Overwinter Movement of Atlantic Puffins (*Fratercula arctica*) Breeding in the Gulf of Maine

by

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Abstract

Atlantic Puffins (*Fratercula arctica*) are pelagic seabirds that breed on offshore islands throughout the North Atlantic. Following the breeding season, puffins spend the non-breeding months at sea and there is a knowledge gap regarding the factors affecting populations away from the colony. I used geolocators to determine the nonbreeding locations of North American puffins breeding on three islands in the Gulf of Maine, examining differences between colonies and within the largest colony. I also examined using stable isotopes in claw tissue to determine general overwinter position.

Puffins sampled in this study typically remained in the Gulf of Maine before moving south in the late winter, though some visited waters around Newfoundland during the autumn. Movement patterns were similar among birds within and between colonies. Attempts to use stable isotope analysis of claw tissue to determine overwinter location were inhibited by the similarity of routes among sampled birds.

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Introduction

Atlantic Puffins (*Fratercula arctica*), hereafter referred to as puffins, are pelagic, pursuit-diving seabirds that breed in large colonies (hundreds to hundreds of thousands of individuals) on offshore islands throughout the North Atlantic during the summer months (Lowther et al. 2002). Following the breeding season, puffins spend the non-breeding months at sea and there is a knowledge gap regarding the factors affecting populations away from the colony. Although broad-scale overwinter movements from and interactions between larger colonies across the range have recently been brought to light (Fayet et al. 2017a), finer details of the movements from North American colonies remain sparse due to the European focus of prior studies.

Puffins spend most of the year at sea and their mortality is highest during the winter, away from observation at colonies (Breton & Diamond 2014). As a long-lived, slow-reproducing species, adult mortality can have a large impact on populations. In a time of changing climatic and oceanographic conditions, it is integral to better understand puffin biology to manage their survival outside of the breeding season. This can be done in part through the creation and maintenance of marine protected areas in important overwinter locations; as such, these locations and their relative importance to the regional metapopulation must first be determined.

Background

Early movement studies of puffins were based primarily on visual observation of individuals and band recoveries (Harris 1984, Gaston et al. 2008). Recent advances in tracking technology (satellite tags, geolocation), especially over the last decade, have begun to provide more insight into movements of some puffin populations (Anker-Nilssen & Aarvak 2009, Fayet et al. 2017a), though much remains to be learned.

Band recoveries:

Among the early efforts to assess the overwinter movements of puffins, Harris (1984) used band recovery data from both sides of the Atlantic and showed varied overwinter locations from different colonies. Notably, several individuals banded in west Britain/Ireland, north Scotland, Norway, the Faeroe Islands, New Brunswick, and Greenland were recovered in Newfoundland. Many of the bands recovered from areas far from their natal colonies were immature birds, suggesting that younger birds disperse further than breeding-age adults.

A follow-up study examined winter band recoveries from birds at least three years of age (considered old enough to attend colonies) from five European colonies (Harris et al. 2005). Consistent with earlier band recoveries, birds from the Isle of May (southeast Scotland) were found throughout the North Sea, while birds from Fair Isle (north Scotland) and Skomer (Wales) were recovered mostly in the Bay of Biscay and Irish Sea. Bands from the Norwegian colonies at Røst and Hornøya remained in the Norwegian Sea and northern North Sea.

Later recoveries of birds banded on the Isle of May again showed most birds in the North Sea but exposed a shift over time from recoveries to the south (Bay of Biscay, English Channel) to recoveries in the North Atlantic (mostly in the Faeroe Islands) (Harris et al. 2010).

A thorough examination of band recoveries throughout Canada between 1921 and 1995 demonstrated some movement, especially of young birds, away from their natal colony with recoveries of Gulf of Maine birds near Newfoundland (Gaston et al. 2008). Overall, fewer bands were recovered from puffins than from co-occurring alcids (Razorbills, *Alca torda*; murres, *Uria* spp.), suggesting that puffins overwinter further from shore where there is a lower likelihood of detection.

Satellite tags:

By the late 1990s, tagging technology had progressed to the point of feasibility for deployment of satellite tags on puffins. Five individuals over three years from the Norwegian colony at Røst were fitted with satellite tags to track post-breeding movements in July and August (Anker-Nilssen & Aarvak 2009). All five birds showed distinct movements towards the Barents Sea to the northeast, contrary to earlier band recoveries collected to the south and west. Satellite tags have the advantage of being highly accurate, but their large size and placement on the bird's back can have a negative impact on bird well-being and breeding success (Anker-Nilssen & Aarvak 2009).

Geolocation:

Light-sensing geolocator tags have become the standard for long-distance seabird movement studies in the last decade. Smaller and lighter than satellite tags, they can be attached to a plastic or metal leg band. Their weakness is their imprecision, with studies suggesting that typical error for seabirds can be on the order of ~185 km (Phillips et al. 2004, Winship et al. 2012), though newer methods of analysis can be more precise

(Ekstrom 2007). While adequate for examining large-scale migrations, geolocators are insufficient for tracking local movements, and though smaller than satellite tags, can still negatively affect the bird. Harris et al. (2013) found that around 60% of birds tagged with geolocators suffered disruption to their breeding efforts through either a delayed (>3 days) return to their burrow or, in some cases, complete nest abandonment, though overwinter survival was unaffected. A study of geolocator-equipped murres found increased levels of corticosterone, an indicator of stress, but no effect on overwinter survival or chick provisioning rates (Elliott et al. 2012).

To complement band recovery data, puffins breeding on the Isle of May were tagged with geolocators in 2007 (Harris et al. 2010). While many remained in the northwestern North Sea, some spent the period from August to December to the west of Scotland in the Atlantic Ocean. All birds returned to the North Sea for January and February, arriving to waters near the colony by April. The winter of 2007/2008 was atypically unfavourable for puffin survival, thus the authors deployed additional geolocators in 2009. Regardless of the conditions (poor in 2007/2008, fair in 2009/2010), about half of the tagged puffins stayed entirely in the North Sea, with the other half venturing into the Atlantic Ocean (Harris et al. 2013). Birds from both overwinter locations returned to the colony around the same time. Overall, this study highlights that geolocators provided novel information on birds far from shore, which would be unlikely to be detected by band recoveries alone.

To determine the extent of route fidelity, adult puffins breeding on Skomer were tagged with geolocators in successive years (Guilford et al. 2011). Birds were found to disperse widely immediately following the breeding season, with some moving west into the

Atlantic and some south to the Bay of Biscay. In autumn, the groups converged in the North Atlantic before southward winter movements; some individuals moved into the Mediterranean Sea during this time. Individuals used similar routes between years, indicating strong route fidelity at the level of the individual if not the population. These dispersive routes are unlikely to be related to genetics or taught by parents, rather, young birds presumably have a wide angle of dispersion, but refine their route as they age, following the proposed "exploration-refinement hypothesis" (Guilford et al. 2011).

Building on prior geolocator work from Skomer, Fayet et al. (2016) identified four distinct strategies of overwinter movement. Individuals either stayed near the colony, travelled into the Atlantic, visited the Atlantic and then the Mediterranean, or stayed local before moving to the Mediterranean. Birds tracked for multiple years showed strong inter-annual route fidelity. Among different puffins using the same migration strategy, there were similarities in timing of movement. Each of the strategies showed different levels of daily energy expenditure, extrapolated from behaviours determined by the wet/dry sensor on the geolocator. Migration strategy was determined to have a significant correlation with subsequent breeding success, with birds visiting the Mediterranean in the spring being most successful.

Another study from Skomer examined the overwinter movements of mated puffin pairs (Fayet et al. 2017b). Pairs with more overwinter route similarity bred earlier the following season and tended to breed more successfully. However, successful prior breeding did not correlate with subsequent route similarity. Pairs migrated separately, even when taking similar routes. Route similarity in pairs persisted for the first three months post-breeding, and then tapered off. There was a positive correlation between winter foraging effort (daily energy expenditure inferred from saltwater immersion data) and reproductive fitness in females, though not in males.

Geolocator tags deployed on puffins from Skellig Michael (Ireland) demonstrated a westward mass movement immediately following the breeding season, with most birds undertaking a transatlantic migration to waters off Newfoundland (Jessopp et al. 2013). The proposed reason for this movement is the reliable abundance of food in these waters at that time of year. A correlation was found between zooplankton (which puffin prey consume) abundance and puffin abundance, lending credibility to this. The degree of movement of an individual bird was determined not to be correlated with the bird's mass or sex.

Recent large-scale comparisons of puffin geolocation data have shown several trends (Fayet et al. 2017a). All puffin populations have at least some overlap in overwinter range with at least one other population for part of the non-breeding season; overlap was highest between August and November. Colony-level productivity was shown to be negatively correlated with four factors: population size, migration distance, wintering latitude, and local water productivity.

eBird:

In addition to traditional scientific study, some incidental data can be gathered from the citizen science program eBird, where bird watchers record their sightings in a large online database. Based on these reports, puffins seem to regularly spend portions of the winter as far south as the waters off North Carolina; puffins have also been occasionally recorded near Bermuda (eBird 2019). These birds are likely breeders from North

America, as there are no other records of European-breeding birds in the western Atlantic south of Newfoundland (Fayet et al. 2017a).

Research Priorities:

Even with the publication of several studies on puffin movement in recent years, there remains a paucity of published data on the movement of North American birds. The deployment and retrieval of geolocator tags on Machias Seal Island, a major puffin breeding colony at the mouth of the Bay of Fundy, and two smaller colonies along mid-coast Maine, Matinicus Rock and Seal Island, will provide insight into the specific movements of puffins from this region. As the core colonies in the Gulf of Maine, understanding the non-breeding movements of these birds is tied to effective management of the regional population (Breton et al. 2006).

Although inter-colony comparisons of overwinter movement have been made from European colonies, the same has not been done within the Gulf of Maine, nor has a thorough examination of puffins nesting in disparate areas within the same colony been attempted. Limited information on puffins at sea in the winter indicates that they are mostly solitary, with very low densities across wide areas (Harris & Wanless 2011). However, large swaths of open ocean remain under-surveyed and it is possible that groups of puffins congregate in certain areas.

Objectives and Predictions

Objective 1: To determine the overwinter range and movements of puffins breeding on three Gulf of Maine colonies: Machias Seal Island, Seal Island, and Matinicus Rock

Prediction 1: Puffins will undergo a dispersive migration, whereby individuals move in different directions to one of several productive overwinter areas in the northwestern Atlantic Ocean between Newfoundland and North Carolina.

Tagged individual puffins in European colonies were found to disperse widely after breeding but followed one of several broad overwintering strategies for the individual colony (Guilford et al. 2011, Fayet et al. 2016). The proposed exploration-refinement hypothesis (Guilford et al. 2011), would support these differences in individual movement, culminating in the development of multiple strategies which may focus on shared high-productivity areas.

Preliminary data suggest that most birds breeding in the Gulf of Maine will remain therein or nearby throughout the winter (Fayet et al. 2017a). Outside of the Gulf of Maine, birds from these colonies could be venturing north to exploit an abundant source of capelin (*Mallotus villosus*) off the coast of Newfoundland as seen in some European breeders (Gaston et al. 2008, Jessopp et al. 2013), south along the continental shelf of the northeastern United States (Gaston et al. 2008, eBird 2019), or further south to the waters off North Carolina or Bermuda (eBird 2019).

Objective 2: To examine differences in overwinter movements at the inter- and intra-colony level

Prediction 2.1: Puffins nesting at each of the three major Gulf of Maine colonies will show similar overwinter movements between colonies.

Previous comparisons of overwinter movement in puffins from different colonies have pooled data from Gulf of Maine colonies due to limited sample size and relative proximity of the islands (Fayet et al. 2017a). The nearness of the colonies provides birds with access to the same resource areas, especially after breeding when puffins are no longer tethered to a colony to feed a chick. Puffins breeding in the Gulf of Maine are also members of the same metapopulation, with colonies connected through natal dispersal and pre-breeding movement of individuals (Breton et al. 2006).

Prediction 2.2: Gulf of Maine colonies will not show differences in overwinter movement based on colony size.

While Fayet et al. (2017a) noted that birds from larger puffin colonies travelled further from their colonies during the winter, the variability in size of the three largest colonies in the Gulf of Maine (~500 pairs at both Matinicus Rock and Seal Island, ~6,000 pairs on Machias Seal Island) is unlikely to place them in different size categories. All three of these colonies would be considered small for the species relative to more northerly colonies with more than 10,000 pairs and the largest colonies in Iceland which exceed 100,000 pairs (Harris & Wanless 2011).

Prediction 2.3: Birds that nest nearer to each other within the same colony will show more similarities in their overwinter movements than those nesting further apart.

Prior overwinter movement studies of seabirds treat breeding colonies as a unit without accounting for intra-colony variability. Subcolony dynamics in seabirds have been studied with a focus on breeding season foraging movement and trophic level (Hipfner et al. 2007, Waggitt et al. 2014), as well as breeding success (Hipfner et al. 2007), but have not examined differences in overwinter strategies. Birds nesting at the same colony may overwinter in widely disparate areas (Jessopp et al. 2013, Fayet et al. 2016), even when comparing members of mated pairs (Fayet et al. 2017b, Davis et al. 2016). There is, however, a lack of published information about the relationship between overwinter connectivity and breeding season nest proximity beyond the pair level.

Historically, puffins did not nest at the northern end of Machias Seal Island; burrows were concentrated along the southern and southwestern portions (A. Diamond, pers. comm.). The newer, northern part of the colony appears to differ from the southern end in timing of pre-breeding arrival to the island (R. Eldridge, pers. comm.), perhaps hinting at differences in overwinter location.

Objective 3: To examine the feasibility of using stable isotope analysis of claw tissue to determine general overwintering position of puffins

Prediction 3: Stable isotope ratios from different overwintering areas will be distinct and recognizable from claw tissue.

A common shortfall of tagging studies is the limitation of sample size due to expense and the difficulty of tag retrieval. If a method could be developed to determine overwinter position without the necessity of tags, it would provide a larger sample from a given population. Isotopes of several elements, notably $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$, vary across marine systems (Hobson 1999), permitting the comparison of overwintering areas in seabirds through analysis of tissue samples (Cherel et al. 2006, Cherel et al. 2007). Steenweg et al. (2017) demonstrated that stable isotopes in claws of Common Eiders (*Somateria mollissima*) collected at the breeding colony could be reliably used to match a specific bird to one of three overwintering destinations known from earlier satellite tracking data and visual confirmation of winter flocks.

With puffins, claw samples taken from geolocator-tagged individuals at the time of tag retrieval could allow for examination of stable isotopes with simultaneous known winter locations. If clear location-based patterns are discernible from tagged birds, samples from other puffins from the colony will be examined for similar patterns. These untagged puffins can then have their overwinter movements estimated with only a claw sample in lieu of geolocators.

Significance

Seabirds face a variety of threats at sea including pollution, commercial fishing, and offshore development. By better understanding their spatial distribution, it will become possible to better assess the precise threats that these birds face and take protective actions, including the creation and maintenance of marine protected areas such as the Northeast Canyons and Seamounts Marine National Monument. While present protected areas are necessary, they may not be sufficient on their own to maintain puffin populations in the Gulf of Maine into the foreseeable future and additional steps (e.g., regulations on fishing gear and offshore energy development) should be taken to limit the impact of the largest at-sea threats.

Previous studies have examined differences in movement between seabird colonies, but not differences within the same colony. An examination of intra-colony differences in overwinter movement could help to elucidate the understanding of community dynamics below the colony level as well as have implications for fine-scale management.

While tagging studies are currently limited by associated costs and the difficulties of tag retrieval, using stable isotope analysis as a complement to tags could permit a greatly increased sample size of any studied population. Locations derived from stable isotope analysis promise to be less expensive, less invasive, and not reliant upon retrieval of tags from specific birds.

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Overwinter Movement of Atlantic Puffins (*Fratercula arctica*) in the Gulf of Maine: Inter- and Intra-Colony Effects

Abstract

To identify potential threats and prioritize areas for protection, modern conservation efforts rely heavily upon spatial data. Determination of priority areas can be complicated, especially in marine systems where distribution of pelagic birds, for example, is not always determined by obvious habitat distinctions. I examined where Atlantic Puffins (*Fratercula arctica*) breeding in the Gulf of Maine spend the nonbreeding season and whether birds from different colonies or parts of the same colony used different overwintering strategies. Between 2013 and 2018, archival light geolocator tags were deployed on puffins breeding on three islands in the Gulf of Maine: Machias Seal Island, Matinicus Rock, and Seal Island. Based on geolocator data, puffins from all three colonies generally remained in and near the Gulf of Maine throughout the autumn and early winter months, venturing southward as far as Cape Hatteras (North Carolina, USA) in February, March, and April, before returning to their respective colonies. A small proportion of individuals travelled to the Gulf of St. Lawrence and waters around Newfoundland immediately after breeding, returning to the Gulf of Maine in mid-winter. I found no evidence of inter- or intra-colony differences in overwinter movement. These overwinter locations can assist development of policy regarding management and protection of important marine areas for all Gulf of Maine puffins.

Introduction

Conservation management decisions have become increasingly reliant upon spatial data to identify potential threats and prioritize areas for protection (Grémillet & Boulinier 2009, McGowan et al. 2013). The impracticality of range-wide preservation for most species has forced managers to generally focus efforts on areas of highest use to designate protection status and implement regulations. In terrestrial systems, these key areas are frequently tied to specific biotic and abiotic factors (e.g., vegetation type, water availability), though information can be supplemented with observations and remote tracking studies. In marine systems, where distribution of pelagic birds, for example, is not always determined by obvious habitat distinctions, the determination of areas of importance can be more complicated. As such, information gained from at-sea surveys and tagging studies has become a powerful tool for the designation of Marine Protected Areas in marine hotspots (Ronconi et al. 2012) and to inform other approaches (Croxall et al 2012).

Colonial seabirds form large aggregations during the breeding season, generally foraging for themselves and their chicks in nearby waters. Breeding season foraging movement has been well studied in a number of species and systems with both observational, radio telemetry (e.g., Anderson & Ricklefs 1987, Irons 1998, Jodice & Collopy 1999), and remotely-collected GPS tag data (e.g., Harris et al. 2012, Pratte et al. 2017, Symons 2018). Movement outside of the breeding season is more difficult to study, as some species (e.g., terns) may travel extreme distances, while others (e.g., puffins) remain far out to sea where encounters with humans are unlikely (Gaston et al. 2008). While banding studies have provided some insight into non-breeding movement of seabirds (e.g., Harris 1984, Gaston et al. 2008), technological advances have permitted the acquisition of more detailed data using bird-borne tracking devices (Burger & Shaffer 2008). Satellite tags can provide highly precise movement data on larger birds such as albatrosses (Hyrenbach & Dotson 2001), but the size of the tags can have negative impacts on smaller species, like puffins (Anker-Nilssen & Aarvak 2009). Archival light geolocator tags are smaller and lighter, permitting use on smaller species at the cost of lower positional precision (e.g., Phillips et al. 2004, Guilford et al. 2011). Geolocator tags may have some effects on seabird condition and breeding success, but these are generally minor and not persistent (Elliott et al. 2012, Harris et al. 2013).

Atlantic Puffins (*Fratercula arctica*), hereafter "puffins", nest colonially on offshore islands across the north Atlantic Ocean (Lowther et al. 2002). These colonies provide an environment to breed and socialize with conspecifics (Harris & Wanless 2011). Due to their proximity, puffins from neighbouring burrows would presumably be more socially connected than birds nesting on opposite sides of the colony, or at different colonies nearby. Subcolony dynamics in seabirds have been studied with a focus on breeding season foraging movements and trophic level (Hipfner et al. 2007, Waggitt et al. 2014) as well as breeding success (Hipfner et al. 2007), but there has been little examination of differences or similarities in overwinter strategies. Birds nesting at the same colony or nearby colonies may overwinter in widely disparate areas (Jessopp et al. 2013, Fayet et al. 2016), even when comparing members of mated pairs (Davis et al. 2016, Fayet et al. 2017a). There is, however, a lack of published information about the relationship beyond the pair level between overwinter connectivity and breeding season nest proximity.

Movements of puffins breeding in the Gulf of Maine during the overwinter period (hereafter defined as the nonbreeding period between August and April) have not been well elucidated. Previous work has found that puffin survival is correlated with Atlantic herring (*Clupea harengus*) abundance (Breton & Diamond 2014), suggesting that overwinter movements are driven, at least partially, by food availability. Several tracks from geolocator-tagged puffins in the Gulf of Maine were included in a range-wide study of puffins (Fayet et al. 2017b), however a specific study of Gulf of Maine birds has not been done. Based on findings from the range-wide study, puffins that breed in the Gulf of Maine appear to remain within and nearby the Gulf of Maine throughout the year, though they likely move offshore based on the relative paucity of winter observations near shore (eBird 2019, Fayet et al. 2017b). eBird records include puffin sightings as far south as Cape Hatteras, North Carolina (USA), peaking in February and March (eBird 2019), though the origin of these birds is unknown. As the nearest breeding colonies are in the Gulf of Maine, it is likely that these observations were of birds from these colonies, though there is some evidence that birds from Newfoundland may visit the Mid-Atlantic Bight (Fifield et al. 2015).

In this study, I used archival light geolocator data to examine where puffins breeding in the Gulf of Maine spend the nonbreeding season and whether birds from different colonies or different parts of the same colony use different overwinter strategies. I predicted that overwinter movements would be generally similar between colonies and unaffected by colony size, though birds nesting nearer one another in the same colony would be more likely to be in closer winter proximity than those nesting farther apart.

Methods

Ethics Statement

The deployment of geolocator tags received both ethical and permit approval for all study locations. Work on Machias Seal Island was approved by the Animal Care Committee at the University of New Brunswick (AUP No. 17005) and the Canadian Wildlife Service (Permit No. ST2728).

Focal Species: Atlantic Puffin

Atlantic Puffins are medium-sized (length 26-29 cm) pursuit-diving seabirds that are members of the family Alcidae, or auks (Lowther et al. 2002). Puffins feed on fish and marine invertebrates, diving to pursue and capture multiple prey items in their bill. Large aggregations of puffins form on offshore islands during the breeding season, where they nest in burrows excavated in sod, between boulders, or in rock crevices.

Study Locations

Puffins breed on several islands in the Gulf of Maine (Figure 1.1); the largest colonies are at Machias Seal Island (MSI), Seal Island (SI), and Matinicus Rock (MR). Machias Seal Island (44°30'N, 67°06'W) lies at the mouth of the Bay of Fundy, where it opens into the Gulf of Maine near the border of Canada and the United States. The island is a Migratory Bird Sanctuary managed by the Canadian Wildlife Service of Environment and Climate Change Canada. Seal Island (43°53'N, 68°44'W) and Matinicus Rock (43°47'N, 68°51'W) are both at the outer edge of Penobscot Bay along mid-coast Maine. Puffins were extirpated from Seal Island in the late 1800s but were reintroduced in the

1980s by translocating and rearing chicks from Newfoundland (Kress & Jackson 2015). Both islands are owned by Maine Coastal Islands National Wildlife Refuge and staffed during the breeding season by the National Audubon Society's Project Puffin.

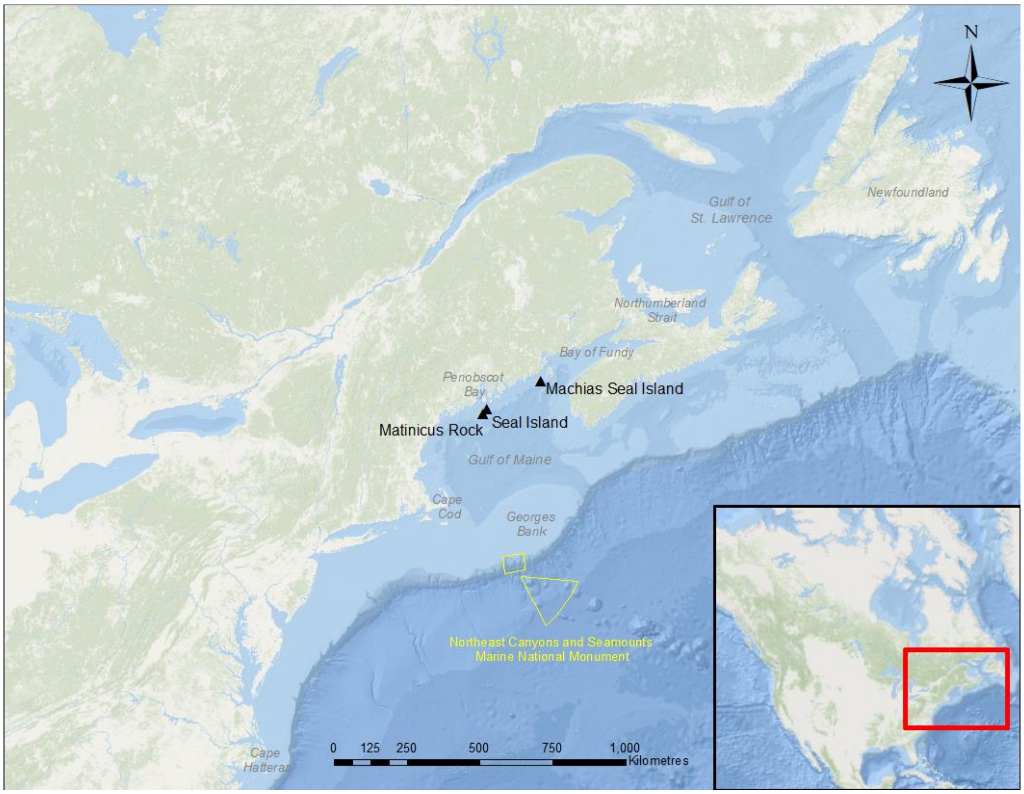

Figure 1.1. Map featuring the three largest puffin colonies in the Gulf of Maine: Machias Seal Island, Seal Island, and Matinicus Rock.

Burrow Selection, Geolocator Deployment and Retrieval

During mid-July, I selected active (chick present) puffin burrows within the colony for tag deployment. I visually examined burrow depth, shape, size, and substrate; I did not consider those deemed too deep, winding, or narrow to reach the end, nor those with multiple routes of egress. Additionally, I preferentially selected burrows in sod backing on rock; pure sod burrows could permit further excavation and possible egress, while wide rock-only burrows risk takeover by Razorbills (*Alca torda*). I chose burrows as far above the tideline as possible to limit the risk of damage from storm surge. I marked burrows with a unique alphanumeric code painted on rocks or 1.5 metre wooden stakes. I recorded burrow GPS locations on MSI to calculate distances between burrows.

I affixed archival light geolocator tags (MSI: MK 3005 & MK 4093 (Biotrack; Wareham, UK; Figure 1.2); SI & MR: LAT 2900 (Lotek; Newmarket, Ontario, Canada) and Intigeo C65 (Migration Technology; Cambridge, UK)) to leg bands with epoxy, fishing line, or cable ties. All tag models record light-level at time data, with some additionally recording temperature and saltwater immersion (wet/dry). Bands with attached tags weighed approximately 2.3 g, which is less than the recommended 3% of the weight (Kenward 2001) of the average adult puffin (310-550 g (Lowther et al. 2002)). In late July, I checked selected burrows twice daily until an adult was found to be present. I weighed, measured, and banded birds with a Bird Banding Lab (BBL) band on one leg and a field readable band with a geolocator on the other; I also collected feathers for genetic sexing. Plastic field readable bands with attached geolocator tags were closed with epoxy, ensuring free movement on the bird's leg. Following tag attachment, I released the bird into its burrow. For tag retrieval, I carefully removed birds from burrows, removed the tag, and weighed and measured birds to ascertain tag effect, the tag having spent at least one complete non-breeding season on the bird. I monitored burrow productivity throughout the breeding season following tag retrieval. Forty-three tags were retrieved (60%) from puffins on Machias Seal Island, representing 43 annual tracks from 41 individuals (one tag was unable to connect; one tag was found at the burrow entrance, having fallen off shortly after deployment; two tags provided two-year tracks), as well as a combined 17 tags (68%) from Seal Island and Matinicus Rock, representing 18 annual tracks from 17 individuals (one tag provided two years of data; Table 1.1). Due to their proximity and the limited number of tags retrieved per year, I pooled the data between the two Penobscot Bay colonies, Seal Island and Matinicus Rock.

Figure 1.2. a) Geolocator tag before deployment. Tags are attached to bands with epoxy and tied with fishing line. **b)** A puffin on Machias Seal Island with a geolocator tag attached to a green plastic field-readable leg band.

Table 1.1. Summary of geolocator tags deployed on and data retrieved from Atlantic Puffins in the Gulf of Maine between 2013 and 2017

Colony	**Deployment Year**	**Tag Type**	**Number Deployed**	**Number Retrieved**	**Number of Annual Tracks***
MSI	2014	Biotrack	26	12	11
MSI	2015	Biotrack	17	11	11
MSI	2016	Biotrack	0	0	1**
MSI	2017	Biotrack	29	20	20
Penobscot Bay	2013	Intigeo	4	2	2
Penobscot Bay	2013	LAT	9	6	6
Penobscot Bay	2014	LAT	12	9	9
Penobscot Bay	2015	LAT	0	0	1**
Total			*97*	*60*	*61*

*Some tags did not yield usable data, while others provided multiyear tracks
**Tag deployed in a previous year

Geolocator Analysis

All tag types produced a single daily position. I analyzed all Biotrack and Intigeo tag data using the *TwilightFree* package (Bindoff et al. 2018) in R 3.4.3 (R Core Team 2017). *TwilightFree* uses a Hidden Markov model with a two-pass forward-backward algorithm to generate locations from light level, and optionally temperature, data extracted from a geolocator tag. For Biotrack MK 3005 tags, I included a sea surface temperature correction in the analysis to improve accuracy; the MK 4093 and Intigeo tags did not record temperature data. If resultant daily locations were deemed unrealistic based on excessive (>300 km/day, which would assume 5 hours of flight at 60 km/h (Harris & Wanless 2011)) or overland movement (>50 km), those days were removed from analysis and tracks were rerun. Tracks that showed plausible overland movements (<50 km) were compared with saltwater immersion data, if available for the given tag.

As the LAT tags calculated daily positions internally rather than producing raw light-level at time data, I could not analyze them with the twilight-free method. Instead, I used the daily positions derived from a template-fit model and applied a 5-day weighted average smoothing of points (at a 1:2:3:2:1 ratio covering a period 2 days before and after (Fifield et al. 2014)). I then removed outliers based on movement in excess of 300 km/day and inland position.

To visualize trends, I created monthly Kernel Density Estimate (KDE) maps, using the *adehabitatHR* package in R 3.4.3 (Calenge 2006, R Core Team 2017), of all individuals pooled by colony, tag type, and year. Maps were not created for months with fewer than 100 total locations between all tracks following outlier removal (Figure 1.3); this only occurred in certain months for LAT tags deployed at the Penobscot Bay colonies in 2013 and 2014, as all other tags were analyzed using *TwilightFree* and were able to produce realistic locations during equinox periods (Bindoff et al. 2018).

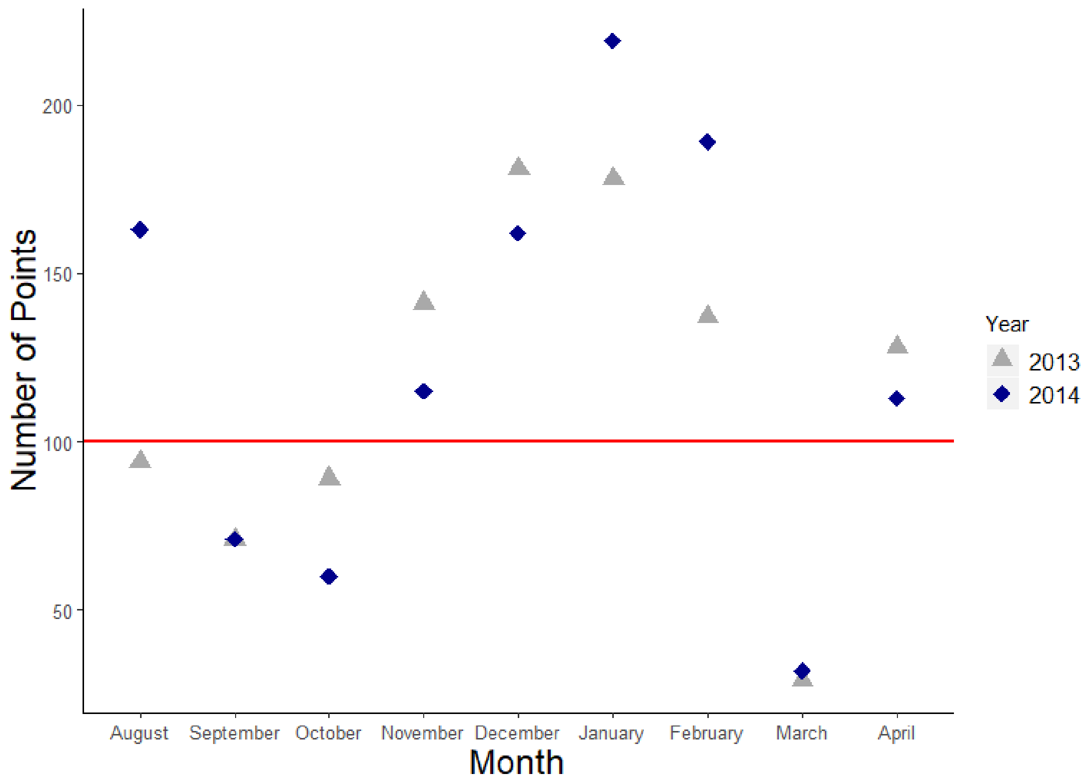

Figure 1.3. Number of points per month for all pooled individuals for Penobscot Bay colonies. Months with fewer than 100 points (red line), typically around the equinox when traditional GLS analysis methods cannot determine accurate latitudes, were not used for monthly KDE maps.

Inter- and Intra-Colony Comparisons

Due to conflating differences in tag type, geolocator analysis, and year, I examined inter-colonial overwinter differences qualitatively, rather than statistically. I created maps of the overlap between KDE plots from each colony for tags deployed in 2014, the one year in which the datasets overlap; these maps focus on the monthly core (50% kernel) and home (95% kernel) ranges. To examine differences in overwinter movement between different nesting areas of Machias Seal Island (Figure 1.4), I ran correlations using the *stats* package in R 3.4.3 (R Core Team 2017) between inter-burrow distance and mean as well as maximum overwinter distance between birds within a given year. Inter-burrow distances were calculated for each within-year burrow pair from GPS positions using the *pointDistance* function in the *raster* package in R 3.4.3 (R Core Team 2017).

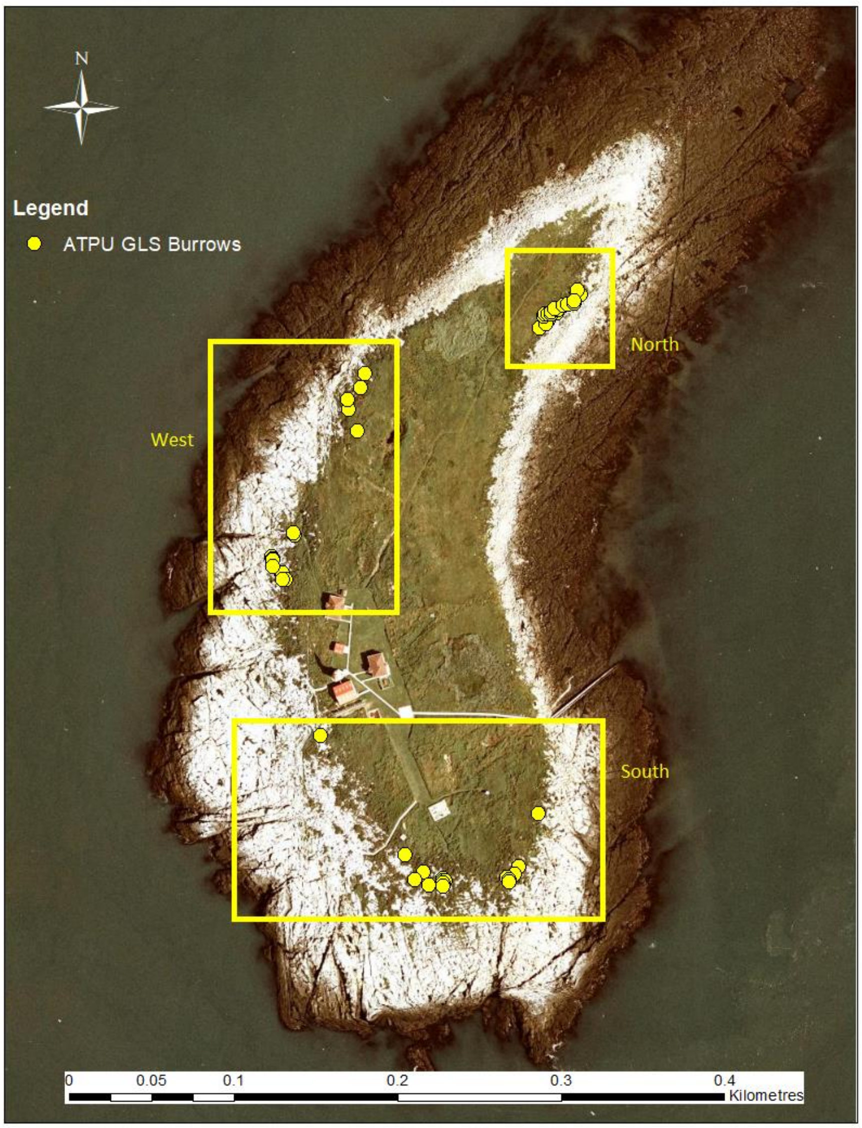

Figure 1.4. Map of Machias Seal Island showing geolocator-tagged burrows. Tag burrows are clustered in groups in three different parts of the colony: North, West, and South.

Results

Overwinter Locations

Puffins tagged on Machias Seal Island typically remained in the Gulf of Maine or around nearby Georges Bank from the end of the breeding season (August) through January in all years (Figure 1.5a-f). By February, many birds began moving south, out of the Gulf of Maine, reaching their southernmost position (southeast of Cape Hatteras, North Carolina) in March or April before returning to the colony (Figure 1.5g-i). Two tagged individuals, one in each of 2014 and 2015, moved immediately after the breeding season to waters around northeastern Newfoundland, then moved to the Gulf of St. Lawrence through December (Figure 1.5a-e). One of these individuals appears to have travelled from the Gulf of Maine to the Gulf of St. Lawrence by flying over land, likely across the Chignecto Isthmus (Figure 1.6); this is corroborated by the tag immersion data (Table 1.2). Movement does not vary based on sex (Appendix III: Table III-1).

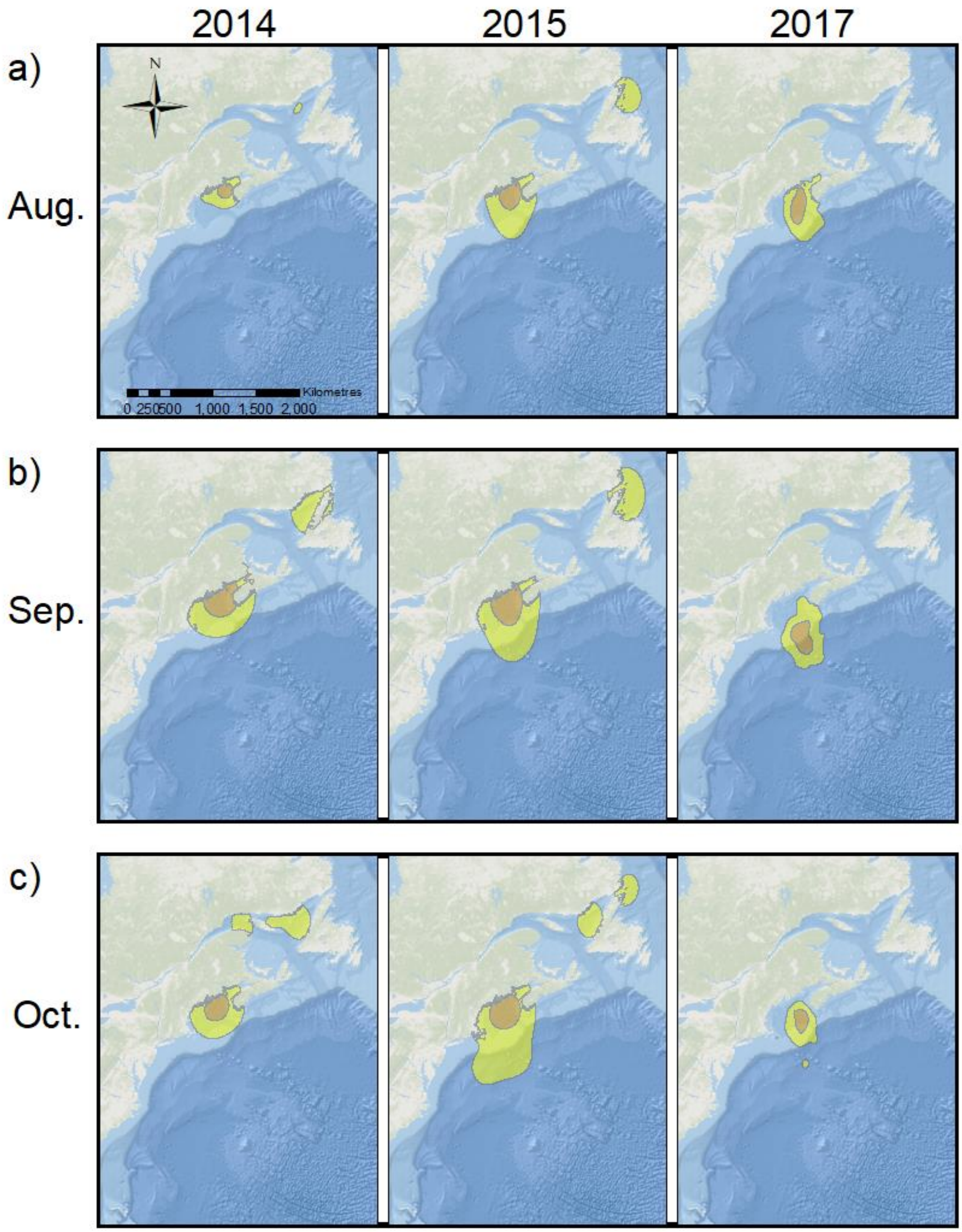

Figure 1.5. Kernel Density Estimate maps showing monthly positions of all birds from Machias Seal Island for a given tag deployment year (2014: n=11, 2015: n=11, 2017: n=20). 50% (orange) and 95% (yellow) occupancy kernels are shown.

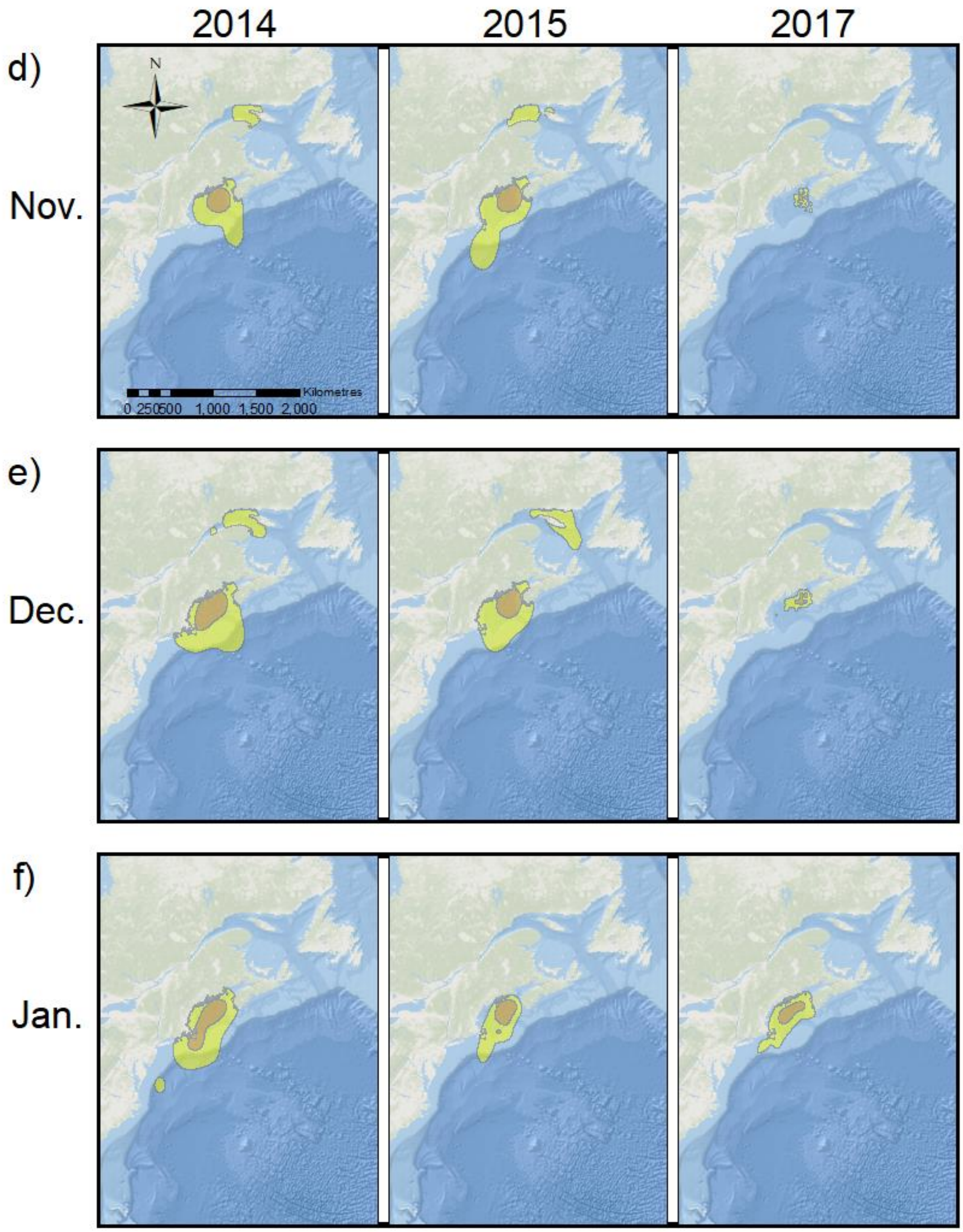

Figure 1.5 (continued). Kernel Density Estimate maps showing monthly positions of all birds from Machias Seal Island for a given tag deployment year (2014: n=11, 2015: n=11, 2017: n=20). 50% (orange) and 95% (yellow) occupancy kernels are shown.

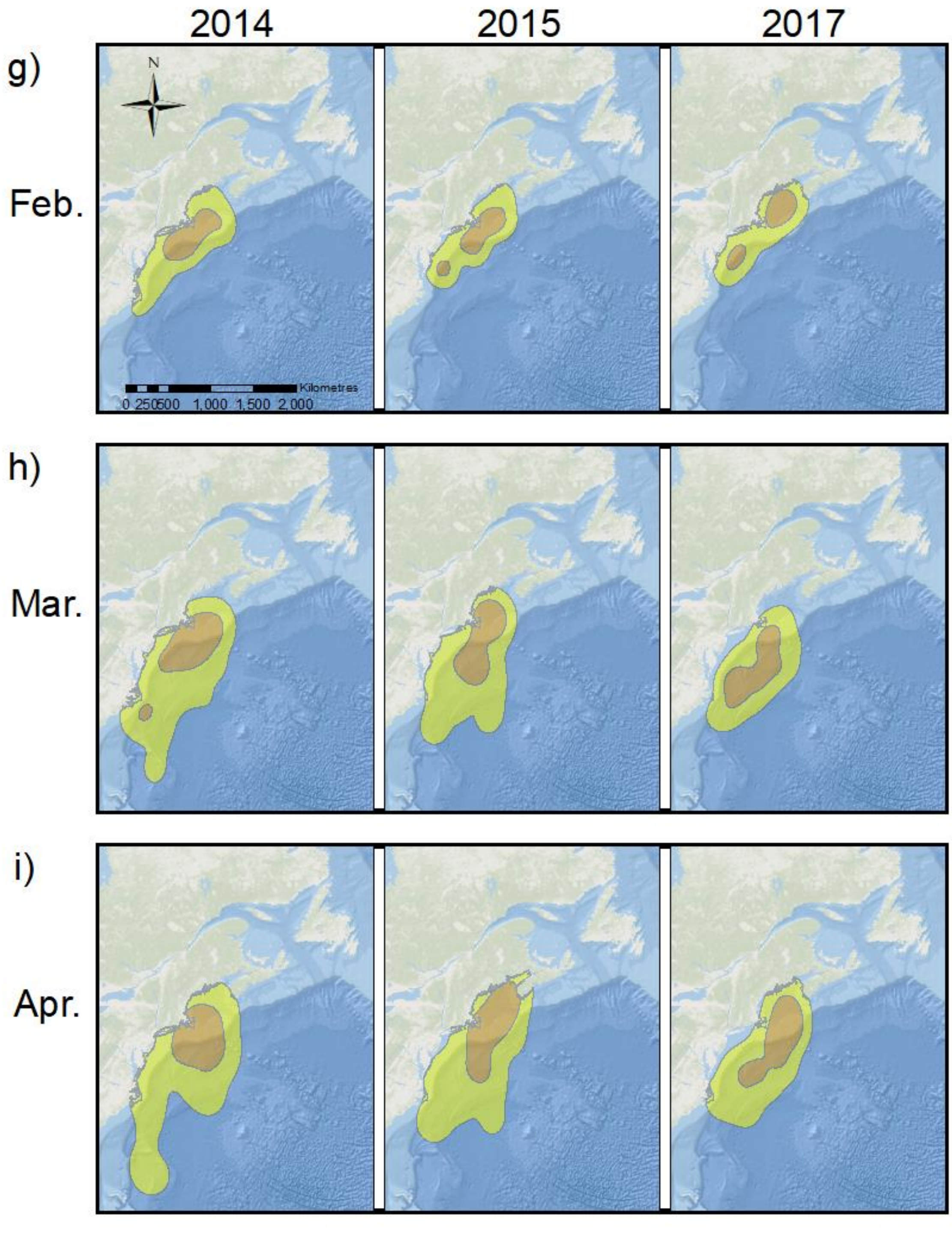

Figure 1.5 (continued). Kernel Density Estimate maps showing monthly positions of all birds from Machias Seal Island for a given tag deployment year (2014: n=11, 2015: n=11, 2017: n=20). 50% (orange) and 95% (yellow) occupancy kernels are shown.

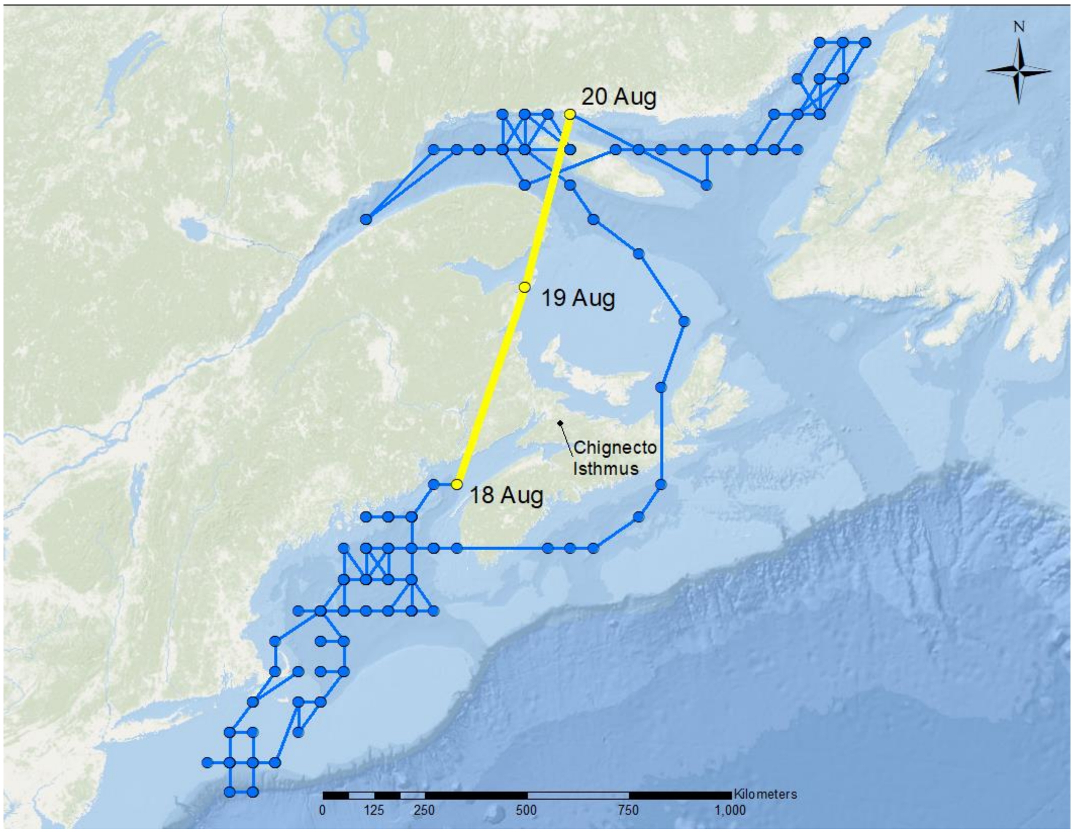

Figure 1.6. Map showing possible movement of tagged puffin 11T across the Chignecto Isthmus. This movement is supported by wet/dry data (Table 1.2) indicating multiple extended (>60 min.) dry periods during these days, suggesting flight. Days of greatest movement highlighted in yellow.

Table 1.2. Duration of dry periods >60 min. from saltwater immersion sensor on tagged puffin 11T. Data shown are the longest dry periods between 15 August (puffin assumed to have left colony) and 24 October (when the sensor stopped recording wet/dry data). There are several instances of lengthy dry periods from 18 August to 20 August, suggesting a period of rapid, flight-based movement.

Date-Time	**Duration (s)**
16-08-2014 10:31	7740
18-08-2014 18:40	*8820*
18-08-2014 21:13	*3759*
19-08-2014 09:45	*3816*
19-08-2014 13:26	*6432*
19-08-2014 16:51	*6546*
20-08-2014 11:27	*3927*

Based on the more limited data from puffins banded at Seal Island and Matinicus Rock, birds from the Penobscot Bay colonies had similar movement patterns to those from Machias Seal Island. Most puffins remained near the Gulf of Maine through the autumn and early winter months, before shifting southward in February; this southerly movement persisted through April (Figure 1.7). Limited resolution around the equinoxes precluded the creation of representative Kernel Density Estimate maps for months with fewer than 100 points among all pooled birds (Figure 1.3). Like two of the Machias Seal Island birds (Figure 1.5a-e), one bird from Seal Island showed an immediate post-breeding movement to Newfoundland. This tag collected two successive years of data and the overall winter pattern was consistent between years, with the bird travelling to Newfoundland, then the Gulf of St. Lawrence, followed by a southerly movement into the Atlantic passing near the Northeast Canyons and Seamounts Marine National Monument before its return to the colony (Figure 1.8).

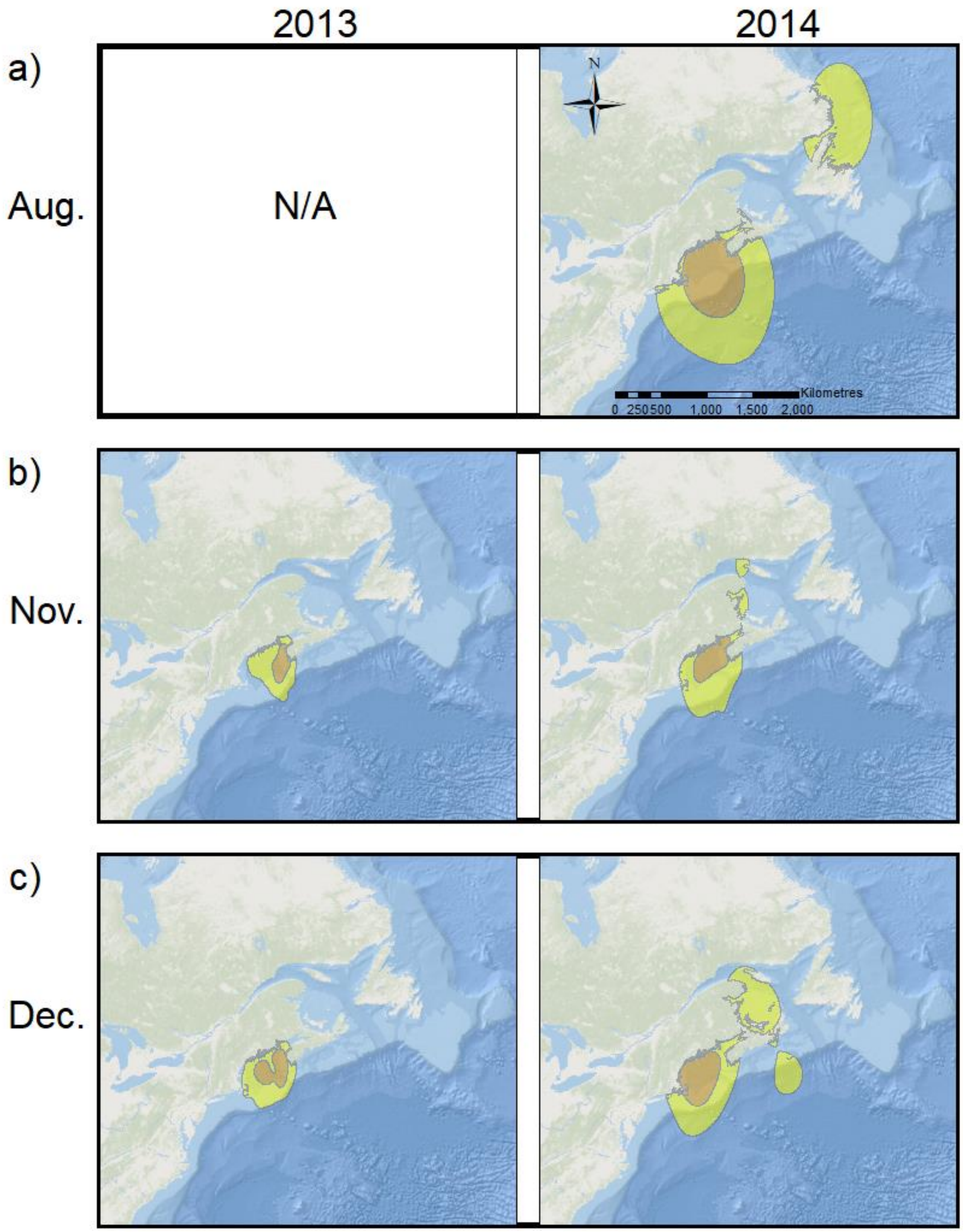

Figure 1.7. Kernel Density Estimate maps showing monthly positions of all LAT-tagged birds from Penobscot Bay colonies for a given tag deployment year (2013: n=6, 2014: n=9). Missing months are those with fewer than 100 points pooled across all tagged individuals. 50% (orange) and 95% (yellow) occupancy kernels are shown.

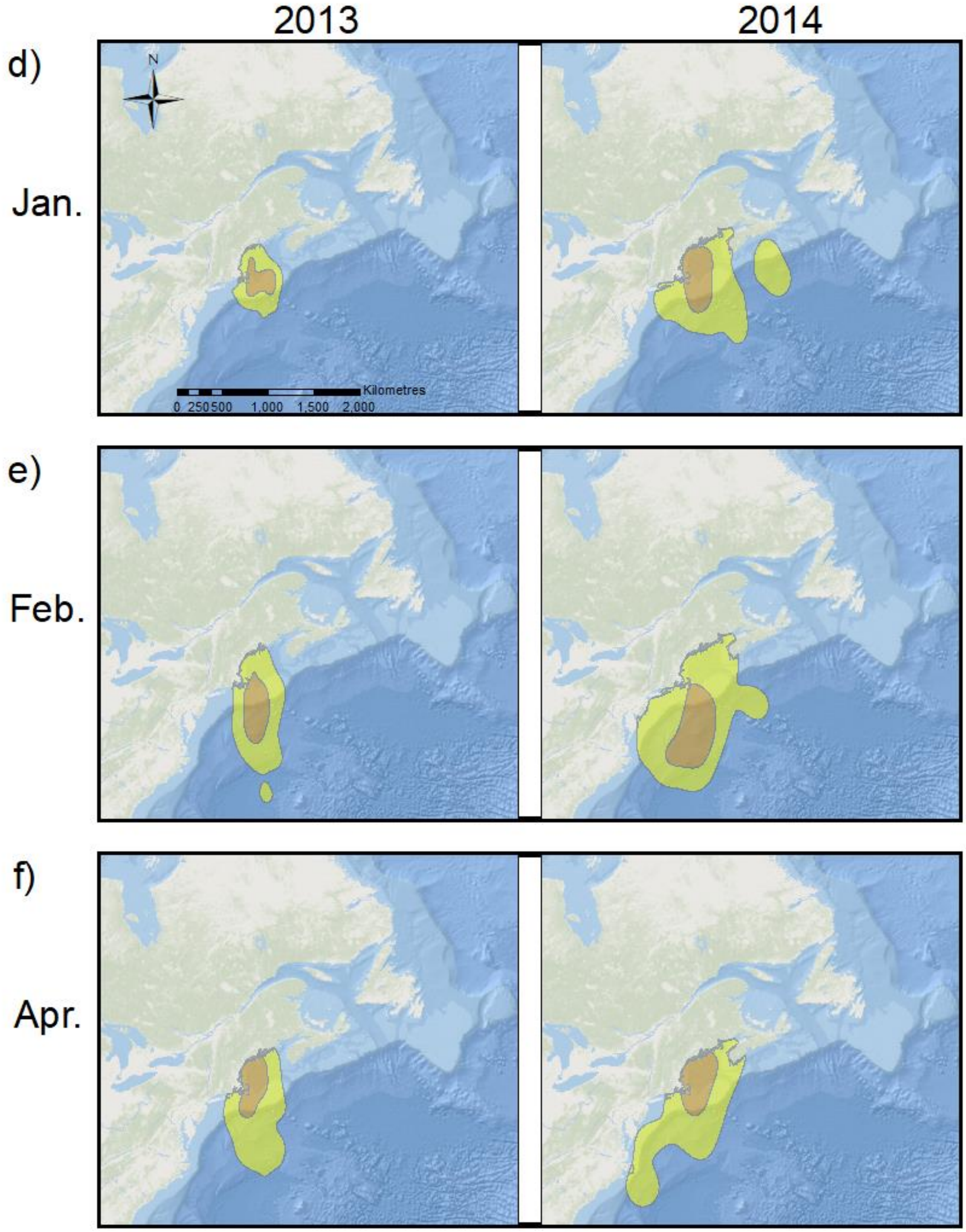

Figure 1.7. (continued). Kernel Density Estimate maps showing monthly positions of all LAT-tagged birds from Penobscot Bay colonies for a given tag deployment year (2013: n=6, 2014: n=9). Missing months are those with fewer than 100 points pooled across all tagged individuals. 50% (orange) and 95% (yellow) occupancy kernels are shown.

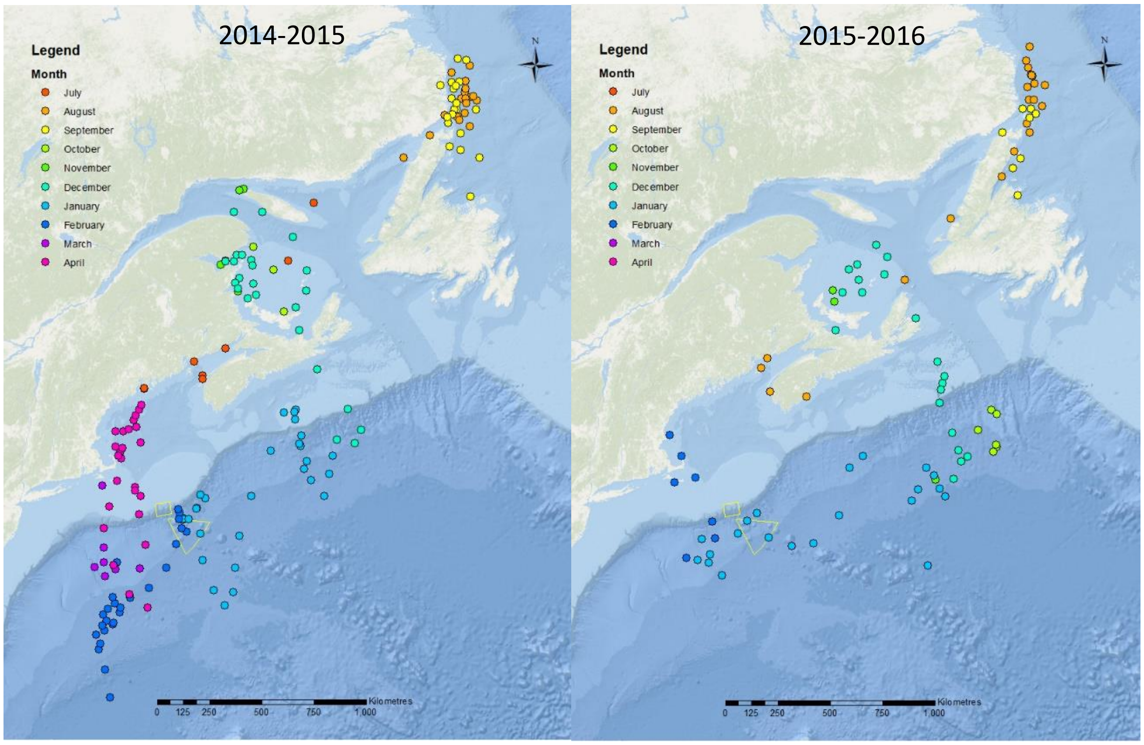

Figure 1.8. Maps showing the two-year track of one tagged individual from Seal Island. This puffin makes a definitive movement to waters around Newfoundland immediately after the breeding season in both years. Outline of Northeast Canyons and Seamounts Marine National Monument shown in yellow. Points indicate 5-day average locations.

Inter-year Effects

Puffin overwinter movements appeared to be generally consistent between years at both the population (Figures 1.5, 1.7) and individual (Figure 1.8) levels; three tags yielded two full winters of data. The most obvious departure came in September 2017 when Machias Seal Island birds spent the month in and around Georges Bank, contrasting with 2014 and 2015 when birds were more centrally located in the Gulf of Maine (Figure 1.5b).

Inter-colony Comparison

Overwinter movements of puffins were similar between the three Gulf of Maine colonies studied. By examining areas of overlap for 2014 (the one overlapping year in the dataset), it is evident that the Gulf of Maine remains the core area for all puffins through the autumn and early winter (Figure 1.9a-d). In late winter and early spring, the Gulf of Maine remains important, but there is a southward shift in the area of overlap for the 50% kernels to an area south of Cape Cod (Figure 1.9e, f). The maps also capture some of the extremes, with a small overlap of the 95% kernel in the northern Gulf of St. Lawrence in December (Figure 1.9c) as well as an area to the south, near Cape Hatteras, in February and April (Figure 1.9e, f).

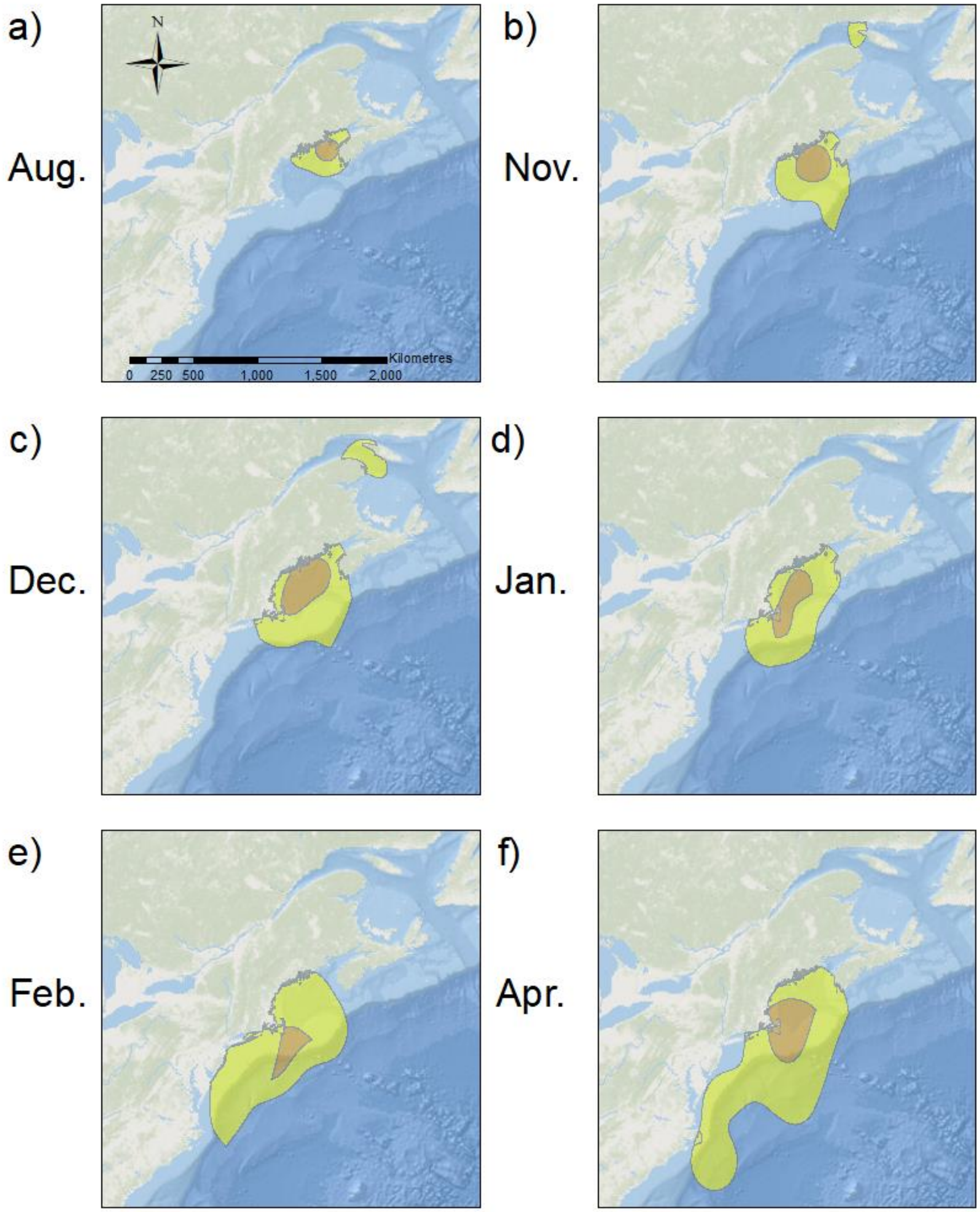

Figure 1.9. Overlapping areas of Kernel Density Estimate maps from both Machias Seal Island (n=11) and Penobscot Bay colonies (n=9, data pooled) in 2014. Dark areas are overlaps of 50% kernels and light areas are overlap of 95% kernels.

Intra-colony Comparison

I found no evidence for any differences in puffin overwinter movement between different nesting areas of Machias Seal Island. There was no correlation between inter-burrow distance and mean (r = -0.08, p = 0.15) or maximum (r = -0.04, p = 0.54) overwinter distance between birds (Figure 1.10).

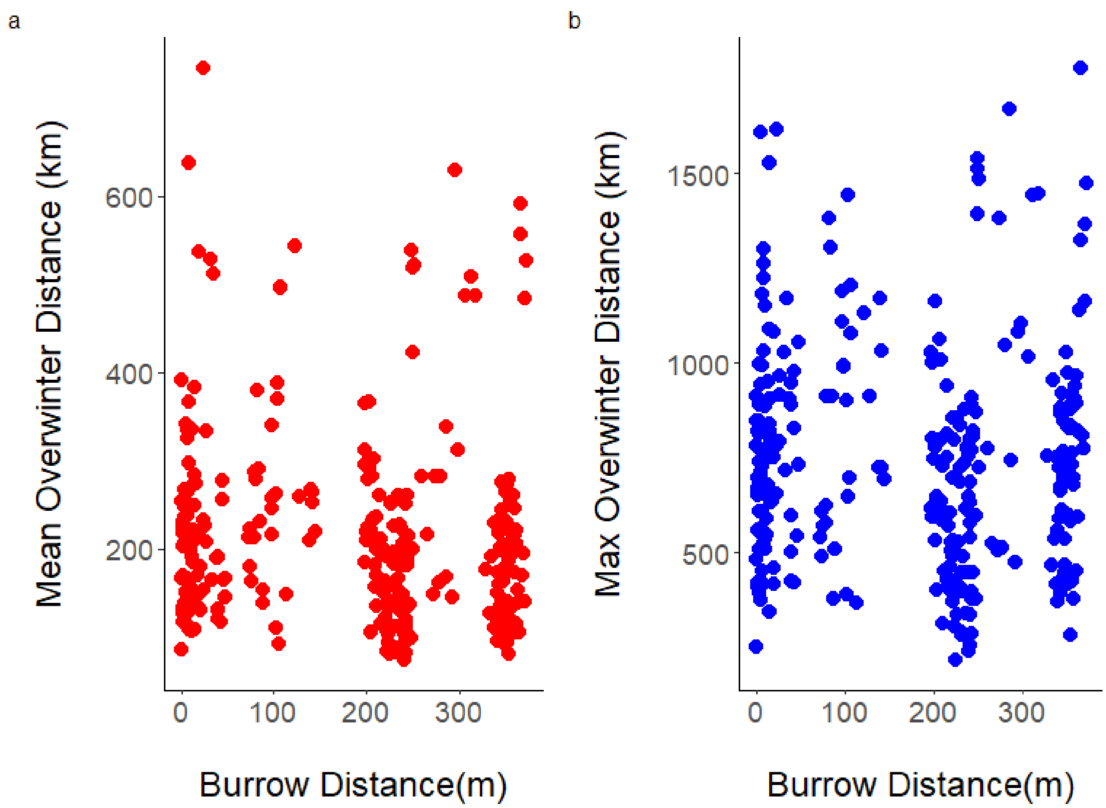

Figure 1.10. Correlation plots of distance between burrows and Mean (a) and Maximum (b) overwinter distance between individuals. There is no evidence of any correlation between burrow distance and mean overwinter distance or maximum overwinter distance.

Tag Effect

Most tagged individuals weighed at both tag deployment and tag retrieval the following year did not show any evidence of lower weight or condition (measured as mass/wing chord); a few birds had slightly lower weights upon retrieval, suggesting a limited overwinter effect in some individuals (Appendix II: Figure II-1). Nesting success of burrows with tagged individuals was generally comparable to that of concurrently-monitored productivity burrows, though there is some evidence of slightly decreased fledging success in the first year after tagging (Appendix II: Figure II-2, Table II-1).

Discussion

Overwinter Movement

Most tagged puffins remained within the Gulf of Maine through much of the non-breeding season. In a range-wide study of puffins, including birds from the Gulf of Maine, Fayet et al. (2017b) found that birds from larger colonies in colder or less productive waters tended to move further from their respective colonies during the winter months. As all three colonies examined are relatively small (MSI is the largest at ~6,000 pairs) and the Gulf of Maine remains relatively warm and productive through the winter (Fayet et al. 2017b), these birds may not be forced to take the lengthy migrations seen in other puffins throughout their range.

The southward movement of birds from February to April is consistent with citizen science reports (via eBird) of puffin presence off Cape Hatteras (Appendix I: Figure I-1). This latitudinal shift may represent an effort by puffins to maximize their incoming breeding condition by foraging in more productive waters prior to the breeding season. The timing of this southward movement aligns with the spring plankton bloom, a bottom-up surge in productivity which generally starts earlier at lower latitudes and gradually works its way north (Friedland et al. 2015). Near Cape Hatteras, as well as the

Nantucket Shoals south of Cape Cod, the bloom begins in late February or early March, well preceding that in colony areas in the Gulf of Maine, which do not typically bloom until April (Friedland et al. 2015). Geolocator-tagged birds appear to be using both of these areas at these times. A similar trend was seen in puffins nesting on Skomer Island, Wales, with individuals that visit the highly productive waters of the Mediterranean Sea during the late winter breeding more successfully than those that remain in the Atlantic Ocean (Fayet et al. 2016).

A small proportion of puffins (3 of 58 individuals tracked) nesting in the Gulf of Maine moved immediately to waters around Newfoundland after breeding. This was likely to take advantage of an abundance of capelin (*Mallotus villosus*) schooling in these waters after spawning in July and August (DFO 2018). Puffins breeding on Skellig Michael, Ireland, are also believed to take advantage of this food resource, undertaking a transatlantic migration to do so (Jessopp et al. 2013). Additionally, historical banding records have shown that immature puffins from MSI will visit Newfoundland, with one individual banded as a chick in 1978 recovered in White Bay on the north coast of Newfoundland during November 1979 (Gaston et al. 2008).

One of the tagged puffins that ventured to Newfoundland appears to have flown across the Chignecto Isthmus to do so. The conception that puffins do not travel far across land (Harris et al. 2010, Fayet et al. 2016), is bolstered by a lack of inland band recoveries (Gaston et al. 2008) and sightings (eBird 2009). The Chignecto Isthmus is a narrow strip of land (24 km at its narrowest) connecting the provinces of New Brunswick and Nova Scotia, separating the Bay of Fundy from the Northumberland Strait (an arm of the Gulf of St. Lawrence). Since puffins can fly at approximately 60 km/h (Harris & Wanless

2011), one would be able to cross this isthmus in under an hour, even accounting for additional distance to permit takeoff and landing several kilometres from shore. To confirm this occurrence, future observers should check for overflying puffins on the Chignecto Isthmus, especially during August. Anecdotally, Razorbills have been occasionally observed flying over the Chignecto Isthmus (A. Kennedy, Canadian Wildlife Service, pers. comm.).

Inter-year comparison

Overwintering areas were similar among all years for each colony. This likely arises from individual overwinter route fidelity, whereby a bird will follow the same overwinter pattern annually. Based on the proposed "exploration-refinement hypothesis", puffins will disperse widely from their natal colony in their first winter, adjusting their route through subsequent winters to maximize overwinter success, before selecting a preferred overwinter strategy (Guilford et al. 2011). Overwinter route fidelity has been documented in puffins from Skomer Island tracked for multiple years (Fayet et al. 2016), as well as in several other seabird species (Phillips et al. 2005, Fifield et al. 2014, McFarlane Tranquilla et al. 2014). Unlike the Skomer birds, which follow one of four winter movement patterns, Gulf of Maine puffins seem to exhibit only two general winter strategies: one where they remain near the Gulf of Maine and venture south in February, and the other where a small proportion of individuals visit Newfoundland and the Gulf of St. Lawrence during the autumn months. The lack of additional overwinter patterns, as seen at other colonies, may be related to the sufficiency of winter food sources in the Gulf of Maine, as well as the presence of the North American continent inhibiting any substantial westward movement.

The largest variation in these movement patterns came in September 2017, when MSI puffins were universally near Georges Bank, contrasting with their position in the central Gulf of Maine in 2014 and 2015. An abundance of prey near the colony in 2017 allowed for high breeding success and relatively good late-breeding condition of puffins, perhaps allowing them to expend more energy following the breeding season to venture to the more productive, but more distant, Georges Bank. Though Georges Bank is a distinct region from the Gulf of Maine, it is immediately adjacent; migratory plasticity at this scale would not require a bird to make large modifications to its behaviour.

Inter-colony comparison

As predicted, I did not observe major differences in overwinter movement of birds tagged at different colonies within the Gulf of Maine. The proximity of the colonies provides birds with access to the same resource areas, especially after breeding when puffins are no longer tethered to a colony to feed a chick. Additionally, the puffins at the three colonies studied are demographically connected within the larger Gulf of Maine puffin metapopulation (Breton et al. 2006). Though the three colonies differ in size (500 – 6,000 pairs), they would all be considered small colonies for the species, relative to those with hundreds of thousands of pairs. Thus, I would not expect to see major inter-colony differences in competition-induced movement as seen at the range-wide scale (Fayet et al. 2017b).

Intra-colony comparison

Contrary to my prediction, I found no indication that the overwinter movements of puffins from MSI are correlated with those of near-nesting individuals. Although social interactions during the breeding season among neighbours are common (e.g., billing), there is no evidence that these social connections persist during the winter, consistent with previous descriptions of low densities of puffins at sea outside the breeding season (Harris & Wanless 2011). The two tagged individuals from MSI that visited Newfoundland after the breeding season nested on opposite ends of the island, both surrounded by neighbours that remained in the Gulf of Maine.

Tag Effect

A few tagged birds showed minor decreases in mass or condition between tag deployment and tag retrieval, possibly indicative of minor effects from the tag. Nest success was generally comparable to that of control burrows, though a slight decrease in fledge success was detected in the first year after tagging. Previous studies of puffins at other colonies have indicated that deployment of geolocator tags can result in disruptions of nest attendance behaviour and occasional desertion leading to nest failure, although overwinter survival was not affected (Harris et al. 2013). Puffins nesting on Machias Seal Island appear to be resilient to researcher disturbance (Kelly et al. 2015) and were observed returning to the colony with prey after tag deployment. Some measures of nest success were higher for tagged birds, perhaps based on the preferential selection of successful breeders for tag deployment. Other indicators of condition (e.g., corticosterone (Elliott et al. 2012)) were not assessed.

The individual from Seal Island that visited Newfoundland (Figure 1.8) appeared to depart the Gulf of Maine in late July 2014, indicating a likely nest failure, possibly brought upon by tagging-related stress. However, this same bird departed the Gulf of

Maine for Newfoundland in late August in 2015, suggesting that individual overwinter route fidelity, rather than a stressor, is the cause of this divergent movement strategy.

Conclusion

Puffins breeding in the Gulf of Maine spent much of the non-breeding season in nearby waters of the Gulf of Maine and Georges Bank. Many birds moved southward, as far as Cape Hatteras, in February, March, and April, possibly to feed in more productive waters and increase their breeding condition prior to their return to the colony in May. Such movements did not appear to differ between colonies or parts of colonies. These overwinter movements can be used as a baseline for other projects and to assist development of policy regarding protection of important marine areas for all Gulf of Maine puffins, such as the Northeast Canyons and Seamounts Marine National Monument at the southern edge of Georges Bank. As geolocator analysis can be limited by its low precision, future work should focus on elucidating the finer-scale movements of these puffins and discerning the factors drawing birds to particular areas. Recent and near-future improvements in tagging technology (both GPS and satellite tags) should allow for more precise examination of long-term movement without the current limitations of these more complex tag types for smaller bird species.

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Appendix I. eBird Maps

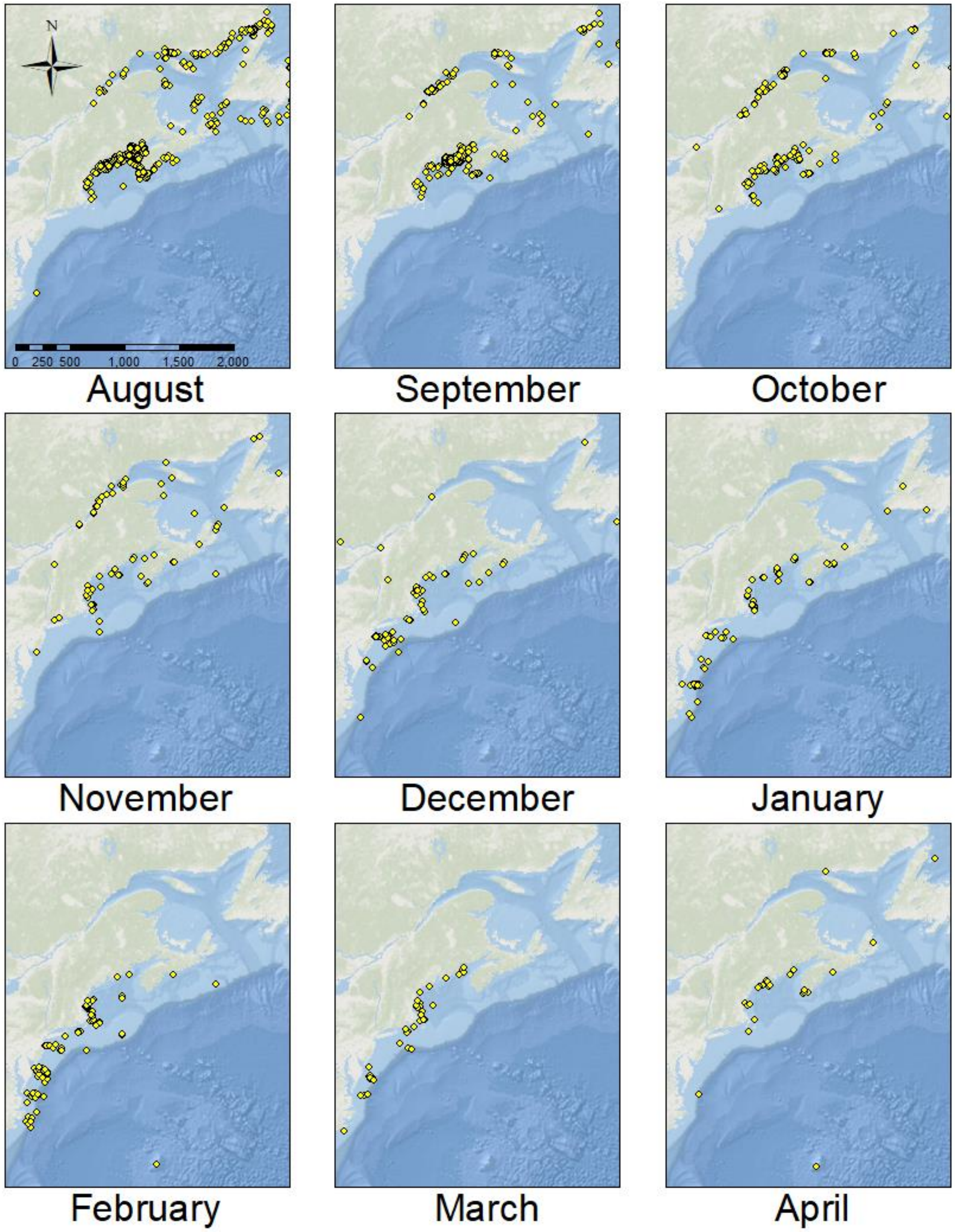

Figure I-1. Maps showing locations of eBird reports including Atlantic Puffins for a given month. Each point represents one checklist. Sightings are most abundant in August, largely in areas around colonies. By December, puffins are being reported south of Cape Cod; this trend continues through March, peaking in February, as far south as Cape Hatteras. Data courtesy of eBird.

Appendix II. Tag Effect

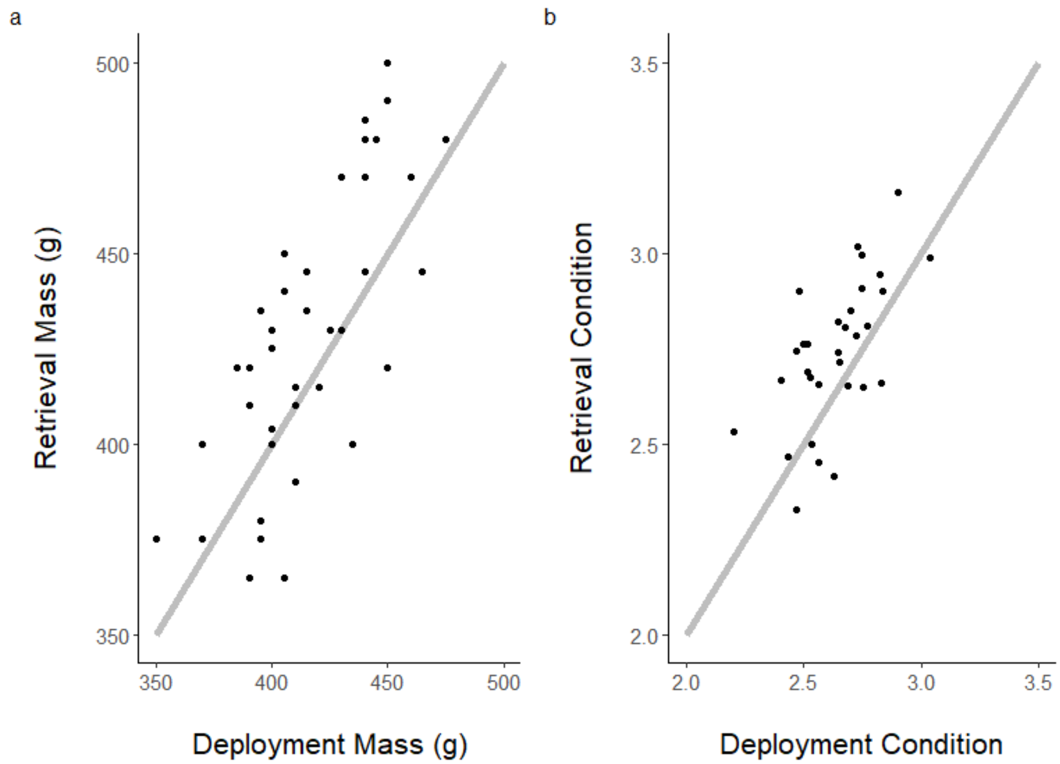

Figure II-1. Graphs comparing mass (a) and condition (b) of tagged birds at time of deployment and retrieval. Condition is measured as mass/wing chord. A 1:1 line is shown in grey. Most birds had higher mass and condition at retrieval than at deployment, suggesting a limited overwinter tag effect, though this may be complicated by annual mass fluctuations associated with chick-rearing.

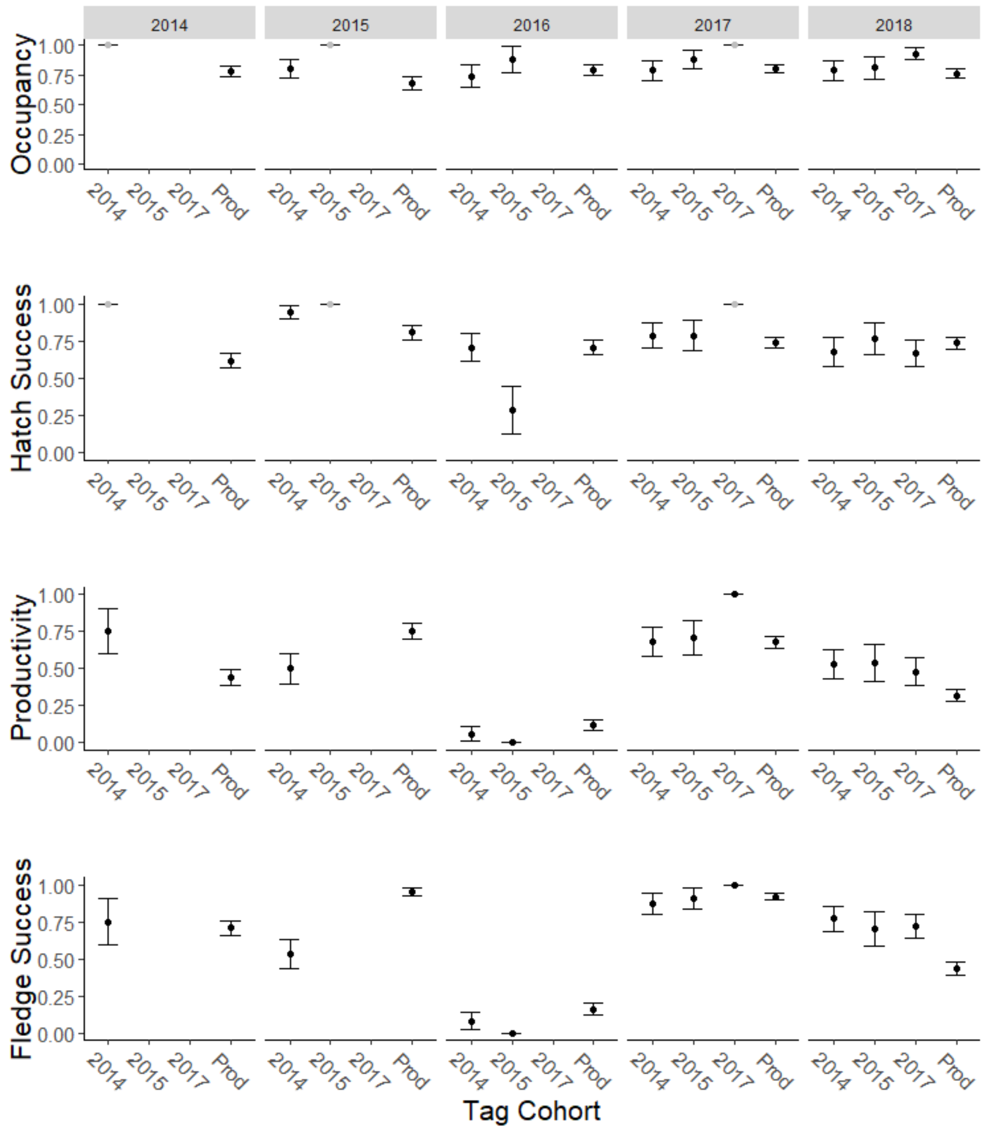

Figure II-2. Nesting success of burrows with tagged individuals by cohort (horizontal axis) and year (column), measured in terms of occupancy, hatch success, productivity (fledge/active nests), and fledge success (fledge/hatch). Means and standard errors are shown. As tags were deployed on birds in active burrows with chicks, occupancy and hatch success in the first year of a tag cohort are always 1. Occupancy and hatch success of tag burrows were generally similar to reference productivity (Prod) burrows. Hatch success was notably low for the 2015 cohort tagged burrows in 2016. Productivity and fledge success were lower for 2014 and 2015 cohorts in their second year than for reference burrows; this trend did not extend to 2017.

Table II-1. Nesting success of burrows with tagged individuals by cohort and year, measured in terms of occupancy, hatch success, productivity (fledge/active nests), and fledge success (fledge/hatch). Means ± SE are shown. As tags were deployed on birds in active burrows with chicks, occupancy and hatch success in the first year of a tag cohort are always 1. Fledging was not assessed for newly-tagged burrows in 2015.

Year	Tag Cohort	n	Occupancy	Hatch Success	Productivity	Fledge Success
2014	2014	8	1 ± 0	1 ± 0	0.75 ± 0.15	0.75 ± 0.15
	Prod	*87*	*0.78 ± 0.04*	*0.62 ± 0.05*	*0.44 ± 0.05*	*0.71 ± 0.05*
2015	2014	25	0.8 ± 0.08	0.95 ± 0.04	0.5 ± 0.1	0.53 ± 0.1
	2015	16	1 ± 0	1 ± 0	NA	NA
	Prod	*67*	*0.68 ± 0.06*	*0.81 ± 0.05*	*0.75 ± 0.05*	*0.95 ± 0.03*
2016	2014	23	0.74 ± 0.09	0.71 ± 0.1	0.06 ± 0.05	0.08 ± 0.06
	2015	8	0.88 ± 0.12	0.29 ± 0.16	0 ± 0	0 ± 0
	Prod	*87*	*0.79 ± 0.04*	*0.71 ± 0.05*	*0.12 ± 0.03*	*0.16 ± 0.04*
2017	2014	24	0.79 ± 0.08	0.79 ± 0.08	0.68 ± 0.09	0.87 ± 0.07
	2015	16	0.88 ± 0.08	0.79 ± 0.1	0.71 ± 0.11	0.91 ± 0.07
	2017	29	1 ± 0	1 ± 0	1 ± 0	1 ± 0
	Prod	*134*	*0.8 ± 0.03*	*0.74 ± 0.04*	*0.68 ± 0.04*	*0.92 ± 0.02*
2018	2014	24	0.79 ± 0.08	0.68 ± 0.09	0.53 ± 0.1	0.77 ± 0.09
	2015	16	0.81 ± 0.1	0.77 ± 0.11	0.54 ± 0.12	0.7 ± 0.11
	2017	29	0.93 ± 0.05	0.67 ± 0.09	0.48 ± 0.09	0.72 ± 0.08
	Prod	*124*	*0.76 ± 0.04*	*0.74 ± 0.04*	*0.32 ± 0.04*	*0.43 ± 0.04*

Appendix III. Sex-based Differences

Table III-1. Comparison of maximum distance from colony (km) and winter range size (longest straight-line distance between most distant points in km) of tagged individuals based on sex. There does not appear to be a significant difference in overwinter movement between the sexes.

Sex	n	Maximum Distance from Colony (Mean ± SE)	Winter Range Size (Mean ± SE)
M	17	980 ± 69	1000 ± 70
F	13	1064 ± 103	1166 ± 131

Stable Isotope Analysis of Claw Tissue to Determine Overwinter Location of Atlantic Puffins (*Fratercula arctica*)

Abstract

Modern ecological and species conservation efforts rely heavily on spatial data acquired from a variety of data-collecting tags for determining areas of highest use. Tagging studies, however, often suffer from a limited sample size, due to the expense and difficulty of tag retrieval. If a non-tag method could be developed to determine overwinter position, then a greater sample could be obtained. As stable isotopes of several elements vary across marine systems, I examined whether stable isotopes from claw tissues could be used to assign general overwinter positions to Atlantic Puffins (*Fratercula arctica*), based on locations obtained via geolocation. Although different birds did not visit distinct overwintering areas, stable isotope results indicated variability in each isotope sampled. This variability is likely diet-based, rather than location-based. If claw samples from more distinct overwinter locations can be obtained, then this technique may be applicable to puffins and other pelagic seabird species.

Introduction

Modern ecological and species conservation efforts rely heavily on spatial data for determining areas of highest use. It is impossible, or at least impractical, to preserve the full annual range for most species, therefore some conservation efforts should focus on key areas instead (Ronconi et al. 2012). A number of factors – such as food availability, climatic conditions, and predator avoidance – can influence the importance of an area for a species or an individual (Shaw 2016).

A wide variety of techniques have been used to study animal movement. In birds, spatial data have traditionally been gathered through banding studies (e.g., Harris 1984, Gaston et al. 2008). Banding data, however, rely on band recoveries and resights, which are limited to areas where people are likely to encounter banded birds. In marine systems, especially among pelagic species, birds may be spending time in areas where direct encounter with humans is extremely unlikely, which can be partly overcome using satellite tags, GPS (Global Positioning System) tags, and geolocators. Satellite tags are highly accurate and do not require recapturing the bird to retrieve data, but their size can negatively impact all but the largest bird species (Hatch et al. 2000, Anker-Nilssen & Aarvak 2009). GPS tags are also highly accurate and do not require retrieval to obtain data; they are, however, severely limited by battery life and therefore not suitable for long-term studies (Harris et al. 2012). Archival light geolocators are smaller and have longer battery life than GPS tags but have much lower precision and require the retrieval of the tag to obtain any data (Phillips et al. 2004, Winship et al. 2012). A major shortfall of tagging studies, regardless of the tag type used, is the limitation of sample size due to tag expense, the difficulty of tag retrieval, and efforts to limit the invasiveness of study procedures. Small sample sizes, while permitting a glimpse into the movement of individuals, may not detect all movement patterns of the population, nor the proportion of the population following them. If a method could be developed to determine overwinter position without the necessity of tags, a greater sample from a given population could be obtained, producing a better understanding at the population level.

Stable isotopes of several elements, notably $\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$, and $\delta^{18}O$, vary across marine systems due to spatial and temporal differences in nutrient origin (benthic vs. pelagic), freshwater inputs, and climate (Hobson 1999). In addition to spatial variation, some stable isotopes (i.e., $\delta^{15}N$, $\delta^{2}H$, and $\delta^{18}O$) are subject to biological variation, with organisms at higher trophic levels having distinctly elevated stable isotope ratios (DeNiro & Epstein 1981, Birchall et al. 2005, Vander Zanden et al. 2016). These isotopes should be considered to be at least partly diet-based in addition to location-based, while $\delta^{13}C$ can be considered solely location-based (Hobson et al. 1994).

This isotopic variation permits the comparison of overwintering areas and diets of seabirds through analysis of tissue samples (Hobson 1999, Cherel et al. 2006, Cherel et al. 2007, Hedd et al. 2010). There are two categories of tissues for stable isotope analysis: metabolically active tissue (e.g., blood, muscle) which have turnover of the constituent elements, and metabolically inert tissue (e.g., feathers, claws) which remain elementally unchanged after growth (Hobson 1999). The stable isotope ratios in these inert tissues mirror those of the location where the tissue was synthesized and will not change over time, regardless of the movement of the animal (Hobson 1999). Steenweg et al. (2017) demonstrated that stable isotopes in claws of Common Eiders (*Somateria mollissima*) collected at the breeding colony could be reliably used to match a specific bird to one of three overwintering destinations known from earlier satellite tracking data and visual confirmation of winter flocks. When pooled, these samples could be used to assign proportions of the breeding colony to overwintering areas, denoting their relative importance to the species and its populations.

Atlantic Puffins (*Fratercula arctica*), hereafter “puffins”, are medium-sized (length 26-29 cm) members of the family Alcidae, or auks (Lowther et al. 2002). During the breeding season, large numbers aggregate on offshore islands to nest; outside the breeding season, puffins remain far offshore (see Chapter 1). While recent studies have shed some light on overwinter movements at a range-wide scale (Fayet et al. 2017), the precise overwintering areas and habits of puffins nesting in the Gulf of Maine remain understudied (but see Chapter 1). As moult timing is highly variable in puffins (Harris & Yule 1977), there is considerable uncertainty in the timeframe represented by the stable isotopes in feathers. Therefore, I examined whether stable isotopes from claw tissues could be used to assign general overwinter positions to puffins breeding on Machias Seal Island in the Gulf of Maine.

Methods

Ethics Statement

This study was approved by the Animal Care Committee at the University of New Brunswick (AUP No. 18004) and the Canadian Wildlife Service (Permit No. ST2728).

Study Site: Machias Seal Island

Machias Seal Island (44°30'N, 67°06'W) is a small (9.5 ha) island at the mouth of the Bay of Fundy, where it opens into the Gulf of Maine near the border of Canada and the United States. The island is a Migratory Bird Sanctuary managed by the Canadian Wildlife Service of Environment and Climate Change Canada. Low vegetation in the interior of the island gives way to a rocky fringe beyond a berm of storm-tossed boulders (Diamond & Devlin 2003). Seven seabird species nest on the island (Arctic

Tern, *Sterna paradisaea*; Common Tern, *S. hirundo*; Common Eider; Leach's Storm-petrel, *Oceanodroma leucorhoa*; Common Murre, *Uria aalge*; Razorbill, *Alca torda*; and Atlantic Puffin), with puffins nesting in sod burrows along the berm or in jumbles of smaller boulders.

Overwinter Locations

I deployed twenty-nine MK 4093 archival light geolocator tags (Biotrack; Wareham, UK) on breeding puffins in late July 2017; of these, I retrieved tags from 20 individuals in 2018 (see Chapter 1). Using the *TwilightFree* package (Bindoff et al. 2018) in R 3.4.3 (R Core Team 2017), I determined approximate daily positions for each individual through the nonbreeding season (August 2017–May 2018). To visualize trends, I created monthly Kernel Density Estimate (KDE) maps (*adehabitatHR* package in R 3.4.3 (Calenge 2006, R Core Team 2017)) of all individuals pooled.

Sample Collection and Stable Isotope Analysis

Upon tag retrieval, I clipped and collected the distal 2 mm of the inner claws (see Figure 2.1a) from both feet, then stored the samples in a freezer (-4 °C) for the remainder of the field season. Of the 20 individuals from which tags were retrieved, I did not collect claw samples from one, as it was retrieved very late in the season; this individual's claws likely represented a different time period than the other 19. In the lab, I washed thawed claw samples with a 2:1 chloroform-methanol solution to remove surficial impurities, rinsed with distilled water, then placed them in a drying oven (60°C) overnight to remove excess water. I weighed out portions of both claw samples, using the oldest material, for each bird for analysis: one claw for carbon and nitrogen analysis (1.00 ±

0.10 mg) and the other for oxygen and hydrogen (0.20 ± 0.02 mg). Non-exchangeable hydrogen was determined using the comparative equilibrium approach (Wassenaar & Hobson 2003) with two secondary keratin standards (caribou hoof, kudu horn). Weighed samples were then run through elemental analyzers to determine the $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, and $\delta^{2}H$ values (C&N: Costech 4010 Elemental Analyzer (Costech; California, USA); O&H: High Temperature Conversion Elemental Analyzer (Thermo Finnigan; Bremen, Germany)). Values are presented relative to international standards: Vienna Pee Dee Belemnite ($\delta^{13}C$), atmospheric air ($\delta^{15}N$), or Vienna Standard Mean Ocean Water ($\delta^{18}O$ and $\delta^{2}H$).

Claw Growth Rate

Bird claws do not grow linearly, instead growing from the base at the edges and from inside the claw in the centre (Bearhop et al. 2003). In addition to growth, bird claws experience constant wear due to contact with rough surfaces. While the middle and outer claws on puffin feet are positioned vertically, the inner claw is rotated inward (see Figure 2.1a) and should be less subject to abrasion than the other claws. To obtain a general rate of growth of the outer edge of the claw, I photographed claws at the time of sample collection and again at a subsequent encounter, at least one month afterward (33-46 days). Claws were photographed against a scale bar (Figure 2.1b), so they could be measured using ImageJ software (Schneider et al. 2012). By comparing the two measurements of the outer edge of the claw, I determined an average rate of claw growth for this time interval. Based on this average, I could calculate an approximate timeframe represented by each claw sample.

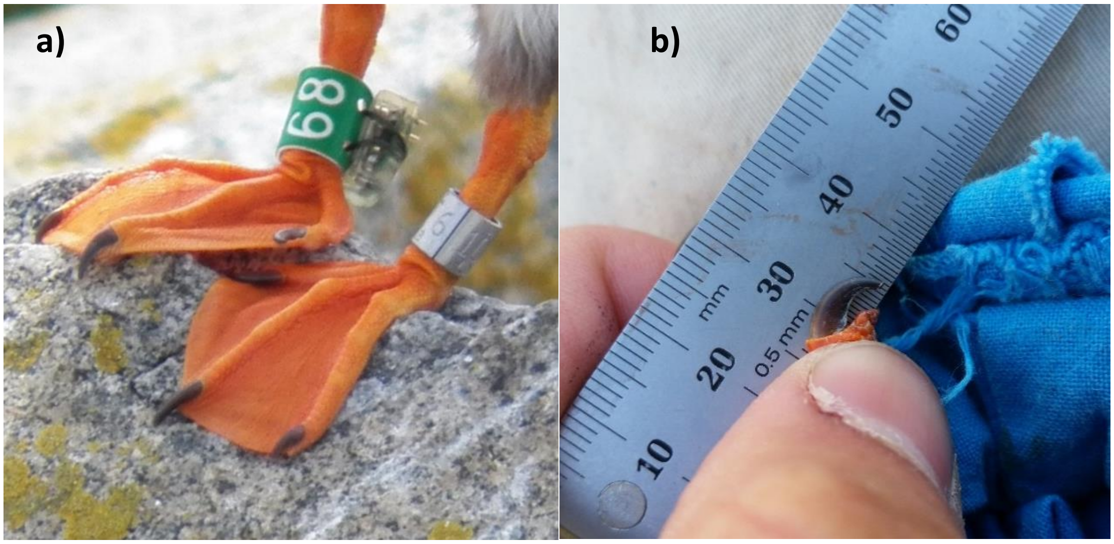

Figure 2.1. a) Feet and legs of a geolocator-tagged puffin. Inner claws are rotated to a horizontal orientation and should not experience as much wear as middle and outer claws. **b)** Puffin claw photographed against a scale bar for measurement.

Statistical Analysis

I separated groups of individuals by comparing isotopic values using hierarchical complete linkage cluster analysis (*vegan* package in R 3.4.3 (Oksanen et al. 2008, R Core Team 2017)); these groups were overlaid on a non-metric multidimensional scaling (NMDS) plot of the data. I subsequently examined those groupings using a one-way ANOVA to determine which isotopes were causing separation and to derive a likely mechanism for this separation.

Results

Overwinter Locations

As interpreted from the geolocators, all puffins tagged in 2017 spent most of the fall and winter within and adjacent to the Gulf of Maine and Georges Bank, venturing south of

Cape Cod in February and March before returning to the Gulf of Maine in April (Figure 2.2). Birds appeared to spread apart more noticeably during the early spring compared to the autumn and early winter months; the 95% occupancy kernel for December covered 50,554 km^2, whereas the area for March was 962,264 km^2.

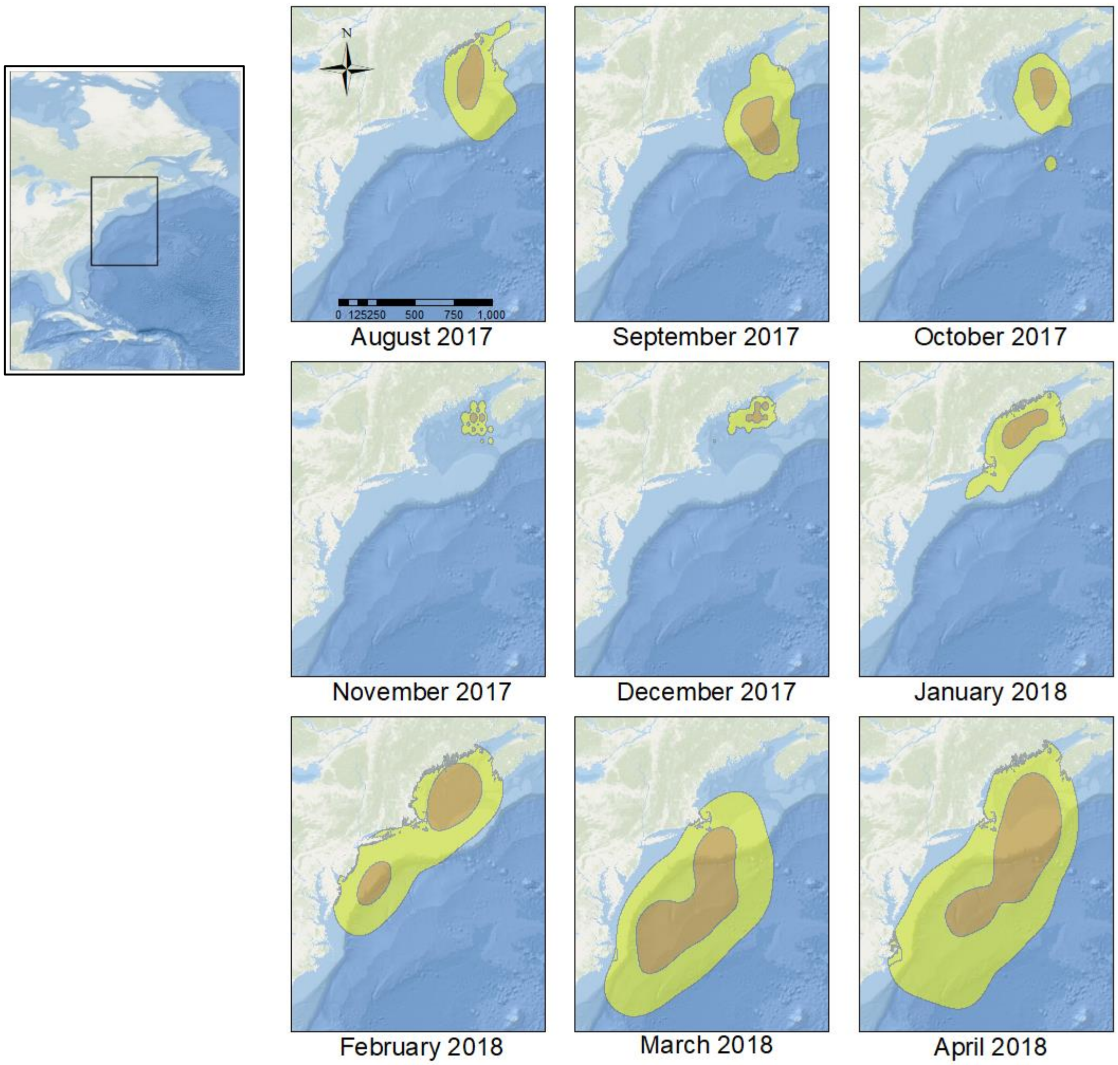

Figure 2.2. Monthly Kernel Density Estimates of puffin (n=20) overwinter position between 2017 and 2018 breeding seasons, inferred from geolocator positions. Occupancy kernels for 50% (orange) and 95% (yellow) are shown. Scale bar shown in kilometres.

Claw Growth Rate

Based on measurements of both claws from nine puffins at both the time of sampling and several weeks subsequent, I found that claws increased in length at an average of 0.02 mm/day, though calculated growth rates were highly variable (-0.01–0.04 mm/day).

Stable Isotope Analysis

Although individual birds did not visit distinct overwintering areas, stable isotope results indicated variability in each isotope sampled (Table 2.1). Based on cluster analysis, I identified three groups of puffins with different isotopic ratios (Figure 2.3).

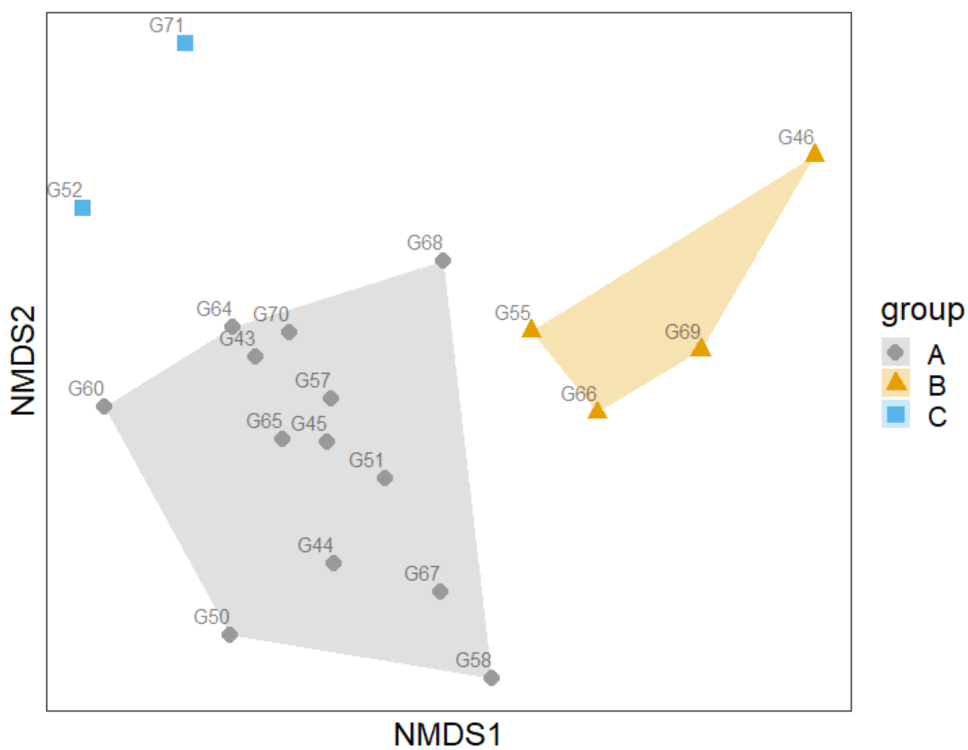

Figure 2.3. NMDS plot of puffin claw (n=19) isotopic ratios, based on four isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$, $\delta^{18}O$). Groups determined by cluster analysis are shown.

When examining each isotope individually using ANOVA, there were significant differences between groups in $\delta^{15}N$ ($F = 12.35$, $p < 0.001$; Figure 2.4a), $\delta^{2}H$ ($F = 9.95$, $p < 0.01$; Figure 2.4b), and $\delta^{18}O$ ($F = 10.49$, $p < 0.01$; Figure 2.4c); isotope ratios did not differ significantly for $\delta^{13}C$ ($F = 3.04$, $p = 0.08$; Figure 2.4d).

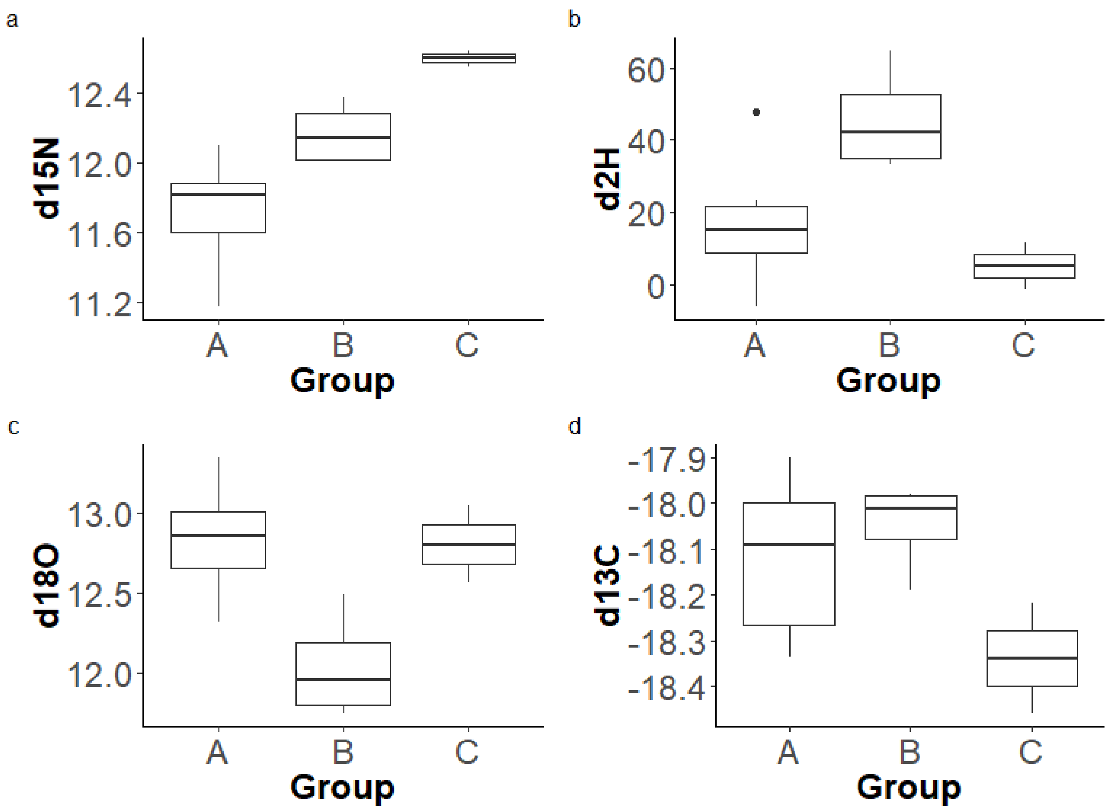

Figure 2.4. Individual isotope boxplots (a: $\delta^{15}N$, b: $\delta^{2}H$, c: $\delta^{18}O$, d: $\delta^{13}C$) based on the groups determined from the cluster analysis. Midpoint line represents median, with boxes representing range between first and third quartile. Whiskers extend to group minimum and maximum.

Table 2.1. Summary of claw sample isotope data. Number of samples, means, and standard deviations are given for all samples pooled and each of the three groups.

Isotope		n	Mean	SD
$\delta^{15}N$	*Total*	*19*	*11.9*	*0.4*
	Group A	13	11.8	0.3
	Group B	4	12.2	0.2
	Group C	2	12.6	0.1
$\delta^{2}H$	*Total*	*19*	*21.2*	*18.0*
	Group A	13	16.1	12.5
	Group B	4	45.6	14.5
	Group C	2	5.3	9.0
$\delta^{18}O$	*Total*	*19*	*12.7*	*0.4*
	Group A	13	12.8	0.3
	Group B	4	12.0	0.3
	Group C	2	12.8	0.3
$\delta^{13}C$	*Total*	*19*	*-18.1*	*0.2*
	Group A	13	-18.1	0.1
	Group B	4	-18.1	0.1
	Group C	2	-18.3	0.2

Separation of group B appears to be based primarily on higher $\delta^{2}H$ and lower $\delta^{18}O$ values than those of groups A and C, whereas group C has higher $\delta^{15}N$ values and somewhat lower $\delta^{13}C$ values relative to the other groups.

Discussion

Overwinter Locations

Puffins tagged in 2017 spent most of the non-breeding season within or near the Gulf of Maine, not travelling to widely disparate areas as documented in studies from other colonies (Guilford et al. 2011, Jessopp et al. 2013, Fayet et al. 2016). A range-wide study, including geolocator data from Machias Seal Island puffins, indicated that puffins near the southern edge of their range do not winter as far from the colony as those from more northerly colonies, perhaps due to differences in water temperature and food availability (Fayet et al. 2017). Colder waters would increase puffins' required energy expenditure, while less productive waters would increase competition for food. As the Gulf of Maine has both the highest water temperatures and highest winter water productivity (as measured by chlorophyll *a*) of the areas studied, birds would have relatively low energy expenditure needs and easier access to food (Fayet et al. 2017). As such, the puffins in the Gulf of Maine may not need to spread as far apart during the winter as birds from other, more northerly, colonies (Fayet et al. 2017).

Claw Growth Rate

I calculated a puffin claw growth rate of 0.02 (± 0.01 SD) mm/day. This growth rate is much lower than studies of other species have suggested (Bearhop et al. 2003, Barquete et al. 2013, Lourenço et al. 2015). During the breeding season, puffin claws are both growing and wearing down due to contact with rock and other solid substrates. Despite using the inner claw, which should experience lower wear rates, two of the eighteen claws measured were shorter at the second encounter than at the time of sampling. It is possible that my sampling increased the subsequent wear rates of these claws through increased sloughing of the outer edge (Bearhop et al. 2003). To approximate the time represented by claw samples, I used a growth rate of 0.11 (± 0.03) mm/day as described for ecologically-similar African Penguins (*Spheniscus demersus*), whose claw wear patterns should be similar (Barquete et al. 2013). From this calculation, I estimated that claw samples represented time periods between December 2017 and March 2018. As puffins remain offshore during the winter, land-based wear is a factor in claw length only during the breeding period. Ideally, future studies examining overwinter claw growth rates could be conducted on puffins at sea, though this would be logistically complicated.

Diet-based Isotopes

While I observed differences between individuals in some isotopes, the differences do not appear to be location-based. One likely explanation for these differences is inter-individual diet variability. Puffins breeding on Machias Seal Island have highly variable diets during the breeding season; diets include a variety of fish species, as well as several invertebrate taxa (Bowser et al. 2013). While I did not have diet data of Gulf of Maine puffins for the non-breeding season, studies of puffins in other parts of their range have indicated that overwinter diet includes both fish and invertebrates, though the relative proportions likely differ from the breeding season (Gaston & Jones 2008, Hedd et al. 2010, Harris et al. 2015). $\delta^{15}N$ has been well documented as an indicator of trophic level (DeNiro & Epstein 1981, Hobson 1990, Kelly 2000), whereas $\delta^{2}H$ and $\delta^{18}O$ are at least partially related to diet (Birchall et al. 2005, Vander Zanden et al. 2016). Organismal hydrogen is derived primarily from diet and drinking water, while oxygen is based on these two sources as well as atmospheric oxygen (Vander Zanden et al. 2016). As puffins are not known to drink water, instead obtaining all metabolic water from their prey (Lowther et al. 2002), I can assume that a high proportion of their hydrogen and oxygen isotopic ratio is directly related to their diet. As species (or individuals) feeding at higher trophic levels generally have higher $\delta^{15}N$ and $\delta^{2}H$ values (Birchall et al. 2005), the significant differences found between individuals in $\delta^{15}N$, $\delta^{2}H$, and $\delta^{18}O$ are all likely explained by dietary variability, with higher $\delta^{15}N$ and $\delta^{2}H$ values representative of piscivore specialists. Individual specialization in breeding season foraging has been previously documented in other alcids (Woo et al. 2008). This finding leads to the possibility that stable isotopes in claw tissue could have future applications for studying diet in pelagic seabirds outside the breeding season.

Location-based Isotopes

Our finding that $\delta^{13}C$ did not differ significantly between groups is consistent with the limited observed overwinter spatial spread of tagged puffins. In Common Eiders, Steenweg et al. (2017) examined $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$ and found significant location-based isotope differences for claws only in $\delta^{13}C$. Eiders were sampled from two distinct overwinter locations (near Nuuk, Greenland and Newfoundland, Canada), which differ in latitude, current-derived nutrients, and freshwater influence. This raises the prospect that the overwinter locations found from geolocation of puffins are not distinct enough to register a location-based $\delta^{13}C$ difference. Unlike eiders, which undergo a directed migration to one of several areas where they will remain through the winter months (Mosbech et al. 2006), puffins are more dispersive and mobile throughout the winter (Fayet et al. 2017). This difference in movement could further muddle the use of location-based isotopes, as claw isotopes would represent a pooled average of locations, rather than one distinct overwintering area.

Although I did not successfully demonstrate the use of location-based isotopes in claw samples, the method remains insufficiently tested to discount its use in puffins. Future efforts should focus on acquiring samples from birds known to travel to different overwinter areas (e.g., Gulf of St. Lawrence, Labrador Sea) to be compared against birds that spend much of the nonbreeding period within and nearby the Gulf of Maine. To avoid complications with trophic signals, the primary focus of such analyses should be on $\delta^{13}C$, though other isotopes may provide additional information if accounting for dietary variability. If claw samples from more distinct overwinter locations can be obtained, then this technique may have applications for puffins and other pelagic seabird species.

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General Discussion

Prior to this study, information about overwinter movements of Atlantic Puffins was strongly based on band recoveries (e.g., Harris 1984, Gaston et al. 2008), tagging studies of European birds (e.g., Anker-Nilssen & Aarvak 2009, Harris et al. 2010, Guilford et al. 2011, Jessopp et al. 2013), and a recent range-wide geolocator study (Fayet et al. 2017). I sought to bridge the knowledge gap on the nonbreeding locations of North American puffins using geolocators deployed on birds breeding on three islands in the Gulf of Maine. Further, I examined differences in movement both among colonies and within the largest colony.

Following a study using claw stable isotopes to determine overwintering locations of Common Eiders (Steenweg et al. 2017), I attempted to replicate their study design in puffins. By collecting claw samples from geolocator-tagged individuals, I attempted to identify isotopic patterns specific to overwintering locations; these patterns could later be used as a baseline for comparison of non-tagged birds to ascertain their overwinter positions and increase sample size from the population.

Overwinter Movement

Objective 1: To determine the overwinter range and movements of puffins breeding on three Gulf of Maine colonies: Machias Seal Island, Seal Island, and Matinicus Rock

Prediction 1: Puffins will undergo a dispersive migration, whereby individuals move in different directions to one of several productive overwinter areas in the northwestern Atlantic Ocean between Newfoundland and North Carolina.

Most puffins from all three colonies spent much of the overwinter period within the Gulf of Maine and nearby waters. Unlike birds nesting at larger, more northerly colonies, puffins from these colonies can remain in the productive Gulf of Maine waters without excessive intraspecies food competition or the energetic costs of long-distance migration inhibiting their survival (Fayet et al. 2017). Some puffins departed the colony in August for waters around Newfoundland, likely to feed on spawning capelin (DFO 2018). This movement to Newfoundland has also been noted in banding records of immature birds from the Gulf of Maine (Gaston et al. 2008) and adult puffins nesting in Ireland (Jessopp et al. 2013). Geolocator tracks suggest that at least one of the puffins from Machias Seal Island that visited Newfoundland may have flown across the Chignecto Isthmus to do so. Although there have been previous observations of larger alcids (i.e., Razorbills) flying across the isthmus, there are no records of puffins doing so (A. Kennedy, Canadian Wildlife Service, pers. comm.).

Many tagged puffins demonstrated a southward shift in late winter and early spring (February through April), likely to maximize their pre-breeding condition by foraging in highly productive waters induced by the spring plankton bloom as it works its way northwards up the coast (Friedland et al. 2015). Similar movements have been documented in European-breeding puffins, where individuals visiting the Mediterranean Sea in late winter bred more successfully than individuals remaining in the Atlantic Ocean (Fayet et al. 2016).

Puffins seemed to use the same overwinter strategies between years at both the population and individual levels, as previously documented in Europe (Fayet et al. 2016). The sole exception to this came in 2017, when all tagged birds from Machias Seal Island visited Georges Bank following breeding, contrasting with their September position in 2014 and 2015 more centrally in the Gulf of Maine. Although distinct oceanographically and highly productive, Georges Bank is geographically adjacent to the Gulf of Maine and would be accessible to birds departing the colony if they were in sufficient condition to travel the extra distance. Abundant prey in 2017 resulted in high puffin breeding productivity and high adult condition at the end of the breeding season, perhaps providing adult puffins with the energy to travel further than in other years.

Following the prediction that puffins would undergo a dispersive migration, birds breeding in the Gulf of Maine seem to use two general overwinter strategies: remaining in the Gulf of Maine and moving south in late winter; or traveling to Newfoundland in the fall and then returning to the Gulf of Maine before making their southward late winter venture. It is likely that there is much more fine-scale variability in overwintering areas which cannot be detected with geolocation alone. Near-future movement studies will benefit from alternative tag types (GPS, satellite) once the current issues with size, expense, and battery life are resolved.

Inter- and Intra-Colony Comparison

Objective 2: To examine differences in overwinter movements at the inter- and intra-colony level

Prediction 2.1: Puffins nesting at each of the three major Gulf of Maine colonies will show similar overwinter movements between colonies.

Prediction 2.2: Gulf of Maine colonies will not show differences in overwinter movement based on colony size.

Prediction 2.3: Birds that nest nearer to each other within the same colony will show more similarities in their overwinter movements than those nesting further apart.

As predicted, puffins from different Gulf of Maine colonies followed similar overwinter patterns, regardless of the colony size. The colonies are in relatively close proximity, sharing the same resource areas, and members of the same metapopulation (Breton et al. 2006). Contrary to the prediction for intra-colony differences, I did not find any pattern to indicate that breeding proximity is correlated with overwinter proximity. It appears that puffin sociality does not extend outside of the breeding season, at least not with the same group of individuals as at the breeding colony. Observational study of overwinter sociality would be logistically difficult due to the preference of these birds to remain far offshore, though advances in technology may one day permit remote study.

Stable Isotopes

Objective 3: To examine the feasibility of using stable isotope analysis of claw tissue to determine general overwintering position of puffins

Prediction 3: Stable isotope ratios from different overwintering areas will be distinct and recognizable from claw tissue.

Contrary to the prediction, observed differences between individuals in some isotopes do not appear to be location-based. Differences in $\delta^{15}N$, $\delta^{2}H$, and $\delta^{18}O$ are all likely attributable to dietary variability, with higher $\delta^{15}N$ and $\delta^{2}H$ values representative of piscivore specialists, rather than generalist feeders. For $\delta^{13}C$, which is less affected by diet, similar values between birds are consistent with the limited overwinter spread seen in the 2017 tag cohort. Ideally, future work could examine stable isotopes from birds visiting distinct areas (such as the Gulf of St. Lawrence, Labrador Sea, and Gulf of Maine), though this is heavily reliant upon the birds' location preferences being different from one another.

Comparisons are further complicated by the uncertain nature of timing of the samples. I chose to use claws in this study as they are inert, continuously growing, and represent the isotopic ratio of the location and time they were grown. However, the difficulty in obtaining accurate claw growth rate information inhibited a clear picture of the timeframe represented by the samples. Feathers are an alternative inert tissue, but timing of puffin moult seems to be highly variable (Harris & Yule 1977). I examined wet/dry data to determine whether a period of moult-related flightlessness (i.e., continuous wet signal) was present at any time during the overwinter period but found no evidence of such. Recent work by St. John Glew et al. (2018) in Europe has used geolocators and stable isotope analysis of feathers to examine overwinter trophic level and foraging area, though this relied on a vast database of oceanic isotope information which is not widely replicated. Future use of stable isotopes to determine puffin overwintering areas may proceed more readily once moult timing or claw growth rates are better understood.

Conclusion

Puffins breeding in the Gulf of Maine follow two general overwinter strategies: remaining in the Gulf of Maine before moving south in the late winter or, alternatively, visiting waters around Newfoundland immediately after breeding before returning to the Gulf of Maine and moving south in the late winter. Movement patterns appear to be similar among birds within and between colonies. Attempts to use stable isotope analysis of claw tissue to determine overwinter location were inhibited by the overwhelming similarity of routes among sampled birds and complications ascertaining a growth rate for the claws to determine the time period represented. Future work should use advances in technology to understand the movement of these birds at a finer spatial scale than is currently possible with geolocation.

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Baran, Mark A., A. W. Diamond, S. W. Kress, and P. Shannon. Overwinter Movement of Atlantic Puffins (*Fraterula arctica*) in the Gulf of Maine: Inter- and Intra-Colony Effects. Presented at Society of Canadian Ornithologists meeting, August 2019, Quebec City, QC.

Baran, Mark A. Overwinter Movement of Atlantic Puffins Breeding in the Gulf of Maine. Presented at Gulf of Maine Seabird Working Group meeting, August 2019, Bremen, ME, USA.

Baran, Mark A. Overwinter Movement of Atlantic Puffins (and Other Alcids) Breeding on Machias Seal Island. Presented at Gulf of Maine Seabird Working Group meeting, March 2019, Bangor, ME, USA.

Baran, Mark A. Overwinter Movements of Atlantic Puffins (*Fratercula arctica*) Breeding on Machias Seal Island and Effects of Subcolony Distribution on Nonbreeding Movements. Presented at the Gulf of Maine Seabird Working Group meeting, March 2018, Bangor, ME USA; Atlantic Canada Seabird Working Group meeting, February 2018, Sackville, NB.