within the kernels (Fieberg & Kochanny 2005). Although there was some variation in UDOI depending on grid cell

size, the relative amount of overlap among species pairs remained the same (Table 2.A2 in the Appendix).

2.3 Stable isotope analysis

Feathers were cleaned of dirt and oils by rinsing twice with 0.25 M sodium hydroxide (NaOH) solution for 30 s, followed by rinsing twice with distilled water for 30 s (Bearhop et al. 2002). All feather samples ($n = 609$) were dried in uncapped glass scintillation vials in a warm oven for a minimum of 2 h, or in a room-temperature sheltered space with low humidity for a minimum of 48 h. Samples were sent to the GLIER Stable Isotopes Lab at the University of Windsor, where they were homogenized, and sub-samples of 0.7-1 mg were analyzed with a continuous-flow isotope ratio mass-spectrometer (Thermo Delta V) to quantify stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). The measured ratios of sample values relative to the ratios of universal standards (Vienna Pee Dee Belemnite for carbon, and atmospheric N_2 for nitrogen) are presented in standard δ notation in units of parts per mil (‰; Bond & Jones 2009). These are calculated as: $\delta^H X = \left[\left(\frac{R_{\text{SAMPLE}}}{R_{\text{STANDARD}}} - 1 \right) \right] * 1000$, where X is the element (C or N), H is the heavy isotope mass of that element, and R is the ratio of the heavy to the light isotope for the element ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). Precision was measured as $\leq 0.48\text{‰}$ for $\delta^{15}\text{N}$ and $\leq 0.17\text{‰}$ for $\delta^{13}\text{C}$ using the standard deviation of replicate analyses of four standards: NIST1577c, tilapia muscle, USGS 40 and Urea ($n = 60$ for all). Instrument accuracy, based on the certified values of USGS 40 ($n = 60$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyzed throughout runs showed a difference from the certified value of 0.08‰ for $\delta^{15}\text{N}$ and 0.11‰ for $\delta^{13}\text{C}$.

We inspected the stable isotope data visually with multivariate histograms and determined that there were no large departures from multivariate normality. A Bayesian multivariate mixed model with Gaussian error was fit to the data. The response variables were the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, with species and feather type as fixed predictors and individual and year as random intercepts. Individuals were nested within years. We ran the model using 13,000 iterations, three chains, a thinning rate of 10, and a burn-in of 3000 (R package 'MCMCglmm', Hadfield 2010). A minimally-informative normal prior was used for the means, and the broadest possible inverse-Wishart distribution was used as a prior for the covariance matrices. Model fit was assessed with visual inspection of trace plots and a posterior predictive check. As the model estimated the covariances between the two response variables and fit different regression slopes for each of the predictor – response combinations in a Bayesian framework, it allows for direct comparison of estimates of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among species for each feather type, based on maximum a posteriori (MAP) and 90% credible intervals. The MAP is the most probable value for $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ (i.e., the mode of the posterior distribution), and the credible intervals provide a 90% probability that the $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ value is within the proscribed range. MAP and 90% credible intervals (CrI) for other model parameters of interest are also reported, along with additional probabilities derived from our posterior distribution estimates. For example, to determine the probability that the effect of year was close to 0, we calculated the proportions of iterations for which the coefficient for each year is higher/lower than 0 and reported the maximum.

Species-specific Standard Ellipse Areas corrected for small sample size (SEA_c) were calculated using the R package 'SIBER', to visually represent isotopic niche breadth for each species and feather type (Jackson et al. 2011). To describe the variability in our estimates of niche breadth and niche overlap, Bayesian Standard Ellipse Areas (SEA_b) and 90% credible intervals (CrI) were also calculated for each species and feather type with a minimally-informative normal prior for the mean and inverse-Wishart prior for the covariance matrices, using a burn-in of 1000, 20,000 iterations, 2 chains, and a thinning rate of 10 (Jackson et al. 2011). Following Jackson (2023), probabilities for pairwise comparisons of niche breadth (P_c) between species within feather types or feather types within species were calculated as proportions of iterations for which SEA is higher/lower for one species/feather type than another. Isotopic niche overlap between species pairs for each feather type was calculated by dividing the area of the portion that overlaps by the total niche area occupied by the two species (Jackson et al. 2011) for the first 1,000 draws from the SEA_b ellipses. Overlap maximum a posteriori (MAP) and 90% credible intervals (CrI) are reported.

Results

Spatiotemporal Analyses

We recovered 35 geolocators over the two years of tracking (Table 2.1). The geolocators from 2 murres and 1 puffin malfunctioned and did not have usable data, and five birds were tracked for two years (2 puffins, 2 razorbills, 1 murre), thus our dataset represents 37 bird-years total. Based on our interest in examining core space use of each species and overlap among species, we used all the available data in our analysis. Every core area polygon (i.e., kernel density) was always based on at least 4 and a maximum of 13 individuals.

In August–September, core use areas (50% kernel density estimates) overlapped to some extent among all three species in the waters off eastern Newfoundland (Fig. 2.2A), but this overlap generally decreased throughout the non-breeding season (Fig. 2.2B-E). As razorbills and murres departed the colony around mid-August, while puffins departed around mid-September (Table 2.1), there may be less overlap during August–September than presented (Fig. 2.2A), depending how quickly birds disperse from the colony vicinity. During August–September, razorbills ranged over a wide area, with some individuals moving farther north (around 60° N, Fig. 2.2A), perhaps because of sex-based differences and/or differences in nest success (Wanless & Harris 1986). After this period, there was no shared core area space use (i.e., $UDOIs = 0$) of murres and razorbills (October–March; Fig. 2.2B-2.2D) until the April–May period (Fig. 2.2E), when returning to the colony. By contrast, puffins were more widely dispersed than murres and razorbills throughout the non-breeding period, which led to varying degrees of overlap with both species (Fig. 2.2B-2.2E). In October–November and December–January, spatial overlap of puffins with the other species decreased (Figs. 2.2B, 2.2C), which continued in February–March (Fig. 2.2D). By February–March, puffins had split into 3 distinct core use areas: east of the shelf break, over the Grand Banks where they overlapped with murres, and towards the Gulf of Maine and U.S. coast where they overlapped with razorbills. During April–May, all three species moved back towards the breeding colonies (Fig. 2.2E).

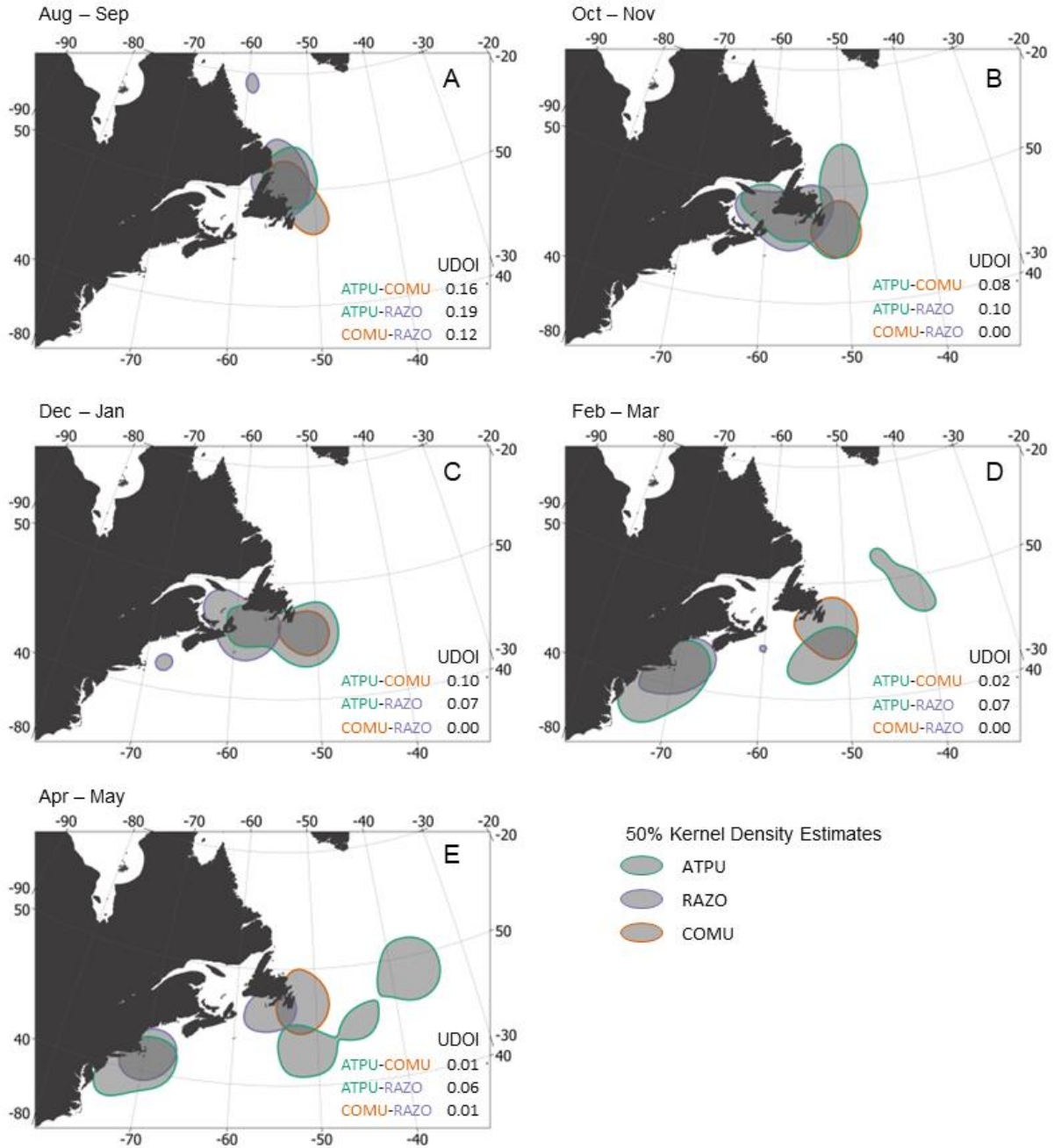


Figure 2.2: 50% Kernel density estimates and Utilization Distribution Overlap Indices (UDOI) during successive two-month periods of the non-breeding season for Atlantic puffins (ATPU), razorbills (RAZO), and common murrelets (COMU) tracked with light-level geolocators.

Isotopic Analyses

The Bayesian multivariate GLMM converged successfully, based on visual inspection of trace plots and density plots of the posteriors. For all feather types, the probability that $\delta^{13}\text{C}$ for

puffins was higher than both of the other two species was 0.75, while $\delta^{15}\text{N}$ differed more among species, with a 0.95 probability that murre $\delta^{15}\text{N}$ was more enriched than razorbills, and 0.99 probability that razorbills were more enriched than puffins (Fig. 2.3). The estimates of covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ centered on 0 (MAP = -0.02, 90% CrI -0.57 – 0.60), indicating no detectable linear relationship between the two response variables in our data. Year did not affect model results (90% CrI included 0, the probability that the effect was either > or < 0 was under 0.71, MAP range: -0.20 – 0.13), except for 2021, when $\delta^{13}\text{C}$ was comparatively much higher than the other years (MAP = 0.46, 90% CI -0.30 – 1.30, $P(2021 > 0) = 0.90$). As feathers were only collected from tagged (geolocator) birds in 2021, sample sizes from all three species were lower that year ($n = 71$) and, thus, we pooled data from 2017-2020 (i.e., excluded 2021) for subsequent niche breadth and overlap analyses.

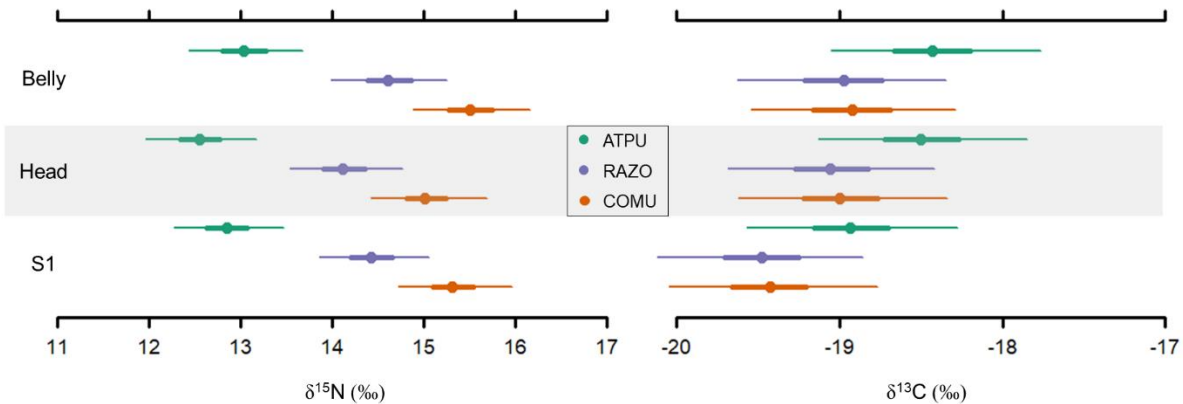


Figure 2.3: Results of a Bayesian multivariate GLMM on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feathers collected in 2017-2021. Maximum a posteriori (MAP) estimates (points), and 50% (thick line) and 90% (thin line) credible intervals for all combinations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, belly, head, and first secondary (S1) feather types, and species - Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU). MAP is the most probable value for the isotope ratio (i.e., the mode of the posterior distribution), and credible intervals provide a 90% or 50% probability that the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value is within the proscribed range.

During secondary feather molt, there was 39% isotopic niche overlap of murres and razorbills (90% CrI 16 – 60%), but no overlap of puffins with murres (90% CrI 0 – 1%) or razorbills (90% CrI 0 – 2%; Fig. 2.4). Murres had a narrower niche breadth (SEA_b) than razorbills ($P_c > 0.99$), although both were less than one third of puffin niche breadth ($P_c > 0.97$; Table 2.2, Fig. 2.4). During belly feather molt, murre isotopic niche expanded relative to secondary feather molt (P_c

> 0.97), while razorbill niche breadth stayed consistent ($P_c = 0.66$) and puffins contracted ($P_c = 0.96$), although puffin niche breadth was still broader than either of the other two alcids ($P_c > 0.94$; Table 2.2, Fig. 2.4). The narrow niches of murres and razorbills during this molt was associated with a large range in the estimates of overlap (90% CrI 0 – 48%), but there was a 0.93 probability that the overlap was < 15%. Puffins had similarly minimal isotopic niche overlap with murres (MAP = 0%, 90% CrI 0 – 32%) and razorbills (MAP = 0%, 90% CrI 0 – 17%) during belly feather molt. During head feather molt (Fig. 2.4), the isotopic niches of these alcids differentiated on the $\delta^{15}\text{N}$ axis, with minimal overlap between only razorbills and puffins (MAP = 0%, 90% CrI 0 – 6%). Razorbill niche breadth expanded by more than 50% during this molting period compared to the other two molt periods ($P_c > 0.93$), while murre niche breadth was similar to belly feather molt ($P_c = 0.49$) and puffin niche was broader than body molt but narrower than secondary feather molt ($P_c > 0.96$).

Table 2.2: Mean ($\pm$ SE) stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) along with estimates of isotopic niche breadth, including SEA_c , the standard ellipse area corrected for small sample sizes, and SEA_b , the MAP of the Bayesian standard ellipse area posterior and associated 90% credible intervals from Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) head, belly, and first secondary (S1) feathers collected during July-August, 2017-2020 on the northeast coast of Newfoundland.

Feather type	Species	SEA_c (‰ ²)	SEA_b (‰ ²)	90% CrI		$\delta^{13}\text{C}$ (‰) mean $\pm$ SE	$\delta^{15}\text{N}$ (‰) mean $\pm$ SE
				lower	upper		
S1	ATPU	2.88	2.85	2.41	3.47	-18.63 $\pm$ 0.10	13.15 $\pm$ 0.14
	RAZO	0.71	0.69	0.59	0.86	-19.81 $\pm$ 0.06	14.66 $\pm$ 0.06
	COMU	0.46	0.45	0.38	0.56	-19.66 $\pm$ 0.04	14.90 $\pm$ 0.05
Belly	ATPU	1.24	1.12	0.85	1.83	-18.73 $\pm$ 0.11	13.69 $\pm$ 0.19
	RAZO	0.66	0.60	0.45	0.94	-18.98 $\pm$ 0.11	14.91 $\pm$ 0.09
	COMU	0.73	0.69	0.52	1.08	-18.83 $\pm$ 0.12	14.49 $\pm$ 0.12
Head	ATPU	2.17	2.15	1.81	2.62	-18.99 $\pm$ 0.07	12.05 $\pm$ 0.14
	RAZO	1.41	1.39	1.17	1.69	-18.95 $\pm$ 0.06	13.90 $\pm$ 0.10
	COMU	0.74	0.73	0.61	0.88	-18.92 $\pm$ 0.05	15.70 $\pm$ 0.06

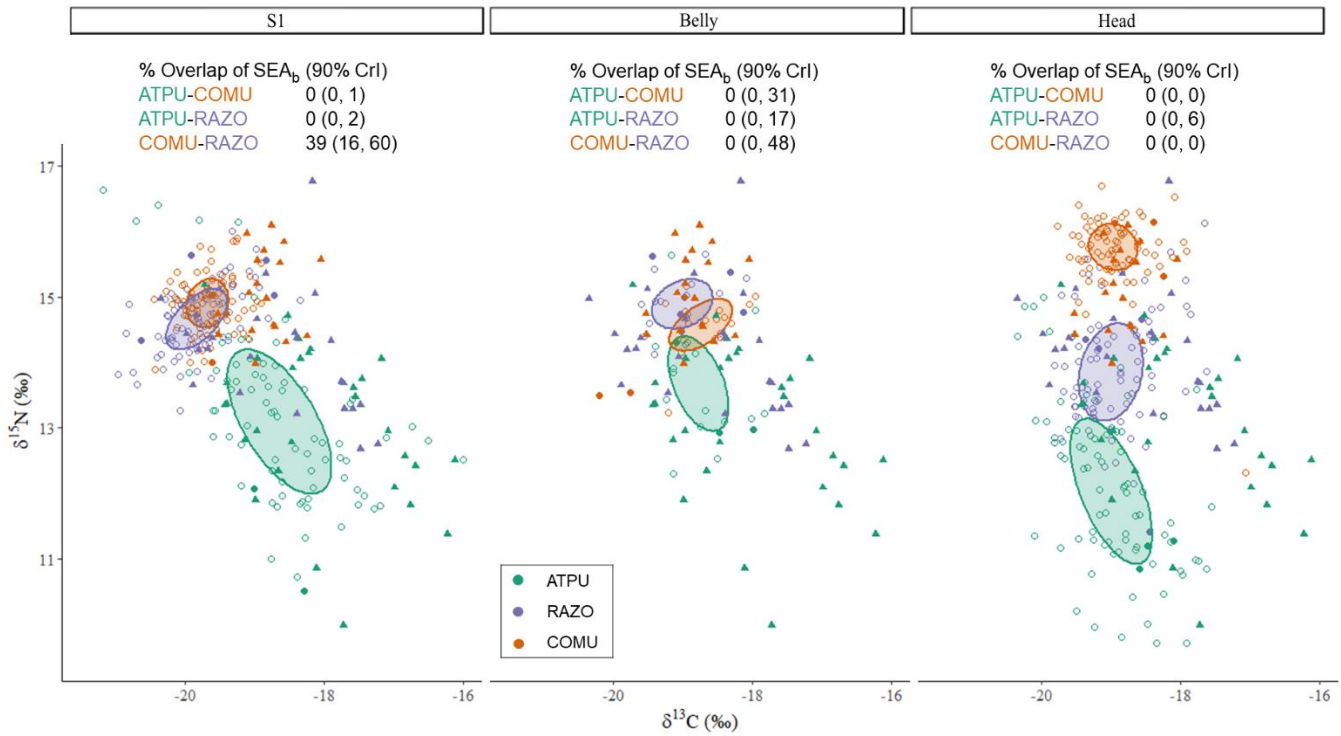


Figure 2.4: Isotopic niche breadth (SEA_c) and isotopic niche overlap (% overlap of SEA_b MAP, 90% CrI) of Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) first secondary (S1), belly, and head feathers. Calculated SEA_c ellipses are plotted for visualization of overlap. The matching calculations of overlap are based on SEA_b, to provide an indication of variability. The MAP is the most probable value for the % overlap (i.e., the mode of the posterior distribution), and credible intervals provide a 90% probability that the overlap is within the proscribed range. SEA and overlap calculations were based on feathers collected in 2017-2020 and included untagged birds (open circles) and geolocator tagged birds (filled circles). Feathers collected from geolocator tracked birds in 2021 (filled triangles) are presented but were not included in SEA or overlap calculations.

Combining Spatial and Isotopic Data

The feather isotope ratios from geolocator tagged birds were used to visually assess whether variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was due to spatial baseline shifts or diet, when the approximate timing of a particular feather molt was known. $\Delta^{13}\text{C}$ values of tagged birds did not show much variation in any of the feather molt periods (ranges of 3.17–4.08‰, Table 2.2, Fig. 2.4) and no apparent geographic gradient (Fig. 2.S1), suggesting minimal baseline shifts within the distributional range of all three species. Therefore, we focused on examining $\delta^{15}\text{N}$ values to determine whether species located in the same general area during a molting period occupied different trophic positions. During fall (September–November), when murre and razorbills molt secondary feathers, all tracked murre and razorbills had $\delta^{15}\text{N}$ ratios within 1.98‰ of each other (Fig. 2.4), suggesting minimal variation in trophic position. We could not include puffins

in this comparison because of uncertainty and variability in when (and therefore where) they molt secondary feathers. During spring (March–May), when all three species molt head feathers, all tracked birds had $\delta^{15}\text{N}$ ratios that ranged $\sim 5.30\text{‰}$ (Fig. 2.5). The range of murre $\delta^{15}\text{N}$ values was 0.82‰ , but the $\delta^{15}\text{N}$ values of puffins varied by 3.30‰ and razorbills by 3.64‰ . There was no clear geographic gradient in $\delta^{15}\text{N}$ values during this molting period, with variation in $\delta^{15}\text{N}$ among closely spaced individuals of the same species apparently greater than the differences between individuals farther apart (Fig. 2.5). The differences in $\delta^{15}\text{N}$ among species in the same general area (Fig. 2.5) reflected the patterns seen in Fig. 2.4, suggesting that murres were feeding at a higher trophic position, razorbills were intermediate, and puffins were at a lower trophic position.

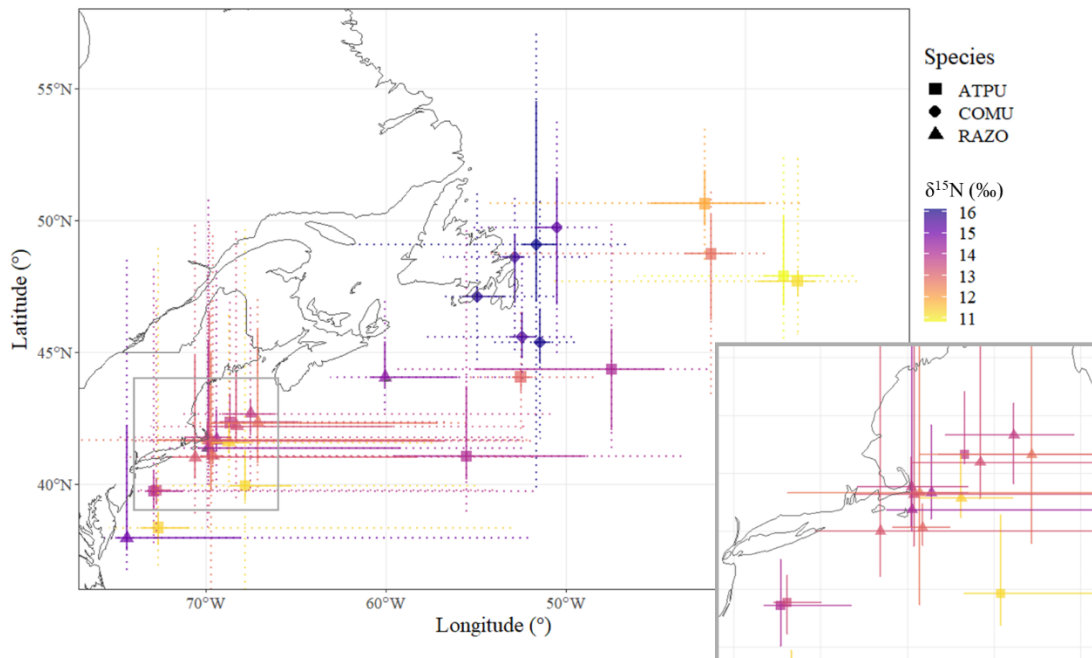


Figure 2.5: Head feather $\delta^{15}\text{N}$ of individual geolocator-tagged Atlantic puffins (ATPU), razorbills (RAZO), and common murres (COMU) at their estimated geographic median locations during March – May, the time of year when head feathers are molted. Solid error bars represent the 25th–75th quantiles of latitude and longitude estimates, and dotted lines indicate the entire range of latitude and longitude estimates during this period.

Discussion

As predicted, we generally found minimal spatiotemporal and isotopic niche overlap during the non-breeding season among sympatrically-breeding Atlantic puffins, razorbills, and common murres, with a few exceptions during certain times of year. Spatial overlap of species-specific core use areas was low among the three species, with two exceptions: overlap was higher just after and before the breeding season, and variability in puffin distributions was associated with some spatial overlap with the other two species at other times. Isotopic niche overlap among the three species was also usually low, especially during head feather molt in the spring, thereby

supporting our prediction that isotopic niche overlap would be low when spatial overlap is high. Our results suggest that these species either have always had separate niches (i.e., always relied on different resources in different places, often referred to as “the Ghost of Competition Past”) during non-breeding, or have co-evolved niche partitioning to allow coexistence (Connell 1983).

One exception to the minimal niche overlap was the high isotopic niche overlap between murres and razorbills during secondary feather molt in the fall, when they also overlapped spatially. Spatial overlap was not surprising during this period, as male razorbills and common murres are limited to swimming-speed movements while flightless during wing molt and the 1–2-month period of post-fledging parental care of flightless offspring (Gaston and Jones 1998). This leaves both species highly vulnerable to certain anthropogenic threats in this area, e.g., vessel traffic, oil spills or chronic oil pollution (Wiese and Ryan 2003, Wilhelm et al. 2009, Lieske et al. 2020). Additionally, the Newfoundland turr hunt, a regulated coastal harvest of murres (Montevecchi et al. 2007), begins in Labrador in September and off northeast Newfoundland in October (ECCC 2023), when razorbills in the area could easily be incorrectly identified as murres (Lavers et al. 2009) and, thus, mistakenly hunted during this period of spatial overlap. The high isotopic niche overlap could be partly because both species rely on available prey near the colony. Interestingly, while all the murres stayed in the same area during September and October, some razorbills, perhaps females or failed breeders (Wanless & Harris 1986), dispersed far to the north, along the Labrador coast. Future research could determine if females or individuals not caring for offspring have different isotopic niches from males performing parental care during flight feather molt (e.g., Burke et al. 2015).

It is difficult to disentangle the effect of different sources of variation on isotopic niche overlap. The spatially varying, basal primary productivity predominantly determines $\delta^{13}\text{C}$ ratios, while $\delta^{15}\text{N}$ ratios mostly increase with trophic position (Hobson et al. 1994, Fry 2006), but both stable isotope ratios incorporate trophic, spatial, environmental, temporal, and physiological variability (Newsome et al. 2007, Shipley & Matich 2020) that we could not control for in this study. Any of these sources of variation may underlie the low isotopic niche overlap among these three alcid species, as we largely do not know when or where certain feather types are molted, nor the physiology of molting in alcids (Pyle 2009). Distribution differences alone could result in low isotopic niche overlap, as there are gradients of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines associated with major water masses such as the Gulf Stream in the northwest Atlantic (McMahon et al. 2013). For feather types where a reasonable molt timespan could be estimated, variation in the feather nitrogen isotope ratios of species occurred in an area where there was little baseline variation, which suggests that differences in $\delta^{15}\text{N}$ values represent occupation of different trophic positions (Hobson et al. 1994). Isotopic niche segregation while co-located during breeding was previously documented among all three species in northwest Newfoundland (Jenkins & Davoren 2020, Lescure 2021) and other regions (Linnebjerg et al. 2013, Pratte et al. 2017, Petalas et al. 2021), with puffins consistently feeding at a lower trophic position while razorbills and murres overlap to varying extents. Our isotope results also align with non-breeding diet studies showing that puffins have a generalist diet with a high proportion of invertebrates (Falk et al. 1992, Harris et al. 2015, Hedd et al. 2010), murre diet contains large proportions of fish (Ainley et al. 1996, Rowe et al. 2000), and razorbills consume both invertebrates (Huettman et al. 2005) and fish (Blake 1984, Ouwehand et al. 2004). As patterns of spatial and dietary overlap are further

confounded by individual variation in when a particular feather was grown, the reason for low isotopic niche overlap remains uncertain.

Species-specific spatial patterns match previous knowledge about non-breeding distribution patterns of birds from Newfoundland colonies. Similar to our tracked birds, Newfoundland common murres do not appear to disperse far from breeding colonies during non-breeding, remaining mostly on the Grand Banks and Orphan Basin and returning toward their colony in late winter (McFarlane Tranquilla et al. 2013, Burke & Montevecchi 2018), where capelin (*Mallotus villosus*) and sand lance (*Ammodytes dubius*) are distributed during this period (DFO 2021, Morrison 2021). Newfoundland razorbills stay near the coast, in shallow areas, but move much farther south than murres (Lavers et al. 2020) and likely cover even larger distances when winter feeding conditions are poor (Diamond et al. 2020), similar to razorbills in other regions (Glew et al. 2019). The razorbills we tracked also moved south along the U.S. coast, where the dominant forage fish are sand lance, herring (*Clupea harengus*) and Atlantic menhaden (*Brevoortia tyrannus*; Anstead et al. 2021, Suca et al. 2021). Puffins used some of the same areas as razorbills and murres throughout non-breeding, eventually overlapping mostly along the U.S. coast and on the Grand Banks, but, as documented previously, they were also found further from the coast (Hedd et al. 2010, Fayet et al. 2017), and towards the mid-Atlantic (Fayet et al. 2017). During late winter, some puffins moved over the Flemish Cap and then towards the Mid-Atlantic Ridge, a recently described hotspot that is used by puffins from eastern Atlantic colonies (Davies et al. 2021b). While this hotspot has been designated as the North Atlantic Current and Evlanov Sea Marine Protected Area (NACES MPA, Fig. 2.1, Davies et al. 2021a), the low spatial overlap among the three alcids underlines the value of establishment and management of functional networks of protected areas to maintain ecosystem processes (Game et al. 2009).

The high spatial variation and broad isotopic niche of puffins during non-breeding could result from displacement from high-quality foraging areas and/or prey types to avoid competitive interactions with larger alcids (e.g., Shealer & Burger 1993, Maniscalco et al. 2001, Carvalho et al. 2020). Puffins are displaced from high-quality prey patches by larger alcids during breeding in coastal Newfoundland (Piatt 1990), and, on a larger scale, they often migrate longer distances from the colony and coast than other sympatrically breeding larger alcids throughout their range (Jessopp et al. 2013, Fayet et al. 2017). The lower trophic position of puffins when spatially overlapped with the other two species suggests displacement from higher trophic level prey. Additionally, puffins occupying the mid-Atlantic had similarly low $\delta^{15}\text{N}$ values, possibly indicating large-scale displacement from high-quality foraging locations occupied by murres and razorbills (e.g., U.S. coast, Grand Banks), or displacement from higher trophic level prey by other species within another known high-quality foraging area, the NACES MPA (Davies et al. 2021a, Davies et al. 2021b). Although puffins' broad secondary feather isotopic niche may be due to individual variability in the timing and, thus, location of feather growth (Harris & Yule 1977, Howell & Pyle 2005, Darby et al. 2022), this variability in molt patterns may also have evolved to reduce overlap of this energetically demanding period with other species. High isotopic variability during belly and head feather molt was possibly related to variation in migration patterns and baselines encountered, but there was also more variation within puffins in the same general area during head feather molt. Despite this evidence for displacement, it is

possible that puffins simply exploit different resources than murres and razorbills, exhibiting greater non-breeding diet flexibility (e.g., Glew et al. 2019) or targeting alternate prey types because their dive depth is comparatively constrained.

The low spatiotemporal and isotopic niche overlap among these alcids during the non-breeding season suggests that different localized threats would impact each species, although there are key exceptions. Murres and puffins that remain on the Grand Banks are likely at increased risk of oil exposure, due to chronic and accidental discharges along high-traffic shipping routes and around offshore oil platforms (Hedd et al. 2011). This would likely affect a greater proportion of the murre population, as many of the tracked puffins left this area, but most of the tracked murres stayed. The U.S. coast, specifically the Gulf of Maine and New York Bight, where extensive offshore wind development is planned (Stenhouse et al. 2020, NROC 2023, Moriarty 2023), is an important area for puffins and razorbills from northeast Newfoundland in mid-winter and early spring. Although alcids have low risk of collision with turbine blades, due to low flight-heights (Johnston et al. 2014), there is evidence that alcids are vulnerable to displacement by offshore wind installations (Vanermen et al. 2015, Welcker & Nehls 2016, Kelsey et al. 2018). Displacement can potentially have population-level impacts (Busch & Garthe 2016, Peschko et al. 2024), but the magnitude of these barrier effects is site specific (Dierschke et al. 2016). Although the consequences of this loss of habitat are unknown, it could increase the spatial overlap between puffins and razorbills. Declines in prey abundance on the U.S. coast or Grand Banks could also be particularly detrimental to puffins (Scopel et al. 2019), especially if they are displaced from high-quality resources in this area of overlap with razorbills.

By combining tracking and stable isotopes, we found evidence of differences in space and resource use during the low-productivity, non-breeding period, in line with predictions based on niche theory. However, remaining knowledge gaps hamper understanding of species interactions during non-breeding. Uncertainty around molt timings, especially for puffin flight feathers, limits our ability to interpret variability in isotope ratios even when combined with tracking. Further studies should focus on this basic aspect of natural history (Pyle 2009), possibly employing compound specific isotope analysis of amino acids (CSIA-aa) to parse out isotopic baseline shifts from trophic position independent of location (McMahon et al. 2015, Ohkouchi et al. 2017). Additionally, multi-colony tracking studies over a wider geographic area (e.g., Buckingham et al. 2022) and analysis of migratory connectivity (e.g., Merkel et al. 2021) would provide a broader picture of important non-breeding foraging areas for alcids in this region.

References

- Ainley DG, Nettleship DN, Carter HR, Storey AE (2020) Common Murre (*Uria aalge*). In: *Birds of the World*, version 1. Billerman SM (ed) Cornell Lab of Ornithology, Ithaca, NY, <https://doi.org/10.2173/bow.commur.01>
- Ainley DG, Spear LB, Allen SG, Ribic CA (1996) Temporal and spatial patterns in the diet of the Common Murre in California waters. *Condor* 98:691–705.

- Anstead KA, Drew K, Chagaris D, Schueller AM, McNamee JE, Buchheister A, Nesslage G, Uphoff JH, Wilberg MJ, Sharov A, Dean MJ, Brust J, Celestino M, Madsen S, Murray S, Appelman M, Ballenger JC, Brito J, Cosby E, Craig C, Flora C, Gottschall K, Latour RJ, Leonard E, Mroch R, Newhard J, Orner D, Swanson C, Tinsman J, Houde ED, Miller TJ, Townsend H (2021) The path to an ecosystem approach for forage fish management: A case study of Atlantic menhaden. *Front Mar Sci* 8:607–657.
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473.
- Ballance LT, Pitman RL, Reilly SB (1997) Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. *Ecology* 78:1502–1518.
- Baran MA, Kress SW, Shannon P, Lyons DE, Major HL, Diamond AW (2022) Overwinter movement of Atlantic puffins (*Fratercula arctica*) breeding in the Gulf of Maine: Inter- and intra-colony effects. *Waterbirds* 45:1–16.
- Barrett RT, Furness RW (1990) The prey and diving depths of seabirds on Hornøy, north Norway after a decrease in the barents sea capelin stocks. *Ornis Scand* 21:1–9.
- Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol Biochem Zool* 75:451–458.
- Bennett S, Harris MP, Wanless S, Green JA, Newell MA, Searle KR, Daunt F (2022) Earlier and more frequent occupation of breeding sites during the non-breeding season increases breeding success in a colonial seabird. *Ecol Evol* 12:1–24.
- Blake BF (1984) Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. *J Exp Mar Bio Ecol* 76:89–103.
- Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, Bearhop S (2018) A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods Ecol Evol* 9:946–955.
- Bond AL, Jones IL (2009) A practical introduction to stable-isotope analysis for seabird biologists: Approaches, cautions and caveats. *Mar Ornithol* 37:183–188.
- Buckingham L, Bogdanova M, Green J, Dunn R, Wanless S, Bennett S, Bevan R, Call A, Canham M, Corse C, Harris M, Heward C, Jardine D, Lennon J, Parnaby D, Redfern C, Scott L, Swann R, Ward R, Weston E, Furness R, Daunt F (2022) Interspecific variation in non-breeding aggregation: A multi-colony tracking study of two sympatric seabirds. *Mar Ecol Prog Ser* 684:181–197.
- Burke CM, Montevecchi WA (2018) Taking the bite out of winter: Common murre (*Uria aalge*) push their dive limits to surmount energy constraints. *Front Mar Sci* 5:1–13.
- Burke CM, Montevecchi WA, Regular PM (2015) Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. *PLoS One* 10:1–22.

- Busch M, Garthe S (2016) Approaching population thresholds in presence of uncertainty: Assessing displacement of seabirds from offshore wind farms. *Environ Impact Assess Rev* 56:31–42.
- Calenge C (2006) The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519.
- Carvalho PC, Maynard LD, Davoren GK (2020) Responses of sympatric shearwaters to supplemental food under varying natural prey availability on the wintering grounds of coastal Newfoundland, Canada. *Mar Ornithol* 48:255–262.
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Am Nat* 122:661–696.
- Darby JH, Harris MP, Wanless S, Quinn JL, Bråthen VS, Fayet AL, Clairbaux M, Hart T, Guilford T, Freeman R, Jessopp MJ (2022) A new biologging approach reveals unique flightless molt strategies of Atlantic puffins. *Ecol Evol* 12:1–13.
- Davies TE, Carneiro APB, Campos B, Hazin C, Dunn DC, Gjerde KM, Johnson DE, Dias MP (2021a) Tracking data and the conservation of the high seas: Opportunities and challenges. *J Appl Ecol* 58:2703–2710.
- Davies TE, Carneiro APB, Tarzia M, Wakefield E, Hennicke JC, Frederiksen M, Hansen ES, Campos B, Hazin C, Lascelles B, Anker-Nilssen T, Arnardóttir H, Barrett RT, Biscoito M, Bollache L, Bouludier T, Catry P, Ceia FR, Chastel O, Christensen-Dalsgaard S, Cruz-Flores M, Danielsen J, Daunt F, Dunn E, Egevang C, Fagundes AI, Fayet AL, Fort J, Furness RW, Gilg O, González-Solís J, Granadeiro JP, Grémillet D, Guilford T, Hanssen SA, Harris MP, Hedd A, Huffeldt NP, Jessopp M, Kolbeinsson Y, Krietsch J, Lang J, Linnebjerg JF, Lorentsen SH, Madeiros J, Magnúsdóttir E, Mallory ML, McFarlane Tranquilla L, Merkel FR, Militão T, Moe B, Montevecchi WA, Morera-Pujol V, Mosbech A, Neves V, Newell MA, Olsen B, Paiva VH, Peter HU, Petersen A, Phillips RA, Ramírez I, Ramos JA, Ramos R, Ronconi RA, Ryan PG, Schmidt NM, Sigurðsson IA, Sittler B, Steen H, Stenhouse IJ, Strøm H, Systad GHR, Thompson P, Thórarinnsson TL, van Bemmelen RSA, Wanless S, Zino F, Dias MP (2021b) Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conserv Lett* 14:1–14.
- DFO - Fisheries and Oceans Canada, Ecosystems and Ocean Science (2021) Assessment of 2J3KL capelin in 2020. <https://www.dfo-mpo.gc.ca/csas-sccs/Publications/S>. (accessed 10 Aug 2023).
- Diamond AW, McNair DB, Ellis JC, Rail J, Whidden ES, Kratter AW, Courchesne SJ, Pokras MA, Wilhelm SI, Kress SW, Farnsworth A, Iliff MJ, Jennings SH, Brown JD, Ballard JR, Schweitzer SH, Okoniewski JC, Gallegos JB, Stanton JD (2020) Two unprecedented auk wrecks in the Northwest Atlantic in winter 2012/13. *Mar Ornithol* 13:185–204.
- Dierschke V, Furness RW, Garthe S (2016) Seabirds and offshore wind farms in European waters: Avoidance and attraction. *Biol Conserv* 202:59–68.

- Dunn RE, Wanless S, Daunt F, Harris MP, Green JA (2020) A year in the life of a North Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Sci Rep* 10:1–11.
- ECCC - Environment and Climate Change Canada (2023) Newfoundland and Labrador Summary of Migratory Birds Hunting Regulations. <https://www.canada.ca/en/environment-climate-change/services/migratory-game-bird-hunting/regulations-provincial-territorial-summaries/newfoundland-labrador.html#toc14> (accessed 10 Aug 2023).
- Elliott KH, Gaston AJ (2014) Dive behaviour and daily energy expenditure in Thick-billed murre *Uria lomvia* after leaving the breeding colony. *Mar Ornithol* 189:183–189.
- Falk K, Jensen J, Kampp KAJ (1992) Winter diet of Atlantic puffins (*Fratercula arctica*) in the Northeast Atlantic. *Colon Waterbirds* 15:230–235.
- Fayet AL, Freeman R, Anker-Nilssen T, Diamond A, Erikstad KE, Fifield D, Fitzsimmons MG, Hansen ES, Harris MP, Jessopp M, Kouwenberg AL, Kress S, Mowat S, Perrins CM, Petersen A, Petersen IK, Reiertsen TK, Robertson GJ, Shannon P, Sigurðsson IA, Shoji A, Wanless S, Guilford T (2017) Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Curr Biol* 27:3871–3878.e3.
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: The importance of the utilization distribution. *J Wildl Manage* 69:1346–1359.
- Fry B (2006) *Stable Isotope Ecology*. Springer, New York, New York.
- Game ET, Grantham HS, Hobday AJ, Pressey RL, Lombard AT, Beckley LE, Gjerde K, Bustamante R, Possingham HP, Richardson AJ (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends Ecol Evol* 24:360–369.
- Gaston AJ, Jones IL (1998) *The Auks: Alcidae, illustrated*. Oxford University Press, New York, USA.
- Geen GR, Robinson RA, Baillie SR (2019) Effects of tracking devices on individual birds – a review of the evidence. *J Avian Biol* 50:1–13.
- Glew KSJ, Wanless S, Harris MP, Daunt F, Erikstad KE, Strøm H, Speakman JR, Kürten B, Trueman CN (2019) Sympatric Atlantic puffins and razorbills show contrasting responses to adverse marine conditions during winter foraging within the North Sea. *Mov Ecol* 7:1–14.
- Glew KSJ, Wanless S, Harris MP, Daunt F, Erikstad KE, Strøm H, Trueman CN (2018) Moulting location and diet of auks in the North Sea inferred from coupled light-based and isotope-based geolocation. *Mar Ecol Prog Ser* 599:239–251.
- Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *J Stat Softw* 33:1–36.
- Halpin LR, Ross JD, Ramos R, Mott R, Carlile N, Golding N, Reyes-González JM, Militão T, De

- Felipe F, Zajková Z, Cruz-Flores M, Saldanha S, Morera-Pujol V, Navarro-Herrero L, Zango L, González-Solís J, Clarke RH (2021) Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods Ecol Evol* 12:2243–2255.
- Harris MP, Leopold MF, Jensen JK, Meesters EH, Wanless S (2015) The winter diet of the Atlantic Puffin *Fratercula arctica* around the Faroe Islands. *Ibis* 157:468–479.
- Harris MP, Yule RF (1977) The moult of the Puffin *Fratercula arctica*. *Ibis* 119:535–541.
- Harrison NM, Whitehouse MJ, Heinemann D, Prince PA, Hunt Jr. GL, Veit RR (1991) Observations of multispecies seabird flocks around South Georgia. *Auk* 108:801–810.
- Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: *Spatial Pattern in Plankton Communities*. Steele JH (ed) Springer, New York, p 277–327
- Hedd A, Fifield DA, Burke CM, Montevecchi WA, Tranquilla LMF, Regular PM, Buren AD, Robertson GJ (2010) Seasonal shift in the foraging niche of Atlantic puffins *Fratercula arctica* revealed by stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses. *Aquat Biol* 9:13–22.
- Hedd A, Montevecchi WA, McFarlane Tranquilla L, Burke CM, Fifield DA, Robertson GJ, Phillips RA, Gjerdrum C, Regular PM (2011) Reducing uncertainty on the Grand Bank: Tracking and vessel surveys indicate mortality risks for common murres in the North-West Atlantic. *Anim Conserv* 14:630–641.
- Hedd A, Regular PM, Montevecchi WA, Buren AD, Burke CM, Fifield DA (2009) Going deep: Common murres dive into frigid water for aggregated, persistent and slow-moving capelin. *Mar Biol* 156:741–751.
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786.
- Howell SNG, Pyle P (2005) Molt, age determination, and identification of puffins. *Birding* 37:412–418.
- Huettman F, Diamond AW, Dalzell B, MacIntosh K (2005) Winter distribution, ecology and movements of Razorbills (*Alca torda*) and other auks in the outer Bay of Fundy, Atlantic Canada. *Mar Ornithol* 33:161–171.
- Hunt GL, Mehlum F, Russell RW, Irons D, Decker B, Becker PH (1999) Physical processes , prey abundance, and the foraging ecology of seabirds. In: *Proc. 22nd International Ornithological Congress*. Adams NJ, Slotow RH (eds) Durban, p 1–21
- Hutchinson GE (1978) *An Introduction to Population Biology*. Yale University Press, New Haven.
- Jackson AL (2023) SIBER 2.1.7 vignette: Comparing populations. <https://cran.r-project.org/web/packages/SIBER/vignettes/siber-comparing-populations.html> (accessed

23 March 2023)

- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602.
- Jenkins E, Gulka J, Maynard L, Davoren G (2018) Seabird population update and trends from six colonies in northeastern Newfoundland. Canadian Wildlife Service Unpublished Report, p 1–27.
- Jenkins EJ, Davoren GK (2021) Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. *Ibis* (Lond 1859) 163:183–196.
- Jessopp MJ, Cronin M, Doyle TK, Wilson M, McQuatters-Gollop A, Newton S, Phillips RA (2013) Transatlantic migration by post-breeding puffins: A strategy to exploit a temporarily abundant food resource? *Mar Biol* 160:2755–2762.
- Johnston A, Cook ASCP, Wright LJ, Humphreys EM, Burton NHK (2014) Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *J Appl Ecol* 51:31–41.
- Karnovsky NJ, Hobson KA, Iverson SJ (2012) From lavage to lipids: Estimating diets of seabirds. *Mar Ecol Prog Ser* 451:263–284.
- Kelsey EC, Felis JJ, Czapanskiy M, Pereksta DM, Adams J (2018) Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. *J Environ Manage* 227:229–247.
- Lack D (1944) Ecological Aspects of Species-formation in Passerine Birds. *Ibis* 86:260–286.
- Lavers J, Hipfner JM, Chapdelaine G (2020) Razorbill (*Alca torda*). In: *Birds of the World*, version 2. Billerman SM (ed) Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.razorb.01>
- Lavers JL, Jones IL, Robertson GJ, Diamond AW (2009) Contrasting population trends at two razorbill colonies in Atlantic Canada: Additive effects of fox predation and hunting mortality? *Avian Conserv Ecol* 4(2):3
- Lescure L (2021) Foraging flexibility of seabirds (Family Alcidae) under varying prey biomass. Master's Thesis. University of Manitoba, Winnipeg, Manitoba, Canada
- Lieske DJ, Tranquilla LMF, Ronconi RA, Abbott S (2020) “Seas of risk”: Assessing the threats to colonial-nesting seabirds in Eastern Canada. *Mar Policy* 115:103863.
- Linnebjerg JF, Fort J, Guilford T, Reuleaux A, Mosbech A, Frederiksen M (2013) Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS One* 8:e72987.

- Lisovski S, Hahn S (2012) GeoLight - processing and analysing light-based geolocator data in R. *Methods Ecol Evol* 3:1055–1059.
- Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: Accuracy and precision affected by environmental factors. *Methods Ecol Evol* 3:603–612.
- Lisovski S, Wotherspoon SJ, Sumner M (2016) TwGeos: Basic data processing for light-level geolocation archival tags. <https://github.com/slisovski/TwGeos> (accessed 10 Aug 2023)
- Lowther PE, Diamond AW, Kress SW, Robertson GJ, Russell K, Nettleship DN, Kirwan GM, Christie D, Sharpe C, Garcia E, Boesman PFD (2020) Atlantic Puffin (*Fratercula arctica*). In: *Birds of the World*, version 1. Billerman SM (ed) Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.atlpuf.01>
- Mancini PL, Hobson KA, Bugoni L (2014) Role of body size in shaping the trophic structure of tropical seabird communities. *Mar Ecol Prog Ser* 497:243–257.
- Maniscalco JM, Ostrand WD, Suryan RM, Irons DB (2001) Passive interference competition by Glaucous-winged Gulls on Black-legged Kittiwakes: A cost of feeding in flocks. *Condor* 103:616–619.
- May RM, MacArthur RH (1972) Niche overlap as a function of environmental variability. *Proc Natl Acad Sci* 69:1109–1113.
- McFarlane Tranquilla L, Montevecchi W, Hedd A, Fifield D, Burke C, Smith P, Regular P, Robertson G, Gaston A, Phillips R (2013) Multiple-colony winter habitat use by murres *Uria* spp. in the Northwest Atlantic Ocean: implications for marine risk assessment. *Mar Ecol Prog Ser* 472:287–303.
- McFarlane Tranquilla L, Montevecchi WA, Hedd A, Regular PM, Robertson GJ, Fifield DA, Devillers R (2015) Ecological segregation among Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*) in the Northwest Atlantic persists through the nonbreeding season. *Can J Zool* 93:447–460.
- McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnol Oceanogr* 58:697–714.
- McMahon KW, Polito MJ, Abel S, McCarthy MD, Thorrold SR (2015) Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (*Pygoscelis papua*). *Ecol Evol* 5:1278–1290.
- Merkel B, Descamps S, Yoccoz NG, Grémillet D, Fauchald P, Danielsen J, Daunt F, Erikstad KE, Ezhov AV, Harris MP, Gavrilov M, Lorentsen SH, Reiertsen TK, Systad GH, Lindberg Thórarinnsson T, Wanless S, Strøm H (2021) Strong migratory connectivity across meta-populations of sympatric North Atlantic seabirds. *Mar Ecol Prog Ser* 676:173–188.
- Merkel B, Phillips RA, Descamps S, Yoccoz NG, Moe B, Strøm H (2016) A probabilistic

- algorithm to process geolocation data. *Mov Ecol* 4:26–37.
- Montevecchi WA, Chaffey H, Burke CM (2007) Hunting for security: Changes in the exploitation of marine birds in Newfoundland and Labrador. In: *Resetting the Kitchen Table*. Parrish CC, Turner NJ, Solberg SM (eds) Nova Science Publishers, Inc., p 99–116
- Moriarty T (2023) BOEM Advances Offshore Wind Leasing Process in the Gulf of Maine. Bureau of Ocean Energy Management press release. <https://www.boem.gov/newsroom/press-releases/boem-advances-offshore-wind-leasing-process-gulf-maine> (accessed 10 Aug 2023).
- Morrison S (2021) Sand lance (*Ammodytes* spp) on the Newfoundland Shelf: Habitat selection, diel behaviour, and synchrony of dynamics with other forage fish. Master's Thesis. University of Manitoba, Winnipeg, Manitoba, Canada
- Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS One* 8:e62897.
- Newsome SD, Rio, Martinez del C, Bearhop S, Phillips DL (2007) A niche for isotope ecology. *Front Ecol Environ* 5:429–436.
- NROC (2023) Northeast ocean data portal energy and infrastructure map. Northeast Regional Ocean Council. <https://www.northeastoceandata.org/data-explorer/?energy-infrastructure> (accessed 4 July 2023).
- Oedekoven CS, Ainley DG, Spear LB (2001) Variable responses of seabirds to change in marine climate: California Current, 1985–1994. *Mar Ecol Prog Ser* 212:265–281.
- Ohkouchi N, Chikaraishi Y, Close HG, Fry B, Larsen T, Madigan DJ, McCarthy MD, McMahon KW, Nagata T, Naito YI, Ogawa NO, Popp BN, Steffan S, Takano Y, Tayasu I, Wyatt ASJ, Yamaguchi YT, Yokoyama Y (2017) Advances in the application of amino acid nitrogen isotopic analysis in ecological and biogeochemical studies. *Org Geochem* 113:150–174.
- Ouwehand J, Leopold MF, Kees CJ (2004) A comparative study of the diet of Guillemots *Uria aalge* and Razorbills *Alca torda* killed during the Tricolor oil incident in the south-eastern North Sea in January 2003. *Atl Seabirds* 6:147–166.
- Pennycuik CJ (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: Ornithodolite observations. *J Exp Biol* 128:335–347.
- Peschko V, Schwemmer H, Mercker M, Markones N, Borkenhagen K, Garthe S (2024) Cumulative effects of offshore wind farms on common guillemots (*Uria aalge*) in the southern North Sea - climate versus biodiversity? *Biodivers Conserv* 33:949–970.
- Petalas C, Lazarus T, Lavoie RA, Elliott KH, Guigueno MF (2021) Foraging niche partitioning in sympatric seabird populations. *Sci Rep* 11:1–12.
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. *Mar Ecol Prog Ser* 266:265–272.

- Piatt JF (1990) The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *Stud Avian Biol*:36–51.
- Piatt JF, Nettleship DN (1985) Diving depths of four alcids. *Auk*:293–297.
- Pratte I, Robertson GJ, Mallory ML (2017) Four sympatrically nesting auks show clear resource segregation in their foraging environment. *Mar Ecol Prog Ser* 572:243–254.
- Pyle P (2009) Age determination and molt strategies in North American alcids. *Mar Ornithol* 37:219–226.
- R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution-blended analyses for sea surface temperature. *J Clim* 20:5473–5496.
- Rowe S, Jones IL, Chardine JW, Elliot RD, Veitch BG (2000) Recent changes in the winter diet of murres (*Uria* spp.) in coastal Newfoundland waters. *Can J Zool* 78:495–500.
- Scopel L, Diamond A, Kress S, Shannon P (2019) Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Mar Ecol Prog Ser* 626:177–196.
- Shealer DA, Burger J (1993) Effects of interference competition on the foraging activity of tropical Roseate Terns. *Condor* 95:322.
- Shipley ON, Matich P (2020) Studying animal niches using bulk stable isotope ratios: An updated synthesis. *Oecologia* 193:27–51.
- Silverman E, Veit R, Nevitt G (2004) Nearest neighbors as foraging cues: Information transfer in a patchy environment. *Mar Ecol Prog Ser* 277:25–36.
- Skov H, Durinck J, Andell P (2000) Associations between wintering avian predators and schooling fish in the Skagerrak-Kattegat suggest reliance on predictable aggregations of herring *Clupea harengus*. *J Avian Biol* 31:135–143.
- Stenhouse IJ, Berlin AM, Gilbert AT, Goodale MW, Gray CE, Montevocchi WA, Savoy L, Spiegel CS (2020) Assessing the exposure of three diving bird species to offshore wind areas on the U.S. Atlantic Outer Continental Shelf using satellite telemetry. *Divers Distrib* 26:1703–1714.
- Strøm H, Descamps S, Ekker M, Fauchald P, Moe B (2021) Tracking the movements of North Atlantic seabirds: Steps towards a better understanding of population dynamics and marine ecosystem conservation. *Mar Ecol Prog Ser* 676:97–116.
- Suca JJ, Deroba JJ, Richardson DE, Ji R, Llopiz JK (2021) Environmental drivers and trends in forage fish occupancy of the Northeast U.S. shelf. *ICES J Mar Sci* 78:3687–3708.
- Thompson CW, Wilson ML, Melvin EF, Pierce DJ (1998) An unusual sequence of flight-feather

- molt in Common Murres and its evolutionary implications. *Auk* 115:653–669.
- Vanermen N, Onkelinx T, Courtens W, Van de walle M, Verstraete H, Stienen EWM (2015) Seabird avoidance and attraction at an offshore wind farm in the Belgian part of the North Sea. *Hydrobiologia* 756:51–61.
- Veit RR, Manne LL (2015) Climate and changing winter distribution of alcids in the Northwest Atlantic. *Front Ecol Evol* 3:1–9.
- Wanless S, Harris JA, Morris MP (1988) Diving behaviour of guillemot *Uria aalge*, puffin *Fratercula arctica* and razorbill *Alca torda* as shown by radio-telemetry. *J Zool Soc London* 216:73–81.
- Wanless S, Harris MP (1986) Time spent at the colony by male and female Guillemots *Uria aalge* and Razorbills *Alca torda*. *Bird Study* 33:168–176.
- Wanless S, Harris MP, Morris JA (1990) A comparison of feeding areas used by individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the breeding season. *Colon Waterbirds* 13:16–24.
- Welcker J, Nehls G (2016) Displacement of seabirds by an offshore wind farm in the North Sea. *Mar Ecol Prog Ser* 554:173–182.
- Wiens JJ, Graham CH (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Evol Syst* 36:519–539.
- Wiese FK, Ryan PC (2003) The extent of chronic marine oil pollution in southeastern Newfoundland waters assessed through beached bird surveys 1984-1999. *Mar Pollut Bull* 46:1090–1101.
- Wilhelm SI, Mailhiot J, Arany J, Chardine JW, Robertson GJ, Ryan PC (2015) Update and trends of three important seabird populations in the western North Atlantic using a geographic information system approach. *Mar Ornithol* 43:211–222.
- Wilhelm SI, Robertson GJ, Ryan PC, Tobin SF, Elliot RD (2009) Re-evaluating the use of beached bird oiling rates to assess long-term trends in chronic oil pollution. *Mar Pollut Bull* 58:249–255.

Supplementary Tables and Figures

Table 2.A1: ‘ProbGLS’ model input parameters for estimating locations using geolocator data from Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU).

	ATPU	RAZO	COMU
wetdry.resolution (s)	30	30	3
max.sst.diff (°)^a	2	2	3
speed.dry (mps)^b	17.6/ 0.2/18.6	16.0/0.2/17.0	19.1/ 0.2/20.1
speed.wet (mps)^b	1/1.3/ 5		
loess.quartile	k = 3		
particle.number	2000		
iteration.number	100		
sunrise.sd^c	2.49/0.94/0		
sunset.sd^c	2.49/0.94/0		
range.solar (°)	-6 to -3		
sst.sd (°)	calculated for each individual		
boundary.box (°)	-85 to -1 longitude, 25 to 70 latitude		
days.around.spring.equinox^d	21 before, 14 after		
days.around.fall.equinox^d	14 before, 21 after		
ice.conc.cutoff	1		
land.mask	T		

^aMaximum tolerance in sea surface temperature (SST) variation

^bMaximum expected speed/speed standard deviation (SD)/maximum speed allowed

^cShape/scale/delay values defining uncertainty for each twilight event, following a log normal distribution

^dNumber of days surrounding equinox for which a random latitude will be assigned

Table 2.A2: Utilization distribution overlap index (UDOI) values of pairwise 50% kernel density distribution overlap between Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) during successive 2-month periods in the non-breeding season, calculated with two different underlying grid sizes (25 km and 150 km). The degree of green shading ranges from the smallest value (white) to the largest in each column (darkest green).

Months	Overlapping species	25 km grid UDOI	150 km grid UDOI
Aug–	ATPU-COMU	0.16	0.12
Sep	ATPU-RAZO	0.19	0.18
	COMU-RAZO	0.12	0.09
Oct–	ATPU-COMU	0.08	0.08
Nov	ATPU-RAZO	0.10	0.11
	COMU-RAZO	0.00	0.00
Dec–	ATPU-COMU	0.10	0.04
Jan	ATPU-RAZO	0.07	0.07
	COMU-RAZO	0.00	0.00
Feb–	ATPU-COMU	0.02	0.02
Mar	ATPU-RAZO	0.07	0.08
	COMU-RAZO	0.00	0.00
Apr–	ATPU-COMU	0.01	0.01
May	ATPU-RAZO	0.06	0.06
	COMU-RAZO	0.01	0.01

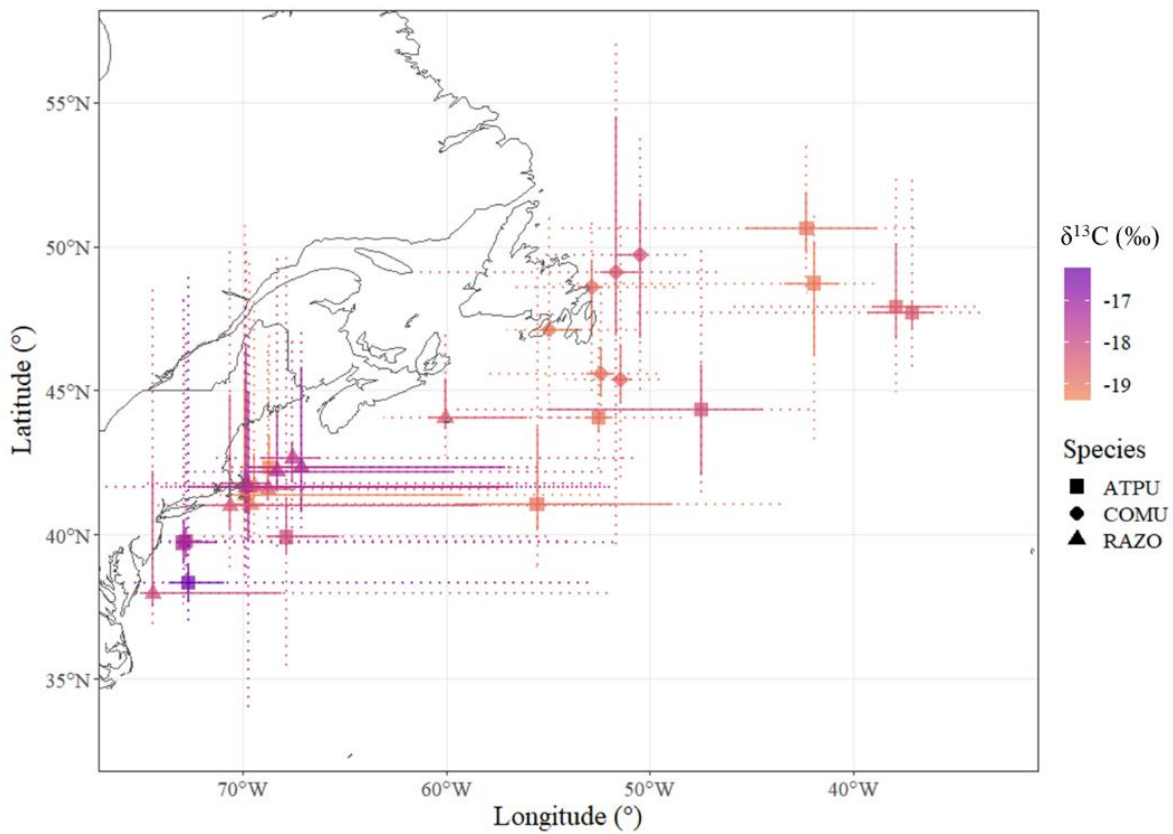


Figure 2.S1: Head feather $\delta^{13}\text{C}$ of individual geolocator-tagged Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) at their estimated geographic median locations during March – May, the time of year when head feathers are molted. Solid error bars represent the 25th-75th quantiles of latitude and longitude estimates, and dotted lines indicate the entire range of latitude and longitude estimates during this period.

Link between Chapters 2 & 3

In Chapter 2, I found mostly low spatiotemporal and isotopic niche overlap among sympatrically breeding Atlantic puffins, razorbills, and common murre during the non-breeding season. There was also some indication that puffins may be displaced by competitive interactions with the larger alcids, as puffin distribution was highly variable and their isotopic niche was comparatively broad. These potential interspecific interactions and their influence on puffins raise questions about intraspecific interactions, specifically whether puffins from different colonies overlap spatiotemporally during non-breeding. The diverse migration paths exhibited by puffins from James Island, Newfoundland in Chapter 2 suggest that they may share space with puffins from other northwest Atlantic colonies during some part of the non-breeding period. I investigated this in Chapter 3 by describing the migratory connectivity of Atlantic puffins from four Canadian colonies across non-breeding.

Chapter 3: Seasonal variability in migratory connectivity for Atlantic Puffins in eastern Canada

Emily S. Runnells¹, Mark A. Baran², Joshua Cunningham³, Antony W. Diamond⁴, David A. Fifield³, Michelle G. Fitzsimmons⁵, April Hedd³, Heather L. Major⁴, Raphael A. Lavoie⁶, Gail K. Davoren¹

¹University of Manitoba, Winnipeg, MB, Canada

²SUNY Plattsburgh, Plattsburgh, NY, USA

³Wildlife Research Division, Environment and Climate Change Canada, Mount Pearl, NL, Canada

⁴University of New Brunswick, St. John, NB, Canada

⁵Fisheries and Oceans Canada, St. John's, NL, Canada

⁶Environment and Climate Change Canada, Quebec, QC, Canada

Prepared for publication in Ornithological Applications

[Return to table of contents](#)

Abstract

Quantifying patterns of migratory connectivity in *Fratercula arctica* (Atlantic Puffin) in the northwest Atlantic is a crucial step for addressing threats to populations of this vulnerable seabird during non-breeding. Variation in migratory connectivity strength across the year indicates both key areas to protect and times when diverse management strategies are needed. Although their migration tends to be gradual, likely proscribed by their high energetic cost of flight, *F. arctica* have been documented covering long distances during migration and exhibiting high inter-individual variability in movement patterns, which could lead to weak migratory connectivity among breeding colonies. Individual migration patterns were derived from light-level geolocators deployed on puffins from four breeding colonies across an over 1000 km stretch of the North American Atlantic coast. Migratory connectivity was quantified during each month of non-breeding using Mantel correlation of the median locations of individuals from the four colonies in various colony-year combinations between 2013 and 2021. The migratory connectivity among the four colonies was strong pre- and post-breeding but generally weakened over the course of the non-breeding period, as individuals traveled to key winter foraging locations, such as the Gulf of Maine. A shift in the pattern of migratory connectivity strength across the temporal span of available data from two colonies suggests that *F. arctica* in the northwest Atlantic are adjusting their migration phenology in response to changing environmental cues. This insight into the migratory connectivity of these long-lived birds allows accurate definition of management units and helps elucidate the population impacts of marine spatial planning efforts.

Introduction

For many birds, regular seasonal movements link breeding locations to non-breeding locations, and learning about these migrations is an important part of understanding species ecology and planning effective conservation (Faaborg et al. 2010, Costa et al. 2012, Lascelles et al. 2014, Allen and Singh 2016, Fraser et al. 2018). Environmental conditions and anthropogenic threats at non-breeding locations, including along migratory routes, have been shown to affect individuals during the breeding season and vice versa (e.g., Marra et al. 1998, Szostek and Becker 2015, Desprez et al. 2018, Wojczulanis-Jakubas et al. 2020). Carry-over effects like these within breeding populations can ultimately influence abundances of species in broader regions, but these seasonal interactions (events occurring in one season that affect individuals or populations in a subsequent season) are often poorly understood (Fretwell 1972, Norris and Marra 2007). Therefore, management of threatened migratory species first requires information on how breeding populations are connected throughout the annual cycle (Taylor and Norris 2010).

One approach to determining how breeding populations are linked across seasons is studying migratory connectivity, which describes the spatial and temporal structure of a migration network by linking individuals, as members of breeding populations, between breeding and non-breeding seasons (Marra et al. 2019). Unlike demographic connectivity (e.g., in fisheries; Cowen and Sponaugle 2009), strong migratory connectivity occurs when there is little mixing among breeding populations during non-breeding periods (Webster et al. 2002). Consequently, the strongest migratory connectivity is when all individuals from the same breeding area migrate to the same non-breeding area, and individuals from different breeding areas migrate to different non-breeding areas. Migratory connectivity weakens with increasing non-breeding spatiotemporal overlap of a greater number of individuals from more distant breeding locations. An advantage of migratory connectivity analysis is that it incorporates information on migration routes, stopover locations, and phenology. As localized anthropogenic threats during non-breeding would have a greater influence on breeding population dynamics if breeding populations also winter together (Marra et al. 2019), migratory connectivity is key to understanding how breeding populations will be affected by changes in survival and reproduction rates due to conditions during non-breeding. For international migratory bird conservation, a diverse management strategy is necessary at the species level when and where migratory connectivity is strong, and instances of weaker migratory connectivity allow identification of areas important to multiple breeding populations, where addressing threats has a broad impact.

Research on avian migratory connectivity has increased in recent years (Marra et al. 2019), and there is growing awareness of its importance for migratory marine species (Dunn et al. 2019, Bentley et al. 2025), including seabirds (González-Solís et al. 2007, Merkel et al. 2021, O'Hanlon et al. 2024, Rexer-Huber et al. 2025). *Fratercula arctica* (Atlantic Puffins, hereafter, 'puffin'), in the Family Alcidae (hereafter 'alcids'), are one example of a migratory seabird. Strongly philopatric during the breeding season (Harris 1983), they move away from their colonies during non-breeding, presumably to areas where they can forage efficiently to replenish energy, molt flight feathers, and survive winter in the north Atlantic Ocean. These movements follow a gradual, continuous travel pattern (Harris et al. 2010, Jessopp et al. 2013, Fayet et al. 2017,

Baran et al. 2022, Runnells et al. 2024) – sometimes termed a “fly and forage” strategy (Amélineau et al. 2021). As alcids, their high wing loading (body mass:wing area, Pennycuik 1987) means that flight is energetically expensive, so it is not efficient for a puffin to fly long distances or for long durations (Elliott et al. 2013). However, compared to other alcids such as *Uria aalge* (McFarlane Tranquilla et al. 2013, Bennett et al. 2022) and *Cepphus grylle* (Baak et al. 2021), they can cover much greater distances during the non-breeding period (Jessopp et al. 2013, Fayet et al. 2017). There is high inter-individual and inter-breeding population variability in dispersal distances, depending partly on colony size and the environmental conditions around the colony (Fayet et al. 2017). Puffin movements match the definition of a dispersive migration (Newton 2024), where individual members of a breeding population move away from the breeding area and then return, but not necessarily all going in the same direction, like *Progne subis* (Purple Martin) north-south migrations (Fraser et al. 2013) or *Ardenna grisea* (Sooty Shearwater) figure eight migrations (Hedd et al. 2012). Research on puffin non-breeding ecology, including migration, is on the IUCN list of recommended conservation actions for this vulnerable species (BirdLife International 2018).

Canadian puffin breeding populations do not seem to be experiencing the declines projected for European populations (BirdLife International 2018), although some are assessed to be at risk of extirpation (NatureServe 2025). Although their breeding range in the Northwest Atlantic spans from 79°N (Jones Sound, Nunavut) to 43°N (Gulf of Maine), half of the puffins in North America breed at colonies in Witless Bay, Newfoundland (Lowther et al. 2020), where they have recovered from historic declines resulting from hunting and bycatch (Regular et al. 2013, *The State of Canada's Birds - Atlantic Puffin* 2024). Much smaller breeding populations in Quebec and New Brunswick have been assessed as vulnerable and critically imperiled, respectively (NatureServe 2025). Threats to all Canadian puffins, during breeding and non-breeding, include climate change impacts such as increasing severe storms (Wilhelm et al. 2015) and shifts in prey abundance or distribution (Scopel et al. 2019, Suca et al. 2021) and chronic and episodic oil pollution (Wiese and Ryan 2003). Migration routes of some puffins from colonies off New Brunswick and the northeast coast of Newfoundland (over 1000 km apart) include the Labrador Sea and the Gulf of Maine (Baran et al. 2022, Runnells et al. 2024), suggesting that at least some birds from different breeding populations may be exposed to similar environmental conditions and localized threats during non-breeding. Recent genetic analysis also suggests that Canadian puffins from four different colonies experience similar selective pressures throughout the year, although New Brunswick breeding populations may be an exception (Carvey et al. 2024). To define management units of Northwest Atlantic puffins, we must understand their migratory connectivity.

Our aim was to determine the migratory connectivity of Atlantic Puffins from four breeding colonies in the Northwest Atlantic during different months throughout the non-breeding period. We predicted that the migratory connectivity among the four colonies would be strong most of the time, because the high energetic costs for puffins to move long distances would result in individuals from the same colony remaining together in areas distinct from other, distant breeding populations. However, we also expect migratory connectivity to vary seasonally. Specifically, migratory connectivity would likely weaken later in the non-breeding season, when individuals from all four colonies have traveled to the same key winter foraging locations. We

also compared temporal variation in migratory connectivity of birds from two of the colonies to inform our understanding of the stability of colony-specific non-breeding spatiotemporal overlap across an older (2013-2015) and more recent (2017-2021) period, expecting minimal change because of puffins' long lifespans. Describing the movement patterns and connectivity of these long-lived birds in this region is an important step in relating non-breeding season threats and conservation to demographic trends.

Methods

Geolocators were deployed and retrieved the following breeding season during recent years (2017-2021) on Atlantic Puffins from four distinct Canadian breeding areas: New Brunswick in the Gulf of Maine (Machias Seal Island), Quebec in the Gulf of St. Lawrence (Mingan Archipelago), Southeastern Newfoundland (Gull Island, Witless Bay), and Northeastern Newfoundland (James Island, Notre Dame Bay; Fig. 3.1, Table 3.1). Additionally, geolocators were deployed on Machias Seal Island and Gull Island during an older period (2013-2015; Table 3.1). The geocator tags measured light-levels, from which estimates of location can be derived twice daily from the timing of sunrise/sunset. We logged the light data for tag models that recorded continuous, full-spectrum light intensity, but did not for tag models that recorded lower resolution, clipped light intensity. Most of the tags also measured immersion status for the entire deployment and some recorded sea surface temperature (SST). The tags from the Mingan Archipelago (MA) and some of the tags from Machias Seal Island (MSI) originally recorded the time of a switch between wet and dry, from which we calculated the number of seconds the tag was wet in 5 minutes, to match the data format from other colonies (i.e., the number of times the tag was wet, based on samples at regular intervals, in a 5 or 10 min period, as in Baran et al. 2022, Runnells et al. 2024). These tags stopped measuring immersion status before the end of the non-breeding period. Migration periods were delineated by determining arrival and departure dates for each bird based on combinations of light and immersion data that indicated burrow attendance (e.g., description in Runnells et al. 2024), with methodology varying by the tag model and nest type because of differences in the data available to characterize behavior.

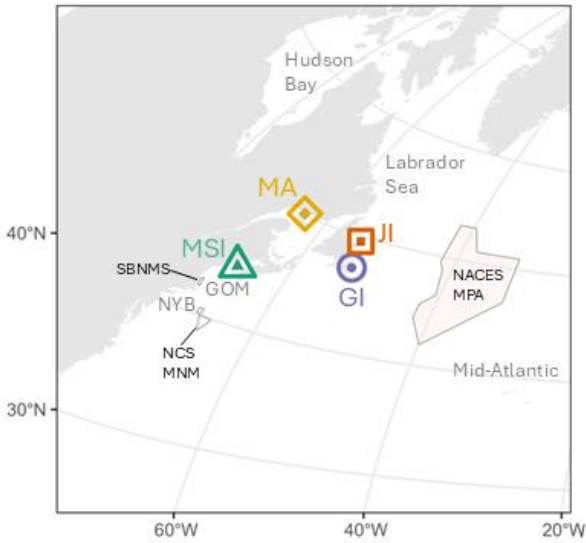


Figure 3.1: Study area in the northwest Atlantic, indicating the breeding colonies of Gull Island (GI), James Island (JI), Machias Seal Island (MSI), and the Mingan Archipelago (MA), along with referenced areas: The New York Bight (NYB), Gulf of Maine (GOM), Labrador Sea, Hudson Bay, Mid- Atlantic, North Atlantic Current and Evlanov Sea basin Marine Protected Area (NACES MPA), Stellwagen Bank National Marine Sanctuary (SBNMS), and Northeast Canyons and Seamounts Marine National Monument (NCS MNM). The MPA boundaries are provided by OSPAR (ospar.org), NOAA (sanctuaries.noaa.gov) and the Northeast Regional Ocean Council (northeastoceandata.org), and the land boundaries are from Natural Earth (naturalearthdata.com).

Table 3.1: Geolocator (GLS) retrieval summary for Atlantic Puffin breeding colonies in this study, with abbreviated colony names, the years included in the tracked migratory periods of puffins from each colony (including both older and recent periods for GI and MSI), the number of GLS tags retrieved in each period, and the colony abundance as estimated number of puffin breeding pairs at each colony (Carvey et al. 2024).

Colony	Abbrev.	Years	Period	No. tags	Abundance
Gull Island	GI	2019-2020	recent	16	140,429
		2013-2015	older	26	
James Island	JI	2019-2021	recent	13	16,859
Mingan Archipelago	MA	2019-2020	recent	9	618
Machias Seal Island	MSI	2017-2020	recent	25	8,635
		2014-2015	older	12	

The geolocator data were processed using ‘probGLS’ (Merkel et al. 2016, see Runnells et al. 2024 for input parameters) in R (R Core Team 2020, 2024), which provided 100 iterations of likely non-breeding movement paths. If temperature data were not available for the entire non-breeding period, the temperature standard deviation was set to 0.5° . ‘ProbGLS’ provides a “most probable track” which is the geographic medians of all the track iteration location estimates. We filtered out locations with a distance over 600 km between the previous location estimate along the most probable track for each bird. These locations were removed based on the assumption that puffins are unlikely to undertake long flights, and thereby adjusting for biased estimates of flight time resulting from long dry periods, which are more likely due to tucking the leg close to the body while sitting on the water rather than long flights, as in other alcids (Elliott and Gaston 2014, Linnebjerg et al. 2014). For each puffin, we calculated the geographic median location estimate for each month from approximately twice daily location estimates that were part of the most probable track during the month. Median locations both below -65° longitude and above 57° latitude (i.e. Hudson Bay, Canada, Fig. 3.1) were considered erroneous and removed, as sea ice would prevent puffins from being in this region during winter months. We also computed monthly error estimates as the 10th and 90th quantiles of latitude and longitude of all 100 iterations for each puffin in each month.

We measured migratory connectivity using the Mantel correlation (r_M) of those geographic medians of individuals for each of the non-breeding months. Mantel correlation is commonly used to indicate the strength of migratory connectivity (Cohen et al. 2018, Marra et al. 2019). In the context of Atlantic Puffins, this correlation relates two matrices of distances to quantify whether birds close together during non-breeding are from the same colony (or close colonies) and birds far apart during non-breeding are from different colonies (or far apart colonies), indicating strong connectivity, or whether birds close during non-breeding are from different (or far apart) colonies (weak connectivity). The range of r_M values is -1 to 1, with $r_M = 1$ indicating that the relative distances between individuals during non-breeding are the same as during breeding (strong connectivity). The farther the r_M value is from 1, the weaker the migratory connectivity among the breeding populations. We calculated Mantel correlation instead of the more recently developed MC (Cohen et al. 2018) because we could not clearly define non-breeding area polygons in the ocean and calculate breeding – non-breeding transition probabilities due to puffins’ dispersive migration and essentially continuous non-breeding area. As these dispersive migration patterns are observed throughout their range (Fayet et al. 2017), we focused our analysis of puffin migratory connectivity on temporal (i.e., monthly) patterns (as in Knight et al. 2021, Korpach et al. 2022). Additionally, because puffins breed on colonies, the distances between breeding locations can be accurately and precisely incorporated into the r_M calculation without measurement error.

By using the ‘estMantel’ function in the ‘MigConnectivity’ R package (Hostetler and Hallworth 2024), we performed a weighted bootstrap of the r_M calculation for each month. Monthly r_M was calculated on four sets of data: all the tracks from all colonies during the ‘recent period’ (2017-2021), all the tracks from all colonies from one year of the recent period (2019-2020), all the tracks from two colonies (GI, MSI) from the recent period, and all tracks from those two colonies from the ‘older period’ (2013-2015). We incorporated error in geolocation estimates into each bootstrapped r_M calculation. First, we measured the distance from the geographic

median of each puffin to both the 90th and 10th quantiles of latitude of each puffin and used the larger of the distances as the error estimate. The same process was completed for longitude. Then, following Cohen et al. (2018), an intercept-only multivariate linear model on those latitude and longitude errors was used to estimate bias (the point estimates of the linear model coefficients – essentially the average error across all birds) and lack of precision (the variance-covariance matrix of the linear model coefficients) in the geolocator-based locations. Breeding locations were provided as the same colony centroid point estimate for each bird from a given colony, and the breeding sites were delineated as a 0.5° buffer around those colony centroid points to meet function requirements. Non-breeding locations were the monthly geographic medians for each bird (described above). We also included the relative abundance of each colony, calculated by dividing the estimated abundance (number of breeding pairs) at a colony (Table 3.1) by the sum of the abundances for all colonies in the analysis. Relative abundances were included to prevent biased r_M estimates, as the sample sizes of tagged birds at each colony were not proportional to the breeding population sizes (“incomplete sampling”, Cohen 2018). The ‘estMantel’ function sampled 10,000 times ($nBoot = 10,000$), proportional to the relative abundances, from a multivariate normal distribution of the latitudinal and longitudinal uncertainty and bias in the non-breeding location with a parametric bootstrap. Output included means, medians and 95% confidence intervals of r_M . As the means and medians were similar for all months in all four datasets, bias-corrected confidence intervals were not needed.

Results

The error in our GLS location estimates was in the range expected for accuracy of these tags (Phillips et al. 2004, Merkel et al. 2016, Halpin et al. 2021), with greater error ranges during the months around the equinoxes (September/October & March/April, Fig. 3.2, Fig. 3.S1), when there is the least accuracy in latitude estimates. Errors can also be introduced when birds spend time in geographically enclosed waters, if the algorithm pushes locations initially estimated on land to the wrong inlet. Filtering out Hudson Bay locations caused three birds to be excluded from the analysis from MSI during February and March, and one bird from MA during January – April. That one bird from MA was also excluded from the 2019-2020 only analysis. Additionally, one MSI bird from the older dataset was excluded from the two-colony analysis during March.

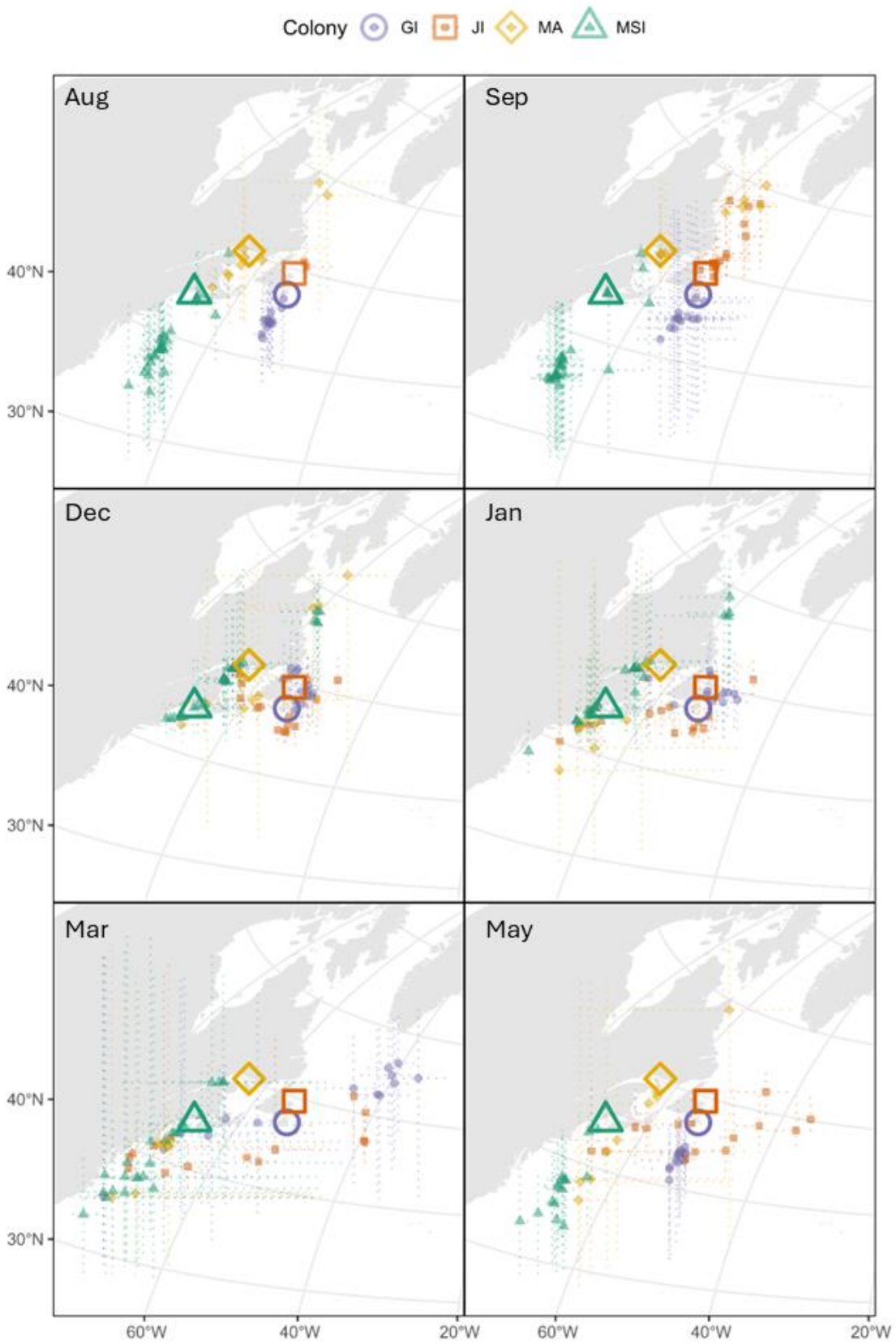


Figure 3.2: Geographic median locations of puffin tracks for select months from the recent period (2017-2021) from four colonies: GI = Gull Is., JI = James Is., MA = Mingan Archipelago, MSI = Machias Seal Is. Shape and color indicate the birds from each breeding colony. Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth ([naturalearthdata.com](https://www.naturalearthdata.com)).

In the recent dataset, the Mantel correlation (r_M) was high during the months after the breeding season (August-December), indicating strong migratory connectivity among birds from all colonies when birds from different colonies were spatially segregated (Fig. 3.3A). During August, puffins mostly remained near the colonies, as not all Newfoundland puffins had finished breeding but MSI puffins had already begun to disperse. September includes the equinox period, so error estimates were larger. However, there was a slight weakening in migratory connectivity in September and October (Fig. 3.3A) associated with birds from two colonies (JI, MA) co-located off in the Labrador Sea, north of Newfoundland (Fig. 3.2). By December, many MSI puffins were in the Labrador Sea, but puffins from other colonies were no longer there, causing continued high r_M . At that point, one or two individuals from MA were farther south with puffins from MSI, birds from the two Newfoundland colonies (JI, GI) were mixed, and there were individuals from three colonies in the Gulf of St. Lawrence (Fig. 3.2). When only considering birds tracked in the same year (Fig. 3.3B), we found almost identical r_M in the fall, except for possibly weaker connectivity around the fall equinox (September mean r_M : 0.72 vs 0.82, October mean r_M : 0.59 vs 0.85), but also larger confidence intervals (as expected with smaller sample sizes).

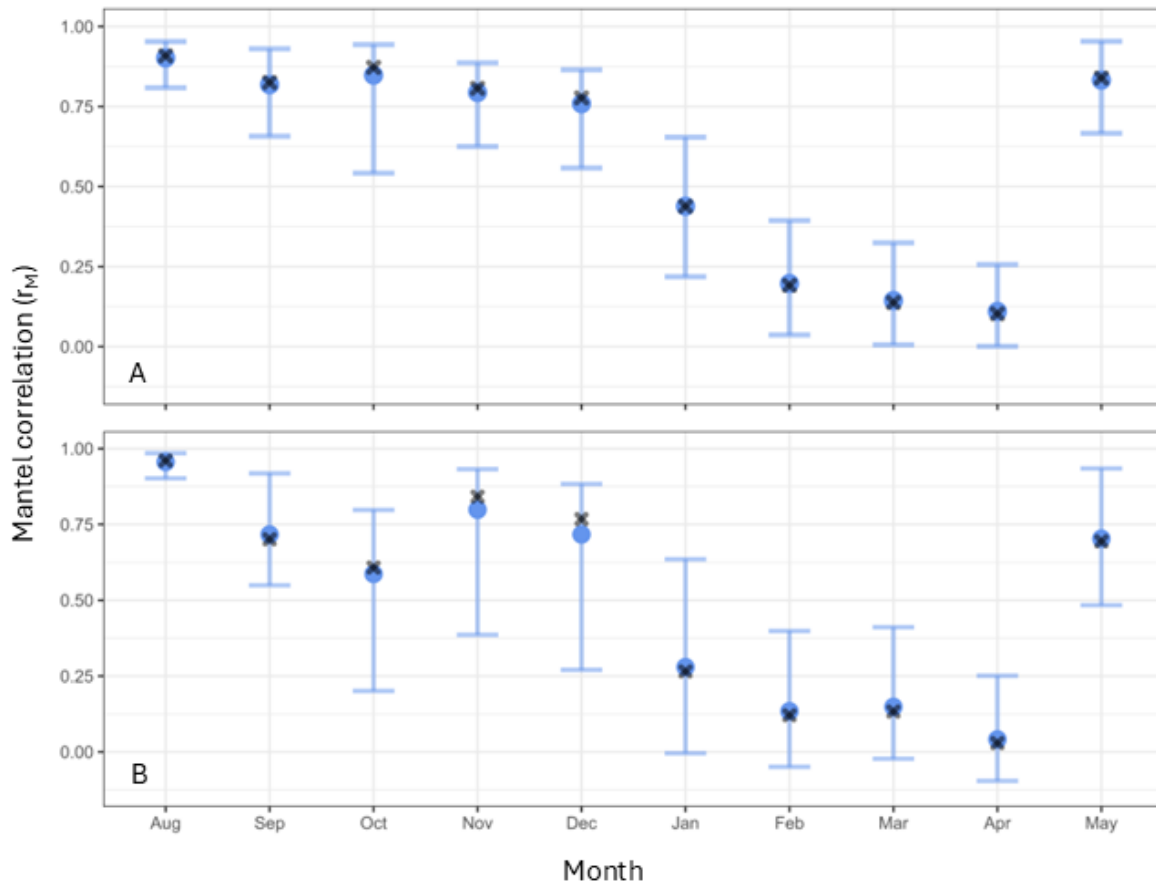


Figure 3.3: Mantel correlation by month for birds from James Is., Gull Is., the Mingan Archipelago, and Machias Seal Is., A) including all years in the recent dataset (2017-2021) and B) only including birds from one year, 2019-2020. Means are represented by a dot, medians by an x, and error bars denote 95% confidence intervals.

Migratory connectivity weakened later into the winter as birds from different colonies moved closer together, with r_M being lower in February, March, and April. The 2019-2020 analysis mean r_M for December was not lower than when all years were included, although the confidence interval was very broad (CI = [0.27, 0.88]). By March, latitudinal errors increased around the spring equinox (Fig. 3.2), but migratory connectivity had weakened (Fig. 3.3A, r_M = 0.14), as there was much spatial overlap among birds from different colonies. Puffins from all colonies were in the Gulf of Maine, and puffins from both Newfoundland colonies (JI and GI) were out in the mid-Atlantic (Fig. 3.2). Only in May did migratory connectivity strengthen again, as birds began to move back towards their colonies (Fig. 3.2), although the confidence interval was wider than in August (Fig. 3.3A). Once again, these patterns in the dataset that included all birds tracked in the recent period were mirrored when only birds tracked in the same year were included (Fig. 3.3B).

There was some indication of subtle shifts in the patterns of migratory connectivity between older and more recent years, based on datasets from GI and MSI only (Fig. 3.4). In the older dataset, in August, many puffins from MSI moved northward, closer to Newfoundland where many GI birds stayed, which resulted in weaker migratory connectivity (Figs. 3.4, 3.5). The migratory connectivity between birds from GI and MSI remained strong through December in the recent dataset, whereas r_M lowered right away in September in the older dataset and migratory connectivity stayed weak through December (Fig. 3.4). These lower r_M values in the older dataset were associated with first more northerly movement of birds from MSI, followed by more southerly movement of birds from GI (Fig. 3.5). During both periods, migratory connectivity weakened from February through April, when r_M values were within a similar range during those months (Fig. 3.4). The average r_M stayed low in May in the older dataset, although there was very wide uncertainty in the estimate (Fig. 3.4), possibly due to some birds from GI taking longer to return to the colony (Fig. 3.5). By contrast, migratory connectivity strengthened in April in the recent dataset.

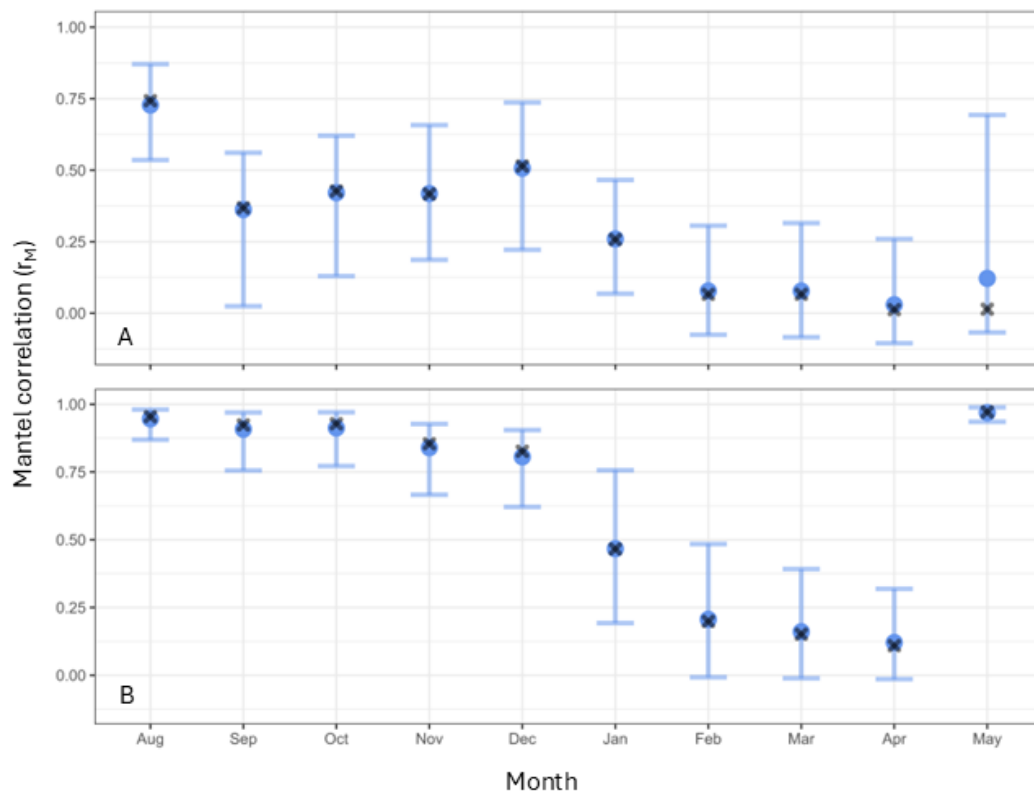


Figure 3.4: Mantel correlation by month for birds only from Gull Island and Machias Seal Island during A) 2013-2015 and B) 2017-2021. Means are represented by a dot, medians by an x, and error bars denote 95% confidence intervals.

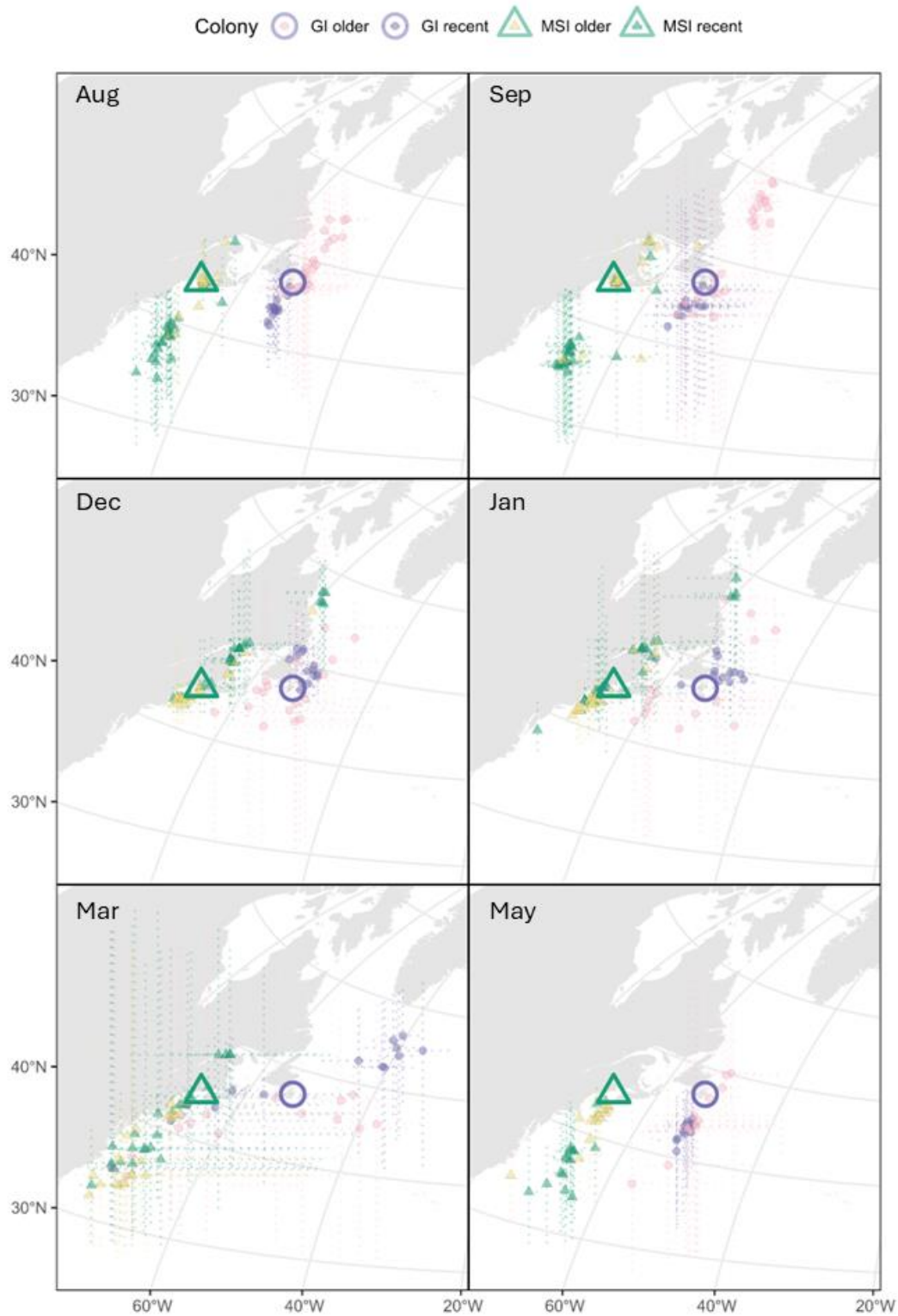


Figure 3.5: Geographic median locations of puffin tracks for select months from recent (teal and purple) and older (pink and yellow) years from two colonies: GI = Gull Is. (circles), MSI = Machias Seal Is. (triangles). Error bars denote the middle 80% of all iteration results in the

month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth ([naturalearthdata.com](https://www.naturalearthdata.com)).

Discussion

As predicted, there was strong migratory connectivity among Atlantic Puffins early in the non-breeding period, weakening later in non-breeding. The month by month weakening of migratory connectivity reflects puffins gradual, dispersive migration as they slowly travel to key wintering locations used by puffins from multiple breeding colonies and indicates that puffins rely on different areas along their route to these key wintering locations. Given their vulnerable IUCN conservation status and suggested conservation actions largely focused on their migratory period (BirdLife International 2018), understanding the migratory connectivity of puffins in the Northwest Atlantic is crucial for differentiating locations where a single or multiple puffin breeding populations are sensitive to marine anthropogenic activity such as offshore energy development and shipping, and climate change impacts. Marine migratory species, like puffins, are generally at high risk, because they are exposed to a wider range of threats over the larger area occupied (Lascelles et al. 2014). Therefore, this shift in migratory connectivity strength allows us to understand when during the non-breeding period conservation actions will address threats to breeding populations on specific colonies and when they will have an impact on multiple colonies throughout the broader region.

Migratory connectivity was strong early in the non-breeding period, when many puffins stayed around their colonies, and as birds returned to their colonies in the spring. Variation in breeding phenology among colonies clearly had an impact on Mantel correlation values at these times. For example, the very strong migratory connectivity in August occurred when birds at some colonies had completed chick rearing and began dispersing to the Labrador Sea, while birds at other colonies were mostly still breeding and, thus, did not move into the Labrador Sea until September. There was also variation in when birds returned to the colonies, with puffins at more southerly colonies starting breeding earlier in the year, but birds from more northerly colonies remaining in the Gulf of Maine, only returning to their colonies late in May. These times of year when connectivity was strong, bookending the breeding season, are periods of high energy requirements, as puffins recover from, and prepare for, laying an egg and provisioning a chick. Chick provisioning is thought to be an annual peak of energy expenditure for many birds (Lack 1968), particularly alcids and penguins (Green et al. 2009, Elliott and Gaston 2014), suggesting that adults need to replenish energy stores immediately post-parental care. Increases in daily energy expenditure just before commencement of breeding have been reported in other alcids (Dunn et al. 2020, Buckingham et al. 2023), and penguins (Green et al. 2009), likely associated with courtship, defending a nest site, and increased foraging as females source the nutrients for an egg (Bond and Diamond 2010, Barrett et al. 2012, Kouwenberg et al. 2016). As quality foraging conditions are crucial pre- and post-breeding, and puffins may already be displaced from the highest quality prey by sympatrically breeding species (Piatt 1990, Runnells et al. 2024), it is important to mitigate threats that may result in lower prey availability, such as fishing practices that lower prey abundance or destroy prey habitat. Strong migratory

connectivity at these times requires addressing threats in multiple areas nearby each colony along with areas that puffins visit sequentially post-breeding, like the Labrador Sea.

The weaker migratory connectivity later in non-breeding, as puffins reached their maximum dispersal extent, was due to spatial overlap of birds from multiple breeding populations in the Gulf of Maine, the New York Bight, and the mid-Atlantic, indicating that these are key wintering areas for puffins from multiple breeding colonies, as suggested in other studies (Baran et al. 2022, Runnells et al. 2024). Fortunately, designated protected areas already exist in those parts of the ocean (Fig. 3.1). In the mid-Atlantic, the North Atlantic Current and Evlanov Sea basin (NACES) marine protected area (MPA) was recently designated by the OSPAR Convention (the Convention for the Protection of the Marine Environment of the North- East Atlantic) specifically to protect 595,196 km² of seabird feeding and foraging grounds (Davies et al. 2021a, 2021b). Off the North American coast, smaller designated areas include the Stellwagen Bank National Marine Sanctuary (2,181 km², SBNMS) and the Northeast Canyons and Seamounts National Marine Monument (12,725 km², NCS MNM), the latter which specifically mentions puffins as relying on the area for food (“Northeast Canyons and Seamounts Marine Monument Mangement Plan” 2024). Although protections in all three areas include prohibitions on disturbance of the seabed, regulations and management capabilities vary, plus there is minimal knowledge of how other current and emerging threats to puffins would be mitigated (Davies et al. 2021a). For instance, offshore wind development is in progress and planned in the New York Bight and Gulf of Maine (Stenhouse et al. 2020, NROC 2023, Moriarty 2023). Although there is low risk of puffins colliding with turbine blades (Bradbury et al. 2014, Johnston et al. 2014), their limited underwater visual field might increase the risk of collisions while diving (Martin and Wanless 2015), and they may be susceptible to displacement, like other alcids (Vanermen et al. 2015, Welcker and Nehls 2016, Kelsey et al. 2018), which could have population-level impacts (Busch and Garthe 2016, Peschko et al. 2024). Another serious, emerging, area-specific threat is warming ocean waters due to climate change. The Gulf of Maine (GOM) and Northwest Atlantic more generally are some of the fastest warming ocean regions (Saba et al. 2016, Pershing et al. 2021), with documented impacts on many marine species (Pershing et al. 2021), including breeding puffins (Major et al. 2021). Increased winter sea surface temperature, presumably associated with reduced food supply, is a strong indicator of poor puffin reproductive success at colonies in the GOM (Scopel et al. 2019), and our finding of weak connectivity January - April implies that GOM winter SST would affect all Canadian breeding populations. Most evidence suggests that the majority of puffins in the Northwest Atlantic are molting primaries during the late winter or early spring (Pyle 2009, Currie et al. 2024), which leaves them flightless and vulnerable with increased energetic demands of feather growth. Molting at this time when migratory connectivity is at its weakest underscores the importance of habitat protection in these key wintering areas used by puffins from multiple colonies.

There was a shift in the monthly patterns of migratory connectivity strength between the older dataset (2013-2015) and recent dataset (2017-2020), with weaker migratory connectivity in most of the fall months and more variability in migratory connectivity strength during May in the earlier period. It appears that puffins from Newfoundland and the Gulf of Maine are staying in the area around their colonies longer after breeding in more recent years, whereas they used

to move longer distances earlier, bringing birds from different colonies closer together sooner. The prompt dispersal in the earlier years may be explained by having higher energy reserves available to begin migrating immediately post-breeding relative to more recent years. Capelin, a key prey for breeding puffins in NL, have shifted towards later peak spawning during 2017-2021 as compared to 2014-2015 throughout the eastern Newfoundland coast (Davoren 2024, Tripp et al. 2025). Later capelin spawning timing creates a mismatch between chick provisioning and high prey availability (Davoren 2024), leading alcids to increase their foraging effort (Gulka and Davoren 2019, Lescure et al. 2023) and therefore energy expenditure. Therefore, higher mismatches in recent years could explain why birds disperse later, because they need to replenish energy reserves post-breeding before beginning migration. At the other end of the non-breeding period, the decreased range in timing of spring arrival at breeding colonies in the recent period may be related to environmental cues in the GOM, where there are documented climate driven impacts leading to a later spring phytoplankton bloom (Record et al. 2019), reduced abundance of key zooplankton (Reygondeau and Beaugrand 2011, Grieve et al. 2017), and shifts in the forage fish community (Suca et al. 2021), among many other ecosystem components (Pershing et al. 2021). These changes in puffin migration phenology suggest a need for continued monitoring of puffin movements to support dynamic management options (Lascelles et al. 2014, Tittensor et al. 2019, Lynch et al. 2021).

In conclusion, the gradual weakening of migratory connectivity strength throughout the non-breeding months means that threats to specific breeding populations need to be addressed at multiple locations in the autumn months (Webster et al. 2002, Norris and Marra 2007, Hooker et al. 2011), and that multi-agency and multi-national collaboration is required to address threats in the latter half of the non-breeding season, including on the high seas (Blasiak and Yagi 2016, Tittensor et al. 2019, Davies et al. 2021a, Gjerde et al. 2022). The at-risk status of puffins in Quebec and New Brunswick, but not Newfoundland (CESCC 2022, NatureServe 2025), suggests that threats associated with periods of strong migratory connectivity are differentially impacting population abundances and trends, and thus need to be addressed for birds breeding at MSI and MA. Although a few of the areas where puffins from multiple colonies aggregate in the winter are partially protected from some threats (Fig. 3.1; Davies et al. 2021b), there are other areas that require consideration, such as the Labrador Sea, and it is important to ensure that the mitigation of pelagic threats is a component of marine protected area designation (Game et al. 2009, Hooker et al. 2011). Although the annual trends in migratory connectivity strength in one year of data were similar to the trends in multiple years of data, the differences between an older tracking dataset and a more recent dataset indicates that puffin migration phenology can change over time, so continued monitoring is important (Hays et al. 2019), especially given the rapidly changing ocean conditions in the region (Halpern et al. 2019, Pershing et al. 2021). Further research into puffin non-breeding habitat characteristics (e.g., Harris et al. 2015) and seasonal interactions, such as carry-over effects, would provide greater insight into the drivers of puffin movement patterns and increase our predictive ability for addressing emerging threats. The handful of seabird migratory connectivity studies to date have elucidated exposure to threats (González-Solís et al. 2007, Rexer-Huber et al. 2025) and refined our understanding of critical habitat (Merkel et al. 2021, O'Hanlon et al. 2024), indicating that an increase in migratory connectivity research is key to addressing conservation of this highly threatened group of birds during non-breeding (Lewison et al. 2012, Dias et al. 2019).

References

- Allen, A. M., and N. J. Singh. 2016. Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution* 3:1–13.
- Amélineau, F., B. Merkel, A. Tarroux, S. Descamps, T. Anker-Nilssen, O. Bjørnstad, V. S. Bråthen, O. Chastel, S. Christensen-Dalsgaard, J. Danielsen, F. Daunt, N. Dehnhard, M. Ekker, K. E. Erikstad, A. Ezhov, P. Fauchald, M. Gavrilov, G. T. Hallgrimsson, E. S. Hansen, M. P. Harris, M. Helberg, H. H. Helgason, M. K. Johansen, J. E. Jónsson, Y. Kolbeinsson, Y. Krasnov, M. Langset, S. H. Lorentsen, E. Lorentzen, M. V. Melnikov, B. Moe, M. A. Newell, B. Olsen, T. Reiertsen, G. H. Systad, P. Thompson, T. L. Thórarinnsson, E. Tolmacheva, S. Wanless, K. Wojczulanis-Jakubas, J. Åström, and H. Strøm. 2021. Six pelagic seabird species of the North Atlantic engage in a fly-and-forage strategy during their migratory movements. *Marine Ecology Progress Series* 676:127–144.
- Baak, J. E., M. L. Leonard, C. Gjerdrum, M. D. Dodds, and R. A. Ronconi. 2021. Non-breeding movements and foraging ecology of the black guillemot *cepphus grylle* in atlantic Canada. *Marine Ornithology* 49:57–70.
- Baran, M. A., S. W. Kress, P. Shannon, D. E. Lyons, H. L. Major, and A. W. Diamond. 2022. Overwinter movement of Atlantic puffins (*Fratercula arctica*) breeding in the Gulf of Maine: Inter- and intra-colony effects. *Waterbirds* 45:1–16.
- Barrett, R. T., E. B. Nilsen, and T. Anker-Nilssen. 2012. Long-term decline in egg size of Atlantic puffins *Fratercula arctica* is related to changes in forage fish stocks and climate conditions. *Marine Ecology Progress Series* 457:1–10.
- Bennett, S., M. P. Harris, S. Wanless, J. A. Green, M. A. Newell, K. R. Searle, and F. Daunt. 2022. Earlier and more frequent occupation of breeding sites during the non-breeding season increases breeding success in a colonial seabird. *Ecology and Evolution* 12:e9213.
- Bentley, L. K., D. Nisthar, E. Fujioka, C. Curtice, S. E. Deland, B. Donnelly, A. Harrison, E. I. Heywood, C. Y. Kot, G. O. Crespo, S. Poulin, P. N. Halpin, and D. C. Dunn. 2025. Marine megavertebrate migrations connect the global ocean. *Nature Communications*.
- BirdLife International. 2018. *Fratercula arctica*, Atlantic Puffin. The IUCN Red List of Threatened Species 8235.
- Blasiak, R., and N. Yagi. 2016. Shaping an international agreement on marine biodiversity beyond areas of national jurisdiction: Lessons from high seas fisheries. *Marine Policy* 71:210–216.
- Bond, A. L., and A. W. Diamond. 2010. Nutrient allocation for egg production in six atlantic seabirds. *Canadian Journal of Zoology* 88:1095–1102.
- Bradbury, G., M. Trinder, B. Furness, A. N. Banks, R. W. G. Caldow, and D. Hume. 2014. Mapping Seabird Sensitivity to offshore wind farms. *PLoS ONE* 9.
- Buckingham, L., F. Daunt, M. I. Bogdanova, R. W. Furness, S. Bennett, J. Duckworth, R. E.

- Dunn, S. Wanless, M. P. Harris, D. C. Jardine, M. A. Newell, R. M. Ward, E. D. Weston, and J. A. Green. 2023. Energetic synchrony throughout the non-breeding season in common guillemots from four colonies. *Journal of Avian Biology* 2023:1–16.
- Busch, M., and S. Garthe. 2016. Approaching population thresholds in presence of uncertainty: Assessing displacement of seabirds from offshore wind farms. *Environmental Impact Assessment Review* 56:31–42.
- Carvey, Q. B., S. A. Pavey, A. W. Diamond, G. K. Davoren, R. A. Lavoie, N. M. LeBlanc, M. J. Legard, G. J. Robertson, E. S. Runnells, C. Petalas, and H. L. Major. 2024. Genetic structure of Atlantic Puffins (*Fratercula arctica*) breeding in Atlantic Canada. *Conservation Genetics*.
- CESCC. 2022. Wild Species 2020: The General Status of Species in Canada.
- Cohen, E. B., J. A. Hostetler, M. T. Hallworth, C. S. Rushing, T. S. Sillett, and P. P. Marra. 2018. Quantifying the strength of migratory connectivity. *Methods in Ecology and Evolution* 9:513–524.
- Costa, D. P., G. a. Breed, and P. W. Robinson. 2012. New Insights into Pelagic Migrations: Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and Systematics* 43:73–96.
- Cowen, R. K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443–466.
- Currie, C. M. V., E. S. Runnells, and G. K. Davoren. 2024. Stable Isotopes Reveal Primary Flight Feather Moults Patterns of Atlantic Puffins (*Fratercula arctica*). *Journal of Ornithology*.
- Davies, T. E., A. P. B. Carneiro, B. Campos, C. Hazin, D. C. Dunn, K. M. Gjerd, D. E. Johnson, and M. P. Dias. 2021a. Tracking data and the conservation of the high seas: Opportunities and challenges. *Journal of Applied Ecology* 58:2703–2710.
- Davies, T. E., A. P. B. Carneiro, M. Tarzia, E. Wakefield, J. C. Hennicke, M. Frederiksen, E. S. Hansen, B. Campos, C. Hazin, B. Lascelles, T. Anker-Nilssen, H. Arnardóttir, R. T. Barrett, M. Bischoff, L. Bollache, T. Boulinier, P. Catry, F. R. Ceia, O. Chastel, S. Christensen-Dalsgaard, M. Cruz-Flores, J. Danielsen, F. Daunt, E. Dunn, C. Egevang, A. I. Fagundes, A. L. Fayet, J. Fort, R. W. Furness, O. Gilg, J. González-Solís, J. P. Granadeiro, D. Grémillet, T. Guilford, S. A. Hanssen, M. P. Harris, A. Hedd, N. P. Huffeldt, M. Jessopp, Y. Kolbeinsson, J. Krietsch, J. Lang, J. F. Linnebjerg, S. H. Lorentsen, J. Madeiros, E. Magnusdottir, M. L. Mallory, L. McFarlane Tranquilla, F. R. Merkel, T. Militão, B. Moe, W. A. Montevecchi, V. Morera-Pujol, A. Mosbech, V. Neves, M. A. Newell, B. Olsen, V. H. Paiva, H. U. Peter, A. Petersen, R. A. Phillips, I. Ramírez, J. A. Ramos, R. Ramos, R. A. Ronconi, P. G. Ryan, N. M. Schmidt, I. A. Sigurðsson, B. Sittler, H. Steen, I. J. Stenhouse, H. Strøm, G. H. R. Systad, P. Thompson, T. L. Thórarinnsson, R. S. A. van Bemmelen, S. Wanless, F. Zino, and M. P. Dias. 2021b. Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conservation Letters* 14:1–14.

- Davoren, G. K. 2024. Variable forage fish biomass and phenology influence marine predator diet, foraging behavior, and species interactions in coastal Newfoundland, Canada. *ICES Journal of Marine Science* 81:629–642.
- Desprez, M., S. Jenouvrier, C. Barbraud, K. Delord, and H. Weimerskirch. 2018. Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. *Functional Ecology* 32:2040–2053.
- Dias, M. P., R. Martin, E. J. Pearmain, I. J. Burfield, C. Small, R. A. Phillips, O. Yates, B. Lascelles, P. G. Borboroglu, and J. P. Croxall. 2019. Threats to seabirds: A global assessment. *Biological Conservation* 237:525–537.
- Dunn, D. C., A. L. Harrison, C. Curtice, S. DeLand, B. Donnelly, E. Fujioka, E. Heywood, C. Y. Kot, S. Poulin, M. Whitten, S. Åkesson, A. Alberini, W. Appeltans, J. M. Arcos, H. Bailey, L. T. Ballance, B. Block, H. Blondin, A. M. Boustany, J. Brenner, P. Catry, D. Cejudo, J. Cleary, P. Corkeron, D. P. Costa, M. Coyne, G. O. Crespo, T. E. Davies, M. P. Dias, F. Douvere, F. Ferretti, A. Formia, D. Freestone, A. S. Friedlaender, H. Frisch-Nwakanma, C. B. Froján, K. M. Gjerde, L. Glowka, B. J. Godley, J. Gonzalez-Solis, J. P. Granadeiro, V. Gunn, Y. Hashimoto, L. M. Hawkes, G. C. Hays, C. Hazin, J. Jimenez, D. E. Johnson, P. Luschi, S. M. Maxwell, C. McClellan, M. Modest, G. N. Di Sciara, A. H. Palacio, D. M. Palacios, A. Pauly, M. Rayner, A. F. Rees, E. R. Salazar, D. Secor, A. M. M. Sequeira, M. Spalding, F. Spina, S. Van Parijs, B. Wallace, N. Varo-Cruz, M. Virtue, H. Weimerskirch, L. Wilson, B. Woodward, and P. N. Halpin. 2019. The importance of migratory connectivity for global ocean policy. *Proceedings of the Royal Society B: Biological Sciences* 286.
- Dunn, R. E., S. Wanless, F. Daunt, M. P. Harris, and J. A. Green. 2020. A year in the life of a North Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Scientific Reports* 10:5993.
- Elliott, K. H., and A. J. Gaston. 2014. Dive behaviour and daily energy expenditure in Thick-billed murrelets *Uria lomvia* after leaving the breeding colony. *Marine Ornithology* 189:183–189.
- Elliott, K. H., R. E. Ricklefs, A. J. Gaston, S. A. Hatch, J. R. Speakman, and G. K. Davoren. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proceedings of the National Academy of Sciences of the United States of America* 110:9380–9384.
- Faaborg, R. T., J. Holmes, A. Anders, K. L. Bildstein, K. Dugger, S. Gauthreaux, P. Heglund, K. Hobson, D. H. Johnson, S. Latta, D. J. Levey, P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. S. Sillett, T. W. Sherry, F. R. Thompson, and N. Warnoc. 2010. Managing migratory landbirds in the New World: do we know enough? *Ecological Applications* 20:398–418.
- Fayet, A. L., R. Freeman, T. Anker-Nilssen, A. Diamond, K. E. Erikstad, D. Fifield, M. G. Fitzsimmons, E. S. Hansen, M. P. Harris, M. Jessopp, A. L. Kouwenberg, S. Kress, S.

- Mowat, C. M. Perrins, A. Petersen, I. K. Petersen, T. K. Reiertsen, G. J. Robertson, P. Shannon, I. A. Sigurðsson, A. Shoji, S. Wanless, and T. Guilford. 2017. Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Current Biology* 27:3871-3878.e3.
- Fraser, K. C., K. T. A. Davies, C. M. Davy, A. T. Ford, D. T. T. Flockhart, and E. G. Martins. 2018. Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution* 6:1–8.
- Fraser, K. C., B. J. M. Stutchbury, P. Kramer, C. Silverio, J. Barrow, D. Newstead, N. Mickle, T. Shaheen, P. Mammenga, K. Applegate, E. Bridge, and J. Tautin. 2013. Consistent range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. *Auk* 130:291–296.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton University Press.
- Game, E. T., H. S. Grantham, A. J. Hobday, R. L. Pressey, A. T. Lombard, L. E. Beckley, K. Gjerde, R. Bustamante, H. P. Possingham, and A. J. Richardson. 2009. Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution* 24:360–369.
- Gjerde, K. M., N. A. Clark, C. Chazot, K. Cremers, H. Harden-Davies, D. Kachelriess, C. R. Payne, M. Rodriguez-Chaves, A. Spadone, T. Thiele, M. Vierros, G. Goettsche-Wanli, and G. Wright. 2022. Getting beyond yes: fast-tracking implementation of the United Nations agreement for marine biodiversity beyond national jurisdiction. *NPJ Ocean Sustainability* 1.
- González-Solís, J., J. P. Croxall, D. Oro, and X. Ruiz. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* 5:297–301.
- Green, J. A., I. L. Boyd, A. J. Woakes, N. L. Warren, and P. J. Butler. 2009. Evaluating the prudence of parents: Daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *Journal of Avian Biology* 40:529–538.
- Grieve, B. D., J. A. Hare, and V. S. Saba. 2017. Projecting the effects of climate change on *Calanus finmarchicus* distribution within the U.S. Northeast Continental Shelf. *Scientific Reports* 7:1–12.
- Gulka, J., and G. K. Davoren. 2019. High individual flexibility in the foraging behavior of a marine predator, the common murre. *Marine Biology* 166:1–16.
- Halpern, B. S., M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, and K. A. Selkoe. 2019. Recent pace of change in human impact on the world's ocean. *Scientific Reports* 9:1–8.
- Halpin, L. R., J. D. Ross, R. Ramos, R. Mott, N. Carlile, N. Golding, J. M. Reyes-González, T.

- Militão, F. De Felipe, Z. Zajková, M. Cruz-Flores, S. Saldanha, V. Morera-Pujol, L. Navarro-Herrero, L. Zango, J. González-Solís, and R. H. Clarke. 2021. Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution* 12:2243–2255.
- Harris, M. P. 1983. Biology and survival of the immature puffin *Fratercula arctica*. *Ibis* 125:56–71.
- Harris, M. P., F. Daunt, M. Newell, R. A. Phillips, and S. Wanless. 2010. Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Marine Biology* 157:827–836.
- Harris, M. P., M. F. Leopold, J. K. Jensen, E. H. Meesters, and S. Wanless. 2015. The winter diet of the Atlantic Puffin *Fratercula arctica* around the Faroe Islands. *Ibis* 157:468–479.
- Hays, G. C., H. Bailey, S. J. Bograd, W. D. Bowen, C. Campagna, R. H. Carmichael, P. Casale, A. Chiaradia, D. P. Costa, E. Cuevas, P. J. Nico de Bruyn, M. P. Dias, C. M. Duarte, D. C. Dunn, P. H. Dutton, N. Esteban, A. Friedlaender, K. T. Goetz, B. J. Godley, P. N. Halpin, M. Hamann, N. Hammerschlag, R. Harcourt, A. L. Harrison, E. L. Hazen, M. R. Heupel, E. Hoyt, N. E. Humphries, C. Y. Kot, J. S. E. Lea, H. Marsh, S. M. Maxwell, C. R. McMahon, G. Notarbartolo di Sciara, D. M. Palacios, R. A. Phillips, D. Righton, G. Schofield, J. A. Seminoff, C. A. Simpfendorfer, D. W. Sims, A. Takahashi, M. J. Tetley, M. Thums, P. N. Trathan, S. Villegas-Amtmann, R. S. Wells, S. D. Whiting, N. E. Wildermann, and A. M. M. Sequeira. 2019. Translating Marine Animal Tracking Data into Conservation Policy and Management. *Trends in Ecology and Evolution* 34:459–473.
- Hedd, A., W. A. Montevecchi, H. Otley, R. A. Phillips, and D. A. Fifield. 2012. Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. *Marine Ecology Progress Series* 449:277–290.
- Hooker, S. K., A. Cañadas, K. D. Hyrenbach, C. Corrigan, J. J. Polovina, and R. R. Reeves. 2011. Making protected area networks effective for marine top predators. *Endangered Species Research* 13:203–218.
- Hostetler, J. A., and M. T. Hallworth. 2024. MigConnectivity: Estimate Migratory Connectivity for Migratory Animals.
- Jessopp, M. J., M. Cronin, T. K. Doyle, M. Wilson, A. McQuatters-Gollop, S. Newton, and R. A. Phillips. 2013. Transatlantic migration by post-breeding puffins: A strategy to exploit a temporarily abundant food resource? *Marine Biology* 160:2755–2762.
- Johnston, A., A. S. C. P. Cook, L. J. Wright, E. M. Humphreys, and N. H. K. Burton. 2014. Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *Journal of Applied Ecology* 51:31–41.
- Kelsey, E. C., J. J. Felis, M. Czapanskiy, D. M. Pereksta, and J. Adams. 2018. Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. *Journal of Environmental Management* 227:229–247.

- Knight, E. C., A. L. Harrison, A. L. Scarpignato, S. L. Van Wilgenburg, E. M. Bayne, J. W. Ng, E. Angell, R. Bowman, R. M. Brigham, B. Drolet, W. E. Easton, T. R. Forrester, J. T. Foster, S. Haché, K. C. Hannah, K. G. Hick, J. Ibarzabal, T. L. Imlay, S. A. Mackenzie, A. Marsh, L. P. McGuire, G. N. Newberry, D. Newstead, A. Sidler, P. H. Sinclair, J. L. Stephens, D. L. Swanson, J. A. Tremblay, and P. P. Marra. 2021. Comprehensive estimation of spatial and temporal migratory connectivity across the annual cycle to direct conservation efforts. *Ecography* 44:665–679.
- Korpach, A. M., C. M. Davy, A. Mills, and K. C. Fraser. 2022. Migratory connectivity and timing for an at-risk Canadian landbird, Eastern Whip-poor-will (*Antrostomus vociferus*), from two geographically distant breeding areas. *Canadian Journal of Zoology* 100:660–668.
- Kouwenberg, A. L., J. M. Hipfner, D. W. McKay, and A. E. Storey. 2016. Corticosterone levels in feathers and blood of rhinoceros auklets *Cerorhinca monocerata* are affected by variation in environmental conditions. *Marine Biology* 163:1–11.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co., London.
- Lascelles, B., G. Notarbartolo Di Sciara, T. Agardy, A. Cuttelod, S. Eckert, L. Glowka, E. Hoyt, F. Llewellyn, M. Louzao, V. Ridoux, and M. J. Tetley. 2014. Migratory marine species: Their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24:111–127.
- Lescure, L., J. Gulka, and G. Davoren. 2023. Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Marine Ecology Progress Series* 709:109–123.
- Lewison, R., D. Oro, B. J. Godley, L. Underhill, S. Bearhop, R. P. Wilson, D. Ainley, J. M. Arcos, P. D. Boersma, P. G. Borboroglu, T. Boulinier, M. Frederiksen, M. Genovart, J. González-Solís, J. A. Green, D. Grémillet, K. C. Hamer, G. M. Hilton, K. D. Hyrenbach, A. Martínez-Abraín, W. A. Montevecchi, R. A. Phillips, P. G. Ryan, P. Sagar, W. J. Sydeman, S. Wanless, Y. Watanuki, H. Weimerskirch, and P. Yorio. 2012. Research priorities for seabirds: Improving conservation and management in the 21st century. *Endangered Species Research* 17:93–121.
- Linnebjerg, J. F., N. P. Huffeldt, K. Falk, F. R. Merkel, A. Mosbech, and M. Frederiksen. 2014. Inferring seabird activity budgets from leg-mounted time-depth recorders. *Journal of Ornithology* 155:301–306.
- Lowther, P. E., A. W. Diamond, S. W. Kress, G. J. Robertson, K. Russell, D. N. Nettleship, G. M. Kirwan, D. Christie, C. Sharpe, E. Garcia, and P. F. D. Boesman. 2020. Atlantic Puffin (*Fratercula arctica*). Page <https://doi.org/10.2173/bow.atlpuf.01> in S. M. Billerman, editor. *Birds of the World*. version 1. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Lynch, A. J., L. M. Thompson, E. A. Beever, D. N. Cole, A. C. Engman, C. Hawkins Hoffman, S. T. Jackson, T. J. Krabbenhoft, D. J. Lawrence, D. Limpinsel, R. T. Magill, T. A. Melvin, J. M. Morton, R. A. Newman, J. O. Peterson, M. T. Porath, F. J. Rahel, G. W. Schuurman, S.

- A. Sethi, and J. L. Wilkening. 2021. Managing for RADical ecosystem change: applying the Resist-Accept-Direct (RAD) framework. *Frontiers in Ecology and the Environment* 19:461–469.
- Major, H. L., S. E. Durham, N. Fana, J. E. Rivers, and A. W. Diamond. 2021. Contrasting phenological and demographic responses of Atlantic Puffin (*Fratercula arctica*) and Razorbill (*Alca torda*) to climate change in the Gulf of Maine. *Elementa* 9:1–19.
- Marra, P. P., E. Cohen, A. L. Harrison, C. E. Studds, and M. Webster. 2019. Migratory Connectivity. *Encyclopedia of Animal Behavior*, Second Edition: Volume 1-5 3:V3-643-V3-654.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable- carbon isotopes. *Science* 282:1884–1886.
- Martin, G. R., and S. Wanless. 2015. The visual fields of Common Guillemots *Uria aalge* and Atlantic Puffins *Fratercula arctica*: Foraging, vigilance and collision vulnerability. *Ibis* 157:798–807.
- McFarlane Tranquilla, L., W. Montevecchi, A. Hedd, D. Fifield, C. Burke, P. Smith, P. Regular, G. Robertson, A. Gaston, and R. Phillips. 2013. Multiple-colony winter habitat use by murrelets *Uria* spp. in the Northwest Atlantic Ocean: implications for marine risk assessment. *Marine Ecology Progress Series* 472:287–303.
- Merkel, B., S. Descamps, N. G. Yoccoz, D. Grémillet, P. Fauchald, J. Danielsen, F. Daunt, K. E. Erikstad, A. V. Ezhov, M. P. Harris, M. Gavrilov, S. H. Lorentsen, T. K. Reiertsen, G. H. Systad, T. Lindberg Thórarinnsson, S. Wanless, and H. Strøm. 2021. Strong migratory connectivity across meta-populations of sympatric North Atlantic seabirds. *Marine Ecology Progress Series* 676:173–188.
- Merkel, B., R. A. Phillips, S. Descamps, N. G. Yoccoz, B. Moe, and H. Strøm. 2016. A probabilistic algorithm to process geolocation data. *Movement Ecology* 4:26–37.
- Moriarty, T. 2023, April 25. BOEM Advances Offshore Wind Leasing Process in the Gulf of Maine. Washington, DC. <https://www.boem.gov/newsroom/press-releases/boem-advances-offshore-wind-leasing-process-gulf-maine>.
- NatureServe. 2025. *Fratercula arctica* account in NatureServe Explorer [web application]. Arlington, VA.
- Newton, I. 2024. *The Migration Ecology of Birds*. Second Edi. Academic Press, London, UK; San Diego, CA; Cambridge, MA.
- Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- Northeast Canyons and Seamounts Marine Monument Mangement Plan. 2024. . United States Fish and Wildlife Service and National Oceanic and Atmospheric Administration.

- NROC. 2023. Northeast Ocean Data Portal Energy and Infrastructure Map.
<https://www.northeastoceandata.org/data-explorer/?energy-infrastructure>.
- O'Hanlon, N., R. van Bemmelen, K. Snell, G. Conway, C. Thaxter, H. Aiton, D. Aiton, D. Balmer, S. Hanssen, J. Calladine, S. Hammer, S. Harris, B. Moe, H. Schekkerman, I. Tulp, and E. Humphreys. 2024. Atlantic populations of a declining oceanic seabird have complex migrations and weak migratory connectivity to staging areas. *Marine Ecology Progress Series* 730:113–129.
- Pennycuik, C. J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: Ornithodolite observations. *Journal of Experimental Biology* 128:335–347.
- Pershing, A. J., M. A. Alexander, D. C. Brady, D. Brickman, E. N. Curchitser, A. W. Diamond, L. McClenachan, K. E. Mills, O. C. Nichols, D. E. Pendleton, N. R. Record, J. D. Scott, M. D. Staudinger, and Y. Wang. 2021. Climate impacts on the Gulf of Maine ecosystem: A review of observed and expected changes in 2050 from rising temperatures. *Elementa* 9:1–18.
- Peschko, V., H. Schwemmer, M. Mercker, N. Markones, K. Borkenhagen, and S. Garthe. 2024. Cumulative effects of offshore wind farms on common guillemots (*Uria aalge*) in the southern North Sea - climate versus biodiversity? *Biodiversity and Conservation* 33:949–970.
- Phillips, R. A., J. R. D. Silk, J. P. Croxall, V. Afanasyev, and D. R. Briggs. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266:265–272.
- Piatt, J. F. 1990. The aggregative response of common murre and Atlantic puffins to schools of capelin. Auks at sea. *Proc. international symposium of the Pacific Seabird Group*, Pacific Grove, 1987:36–51.
- Pyle, P. 2009. Age determination and molt strategies in North American alcids. *Marine Ornithology* 37:219–226.
- R Core Team. 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- R Core Team. 2024. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Record, N. R., W. M. Balch, and K. Stamieszkin. 2019. Century-scale changes in phytoplankton phenology in the Gulf of Maine. *PeerJ* 2019.
- Regular, P., W. Montevecchi, A. Hedd, G. Robertson, and S. Wilhelm. 2013. Canadian fishery closures provide a largescale test of the impact of gillnet bycatch on seabird populations. *Biology Letters* 9.
- Rexer-Huber, K., T. A. Clay, P. Catry, I. Debski, G. Parker, R. Ramos, B. C. Robertson, P. G. Ryan, P. M. Sagar, A. Stanworth, D. R. Thompson, G. N. Tuck, H. Weimerskirch, and R. A. Phillips. 2025. Metapopulation distribution shapes year-round overlap with fisheries for a circumpolar seabird. *Ecological applications* : a publication of the Ecological Society of

America 35:e70019.

- Reygondeau, G., and G. Beaugrand. 2011. Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Global Change Biology* 17:756–766.
- Runnells, E. S., W. A. Montevecchi, and G. K. Davoren. 2024. Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murre during the non-breeding season in the Northwest Atlantic. *Marine Ecology Progress Series* 739:241–256.
- Saba, V. S., S. M. Griffies, W. G. Anderson, M. Winton, M. A. Alexander, T. L. Delworth, J. A. Hare, M. J. Harrison, A. Rosati, and G. A. Vecchi. 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. *Journal of Geophysical Research: Oceans* 121:118–132.
- Scopel, L. C., A. Diamond, S. Kress, and P. Shannon. 2019. Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Marine Ecology Progress Series* 626:177–196.
- Stenhouse, I. J., A. M. Berlin, A. T. Gilbert, M. W. Goodale, C. E. Gray, W. A. Montevecchi, L. Savoy, and C. S. Spiegel. 2020. Assessing the exposure of three diving bird species to offshore wind areas on the U.S. Atlantic Outer Continental Shelf using satellite telemetry. *Diversity and Distributions* 26:1703–1714.
- Suca, J. J., J. J. Deroba, D. E. Richardson, R. Ji, and J. K. Llopiz. 2021. Environmental drivers and trends in forage fish occupancy of the Northeast US shelf. *ICES Journal of Marine Science* 78:3687–3708.
- Szostek, K. L., and P. H. Becker. 2015. Survival and local recruitment are driven by environmental carry-over effects from the wintering area in a migratory seabird. *Oecologia* 178:643–657.
- Taylor, C. M., and D. R. Norris. 2010. Population dynamics in migratory networks. *Theoretical Ecology* 3:65–73.
- The State of Canada's Birds - Atlantic Puffin. 2024. . Data Accessed from NatureCounts, Birds Canada.
- Tittensor, D. P., M. Beger, K. Boerder, D. G. Boyce, R. D. Cavanagh, A. Cosandey-Godin, G. O. Crespo, D. C. Dunn, W. Ghiffary, S. M. Grant, L. Hannah, P. N. Halpin, M. Harfoot, S. G. Heaslip, N. W. Jeffery, N. Kingston, H. K. Lotze, J. McGowan, E. McLeod, C. J. McOwen, B. C. O'Leary, L. Schiller, R. R. E. Stanley, M. Westhead, K. L. Wilson, and B. Worm. 2019. Integrating climate adaptation and biodiversity conservation in the global ocean. *Science Advances* 5:1–15.
- Tripp, A., H. M. Murphy, P. M. Penton, and G. K. Davoren. 2025. Trends in larval densities, spawning timing, and site quality of capelin (*Mallotus villosus*) across bays and habitats in Newfoundland, Canada. *ICES Journal of Marine Science* 82:1–13.

- Vanermen, N., T. Onkelinx, W. Courtens, M. Van de walle, H. Verstraete, and E. W. M. Stienen. 2015. Seabird avoidance and attraction at an offshore wind farm in the Belgian part of the North Sea. *Hydrobiologia* 756:51–61.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76–83.
- Welcker, J., and G. Nehls. 2016. Displacement of seabirds by an offshore wind farm in the North Sea. *Marine Ecology Progress Series* 554:173–182.
- Wiese, F. K., and P. C. Ryan. 2003. The extent of chronic marine oil pollution in southeastern Newfoundland waters assessed through beached bird surveys 1984-1999. *Marine Pollution Bulletin* 46:1090–1101.
- Wilhelm, S. I., J. Mailhiot, J. Arany, J. W. Chardine, G. J. Robertson, and P. C. Ryan. 2015. Update and trends of three important seabird populations in the western North Atlantic using a geographic information system approach. *Marine Ornithology* 43:211–222.
- Wojczulanis-Jakubas, K., M. Jiménez-Muñoz, D. Jakubas, D. Kidawa, N. Karnovsky, D. Cole, and E. Matechou. 2020. Duration of female parental care and their survival in the little auk *Alle alle* - are these two traits linked? *Behavioral Ecology and Sociobiology* 74.

Supplementary Figures

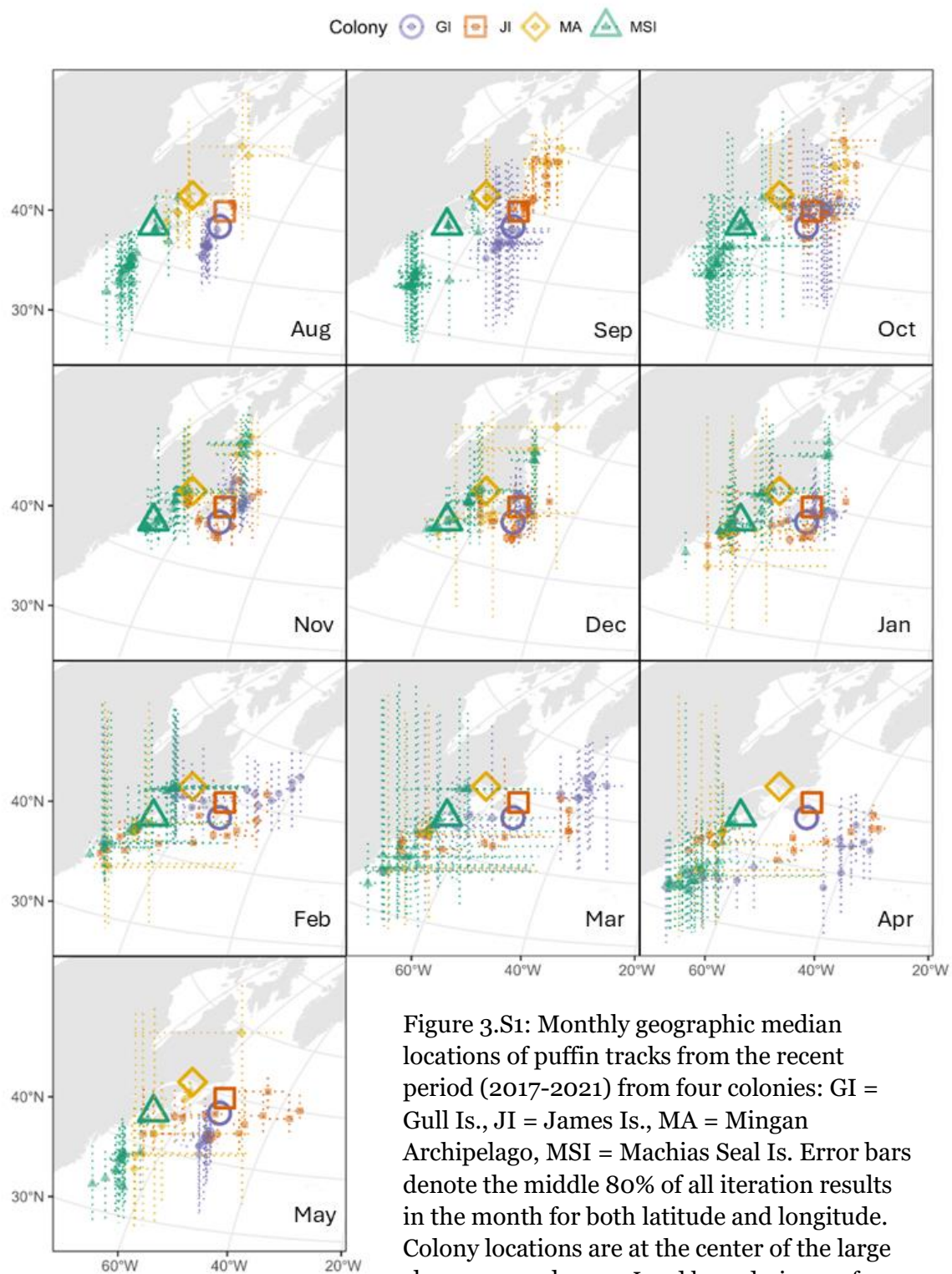


Figure 3.S1: Monthly geographic median locations of puffin tracks from the recent period (2017-2021) from four colonies: GI = Gull Is., JI = James Is., MA = Mingan Archipelago, MSI = Machias Seal Is. Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth ([naturalearthdata.com](https://www.naturalearthdata.com)).

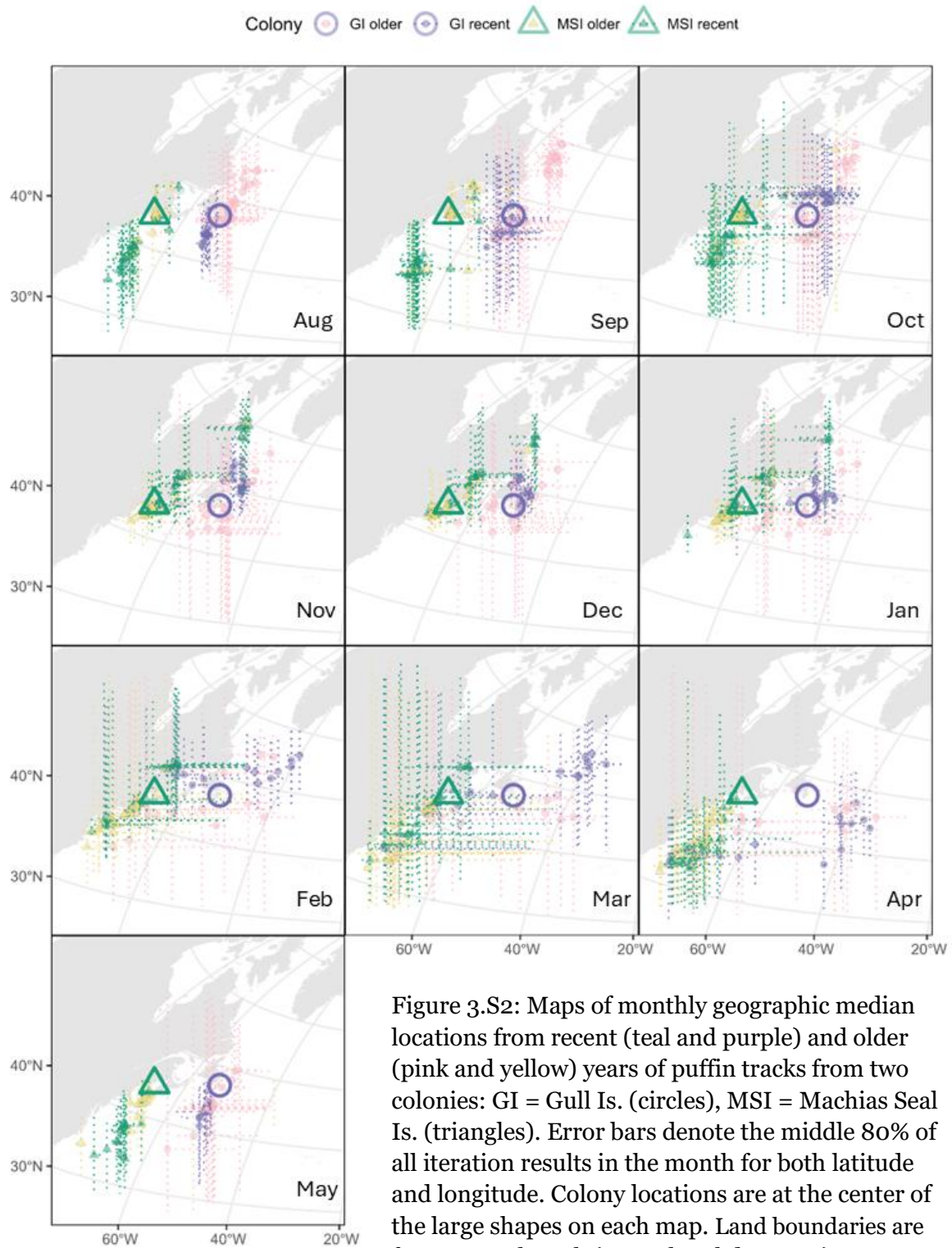


Figure 3.S2: Maps of monthly geographic median locations from recent (teal and purple) and older (pink and yellow) years of puffin tracks from two colonies: GI = Gull Is. (circles), MSI = Machias Seal Is. (triangles). Error bars denote the middle 80% of all iteration results in the month for both latitude and longitude. Colony locations are at the center of the large shapes on each map. Land boundaries are from Natural Earth (naturalearthdata.com).

Link between Chapters 3 & 4

In Chapter 3, I found strong migratory connectivity among Atlantic Puffins early in the non-breeding period, followed by a month by month weakening of migratory connectivity culminating in shared space use at key winter foraging areas. This pattern reflects the gradual migration characteristic of alcids and indicates that they rely on different areas along their route. As environmental conditions and anthropogenic threats at non-breeding locations have been shown to affect individuals during the breeding season, understanding when and where different breeding populations overlap informs the targeting of conservation efforts. Breeding season conditions that excessively deplete energy reserves might also affect alcids during migration, but these carry-over effects from breeding to non-breeding have only rarely been studied in seabirds and have not been studied in alcids. In Chapter 4, I investigate the influence of breeding season energy expenditure on razorbill non-breeding energy expenditure and foraging activity.

Chapter 4: Influence of breeding season energy expenditure on Razorbill fall and winter foraging and energy

Emily S. Runnells¹, and Gail K. Davoren¹

¹Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

This chapter is being prepared for publication in Journal of Animal Ecology

[*Return to table of contents*](#)

Abstract

Carry-over effects, where conditions during one season incur costs that may affect how an individual allocates resources in subsequent seasons, have been demonstrated for several migratory bird species. Wintering conditions are well known to affect breeding success, but fewer studies have examined how breeding conditions affect birds during migration and winter. For seabirds, high energetic costs in the breeding season deplete energy stores, which may compromise winter survival, as mortality risks are higher during migration and winter. Our aim was to determine if breeding season energy expenditure carries over to influence razorbill (*Alca torda*) foraging behavior and energy expenditure in the fall and early winter. GLS-TDRs were deployed on chick-rearing razorbills during two breeding seasons (2021, 2022) with varying prey biomass. Time-activity budgets and Daily Energy Expenditure (DEE) were summarized for the breeding period and the non-breeding months of September – December. Breeding DEE varied among individuals but was lower in a year with high prey biomass. Based on our Bayesian analysis, the existence of carry-over effects on non-breeding DEE could not be confirmed, but there were high probabilities of a positive effect in the average prey biomass year and the opposite in the high prey biomass year. Higher breeding DEE led to increased time spent diving in September following the breeding season with high prey biomass, but otherwise there were no carry-over effects on foraging effort. These insights into carry-over effects on behavior and energy expenditure emphasize how environmental conditions mediate seasonal interactions and inform future research priorities.

Introduction

Organisms must continually make trade-offs in how they allot their limited energy reserves to meet energetic demands throughout their lifetime. Energetic debts or surpluses can affect an individual's behavior not only immediately, but also by carrying over into the next season. Although the concept of seasonal interactions is not new (Fretwell 1972), most research on vertebrates has been conducted during only one season, primarily the breeding season, and only a small percentage of studies consider seasonal interactions (Marra et al. 2015). It is important to understand these carry-over effects, where the conditions during one season affect the energetic state of an individual as it transitions to the next season, because they can have impacts on fitness and ultimately population dynamics (Norris & Taylor 2006, Norris & Marra 2007, Harrison et al. 2011). If fewer resources are available and more energy is used in one season, then less will be available for the next season, or vice versa, and individuals would be expected to show associated changes in behavior.

Studies, mostly on birds, have shown how winter habitat quality, foraging conditions, and migration distance influence breeding success (Norris and Marra 2007, Harrison et al. 2011). This includes research on seabirds, such as a study on how changes in winter foraging conditions affect the reproductive timing and egg size of Cassin's Auklet (*Ptychoramphus aleuticus*, Sorensen et al. 2009), and a study on Atlantic Puffins (*Fratercula arctica*) showing winter diet and stress hormone levels influence egg size (Kouwenberg et al. 2013). Far fewer studies connect breeding season conditions to movement and foraging the following winter (Harrison et al. 2011). Links between breeding success, migration timing, and dispersal extent have been demonstrated for two seabird species (Bogdanova et al. 2011, Catry et al. 2013), and a recent study on Black-legged Kittiwakes (*Rissa tridactyla*) experimentally demonstrated that supplemental summer food supply resulted in earlier departure of successful breeders from the colony and shorter non-breeding travel distances (Whelan et al. 2020). However, the effect of breeding season prey availability and energy expenditure on post-breeding energy expenditure have yet to be considered for seabirds, and carry-over effects on fall and winter behavior remain unexplored in species of the family Alcidae (hereafter 'alcid').

Alcids have exceptionally high wing-loading, leading to very high energetic costs of flight. These flight costs magnify the energy expenditure required during the breeding season and may constrain their migratory behavior during nonbreeding. Breeding is a period of high energy expenditure for many seabird species (e.g., Green et al. 2009, Dunn et al. 2020, Tremblay et al. 2022). Razorbills, one of the larger alcids, are close relatives of the extinct, flightless Great Auk (*Pinguinus impennis*), and the extant, similarly proportioned, murres (*Uria* spp.; Strauch 1985, Mowm et al. 1994, Friesen et al. 1996), which have the highest recorded flight costs of all vertebrates (Elliott et al. 2013). Therefore, flying is an energetically expensive activity for razorbills, but their wing-propelled diving is very efficient (Thaxter et al. 2010, Elliott et al. 2013). Their breeding biology is also similar to murres, with a short chick-rearing period (15-21 days), during which a pair shares provisioning duties, flying to and from the colony, searching for and delivering prey (Lavers et al. 2020). In Northeast Newfoundland, Canada, capelin (*Mallotus villosus*) are the main prey returned by breeding razorbills (Gulka et al. 2019, Lescure et al. 2023). During years with reduced capelin abundance, razorbill foraging trips have longer flight distances (Lescure et al. 2023), which increases their energy expenditure. Like murres,

razorbills depart the colony when flightless but fully-feathered fledglings at ~25% of adult body mass follow the male parent out to sea (Hope Jones & Rees 1985), where they are provisioned for an additional 1-2 months, effectively rendering that accompanying parent flightless and requiring additional foraging (Gaston & Jones 1998). During the early fall, adults also molt their flight feathers (Pyle 2009), another energetic expense that physically renders them flightless (Elliott & Gaston 2014).

The objective of this research was to determine if carry-over effects from energy expenditure during the breeding season affect razorbills in the fall and early winter across two years (2021, 2022). We hypothesized that energy expenditure during the breeding season will influence energy expenditure and foraging activity in the post-breeding period. Specifically, we predicted that birds that expend more energy during the breeding season would increase daily energy expenditure, to search for prey, and spend more time diving during non-breeding, to replenish energy stores that were depleted during breeding. These patterns were expected during 2021, when capelin biomass at accessible depths (< 50 m) during breeding was near the long-term average (Legard et al. 2025), but we expected no relationship in 2022, when capelin biomass was nearly double the long-term average during breeding (Legard et al. 2025), which would have allowed razorbills to minimize depletion of their energy reserves. As flight feather molt, another energetically demanding stage of the annual cycle, occurs in the early fall, we expected carry-over effects to be stronger in late-fall and early-winter, when razorbills may have more opportunity to increase energy stores.

Methods

All field work was carried out in a razorbill colony on James Island, off of NE Newfoundland, Canada, in the Northwest Atlantic (Fig. 4.1). Lotek LAT 2800 geolocator time-depth recorders (GLS-TDRs) were mounted to leg bands and deployed on hand-captured, chick-rearing razorbills. In 2021, 19 GLS-TDRs were deployed, and an additional 11 were deployed in 2022, 7 of which were on individuals that loggers were retrieved from, to allow for direct inter-year comparisons. All tags were under 1% of the bird's body weight to reduce device effects (Bodey et al. 2018, Geen et al. 2019). Razorbill handling was conducted between midnight and sunrise (approximately 3 h work periods), to minimize colony disturbance. Therefore, following nests to determine breeding success and fledge dates was not feasible. Overall, 17 GLS-TDRs were retrieved during the 2022-2025 breeding seasons, 10 of the tags deployed in 2021 and 7 from 2022, 5 of which were the same individual tracked in both years. Body mass of all individuals was measured at deployment and retrieval, and a drop of blood was collected on FTA cards at retrieval for later sex determination when sex had not been previously determined. All fieldwork followed ethical protocols according to the Canadian Council on Animal Care (University of Manitoba Protocols F20-017, F24-006) and Canadian Bird Banding Office (Banding Permit 10873).

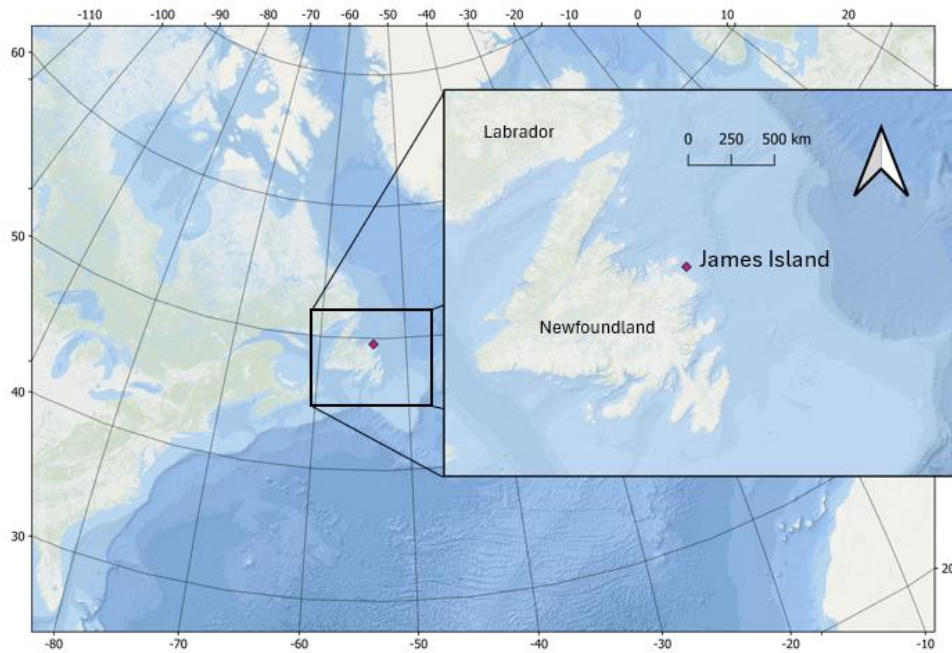


Figure 4.1: Location of James Island, where GLS-TDR loggers were deployed and retrieved. Background from services.arcgisonline.com, map produced in QGIS 3.16.1 (qgis.osgeo.org).

The GLS-TDR loggers collected data that allowed the determination of sea surface temperature and time activity budgets in the breeding and non-breeding seasons, following procedures used in Patterson et al. (2022). Razorbills depart James Island in mid-August (Runnells et al. 2024), so data from July were used to represent the breeding season, and data from September–December represented non-breeding. The tags recorded light intensity (full resolution), pressure (dbar), temperature ($^{\circ}\text{C}$), and immersion status (binary wet/dry) every 10 s. To adjust for the submerged position of razorbill legs and compensate for noise in the pressure data, a zero-offset correction of 1 m was applied to the pressure data using DiveMove (Luque 2007). Depth was determined based on the conversion ratio of every 1 m of depth in the ocean adding approximately 1 dbar.

Time-activity budgets were determined based on the following criteria. Diving was classified as any period when depth was greater than 1.5 m (Fig. 4.2). Then, dive bouts were defined as groups of dives less than 300 s apart, when the tag was never dry for more than 30 s. Time in a dive bout but not diving was classified as swimming (Fig. 4.2). Temperature measurements were assumed to represent sea surface temperature (SST) when the tag was wet but the bird was not diving, and the range during each 180 s period was less than 0.5°C and was within the daily 5th to 95th temperature quantiles recorded during dives ($\pm 1^{\circ}\text{C}$). Intervening SST measurements were then interpolated. If the tag was wet and the temperature measurement was less than 0.5°C from SST, then the bird’s activity was classified as swimming (Fig. 4.2). If the logger was dry for less than 30 s during a period in between dives, this time was classified as swimming (Fig. 4.2). If the logger was dry for at least 60 s and the maximum temperature while dry was less

than a certain threshold, razorbill activity was classified as flying (Fig. 4.2). If the temperature was greater than the threshold, this was classified as resting, when the tagged leg is tucked into body feathers (Fig. 4.2). The temperature threshold used during breeding, when the air temperatures are warmer, was 28 °C, while the temperature threshold during non-breeding was 13 °C. The times when razorbills tuck the other leg are unknown and thus were not included as resting. Therefore, this method underestimates the time resting. As there is evidence that alcid do not tuck both legs equal amounts of time, along with individual variation in the amount of leg tucking per leg (Darby et al. 2022), we chose to limit assumptions by using only logger-detected tucking events. Finally, any remaining activity was classified as swimming during non-breeding, or as ‘unknown colony’ during breeding when the tag was dry (e.g., standing on rocks, in nesting crevice, Fig. 4.2).

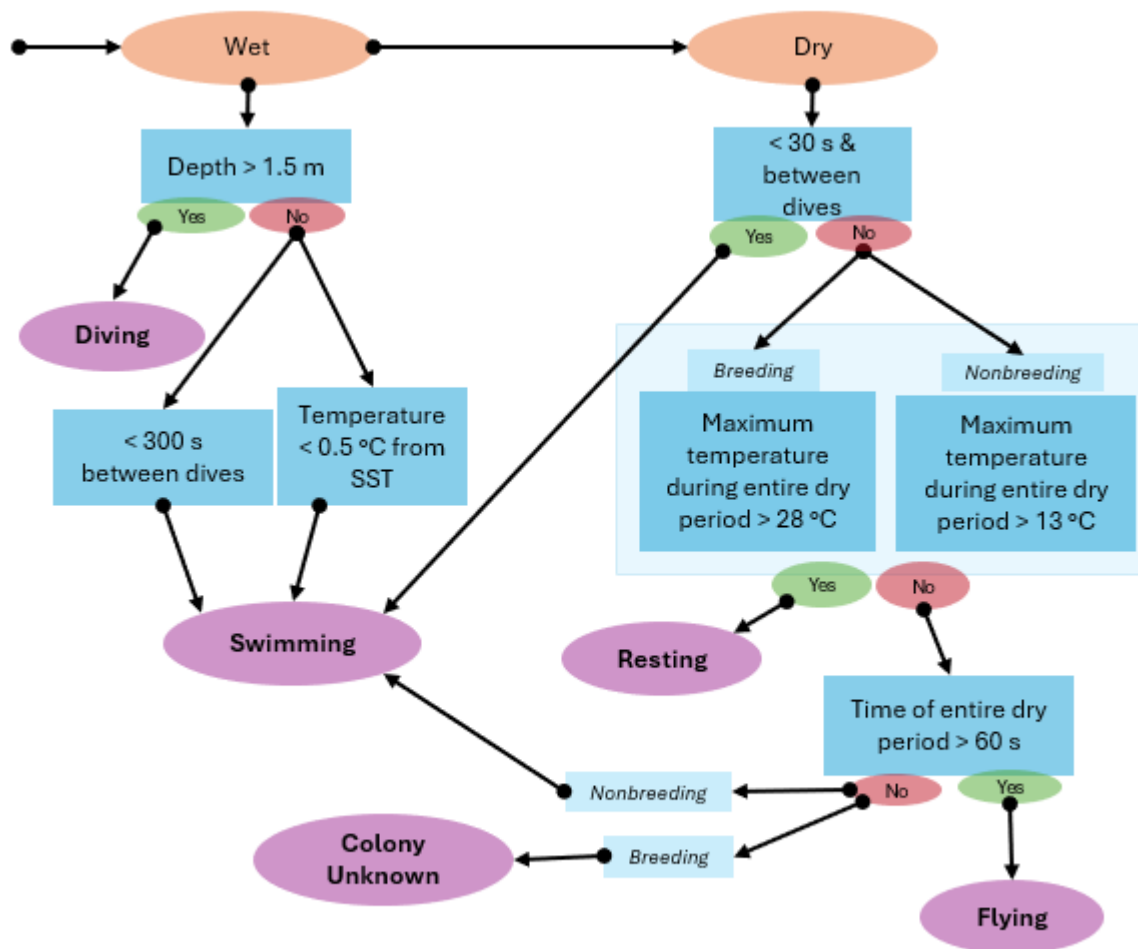


Figure 4.2: Flow chart of activity category classification based on immersion, pressure, and temperature data from GLS-TDR loggers.

The resulting time activity budgets and SST were then used to calculate Daily Energy Expenditure (DEE, kJ) during both breeding and non-breeding periods. Model-derived estimates of activity-specific energy expenditures for Thick-billed Murres (*Uria lomvia*; Elliott et al. 2013), a closely related and physiologically similar alcid, were applied to daily time-activity budgets. The amount of time spent in each activity category each day was calculated and inserted into an equation modified from Elliott and Gaston (2014) to correct conversion errors and adapt to the non-breeding season when needed (Burke & Montevecchi 2018, Patterson et al. 2022).

For non-breeding:

$$DEE = 508 * T_f + 3.64 * \sum \left[1 - e^{\left(\frac{-d}{1.23}\right)} \right] + (113 - 2.75 * SST) * T_s + (72.2 - 2.75 * SST) * T_r$$

For breeding:

$$DEE = 508 * T_f + 33 * T_c + 3.64 * \sum \left[1 - e^{\left(\frac{-d}{1.23}\right)} \right] + (113 - 2.75 * SST) * T_s \\ + (72.2 - 2.75 * SST) * T_r$$

Here, T_f is hours spent flying, d is minutes of each dive, SST is sea surface temperature ($^{\circ}C$), T_s is hours spent swimming, T_r is hours spent resting on the water (with leg tucked), and T_c is hours spent dry on the colony. The duration of all time metrics (i.e., T_x) were calculated per day. DEE was summarized into monthly values for breeding (July), and for each month of post-breeding (September, October, November, and December), when time activity budgets and dive characteristics (i.e. maximum depth, number of dives per day) were also summarized. The distributions of these measurements were typically left skewed, with occasional extreme values that pulled the monthly medians away from the most frequently observed values (Figs. 4.S1, 4.S2). Therefore, modes were calculated from the depths of all the dives in the month, the DEE, the daily maximum depth, the daily number of dives, and the hours per day spent flying, diving, and resting, along with the 10th and 90th quantiles of each of those measures, and the maximum dive depth in the month.

After exploratory analyses, we focused on non-breeding DEE and time spent diving, as these variables best addressed my hypothesis. Although based on a number of assumptions, DEE incorporates time activity budgets and SST, and is the best available representation of overall energy use. Time diving directly addresses questions about foraging effort for pursuit-diving razorbills and effectively integrates information on the number of dives and dive duration, the latter of which is correlated with dive depth in razorbills from this colony (Lescure et al. 2023, Legard et al. 2025). The effect of breeding season energy expenditure (i.e., mode of DEE during breeding) on monthly modal DEE and monthly modal time diving per day during non-breeding

were analyzed with Bayesian Generalized Linear Mixed Models (GLMMs), using 'brms' (Bürkner 2017) in R version 4.4.2 (R Core Team 2024). Models included an interaction between year and breeding DEE, and band number was included as a random effect to account for repeated measures. Models of non-breeding DEE were fit using a Gaussian distribution, with an identity link function, and models of diving time were fit using a skewed normal distribution with identity link. Default priors were used, which were an improper flat prior for the slope, a Student's T distribution with $df = 3$, $\mu = \text{median of the response variable}$, and $\sigma = \text{median absolute deviation of the response variable for the intercept}$, and a Student's T distribution bounded at 0 with $df = 3$, $\mu = 0$, and $\sigma = \text{median absolute deviation of the response variable for the standard deviation}$. The skewness prior for the dive time model was a normal distribution with $\mu = 0$ and $\sigma = 4$. We ran 4 chains of 50,000 iterations, with a thinning rate of 10. Visual inspection of trace plots confirmed that all chains mixed and converged, and all r-hat values were 1.0, supporting chain convergence.

Posterior distributions from the GLMMs provided the evidence needed to assess our hypotheses. Bayesian credible intervals are not equivalent to tests of statistical significance but describe the shape of the posterior distribution, such that a broader interval indicates more uncertainty in the estimate (McElreath 2018). In this analysis, the extent to which the posterior distribution for the slope parameter overlaps with zero is evidence for/against the existence of carry-over effects. If the 95% credible interval does not overlap with zero, we consider this to indicate high confidence for the presence of a relationship between breeding DEE and a non-breeding variable. The proportion of the slope posterior distribution that was above zero, denoted $p(\beta_1 > 0)$, for both DEE and time diving was calculated to directly assess the probability of my predictions (i.e. positive relationships). Maximum a posteriori (MAP), indicating the most probable values for the slopes (i.e. the mode of the posterior distributions), were also calculated. The mean of the posterior for the intercept and slope in each year were used to describe the linear relationship, and 95% credible intervals were produced using 'marginaleffects::predictions' (Arel-Bundock et al. 2024) to visualize the uncertainty in the modeled relationship.

Results

All 17 retrieved loggers yielded data that were usable for determining time-activity budgets. Four females (ZW) and one bird of unknown sex were tracked in both years, but only two males (ZZ) were tracked in 2022, compared to five in 2021. This resulted in different proportions of males tracked in each year (2021: 50%; 2022: 29%). There was greater variation in the breeding DEE values, including higher values, in 2021 relative to 2022 (Fig. 4.3). Minimum and maximum non-breeding DEE values were lower in September relative to the other months, slightly increasing in October, and highest in November and December (Fig. 4.3). Non-breeding modal diving times were highly variable, but more razorbills spent less time diving in November and December than in September and October, particularly in 2021, when there were a higher proportion of males tracked (Fig. 4.4).

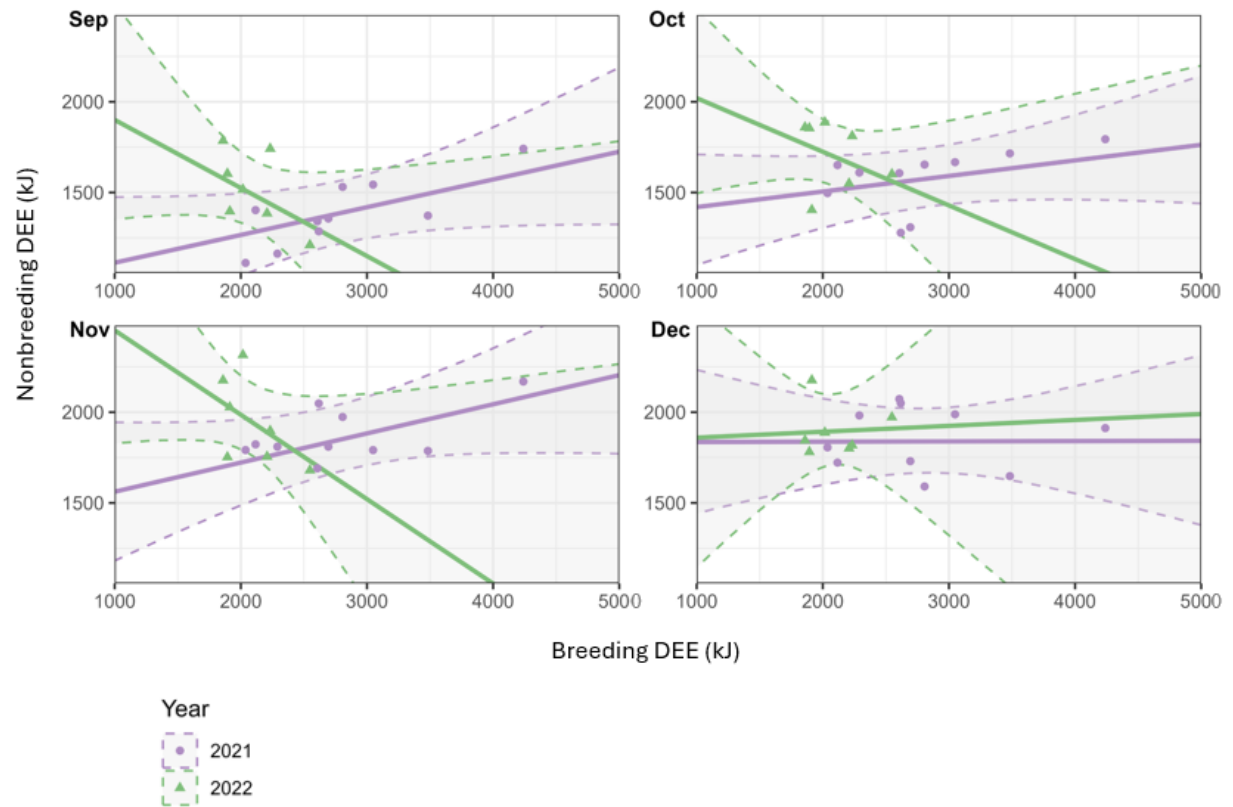


Figure 4.3: Modeled relationships between breeding and non-breeding DEE in 2021 (purple) and 2022 (green) with their associated 95% credible intervals (gray shading). Monthly modes of each tag are included as points.

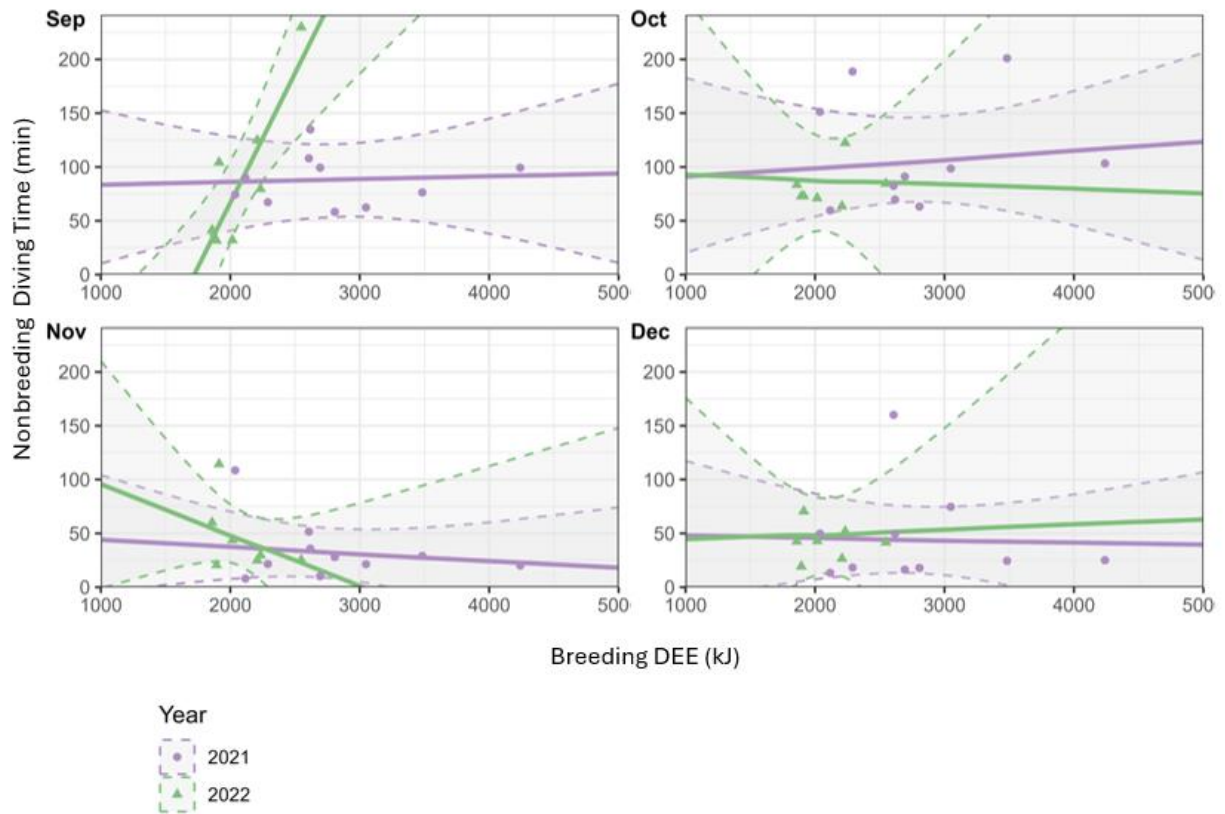


Figure 4.4: Modeled relationships between breeding DEE and non-breeding diving time in 2021 (purple) and 2022 (green) with their associated 95% credible intervals (gray shading). Monthly modes are included as points (each point represents a single tag).

The relationship between breeding DEE and non-breeding DEE showed contrasting patterns in the two years during all non-breeding months except December (Fig. 4.3), but all the 95% credible intervals overlapped with zero (Fig. 4.3, Fig. 4.5, Table 4.S1), indicating we do not have high confidence that a relationship exists. In 2021, the more energy expended during breeding, the more energy expended in the fall, while the opposite trend was observed in 2022 (Fig. 4.3). There was a high probability of a positive slope in September, October, and November ($p[\beta_1 > 0] \geq 0.91$, Table 4.S1) in 2021, while in 2022 the probability of a positive slope was very low during those months ($p[\beta_1 > 0] \leq 0.08$, Table 4.S1). Among those three months, slopes were shallower in October (Fig. 4.3, Fig. 4.5, Table 4.S1) and the probability of a positive slope lowest ($p[\beta_1 > 0] = 0.91$) in 2021 or highest ($p[\beta_1 > 0] = 0.08$) in 2022. Although the MAP of the negative slopes in 2022 indicated stronger effects (i.e., higher absolute value of the slope) of breeding DEE on non-breeding DEE when compared to the positive slopes in 2021 (Fig. 4.5, Table 4.S1), there was more uncertainty in the slope estimates (i.e., wider credible interval) in 2022 relative to 2021 (Fig. 4.3, Fig. 4.5, Table 4.S1). The narrower credible intervals in 2021 (Fig. 4.3, Fig. 4.5, Table 4.S1) indicate that the reported slope estimate is more likely. In December, any indication

of a relationship between breeding and non-breeding DEE disappeared, with a 0.5 probability of a positive slope in both years (Table 4.S1).

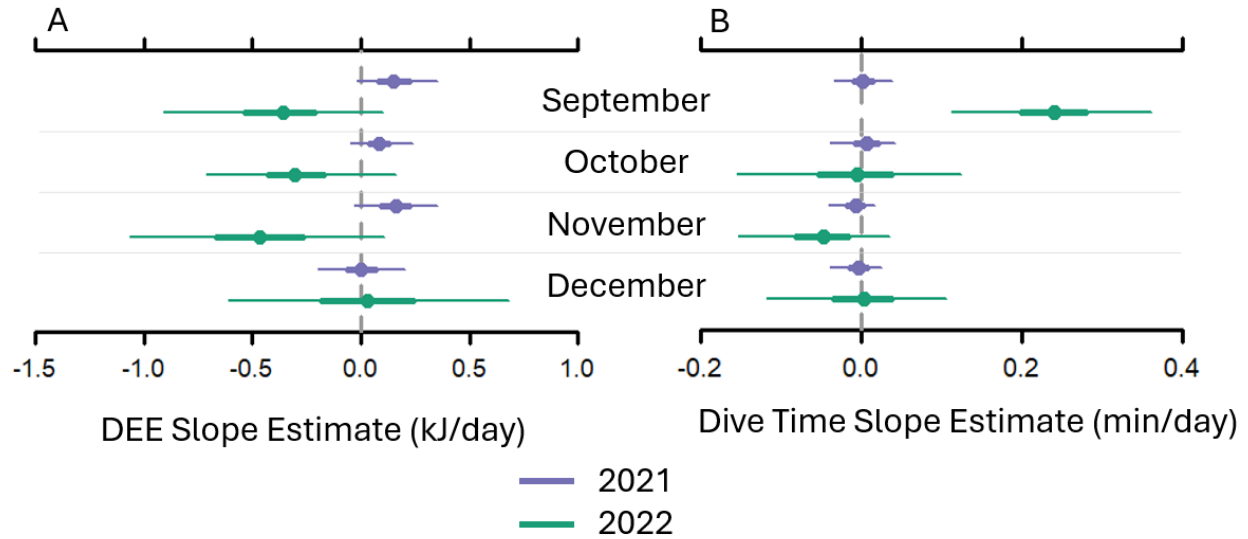


Figure 4.5: Posterior distributions of the slope parameter from Bayesian generalized linear mixed models of non-breeding DEE (A) and time diving (B). Maximum a posteriori (MAP) estimates (points), and 50% (thick line) and 95% (thin line) credible intervals for slope values from 2021 and 2022. MAP is the most probable value for the slope (i.e. the mode of the posterior distribution), and credible intervals provide a 95% or 50% probability that the slope value is within the given range.

There did not appear to be a relationship between breeding DEE and non-breeding daily diving time in either year during most non-breeding months, with one exception (Fig. 4.4). In 2022, the more energy expended during breeding, the more time razorbills spent diving in September (Fig. 4.4), as evidenced by a high probability of a positive slope in September 2022 ($p[\beta_1 > 0] = 0.99$), and narrow credible intervals that did not overlap with zero, indicating high confidence in that trend (Fig. 4.4, Fig. 4.5, Table 4.S2). In November, there was a weak indication that increased breeding energy expenditure led to less time spent diving, with a mid-range probability of a negative slope in 2021 ($p[\beta_1 < 0] = 0.69$) and even higher probability in 2022 ($p[\beta_1 < 0] = 0.86$). However, there was high uncertainty in both trend lines, as demonstrated by wide credible intervals (Fig. 4.4) overlapping with zero (Fig. 4.5), and the effect was not strong, as indicated by the near zero MAP of slopes in both years (Fig. 4.5, Table 4.S2). There was no indication that breeding DEE effects non-breeding diving time in October and December (Fig. 4.4), with mid-range probabilities of positive slopes in both 2021 and 2022 ($0.44 \leq p[\beta_1 > 0] \leq 0.65$, Table 4.S2). Overall, September 2022 was the only time when there was high confidence in an effect of breeding DEE on time spent diving.

Discussion

Overall, we did not find strong evidence of carry-over effects from breeding to non-breeding in razorbills. The higher and more variable energy expenditure during breeding in 2021, when capelin biomass was near the long-term average (hereafter ‘average prey biomass year’), relative to 2022, when capelin biomass was nearly double the long-term average (hereafter ‘high prey biomass year’), supports our predictions of differences between years and aligns with previous research on razorbills in the study area (Lescure et al. 2023, Legard et al. 2025). In both years, however, there was a slightly greater than 5% probability that a relationship between breeding and non-breeding DEE did not exist, along with different strength and directionality of the trends among years. Similar to our prediction, in the average prey biomass year (2021), increased energy expenditure during chick rearing tended to lead to higher energy expenditure in the fall; however, in the year with high prey biomass (2022), when razorbills expended more energy during the breeding season, they seemed to expend less energy during the fall. The greater variation in breeding DEE during 2021 also contributed to greater confidence that there was a weakly positive carry-over effect on non-breeding energy expenditure that year, while the lower variation and smaller sample size in 2022 resulted in lower confidence in a stronger negative carry-over effect in that year. These trends, however, are likely also influenced by the different sex ratios among years, as at-sea parental care by males would influence post-breeding energy expenditure. Contrary to our prediction, increased breeding season energy expenditure did not lead to increased time spent diving during non-breeding, suggesting there was no carry-over effect on foraging effort in most months across both years. One exception was in September 2022, when there was high confidence of a positive relationship between breeding energy expenditure and time spent diving. Finally, any relationships between breeding and non-breeding DEE disappeared in December in both years, supporting the idea that razorbills need to recover from breeding as soon as possible, regardless of the additional energetic demands of molt and parental care.

The results suggest that the environmental conditions experienced, particularly foraging conditions during breeding, affect the directionality of carry-over effects on energy expenditure from breeding to non-breeding. We expected increased breeding DEE would lead to increased non-breeding DEE in a year with average prey biomass during the breeding season (2021) and expected no carry-over effects in a year with high prey biomass (2022). The trends matched my prediction in 2021, but, instead of no relationship in 2022, there was some indication that lower breeding DEE led to higher non-breeding DEE. Conversely, Black-legged Kittiwakes that expended less energy during breeding (through supplemental feeding or failed breeding) expended less energy during non-breeding (illustrated by lower dispersal from the colony) during a year of high prey abundance (Whelan et al. 2020), and expended more energy during non-breeding (higher dispersal) during a year of poor environmental conditions during breeding (Bogdanova et al. 2011). It is possible that we did not see these trends because prey biomass was not low enough during the average capelin biomass year. Indeed, razorbills experiencing substantially lower prey biomass may show a stronger positive relationship between breeding and non-breeding energy expenditure. By contrast, the high biomass of capelin near the razorbill study colony during summer 2022 (Lescure et al. 2023, Legard et al. 2025) may have led to conditions where razorbill energy stores were not as depleted during breeding and, thus, they were not energy limited during non-breeding. In support, there was a lower range of

breeding DEE in 2022, as razorbills were expending less energy flying in search of prey (Legard et al. 2025) as shown in previous years at this colony (Lescure et al. 2023). Therefore, if razorbills do not deplete their energy stores to a high extent during breeding, they may not have to work hard to replenish energy stores during non-breeding. This might result in their non-breeding behaviors and DEE more directly matching their non-breeding energy requirements. Even a year with average prey biomass likely requires high energy expenditure for chick provisioning in seabirds adapted for pursuit diving (Green et al. 2009, Elliott & Gaston 2014, Dunn et al. 2020).

The contrasting trends across years of this study, however, may also be related to interannual variation in sex ratios of tracked birds. Female razorbills have the option to expend energy flying between departing the colony and beginning wing feather molt, while males taking care of fledglings at sea do not have that option (Gaston & Jones 1998). As we tracked a higher proportion of females in 2022, and very few confirmed males, we might expect higher non-breeding DEE during September in this year in females flying to high-quality prey patches to replenish energy. However, by quantifying the modal DEE values, we focused analysis on the most common daily time-activity budget in each month. Therefore, if females concentrated post-breeding flying movements during September across a few days, the modal value would not incorporate these days of higher DEE. Overall, the lower non-breeding DEE in (mostly female) birds that expended more energy during 2022, suggests that they spend only one or two days in flight to a location where they could spend the remaining days of the month foraging and otherwise resting and conserving energy during flight feather molt. In support, female thick-billed murres tend to make long-distance post-breeding movements over 1-2 days (Elliott & Gaston 2014), and the lower modal DEE in September matches the flightless molt timing (Pyle 2009). Additionally, the positive relationship between breeding and non-breeding energy expenditure in 2021, when a higher proportion of males were tracked, aligns with the consistent extra diving effort likely required to replenish their own energy stores enough to provision a chick at sea for 1-2 months (Gaston & Jones 1998).

The relationships between breeding and non-breeding DEE disappeared in December, contrary to my prediction. Indeed, we predicted an increased effect in later months as birds may not be able to replenish energy stores until after the energetically demanding molt period in fall months. Therefore, our findings suggest that carry-over effects from breeding season energy expenditure do not get extended through molting and parental care, despite the extra limitations and energetic costs of those periods (Bridge 2004, Elliott & Gaston 2014). Other factors instead may be affecting non-breeding DEE more than breeding DEE by this time, such as colder temperatures, winter weather, and less daylight for foraging (Dunn et al. 2020, Moe et al. 2021). In support, razorbill non-breeding distribution is related to environmental conditions in the northwest Atlantic (Veit & Manne 2015), with birds traveling further in years of poor winter conditions (Diamond et al. 2020). However, razorbills on both sides of the Atlantic seem to have relatively consistent migratory paths post-molt and parental care (Buckingham et al. 2022, Runnells et al. 2024), which may limit variation in flying time later during non-breeding. As flying is the behavior that most influences DEE, information on the timing and extent of dispersal would inform more appropriate periods to examine carry-over effects.

The only time there was a carry-over effect on foraging effort was in September 2022, immediately following a breeding season with above average prey abundance, when expending more energy during breeding increased razorbill time spent diving, as predicted. Once synchronous flight feather molt begins post-breeding, razorbill movement is limited. Therefore, increased diving may be the only option for replenishing energy stores in September and October, which is when molt is predicted to occur (Pyle 2009). As flight feather molt is an energy intensive process (Bridge 2006), an increase in foraging when there is prey available would help offset that energetic expense. High capelin biomass in the vicinity of the colony in 2022 could have continued into September (Flynn et al. 2001, Magnaye et al. 2019), offering razorbills a chance to easily refuel proportional to their energetic needs. Alternately, the carry-over effects in September 2022 could be related to the higher proportion of females tracked that year. For murres, females do more chick provisioning on the colony, reducing their own energy stores, while males spend more time foraging for themselves, maintaining energy stores in preparation for at sea provisioning (Paredes et al. 2006, Thaxter et al. 2009, Elliott et al. 2010, Elliott & Gaston 2014). Therefore, female razorbills may have a greater need to replenish energy, which they could achieve by flying to a prey-rich location where they can forage until they have replenished energy stores depleted during breeding. However, there is some evidence that diving uses more energy during wing feather molt in alcids (Bridge 2004), and thus diving more may result in higher energy expenditure during the fall that could cancel out the benefits of increased foraging, unless high-quality prey were plentiful.

Although diving time generally was not affected by the amount of energy expended during breeding, it is possible that razorbills are instead changing which prey types they are consuming during non-breeding to replenish energy spent during breeding. Although we do not have information on what our tagged razorbills consumed, it is possible that high-quality prey were available during non-breeding. Winter stomach contents of razorbills indicate they consume invertebrates (Huettman et al. 2005) and fish (Blake 1984, Ouwehand et al. 2004) in varying proportions, depending on location, and therefore, likely, availability. Razorbills from the study colony, like murres also breeding in the area, move north towards Labrador immediately post-breeding (Legard et al. In press, Davoren et al. 2002). During secondary feather molt, in the early fall, high spatial and isotopic niche overlap between murres and razorbills from northeastern Newfoundland (Runnells et al. 2024), suggests that they are relying on both capelin and invertebrates (Davoren et al. 2002). There may be no point in increased diving if high quality prey, such as capelin, are available and provide the energy needed.

In conclusion, there are many factors that likely influence razorbill DEE and time spent diving during non-breeding. Therefore, it is challenging to determine whether there are carry-over effects from breeding season energy depletion. Foraging conditions during breeding and non-breeding may mediate the strength and direction of carry-over effects, and may integrate with non-breeding environmental conditions to alter razorbills' timeline and capacity for replenishing energy reserves before the winter. Sex differences in parental care, as in murres (Paredes et al. 2006, Thaxter et al. 2009, Elliott et al. 2010), may also affect how razorbills spend their time and energy, both on the colony and during post-fledging. In future studies, determining individual razorbill trophic position during molt and dispersal distance in each month would help to interpret non-breeding energy expenditure patterns. Additionally,

increased numbers of tracked birds may narrow estimates of carry-over effect strength, increase confidence that relationships exist and increase the ability to examine sex-based differences. Finally, incorporating tracking years when breeding season foraging conditions are poor, while considering the influence of nest success and breeding phenology, may increase the ability to detect carry-over effect timing and strength.

References

- Arel-Bundock V, Greifer N, Heiss A (2024) How to Interpret Statistical Models Using ‘marginaleffects’ for R and Python. *J Stat Softw* 111.
- Blake BF (1984) Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. *J Exp Mar Bio Ecol* 76:89–103.
- Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, Bearhop S (2018) A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods Ecol Evol* 9:946–955.
- Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S (2011) Seasonal interactions in the black-legged kittiwake, *rissa tridactyla*: Links between breeding performance and winter distribution. *Proc R Soc B Biol Sci* 278:2412–2418.
- Bridge ES (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. *Mar Ornithol* 34:7–19.
- Bridge ES (2004) The effects of intense wing molt on diving in alcids and potential influences on the evolution of molt patterns. *J Exp Biol* 207:3003–3014.
- Buckingham L, Bogdanova MI, Green J, Dunn RE, Wanless S, Bennett S, Bevan R, Call A, Canham M, Corse C, Harris M, Heward C, Jardine D, Lennon J, Parnaby D, Redfern C, Scott L, Swann R, Ward R, Weston E, Furness R, Daunt F (2022) Interspecific variation in non-breeding aggregation: A multi-colony tracking study of two sympatric seabirds. *Mar Ecol Prog Ser* 684:181–197.
- Burke CM, Montevecchi WA (2018) Taking the bite out of winter: Common murres (*Uria aalge*) push their dive limits to surmount energy constraints. *Front Mar Sci* 5:63.
- Bürkner PC (2017) Brms: An R package for Bayesian multilevel models using Stan. *J Stat Softw* 80.
- Catry P, Dias MP, Phillips RA, Granadeiro JP (2013) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* 94:1230–1235.
- Darby JH, Harris MP, Wanless S, Quinn JL, Bråthen VS, Fayet AL, Clairbaux M, Hart T, Guilford T, Freeman R, Jessopp MJ (2022) A new biologging approach reveals unique flightless molt strategies of Atlantic puffins. *Ecol Evol* 12:e9579.
- Davoren GK, Montevecchi WA, Anderson JT (2002) Scale-dependent associations of predators and prey: Constraints imposed by flightlessness of common murres. *Mar Ecol Prog Ser* 245:259–272.

- Diamond AW, McNair DB, Ellis JC, Rail J, Whidden ES, Kratter AW, Courchesne SJ, Pokras MA, Wilhelm SI, Kress SW, Farnsworth A, Iliff MJ, Jennings SH, Brown JD, Ballard JR, Schweitzer SH, Okoniewski JC, Gallegos JB, Stanton JD (2020) Two unprecedented auk wrecks in the Northwest Atlantic in winter 2012/13. *Mar Ornithol* 13:185–204.
- Dunn RE, Wanless S, Daunt F, Harris MP, Green JA (2020) A year in the life of a North Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Sci Rep* 10:5993.
- Elliott KH, Gaston AJ (2014) Dive behaviour and daily energy expenditure in Thick-billed murres *Uria lomvia* after leaving the breeding colony. *Mar Ornithol* 189:183–189.
- Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behavior by a monomorphic seabird represents risk partitioning. *Behav Ecol* 21:1024–1032.
- Elliott KH, Ricklefs RE, Gaston AJ, Hatch SA, Speakman JR, Davoren GK (2013) High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc Natl Acad Sci U S A* 110:9380–9384.
- Flynn SR, Nakashima BS, Burton MPM (2001) Direct assessment of post-spawning survival of female capelin, *Mallotus villosus*. *J Mar Biol Assoc United Kingdom* 81:307–312.
- Fretwell SD (1972) *Populations in a Seasonal Environment*. Princeton University Press.
- Friesen VL, Baker AJ, Piatt JF (1996) Phylogenetic relationships within the Alcidae (charadriiformes: Aves) inferred from total molecular evidence. *Mol Biol Evol* 13:359–367.
- Gaston AJ, Jones IL (1998) *The Auks: Alcidae*, illustrate. Oxford University Press, Oxford, UK.
- Geen GR, Robinson RA, Baillie SR (2019) Effects of tracking devices on individual birds – a review of the evidence. *J Avian Biol* 50:1–13.
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: Daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538.
- Gulka J, Ronconi RA, Davoren GK (2019) Spatial segregation contrasting dietary overlap: niche partitioning of two sympatric alcids during shifting resource availability. *Mar Biol* 166.
- Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* 80:4–18.
- Hope Jones P, Rees EIS (1985) Appearance and behavior of immature guillemots and razorbills at sea. *Br Birds* 78:370–377.
- Huettman F, Diamond AW, Dalzell B, MacIntosh K (2005) Winter distribution, ecology and movements of Razorbills (*Alca torda*) and other auks in the outer Bay of Fundy, Atlantic Canada. *Mar Ornithol* 33:161–171.
- Kouwenberg AL, Mark Hipfner J, McKay DW, Storey AE (2013) Corticosterone and stable isotopes in feathers predict egg size in Atlantic Puffins *Fratercula arctica*. *Ibis (Lond 1859)* 155:413–418.
- Lavers J, Hipfner JM, Chapdelaine G (2020) Razorbill (*Alca torda*). In: *Birds of the World*, version 1. Billerman SM (ed) Cornell Lab of Ornithology, Ithaca, NY, USA, p <https://doi.org/10.2173/bow.razorb.01>

- Legard MJ, Diamond AW, Fifield DA, Major HL, Ronconi RA, Davoren GK (no date) The behaviour of individual razorbills (*Alca torda*) during the non-breeding season is consistent but not related to personality. *Mar Ecol Prog Ser* In press.
- Legard MJ, Lescure L, Davoren GK (2025) Individual consistency in foraging behaviour is influenced by prey availability in a breeding seabird.
- Lescure L, Gulka J, Davoren GK (2023) Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Mar Ecol Prog Ser* 709:109–123.
- Luque S (2007) An Introduction to the diveMove Package. *R News*:1–11.
- Magnaye M, Rideout RM, Davoren GK (2019) Irregular growth patterns in the otoliths of a short-lived forage fish do not reliably indicate reproductive history. *Fish Res* 218:120–126.
- Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM (2015) A call for full annual cycle research in animal ecology. *Biol Lett* 11.
- McElreath R (2018) *Statistical Rethinking - A Bayesian Course with Examples in R and STAN*, Second Edi. Chapman and Hall/CRC.
- Moe B, Daunt F, Bråthen VS, Barrett RT, Ballesteros M, Bjørnstad O, Bogdanova MI, Dehnhard N, Erikstad KE, Follestad A, Gíslason S, Hallgrímsson GT, Lorentsen S, Newell M, Petersen A, Phillips RA, Ragnarsdóttir SB, Reiertsen TK, Åström J, Wanless S (2021) Twilight foraging enables European shags to survive the winter across their latitudinal range. *Mar Ecol Prog Ser* 676:145–157.
- Moum T, Johansen S, Erikstad KE, Piatt JF (1994) Phylogeny and evolution of the auks (subfamily alcinæ) based on mitochondrial DNA sequences. *Proc Natl Acad Sci U S A* 91:7912–7916.
- Norris DR, Marra PP (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- Norris DR, Taylor CM (2006) Predicting the consequences of carry-over effects for migratory populations. *Biol Lett* 2:148–151.
- Ouwehand J, Leopold MF, Kees CJ (2004) A comparative study of the diet of Guillemots *Uria aalge* and Razorbills *Alca torda* killed during the Tricolor oil incident in the south-eastern North Sea in January 2003. *Atl Seabirds* 6:147–166.
- Paredes R, Jones IL, Boness DJ (2006) Parental roles of male and female thick-billed murrelets and razorbills at the Gannet Islands, Labrador. *Behaviour* 143:451–481.
- Patterson A, Gilchrist HG, Robertson GJ, Hedd A, Fifield DA, Elliott KH (2022) Behavioural flexibility in an Arctic seabird using two distinct marine habitats to survive the energetic constraints of winter. *Mov Ecol* 10:1–16.
- Pyle P (2009) Age determination and molt strategies in North American alcids. *Mar Ornithol* 37:219–226.
- R Core Team (2024) *R: A Language and Environment for Statistical Computing*.
- Runnells ES, Montevecchi WA, Davoren GK (2024) Spatiotemporal and isotopic niche overlap

- among Atlantic puffins, razorbills, and common murre during the non-breeding season in the Northwest Atlantic. *Mar Ecol Prog Ser* 739:241–256.
- Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: Stable isotope evidence that pre-breeding diet quality influences reproductive success. *J Anim Ecol* 78:460–467.
- Strauch JG (1985) The Phylogeny of the Alcidae. *Auk* 102:520–539.
- Thaxter CB, Daunt F, Hamer KC, Watanuki Y, Harris MP, Grémillet D, Peters G, Wanless S (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: Nest defence, foraging efficiency or parental effort? *J Avian Biol* 40:75–84.
- Thaxter CB, Wanless S, Daunt F, Harris MP, Benvenuti S, Watanuki Y, Grémillet D, Hamer KC (2010) Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *J Exp Biol* 213:1018–1025.
- Tremblay F, Whelan S, Choy ES, Hatch SA, Elliott KH (2022) Resting costs too: The relative importance of active and resting energy expenditure in a sub-arctic seabird. *J Exp Biol* 225.
- Veit RR, Manne LL (2015) Climate and changing winter distribution of alcids in the Northwest Atlantic. *Front Ecol Evol* 3:1–9.
- Whelan S, Hatch SA, Irons DB, McKnight A, Elliott KH (2020) Increased summer food supply decreases non-breeding movement in black-legged kittiwakes. *Biol Lett* 16.

Supplemental Figures

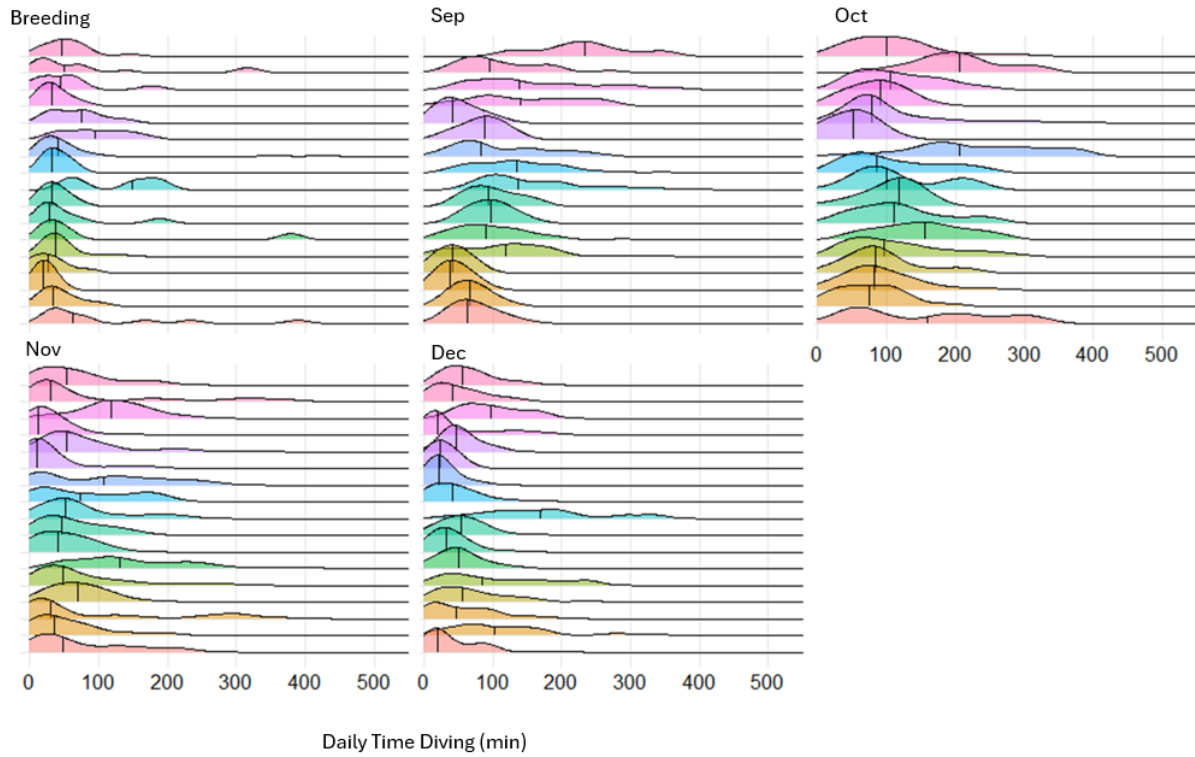


Figure 4.S1: Probability density of daily time spent diving for each tag deployment during breeding and 4 nonbreeding months. Colors represent individuals. The vertical line is at the median, and the mode is at the highest peak. During breeding, sample sizes range between 6-24 days of data.

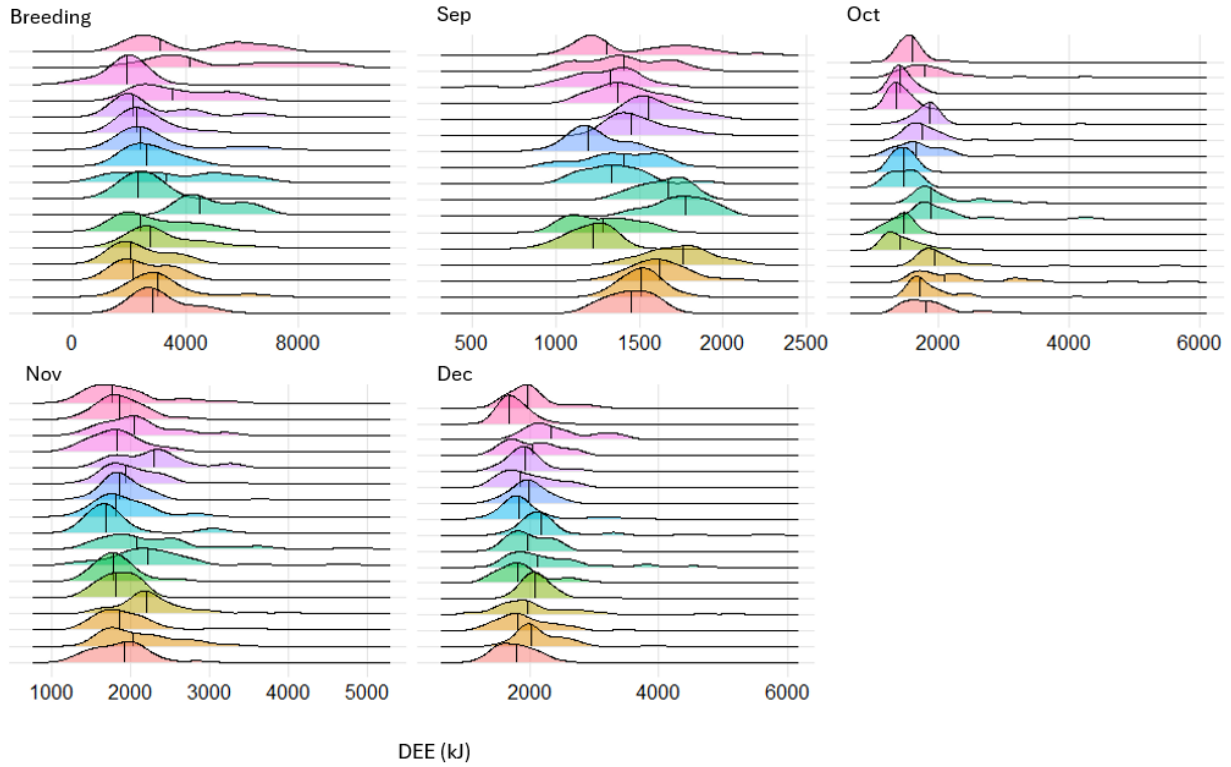


Fig 4.S2: Probability density of daily energy expenditure (DEE) for each tag deployment during breeding and 4 nonbreeding months. Colors represent individuals. The vertical line is at the median, and the mode is at the highest peak. During breeding, sample sizes range between 6-24 days of data.

Table 4.S1: Probability that the relationship between breeding and non-breeding DEE has a positive slope (*i.e.*, $p[\beta_1 > 0]$) or a negative slope, and the maximum a posteriori (MAP) and 95% credible interval (95% CrI) of the slope for each non-breeding month of 2021 and 2022.

	2021				2022			
Month	$p[\beta_1 < 0]$	$p[\beta_1 > 0]$	MAP	95% CrI	$p[\beta_1 < 0]$	$p[\beta_1 > 0]$	MAP	95% CrI
Sep	0.047	0.953	0.17	(-0.02, 0.35)	0.944	0.056	-0.33	(-0.91, 0.10)
Oct	0.091	0.909	0.07	(-0.05, 0.24)	0.921	0.079	-0.31	(-0.71, 0.16)
Nov	0.049	0.952	0.15	(-0.03, 0.35)	0.943	0.057	-0.46	(-1.06, 0.11)
Dec	0.499	0.501	-0.01	(-0.20, 0.20)	0.459	0.541	0.02	(-0.61, 0.68)

Table 4.S2: Probability that the relationship between breeding DEE and non-breeding time diving has a positive slope (*i.e.*, $p[\beta_1 > 0]$), and the maximum a posteriori and 95% credible interval of the slope for each non-breeding month of 2021 and 2022

	2021			2022		
Month	$p[\beta_1 > 0]$	MAP	95% CrI	$p[\beta_1 > 0]$	MAP	95% CrI
Sep	0.564	1.04e-4	(-0.032, 0.038)	0.999	0.24	(0.113, 0.362)
Oct	0.652	0.01	(-0.037, 0.043)	0.468	3.16e-3	(-0.155, 0.124)
Nov	0.307	-3.31e-3	(-0.040, 0.017)	0.138	-0.04	(-0.152, 0.035)
Dec	0.443	-4.70e-5	(-0.038, 0.026)	0.531	4.21e-3	(-0.117, 0.107)

General Discussion & Conclusions

A growing body of ecology literature is based on light-level geolocator tracking technology, and a variety of methods are now available for obtaining location estimates from geolocator data. Historically, it has been unclear what factors to consider when choosing a processing method or whether all geolocator-based location estimates are directly comparable. In Chapter 1, we addressed this knowledge gap by aiming to show how location estimates of non-breeding Atlantic puffins differ depending on the GLS processing method and the GLS tag model and settings used. We found that location estimates produced by most of the commonly used processing methods were comparable outside of equinox periods, based on previous studies of geolocator accuracy (Phillips et al. 2004, Shaffer et al. 2005, Lisovski et al. 2012, Merkel et al. 2016, Halpin et al. 2021); however, the characteristics of the data collected by different tag types had an effect for some of the methods. Therefore, researchers trying to choose a GLS data processing method should consider tag type and selected settings but can also weigh the different time and effort commitments of each method against how the data outputs suit their research objectives. Location estimates from GLS data are often used in further analysis, such as the analyses in Chapters 2 and 3. In Chapter 1, differences between processing methods in a subsequent analysis of distribution similarity suggest that the same method should be used for all GLS data processing. Based on all these results, we used one processing method that facilitated incorporation of environmental data and provided location estimate uncertainty when examining niche overlap (Chapter 2) and migratory connectivity (Chapter 3).

Little is known about the spatial and dietary overlap of seabird species during the non-breeding season, when scarce and patchy marine food resources could lead to interspecific competition. Therefore, in Chapter 2, we aimed to quantify spatiotemporal and isotopic niche overlap among common murres (*Uria aalge*), razorbills (*Alca torda*), and Atlantic puffins (*Fratercula arctica*) outside the breeding season. By combining GLS tracking and stable isotope ratios of carbon and nitrogen, we found evidence of differences in space and resource use during the low-productivity, non-breeding period. These findings are in line with predictions based on niche theory. Indeed, the minimal overlap of these three alcid species during an understudied phase of their annual cycle suggests that they segregate spatially and partition resources. Similar patterns are seen among other closely-related, high-latitude seabirds during non-breeding (Orben et al. 2015), as expected in environments where resources are limited (Wiens 1977). Although findings may indicate that these species co-evolved niche partitioning to allow coexistence, it is also possible that each species has always relied on different resources in different places during non-breeding and, thus, coexist because their niches differ sufficiently (Connell 1980).

Interestingly, there was high variability in migratory paths among puffins, which led to some spatial overlap with each of the other alcids. The spatial but not isotopic niche overlap, particularly with puffins occupying a lower trophic position when spatially overlapped with the larger species, suggests displacement from higher trophic level prey. These interspecific interactions also raise questions about intraspecific interactions, such as whether puffins from other northwest Atlantic colonies are also relying on the same winter foraging areas. The diverse migration paths exhibited by puffins from James Island, Newfoundland in Chapter 2 suggest that they may share space with puffins from other northwest Atlantic colonies. Describing the

movement patterns and migratory connectivity of multiple puffin populations in this region is an important step in relating non-breeding season distributions to demographic trends.

This led to Chapter 3, where we aimed to determine the migratory connectivity of Atlantic puffins from four Canadian breeding colonies during different months throughout the non-breeding period. Research on avian migratory connectivity has increased in recent years (Marra et al. 2019), and there is growing awareness of its' importance for migratory marine species (Dunn et al. 2019, Bentley et al. 2025), including seabirds (González-Solís et al. 2007, Merkel et al. 2021, O'Hanlon et al. 2024, Rexer-Huber et al. 2025), as an important component of planning effective conservation (Costa et al. 2012, Lascelles et al. 2014, Allen & Singh 2016, Fraser et al. 2018). Findings indicated that the migratory connectivity among the four colonies was strong pre- and post-breeding and the progressive weakening of migratory connectivity across most of the non-breeding period reflects puffins gradual, dispersive migration towards key wintering locations used by puffins from multiple breeding colonies, such as the Gulf of Maine. This could indicate intraspecific competition for puffins during this period if prey are limited in these areas of high spatial overlap.

These times of year when puffin migratory connectivity was strong, bookending the breeding season, are periods of high energy requirements. Chick provisioning is thought to be an annual peak of energy expenditure for many birds (Lack 1968), particularly alcids and penguins (Green et al. 2009, Elliott & Gaston 2014), suggesting that adults need to replenish energy stores as soon as possible post-parental care. Studies of carry-over effects, where conditions during one season incur costs that may affect how an individual allocates resources in subsequent seasons, have focused on how wintering conditions affect breeding success (e.g., Sorensen et al. 2009, Kouwenberg et al. 2013). Only a few studies, however, have examined how breeding conditions affect seabirds during migration and winter (Bogdanova et al. 2011, Catry et al. 2013, Whelan et al. 2020). In Chapter 4, we provide one of the first investigations of breeding to non-breeding carry-over effects in a species of the family Alcidae (Young et al. 2017, Daunt et al. 2020). Specifically, our aim was to determine if breeding season energy expenditure carries over to influence razorbill foraging behavior and energy expenditure in the fall and early winter. Although the existence of carry-over effects could not be confirmed in our Bayesian analysis, we found supporting evidence that foraging conditions during breeding and non-breeding mediate the strength and direction of carry-over effects, and may combine with sex differences in parental care (Paredes et al. 2006, Thaxter et al. 2009, Elliott et al. 2010), to alter razorbills' timeline and capacity for replenishing energy reserves before the winter. Although the concept of seasonal interactions is not new (Fretwell 1972), most research on vertebrates has been conducted during the breeding season, and only a small percentage of studies consider seasonal interactions (Marra et al. 2015), so this work fills an important knowledge gap and advances our understanding of carry-over effects into the non-breeding season.

Significance

Research on puffin non-breeding ecology is on the IUCN list of recommended conservation actions for this vulnerable species (BirdLife International 2018). Marine migratory species are

generally at high risk, because they are exposed to a wider range of threats over the larger area occupied (Lascelles et al. 2014). For pursuit-diving seabirds, high energetic costs in the breeding season deplete energy stores (Green et al. 2009, Elliott & Gaston 2014, Dunn et al. 2020), which may compromise winter survival, as mortality risks may be higher during migration and winter (e.g., Barbraud & Weimerskirch 2003, Gaston 2003, Sandvik et al. 2005). Understanding daily energy expenditure during non-breeding, and the factors that influence it, is an important step for identification of energetic bottleneck periods (Fort et al. 2009). Together with location information, this could lead to developing protected area networks in areas where energy requirements are the highest in their annual cycle. The results of our geolocator processing method comparison provide a resource to help managers effectively and appropriately compile archived geolocator data for such marine spatial planning.

Identifying the non-breeding distributions of puffins, razorbills, and common murre and the key areas they rely on in the northwest Atlantic will help target marine spatial planning and offset threats to all three species. The low spatial overlap among the three alcids, along with the strong migratory connectivity of puffins pre- and post-breeding, indicate the value of establishment and management of functional networks of protected areas (Game et al. 2009). The Gulf of Maine, New York Bight, and the Grand Banks emerged as key wintering areas used by multiple alcid species and by puffins from multiple colonies, where addressing threats will require multi-agency and multi-national collaboration (Blasiak & Yagi 2016, Tittensor et al. 2019, Davies et al. 2021, Gjerde et al. 2022). For instance, offshore wind development is in progress and planned in the New York Bight and Gulf of Maine (Stenhouse et al. 2020, NROC 2023, Moriarty 2023). Although there is low risk of alcids colliding with turbine blades (Bradbury et al. 2014, Johnston et al. 2014), they may be susceptible to displacement (Vanermen et al. 2015, Welcker & Nehls 2016, Kelsey et al. 2018), which could have population-level impacts (Busch & Garthe 2016, Peschko et al. 2024). If puffins are displaced from high-quality resources in areas of overlap with other alcids, then further displacement through offshore development, or declines in prey abundance, could also be particularly detrimental to puffins (Scopel et al. 2019). The Gulf of Maine and Northwest Atlantic more generally are some of the fastest warming ocean regions (Saba et al. 2016, Pershing et al. 2021), with documented impacts on many marine species (Pershing et al. 2021), including breeding alcids (Scopel et al. 2019, Major et al. 2021), and our finding of weak migratory connectivity in puffins January – April implies that climate change driven ecosystem impacts could affect all Canadian breeding populations.

Future Directions

Along with the scientific advances made in this thesis, our findings have also revealed more knowledge gaps. Many of these questions can be addressed with data from light-level geolocator deployments. Our comparison of geolocator data processing methods focused on one species with movement characteristics and distribution patterns that would limit the impact of confounding effects on our comparison. Therefore, opportunities for building on this research include comparing how different processing methods perform under conditions that make light-level geolocation more challenging. Future research could also consider adding processing steps

and environmental information to understand how much these additional choices would influence location estimates. This work would elucidate the implications of data processing choices for research on different species.

Uncertainty around molt timings, especially for puffin flight feathers, limited our ability to interpret variability in isotope ratios even when combined with tracking. Further studies should focus on this basic aspect of natural history (Pyle 2009), as in Currie et al. (2024). Compound specific isotope analysis of amino acids (CSIA-aa) could also be a useful methodology to parse out isotopic baseline shifts from trophic position independent of location (McMahon et al. 2015, Ohkouchi et al. 2017). Future stable isotope research could also determine if razorbill and murre females or individuals not caring for offspring have different isotopic niches from males performing parental care during flight feather molt (e.g., Burke et al. 2015).

Additionally, multi-colony tracking studies over a wider geographic area (e.g., Buckingham et al. 2022) and analysis of migratory connectivity in additional species besides puffins (e.g., Merkel et al. 2021) would provide a broader picture of important non-breeding foraging areas for alcids in this region. We learned that migration phenology may change over time, so continued, coordinated monitoring is important (Hays et al. 2019), especially given the rapidly changing ocean conditions in locations we found to be important for alcids in the northwest Atlantic (Halpern et al. 2019, Pershing et al. 2021). Further research into non-breeding habitat characteristics (e.g., Harris et al. 2015) and seasonal interactions, such as carry-over effects, would provide greater insight into the drivers of alcid movement patterns and increase our predictive ability for addressing emerging threats.

Our study of carry-over effects in razorbills indicated that there are many factors influencing alcid time-activity budgets throughout the year. In future studies, determining individual razorbill trophic position during molt and dispersal distance in each month would help to interpret non-breeding energy expenditure patterns. Additionally, increased numbers of tracked birds may narrow estimates of carry-over effect strength, increase confidence in the presence or absence of relationships, and increase the ability to examine sex-based differences. Finally, incorporating tracking years when breeding season foraging conditions are poor, while considering the influence of nest success and breeding phenology, may increase the ability to detect carry-over effect timing and strength.

Overall, the research in this thesis is based on alcids that survived the winter, and to understand the threats to non-breeding alcids, we need advances in technology and support for at-sea research that allows us to learn about the movements, behavior, and diets of birds that do not return to the breeding colony. Moreover, alcids are not the only species for whom we know much less about their lives outside of the breeding season. Ecology studies on the full annual cycle are needed across vertebrate taxa.

References

- Allen AM, Singh NJ (2016) Linking movement ecology with wildlife management and conservation. *Front Ecol Evol* 3:1–13.
- Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. *Proc R Soc B Biol Sci* 270:2111–2116.
- Bentley LK, Nisthar D, Fujioka E, Curtice C, Deland SE, Donnelly B, Harrison A, Heywood EI, Kot CY, Crespo GO, Poulin S, Halpin PN, Dunn DC (2025) Marine megavertebrate migrations connect the global ocean. *Nat Commun*.
- BirdLife International (2018) *Fratercula arctica*, Atlantic Puffin. IUCN Red List Threat Species 8235.
- Blasiak R, Yagi N (2016) Shaping an international agreement on marine biodiversity beyond areas of national jurisdiction: Lessons from high seas fisheries. *Mar Policy* 71:210–216.
- Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S (2011) Seasonal interactions in the black-legged kittiwake, *rissa tridactyla*: Links between breeding performance and winter distribution. *Proc R Soc B Biol Sci* 278:2412–2418.
- Bradbury G, Trinder M, Furness B, Banks AN, Caldow RWG, Hume D (2014) Mapping Seabird Sensitivity to offshore wind farms. *PLoS One* 9.
- Buckingham L, Bogdanova MI, Green J, Dunn RE, Wanless S, Bennett S, Bevan R, Call A, Canham M, Corse C, Harris M, Heward C, Jardine D, Lennon J, Parnaby D, Redfern C, Scott L, Swann R, Ward R, Weston E, Furness R, Daunt F (2022) Interspecific variation in non-breeding aggregation: A multi-colony tracking study of two sympatric seabirds. *Mar Ecol Prog Ser* 684:181–197.
- Burke CM, Montevecchi WA, Regular PM (2015) Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. *PLoS One* 10:e0141190.
- Busch M, Garthe S (2016) Approaching population thresholds in presence of uncertainty: Assessing displacement of seabirds from offshore wind farms. *Environ Impact Assess Rev* 56:31–42.
- Catry P, Dias MP, Phillips RA, Granadeiro JP (2013) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* 94:1230–1235.
- Connell JH (1980) Diversity and the coevolution of competitors, or the Ghost of Competition Past. *Oikos* 35:131–138.
- Costa DP, Breed G a., Robinson PW (2012) New Insights into Pelagic Migrations: Implications for Ecology and Conservation. *Annu Rev Ecol Evol Syst* 43:73–96.
- Currie CMV, Runnells ES, Davoren GK (2024) Stable Isotopes Reveal Primary Flight Feather Moults Patterns of Atlantic Puffins (*Fratercula arctica*). *J Ornithol*.
- Daunt F, Fang Z, Howells R, Harris M, Wanless S, Searle K, Elston D (2020) Improving estimates of seabird body-mass survival rates. *Scottish Mar Freshw Sci* 11.
- Davies TE, Carneiro APB, Campos B, Hazin C, Dunn DC, Gjerde KM, Johnson DE, Dias MP

- (2021) Tracking data and the conservation of the high seas: Opportunities and challenges. *J Appl Ecol* 58:2703–2710.
- Dunn DC, Harrison AL, Curtice C, DeLand S, Donnelly B, Fujioka E, Heywood E, Kot CY, Poulin S, Whitten M, Åkesson S, Alberini A, Appeltans W, Arcos JM, Bailey H, Ballance LT, Block B, Blondin H, Boustany AM, Brenner J, Catry P, Cejudo D, Cleary J, Corkeron P, Costa DP, Coyne M, Crespo GO, Davies TE, Dias MP, Douvère F, Ferretti F, Formia A, Freestone D, Friedlaender AS, Frisch-Nwakanma H, Froján CB, Gjerde KM, Glowka L, Godley BJ, Gonzalez-Solis J, Granadeiro JP, Gunn V, Hashimoto Y, Hawkes LM, Hays GC, Hazin C, Jimenez J, Johnson DE, Luschi P, Maxwell SM, McClellan C, Modest M, Di Sciara GN, Palacio AH, Palacios DM, Pauly A, Rayner M, Rees AF, Salazar ER, Secor D, Sequeira AMM, Spalding M, Spina F, Van Parijs S, Wallace B, Varo-Cruz N, Virtue M, Weimerskirch H, Wilson L, Woodward B, Halpin PN (2019) The importance of migratory connectivity for global ocean policy. *Proc R Soc B Biol Sci* 286.
- Dunn RE, Wanless S, Daunt F, Harris MP, Green JA (2020) A year in the life of a North Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Sci Rep* 10:5993.
- Elliott KH, Gaston AJ (2014) Dive behaviour and daily energy expenditure in Thick-billed murres *Uria lomvia* after leaving the breeding colony. *Mar Ornithol* 189:183–189.
- Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behavior by a monomorphic seabird represents risk partitioning. *Behav Ecol* 21:1024–1032.
- Fort J, Porter WP, Grémillet D (2009) Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *J Exp Biol* 212:2483–2490.
- Fraser KC, Davies KTA, Davy CM, Ford AT, Flockhart DTT, Martins EG (2018) Tracking the conservation promise of movement ecology. *Front Ecol Evol* 6:1–8.
- Fretwell SD (1972) *Populations in a Seasonal Environment*. Princeton University Press.
- Gaston AJ (2003) Synchronous fluctuations of thick-billed murre (*Uria lomvia*) colonies in the eastern Canadian Arctic suggest population regulation in winter. *Auk* 120:362–370.
- Gjerde KM, Clark NA, Chazot C, Cremers K, Harden-Davies H, Kachelriess D, Payne CR, Rodriguez-Chaves M, Spadone A, Thiele T, Vierros M, Goettsche-Wanli G, Wright G (2022) Getting beyond yes: fast-tracking implementation of the United Nations agreement for marine biodiversity beyond national jurisdiction. *NPJ Ocean Sustain* 1.
- González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front Ecol Environ* 5:297–301.
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: Daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538.
- Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world's ocean. *Sci Rep* 9:1–8.
- Halpin LR, Ross JD, Ramos R, Mott R, Carlile N, Golding N, Reyes-González JM, Militão T, De Felipe F, Zajková Z, Cruz-Flores M, Saldanha S, Morera-Pujol V, Navarro-Herrero L, Zango L, González-Solís J, Clarke RH (2021) Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles.

- Harris MP, Leopold MF, Jensen JK, Meesters EH, Wanless S (2015) The winter diet of the Atlantic Puffin *Fratercula arctica* around the Faroe Islands. *Ibis* (Lond 1859) 157:468–479.
- Hays GC, Bailey H, Bograd SJ, Bowen WD, Campagna C, Carmichael RH, Casale P, Chiaradia A, Costa DP, Cuevas E, Nico de Bruyn PJ, Dias MP, Duarte CM, Dunn DC, Dutton PH, Esteban N, Friedlaender A, Goetz KT, Godley BJ, Halpin PN, Hamann M, Hammerschlag N, Harcourt R, Harrison AL, Hazen EL, Heupel MR, Hoyt E, Humphries NE, Kot CY, Lea JSE, Marsh H, Maxwell SM, McMahon CR, Notarbartolo di Sciara G, Palacios DM, Phillips RA, Righton D, Schofield G, Seminoff JA, Simpfendorfer CA, Sims DW, Takahashi A, Tetley MJ, Thums M, Trathan PN, Villegas-Amtmann S, Wells RS, Whiting SD, Wildermann NE, Sequeira AMM (2019) Translating Marine Animal Tracking Data into Conservation Policy and Management. *Trends Ecol Evol* 34:459–473.
- Johnston A, Cook ASCP, Wright LJ, Humphreys EM, Burton NHK (2014) Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *J Appl Ecol* 51:31–41.
- Kelsey EC, Felis JJ, Czapanskiy M, Pereksta DM, Adams J (2018) Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. *J Environ Manage* 227:229–247.
- Kouwenberg AL, Mark Hipfner J, McKay DW, Storey AE (2013) Corticosterone and stable isotopes in feathers predict egg size in Atlantic Puffins *Fratercula arctica*. *Ibis* (Lond 1859) 155:413–418.
- Lack D (1968) Ecological adaptations for breeding in birds. Methuen & Co., London.
- Lascelles B, Notarbartolo Di Sciara G, Agardy T, Cuttelod A, Eckert S, Glowka L, Hoyt E, Llewellyn F, Louzao M, Ridoux V, Tetley MJ (2014) Migratory marine species: Their status, threats and conservation management needs. *Aquat Conserv Mar Freshw Ecosyst* 24:111–127.
- Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: Accuracy and precision affected by environmental factors. *Methods Ecol Evol* 3:603–612.
- Major HL, Durham SE, Fana N, Rivers JE, Diamond AW (2021) Contrasting phenological and demographic responses of Atlantic Puffin (*Fratercula arctica*) and Razorbill (*Alca torda*) to climate change in the Gulf of Maine. *Elementa* 9:1–19.
- Marra PP, Cohen E, Harrison AL, Studds CE, Webster M (2019) Migratory Connectivity. *Encycl Anim Behav Second Ed Vol 1-5* 3:V3-643-V3-654.
- Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM (2015) A call for full annual cycle research in animal ecology. *Biol Lett* 11.
- McMahon KW, Polito MJ, Abel S, McCarthy MD, Thorrold SR (2015) Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (*Pygoscelis papua*). *Ecol Evol* 5:1278–1290.
- Merkel B, Descamps S, Yoccoz NG, Grémillet D, Fauchald P, Danielsen J, Daunt F, Erikstad KE, Ezhov AV, Harris MP, Gavrilov M, Lorentsen SH, Reiertsen TK, Systad GH, Lindberg

- Thórarinnsson T, Wanless S, Strøm H (2021) Strong migratory connectivity across meta-populations of sympatric North Atlantic seabirds. *Mar Ecol Prog Ser* 676:173–188.
- Merkel B, Phillips RA, Descamps S, Yoccoz NG, Moe B, Strøm H (2016) A probabilistic algorithm to process geolocation data. *Mov Ecol* 4:26–37.
- Moriarty T (2023) BOEM Advances Offshore Wind Leasing Process in the Gulf of Maine. <https://www.boem.gov/newsroom/press-releases/boem-advances-offshore-wind-leasing-process-gulf-maine>
- NROC (2023) Northeast Ocean Data Portal Energy and Infrastructure Map. <https://www.northeastoceandata.org/data-explorer/?energy-infrastructure> (accessed 4 July 2023)
- O’Hanlon N, van Bemmelen R, Snell K, Conway G, Thaxter C, Aiton H, Aiton D, Balmer D, Hanssen S, Calladine J, Hammer S, Harris S, Moe B, Schekkerman H, Tulp I, Humphreys E (2024) Atlantic populations of a declining oceanic seabird have complex migrations and weak migratory connectivity to staging areas. *Mar Ecol Prog Ser* 730:113–129.
- Ohkouchi N, Chikaraishi Y, Close HG, Fry B, Larsen T, Madigan DJ, McCarthy MD, McMahon KW, Nagata T, Naito YI, Ogawa NO, Popp BN, Steffan S, Takano Y, Tayasu I, Wyatt ASJ, Yamaguchi YT, Yokoyama Y (2017) Advances in the application of amino acid nitrogen isotopic analysis in ecological and biogeochemical studies. *Org Geochem* 113:150–174.
- Orben RA, Irons DB, Paredes R, Roby DD, Phillips RA, Shaffer SA (2015) North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. *J Biogeogr* 42:401–412.
- Paredes R, Jones IL, Boness DJ (2006) Parental roles of male and female thick-billed murre and razorbills at the Gannet Islands, Labrador. *Behaviour* 143:451–481.
- Pershing AJ, Alexander MA, Brady DC, Brickman D, Curchitser EN, Diamond AW, McClenachan L, Mills KE, Nichols OC, Pendleton DE, Record NR, Scott JD, Staudinger MD, Wang Y (2021) Climate impacts on the Gulf of Maine ecosystem: A review of observed and expected changes in 2050 from rising temperatures. *Elementa* 9:1–18.
- Peschko V, Schwemmer H, Mercker M, Markones N, Borkenhagen K, Garthe S (2024) Cumulative effects of offshore wind farms on common guillemots (*Uria aalge*) in the southern North Sea - climate versus biodiversity? *Biodivers Conserv* 33:949–970.
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. *Mar Ecol Prog Ser* 266:265–272.
- Pyle P (2009) Age determination and molt strategies in North American alcids. *Mar Ornithol* 37:219–226.
- Rexer-Huber K, Clay TA, Catry P, Debski I, Parker G, Ramos R, Robertson BC, Ryan PG, Sagar PM, Stanworth A, Thompson DR, Tuck GN, Weimerskirch H, Phillips RA (2025) Metapopulation distribution shapes year-round overlap with fisheries for a circumpolar seabird. *Ecol Appl* 35:e70019.
- Saba VS, Griffies SM, Anderson WG, Winton M, Alexander MA, Delworth TL, Hare JA, Harrison MJ, Rosati A, Vecchi GA (2016) Enhanced warming of the Northwest Atlantic Ocean under climate change. *J Geophys Res Ocean* 121:118–132.

- Sandvik H, Erikstad KE, Barrett RT, Yoccoz NG (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *J Anim Ecol* 74:817–831.
- Scopel LC, Diamond A, Kress S, Shannon P (2019) Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Mar Ecol Prog Ser* 626:177–196.
- Shaffer SA, Tremblay Y, Awkerman JA, Henry RW, Teo SLH, Anderson DJ, Croll DA, Block BA, Costa DP (2005) Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Mar Biol* 147:833–843.
- Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: Stable isotope evidence that pre-breeding diet quality influences reproductive success. *J Anim Ecol* 78:460–467.
- Stenhouse IJ, Berlin AM, Gilbert AT, Goodale MW, Gray CE, Montevecchi WA, Savoy L, Spiegel CS (2020) Assessing the exposure of three diving bird species to offshore wind areas on the U.S. Atlantic Outer Continental Shelf using satellite telemetry. *Divers Distrib* 26:1703–1714.
- Thaxter CB, Daunt F, Hamer KC, Watanuki Y, Harris MP, Grémillet D, Peters G, Wanless S (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: Nest defence, foraging efficiency or parental effort? *J Avian Biol* 40:75–84.
- Tittensor DP, Beger M, Boerder K, Boyce DG, Cavanagh RD, Cosandey-Godin A, Crespo GO, Dunn DC, Ghiffary W, Grant SM, Hannah L, Halpin PN, Harfoot M, Heaslip SG, Jeffery NW, Kingston N, Lotze HK, McGowan J, McLeod E, McOwen CJ, O’Leary BC, Schiller L, Stanley RRE, Westhead M, Wilson KL, Worm B (2019) Integrating climate adaptation and biodiversity conservation in the global ocean. *Sci Adv* 5:1–15.
- Vanermen N, Onkelinx T, Courtens W, Van de walle M, Verstraete H, Stienen EWM (2015) Seabird avoidance and attraction at an offshore wind farm in the Belgian part of the North Sea. *Hydrobiologia* 756:51–61.
- Welcker J, Nehls G (2016) Displacement of seabirds by an offshore wind farm in the North Sea. *Mar Ecol Prog Ser* 554:173–182.
- Whelan S, Hatch SA, Irons DB, McKnight A, Elliott KH (2020) Increased summer food supply decreases non-breeding movement in black-legged kittiwakes. *Biol Lett* 16.
- Wiens JA (1977) On Competition and Variable Environments: Populations may experience ‘ecological crunches’ in variable climates, nullifying the assumptions of competition theory and limiting the usefulness of short-term studies of population patterns. *Am Sci* 65:590–597.
- Young RC, Orben RA, Will AP, Kitaysky AS (2017) Relationship between telomere dynamics and movement and behavior during winter in the thick-billed murre. *Mar Ecol Prog Ser* 578:253–261.