Influence of Extrinsic Factors on Movements and Reproductive Success of Leach's Storm-Petrels (*Oceanodroma leucorhoa*).

By

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Abstract

Small pelagic seabirds are valuable indicators of changes in marine ecosystems because they range widely and feed at low trophic levels, and so respond rapidly to changes in ocean conditions. Globally, rapid climatic changes and increased pollution are changing marine environments. Determining how foraging and migratory movements in the face of these changes affect reproductive success of pelagic seabirds allows for a better understanding of the state of ocean ecosystems. However, until a decade ago, it was difficult to track smaller species (< 100 g). The objective of my thesis was to evaluate extrinsic factors influencing the reproductive success of small procellariform seabirds, using the Leach's storm-petrel (*Oceanodroma leucorhoa*) as a model species. In Chapter 2, I tracked movements of Leach's storm-petrels from two colonies in Nova Scotia during the incubation period, to determine what ocean conditions they faced. In Chapter 3, I evaluated ocean conditions associated with reproductive success during the breeding season. In Chapter 4, I described migratory patterns and ocean conditions in wintering areas. Finally, in Chapter 5, I evaluated effects of mercury, a neurotoxin present globally in marine ecosystems, on reproductive success. Results indicated that during the incubation period Leach's storm-petrels foraged about 800 km from their breeding colonies, beyond the continental shelf, further than expected based on allometry. High sea-surface temperatures during the breeding season and a high North Atlantic Oscillation index were negatively associated with storm-petrel reproductive success, probably through indirect effects on prey abundance. Migration patterns were variable across individuals, but I found that storm-petrels used the productive waters of the Equatorial and Benguela Currents as wintering areas. Finally, there was no association between mercury concentrations and storm-petrel reproductive success. Overall, my results suggested that extrinsic factors associated with climate change, changing sea-surface temperature and the North Atlantic Oscillation index, are likely to have negative effects on the reproductive success of Leach's storm-petrels. Climate projections suggest the Scotian Shelf will continue warming and the North Atlantic Oscillation index will mostly be positive, which is worrying for North Atlantic seabirds. My research serves to predict seabird responses to environmental change by linking extrinsic factors to reproductive success.

List of Abbreviations Used

Abbreviation	Description
AUC	Area under the curve
BP	Bon Portage Island
Chl-a	Chlorophyll-a concentration
CI	Country Island
g	gram
GLS	Global Location Sensor
Hg	mercury
hr	hour
KUD	kernel utilization distribution
MeHG	Methylmercury
mg	milligram
NAO	North Atlantic Oscillation
ng	nanogram
SDM	Species Distribution Modelling
SOI	Southern Oscillation Index
SST	Sea Surface Temperature
SSTa	Sea Surface Temperature anomalies
THg	Total mercury
VHF	Very High Frequency

Acknowledgments

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Chapter 1 – Introduction

Energetic costs associated with reproduction are high (Harshman and Zera 2006, Speakman 2008), and reproductive instinct influences the behavior and life-histories of most species. The costs associated with reproduction produce the largest trade-offs in life-history, between current reproduction and survival or future reproduction (Calow 1979, Reznick 1985, Stearns 1989). However, investment in reproductive activities does not necessarily guarantee reproductive success, because intrinsic and extrinsic factors both play a role in the reproductive success of individuals.

1.1 Intrinsic Factors Influencing Reproductive Success

Intrinsic factors such as age and experience can affect reproductive success. During the early period of sexual maturity, reproductive success may increase as individuals form pair bonds, gain reproductive experience, or acquire higher rank status in their social system (Curio 1983, Nol and Smith 1987, Bradley et al. 1995, Woodard and Murphy 1999). In contrast, in older reproducing animals, individuals may experience reproductive senescence, which translates into lower reproductive success or complete cessation of reproduction (Bérubé et al. 1999, Reed et al. 2008).

In addition to age and breeding experience, body condition, another intrinsic factor, also influences reproductive success. All the different steps of the life-cycle are linked to one another, and the reproductive phase is dependent on previous phases (Williams 2012). Body condition at the start of a breeding season may be dependent on the quality of an animal's environment before a breeding season (Norris et al. 2004). When body condition is low, individuals may experience poor reproductive success (Guinet et al. 1998a, Marra et al. 1998, Drent et al. 2003), or they may forgo reproduction altogether for that season (Crossin et al. 2012).

Differences in reproductive success due to age, breeding experience, or body condition tend to be accentuated when extrinsic factors such as weather events worsen breeding conditions, as in periods of food shortage (Daunt et al. 2007, Haug et al. 2015).

1.2 Extrinsic Factors Influencing Reproductive Success

Extrinsic factors that affect reproductive success in free-ranging animals, the main focus of my thesis, are of particular interest because they are rapidly changing due to human-induced changes to the environment, with potential evolutionary and conservation consequences. Extrinsic factors capable of influencing reproductive success in birds include biotic factors such as predation, competition, and brood parasitism (Ricklefs 1969, Montgomerie and Weatherhead 1988, Payne 1998, Benson et al. 2010), and abiotic factors such as climate change, stochastic weather events, and pollution (Jones and Reynolds 1997, García and Arroyo 2001, Visser et al. 2006, Post and Forchhammer 2008). For the purposes of this dissertation, I will focus on the influence of abiotic factors.

There is a growing body of work that documents effects of climate change on a wide range of terrestrial and marine organisms across diverse taxa (Walther et al. 2002, Hoegh-Guldberg and Bruno 2010). For example, in migrating caribou (*Rangifer tarandus*), the emergence of the caribou's forage plants is influenced by local temperature. With recent increases in temperature due to climate change, emergence in key forage species occurs earlier in the season. This creates a mismatch between the peak abundance of food and the peak foraging demand by caribou calves. The result is an increase in juvenile caribou mortality, and a decline in reproductive success in some caribou populations (Post and Forchhammer 2008).

Similar to mammals, the impact of climate change on the reproductive success of birds is most evident through its influence on food availability during breeding (Hogstedt 1981, Phillips et al. 1996, Siikamäki 1998). Climate change can result in a decline in food abundance, or a shift in timing of peak food abundance, creating a temporal mismatch between peak abundance of food and when birds are feeding their offspring (Stenseth and Mysterud 2002). For instance, in great tits (*Parus major*) a temporal mismatch between offspring needs and peak abundance in caterpillars, which constitute their main diet component, influence their reproductive success (Visser et al. 2006). For some migratory birds, climate change can affect the timing of arrival on over-wintering and breeding grounds, which is key for survival and reproductive success (Marra et al. 1998, Calvert et al. 2009).

Another important extrinsic factor that can affect reproductive success is pollution. Mercury (Hg), for example, is released naturally in small quantities in the environment, but now most releases to the environment are anthropogenic. Mercury is easily volatilized so that it can be transported globally, even to areas far from release points (Morel et al. 1998). In aquatic food webs, elemental Hg is transformed into more toxic methylmercury (MeHg, Mason and Sheu 2002), resulting in higher MeHg concentrations in freshwater and marine species than in terrestrial species (Ackerman et al. 2016a). However, high levels of Hg can be found in terrestrial birds, resulting in decreased reproductive success through nest desertion (Jackson et al. 2011) or low egg hatchability (Custer et al. 2007).

Extrinsic factors such as climate change and pollution can affect organisms in different ways and can reduce reproductive success through altered behavioral responses, reduced fertility, and premature death (Heinz 1976, Evers et al. 2008, Heinz et al. 2009). Animals have no control over those extrinsic factors, yet through their movements they may either avoid or be subjected to these factors, which may, in turn, alter their reproductive success.

1.3 Trade-Offs Between Animal Movement and Reproduction

Extrinsic factors affecting reproductive success, such as those mentioned earlier, can influence the movement patterns of animals. Animal movements can be examined at different spatiotemporal scales, from regional (involving foraging movements around a central breeding place for central-place foragers) to global (involving migratory movements between successive breeding events) that can be influenced by extrinsic factors. During foraging movements from a central place, animals may have to forage further or in discrete patches as prey density decreases or spatiotemporal shifts in prey availability occur due to climate change (Seyboth et al. 2016). Furthermore, during migration animals may have to change the timing or pattern of their migration if climatic changes modify the quality of stop-over habitats (Galbraith et al. 2011). Movement is favoured when benefits gained from moving offset energetic costs associated with such movement (Lack 1954), and the costs incurred by those movements may create trade-offs between central-place foraging or migration and current or subsequent reproductive success (Fenkes et al. 2016).

1.3.1 Trade-Offs Between Central-Place Foraging Movements and Reproductive Success

For central-place foragers, foraging periods are defined by outward movement to a foraging area, and return movement to a central location, usually a breeding site (Orians and Pearson 1979). As a consequence of being tied to a breeding site, central-place foragers have limited ability to shift their foraging ranges. Increasing the foraging range, due to prey depletion or shifts in prey location, may increase the energy cost of travel, and threaten the reproductive success of central-place foragers. For example, in a newly formed colony of northern fur seals (*Callorhinus ursinus*), as the colony grew, local resources were depleted and lactating females had to forage further from the colony. The increase in foraging distance resulted in lower reproductive success (Kuhn et al. 2014).

In birds, when prey density decreased, adult water pipits (*Anthus spinoletta*) and common murres (*Uria aalge*) foraged further from their nests. This increase in foraging distance decreased food deliveries to chicks and, ultimately, decreased reproductive success (Frey-Roos et al. 1995, Burke and Montevecchi 2009).

1.3.2 Trade-Offs Between Migration Movements and Reproductive Success

In this thesis, I consider migration as a large scale movement that leads to the relocation of all or part of a population between two breeding seasons (Dingle and Drake 2007). Benefits to migrating include exploitation of abundant foraging resources that are available for a short period of the year (e.g., during the breeding season) in one habitat (Dingle 2014). Other benefits include avoiding predators and inclement weather, and shedding parasites (Alerstam et al. 2003, McKinnon et al. 2010). However, migration, can also be energetically expensive because it can necessitate specialized morphological, physiological, and behavioral adaptations. Costs can include a prolonged increase in metabolic rate, increased time required to build energy (fat) reserves, and predation risks of transiting through unfamiliar landscapes. For example, in addition to the high energetic costs associated with long-distance movement, migrating salmon must make physiological adaptations in osmoregulation to move from fresh to salt water, and back to fresh water (Hoar 1988). Some migratory birds experience severe atrophy of some organs that are metabolically costly to maintain when they ready themselves for migration (Piersma and Lindström 1997, Piersma et al. 1999, Landys-Ciannelli et al. 2003). The costs incurred through migration may impede reproductive success the following breeding season. For example, upon returning from winter migration, some female black-browed albatrosses (*Thalassarche melanophris*) may not breed in the upcoming season depending on their body condition upon arriving at their colony (Crossin et al. 2012). For American redstarts (*Setophaga ruticilla*), the quality of their winter habitat influences body condition, migration departure date, and ultimately reproductive success (Marra et al. 1998, Reudink et al. 2009).

1.4 Extrinsic Factors in the Marine Environment

Foraging and migratory movements may also be affected by human-generated factors that can potentially increase costs associated with movement and ultimately affect reproductive success and survival. In the marine environment, these factors include climate change, human exploitation (fisheries, off-shore oil and gas development), and pollution (chronic contamination, plastic pollution; Wiese and Robertson 2004, Tuck et al. 2011, Provencher et al. 2015, Ronconi et al. 2015). For instance, climate change may alter the climatic cues an animal receives at the start of a migratory journey that may no longer be synchronised with cues at the end of the journey (Durant et al. 2007, Watanuki et al. 2009). This mismatch can potentially have a bottom-up impact on marine predators, decreasing reproductive success, because peak resources are not available during peak requirements (Barbraud and Weimerskirch 2006, Bertram et al. 2009).

Similarly, the wide-spread occurrence of pollutants in the marine environment may or may not increase exposure for wide-ranging individuals. Pollutants can affect reproductive success directly during breeding, or indirectly through carry-over effects, where animals are exposed to pollutants at one stage of their life cycle but will experience negative effects during subsequent breeding seasons (Barros et al. 2014, Goutte et al. 2014a).

Human impacts on the environment, such as climate change or pollution, can alter the movement patterns of animals and impede their reproductive success. Seabirds are excellent model organisms for examining fitness consequences of animal movement in an environment increasingly affected by humans. Below, I discuss reasons why seabirds are well suited for studying how movement and extrinsic factors, such as climate change, and Hg pollution affect reproductive success. I then detail the breeding biology of my study species, my study sites, and techniques used in this thesis to study movement ecology.

1.5 Seabirds as Models

Seabirds are generally long-lived, with high rates of adult survival, and high variability in reproductive success from year to year (Warham 1990, Weimerskirch 1998). Seabirds are highly philopatric, returning annually to the same breeding colonies and even the same nest site. High nest fidelity and colonial nesting behavior means that seabirds are generally accessible in large numbers and can be recaptured in successive breeding seasons. Seabirds are central-place foragers during the breeding season, and many undergo long foraging movements during the breeding season as well as long-distance migration to and from their breeding colonies and wintering sites. During these movements seabirds can be exposed to changes in food quantity and quality, and to pollutants (Robinson et al. 2008, Lavoie et al. 2014). All of these characteristics make seabirds ideal models for studying the effects of extrinsic factors on movements and reproductive success. Broad movements of seabirds also make them good indicators of the condition of marine ecosystems (Chastel et al. 1993, Berman et al. 2009). In addition, because different species feed at different trophic levels, and collectively use a broad variety of marine habitats, seabirds are exposed to a multitude of ocean conditions within marine ecosystems that could affect reproductive success (Cairns 1988, Frederiksen et al. 2007, Mallory et al. 2010). Indeed, changes in the health and condition of marine environments, such as those related to climatic changes and contaminants, are often monitored using data on seabird survivorship, reproductive success, or chick growth (Hobson et al. 1994, Monteiro and Furness 1995, Diamond and Devlin 2003, Burger and Gochfeld 2004, Iverson et al. 2007, Parsons et al. 2008).

1.5.1 Seabird Movements

Declines in seabird populations have been observed in all parts of the world (Kitaysky et al. 2006, Catry et al. 2011, Croxall et al. 2012). Thus an understanding of the factors affecting population declines is important for recognizing where future conservation efforts should be directed (Webster et al. 2002). A key to conservation of most species is knowledge of their foraging ecology and migratory movements through the different phases of their life-cycle, and an understanding of the drivers of those movements. For example, determining migratory routes and winter or breeding destinations helps to identify important habitat and potential threats to seabirds in those areas (Lawler et al. 2013, Allen and Singh 2016).

Although it is important to document and describe seabird movements, this is challenging because they can span great distances and are often found in remote areas. Indeed, seabirds can easily move tens of thousands of kilometers in a matter of weeks (Stone et al. 1990, Egevang et al. 2010). For many decades, tracking animals for long periods of time with electronic devices was restricted to large land animals due to the historically large size of the tracking devices (Hoskinson and Mech 1976, Addison et al. 1980). Miniaturization of these devices now allows tracking of small animals. However, there are still knowledge gaps regarding regional and global movements of many species (Wilcove and Wikelski 2008, Hein et al. 2012).

Extrinsic factors faced by seabirds during regional foraging movements, such as severe storms, oil spills, and food availability, can have direct effects on reproductive success during a given breeding season (Eppley and Rubega 1990, Yannic et al. 2014). Extrinsic factors can also have indirect effects. For example, prey abundance influences the foraging distance, which determines the frequency with which chicks are provisioned by parents, and ultimately influence breeding success. This in turn, can affect chick growth rates (Ricklefs et al. 1994, Lyons and Roby 2011, Shoji et al. 2011) and, ultimately, reproductive success (Monaghan et al. 1989, Golet et al. 2000, Busser et al. 2004, Wanless et al. 2005).

Conditions encountered during migratory movements and where individuals over-winter can affect reproductive success the following breeding season (Shoji et al. 2015). Adults that over-winter in high quality habitat, which allows them to replenish their body reserves, may arrive at breeding sites in better condition, and lay eggs earlier and/or produce larger eggs than adults wintering in poorer quality habitat (Robb et al. 2008, Sorensen et al. 2009). Earlier laying dates and larger eggs can increase reproductive success (Croxall et al. 1992, Reed et al. 2009). Consequently, identifying migratory routes and destinations is an important step in understanding how quality of wintering habitats affects reproductive success.

1.5.2 Seabirds and Climate Change

In the oceans, climate change is linked to change in water temperatures, stratification, and ocean acidification, which can result in altered primary productivity, altered food-web dynamics, and shifts in species distributions (Hoegh-Guldberg and Bruno 2010, Doney et al. 2012). Effects of climate change are not uniform across the globe. For example, the Arctic is considered more severely affected by climate change than most other regions (Walsh 2008). Thus, effects of climate change on seabird populations will not be uniform across the globe.

In the Atlantic Ocean, the North Atlantic Oscillation (NAO) index is defined as the difference in atmospheric pressure at sea level between Iceland and the Azores (Hurrell 1995). The NAO index is associated with climatic conditions over much of the Atlantic and part of Europe (Hurrell and Deser 2010). Positive NAO index values are associated with stronger than usual westerly winds over middle latitudes, low pressure anomalies over the Icelandic region, and anomalously high pressure across the subtropical Atlantic.

Positive values observed since the 1980s have been associated with intensified winter storms from Newfoundland to northern Europe, increased wave height over the northeast Atlantic, and warmer, moister winters (Stenseth et al. 2002, Hurrell and Deser 2010).

The NAO index has been associated with timing of migration, onset of reproduction, body condition upon arrival at a breeding colony, breeding productivity, and survival of many seabird species (Thompson and Ollason 2001, Forchhammer et al. 2002, Sandvik et al. 2005). Mechanisms for the observed effects associated with the NAO index are indirect, either affecting food availability, or influencing wind and precipitation (Sandvik and Erikstad 2008, Bustnes et al. 2013). For these seabird species, effects associated with the NAO index can differ among regions (Sæther et al. 2003, Sandvik et al. 2008). For example, pre-laying body masses of common eiders (*Somateria mollissima*) from the Canadian Arctic are related to the NAO index within the same year, whereas those from Norway are related to the NAO index with a lagged response of one year (Descamps et al. 2010). This suggests that the NAO index conditions can have an indirect effect through climate, or a delayed effect through the food web, and might differ among geographic regions. Therefore, it is necessary to understand how each population is affected by this global weather phenomenon.

1.5.3 Seabirds and Mercury (Hg) Pollution

Seabirds face several types of at-sea pollution, including artificial light, hydrocarbons, plastic pollution, and Hg (Wiese and Robertson 2004, Provencher et al. 2015, Rodríguez et al. 2015). Time series of Hg profiles in seabirds from the Arctic and the North Atlantic over 100 years show increased Hg burdens (Monteiro and Furness 1997, Bond et al. 2015). This is of particular concern because ingestion of Hg in seabirds is related to reduced hatching success through either early embryonic death or decreased egg fertility (Scheuhammer 1987, Wolfe et al. 1998). Although many studies have monitored levels of Hg in seabirds (Burger and Gochfeld 2000, Carravieri et al. 2014, Mallory et al. 2015), few have evaluated the effects of Hg burdens on reproductive success or survival.

1.6 Study Species

The family Hydrobatidae (storm-petrels) belongs to the procellariform order. It has 25 species in seven genera, including 15 species in the genus *Oceanodroma.* Storm-petrels feed on small prey items at the surface of the water while hovering. Their diet responds rapidly to changing environmental conditions, which makes hydrobatids ideal indicators of ocean productivity. They are strictly pelagic and found throughout the world's oceans. Because of their small size, little is known about their foraging ecology, particularly their movement patterns and distribution at sea (Warham 1990, Spear 2008).

Leach’s storm-petrels (*Oceanodroma leucorhoa*) are small (~ 45 g) seabirds that breed mostly in the northern hemisphere (Huntington et al. 1996). The estimated world population of 8 million (Huntington et al. 1996) makes Leach’s storm-petrels the most abundant species of procellariiform in the North Atlantic (Barrett et al. 2006). The largest colony (~ 3 million pairs) breeds on Baccalieu Island, Newfoundland (Sklepkovych and Montevecchi 1989). However, populations at many surveyed colonies have declined in the past 50 years, and some colonies have been abandoned (Robertson et al. 2006, Newson et al. 2008, Wilhelm et al. 2015). This motivated the International Union for the Conservation of Nature (IUCN) at the end of 2016, to change the status of Leach's storm-petrel from least concern to vulnerable. Currently, we know little about what factors are affecting the reproductive success, or the survival of Leach's storm-petrels (Gilmour et al. 2015).

Leach's storm-petrels breed on islands mostly free of mammalian predators (Huntington et al. 1996) because small seabirds are especially vulnerable to mammalian predation (Croxall et al. 2012). They are nocturnal at their colonies to avoid diurnal avian predators (Votier et al. 2006). Pairs arrive on the breeding grounds in May following their return migration from wintering areas. They excavate burrows, preferably in peaty soil (Stenhouse and Montevecchi 2000), to which they return with high fidelity across years (Huntington et al. 1996). Females lay a single large egg, representing 22% of average female body mass, at the end of June and both adults incubate in 1- to 5-day incubation shifts. While one adult incubates, the other is assumed to forage an estimated 200 km from their colony (Ricklefs and Schew 1994, Huntington et al. 1996, Thaxter et al. 2012). Food captured during foraging trips includes small fish, such as myctophids, lanternfish, and sandlance (Hedd et al. 2009), as well as mesopelagic crustaceans (Steele and Montevecchi 1994) captured when the latter make diel vertical migrations in the water column. Incubation lasts ~ 45 days. Once eggs hatch, chicks are brooded for several days and then are left on their own while adults forage at sea. Adults return independently to feed their chick every night, or every other night (Ricklefs et al. 1985).

For the first part of the nestling period, chicks are fed prey items, transformed into nutritious oil in the adult's proventriculus; later on, chicks are fed whole prey items. Nestlings accumulate significant fat reserves, and after reaching masses up to twice those of adults, they begin a fasting period, during which they lose fat and gain muscle mass to be able to fly. Nestling periods last ~ 65 days. Sexual maturity is reached at around 5 or 6 years of age, but little is known about pre-adult periods of the storm-petrel lifecycle. Leach’s storm-petrels undertake winter migrations, but information about the routes they use is limited. On the Atlantic Ocean, the migration range of Leach’s storm-petrels covers the equatorial area, ranging from coastal areas of Brazil to the entire coast of West Africa (Huntington et al. 1996).

1.7 Study Sites

1.7.1 Bon Portage Island

The majority of field work for this thesis took place on Bon Portage Island (Outer Island on some maps, 43° 28' N, 65° 44' W), which is 3 km off the southwestern tip of Nova Scotia, Canada. The ~ 0.5 × 3-km island is dominated by white spruce (*Picea glauca*), black spruce (*P. mariana*), and balsam fir (*Abies balsamea*). The island has an estimated 50,000 pairs of breeding Leach’s storm-petrels (Oxley 1999). A recent short-term study on Bon Portage suggested that apparent survival rates of Leach’s storm-petrels was 0.78 ± 0.04 (Fife et al. 2015), which is low for long-lived seabirds (Beck and Brown 1972, Sandvik et al. 2005, Zabala et al. 2011). The main threat to storm-petrels at this colony is predation, mainly by great black-backed gulls *(Larus marinus*), herring gulls (*L.*

argentus), and great horned owls (*Bubo virginianus*). Threats from oil and gas infrastructure are likely relatively low at this site because the foraging ranges of storm-petrels at this colony do not overlap with the location of offshore oil and gas platforms (Pollet et al. 2014a). Several other seabird species also breed on Bon Portage. Great black-backed gulls and common eiders (*Somateria mollissima*) breed on the outskirts of the island, whereas herring gulls breed in open habitat throughout the island. There is a small rookery on the north end of the island that is shared by great blue herons (*Ardea herodias*) and black-crowned night-herons (*Nycticorax nycticorax*). Two pairs of great horned owls also breed on the island. Bon Portage also has several breeding songbird species.

Starting in 2010, Leach's storm-petrels were monitored in ~300 burrows from twelve 12 × 12-m plots, randomly situated along an east-west path, located primarily in a loosely forested area, although a few plots are in more open habitat with only a few standing dead trees. Plots contained an average of 29.1 (range: ~ 15–53) uniquely numbered marked burrows.

1.7.2 Country Island

Data for this thesis were also collected on Country Island (45° 06' N, 61° 32' W), located on the eastern shore of Nova Scotia, about 340 km NE of Bon Portage. The island has a circular shape with a diameter of ~ 500 m. It has an estimated 8,700 breeding pairs of Leach's storm-petrels (S. Wilhelm, pers. comm.). There is also a mixed population of common (*Sterna hirundo*), Arctic (*S. paradisaea*), and roseate terns (*S. dougallii*) breeding on the island, as well as common eiders and several songbird species. As part of roseate tern management, avian predators (larids, corvids, and raptors) are prevented from breeding on the island. However, meadow voles (*Microtus pennsylvanicus*) have been present on the island in high numbers since the beginning of this study. Many Leach's storm-petrel eggs have been found outside of their burrows and some chicks were found inside burrows with physical wounds, which were attributed to vole predation. Starting in 2011, 80 randomly selected Leach's storm-petrel burrows were monitored.

1.8 Bio-Logging Tags

1.8.1 Very High Frequency Tags

Short-range Very High Frequency (VHF) tags emit a signal at a specified frequency but do not store data. VHF tags were first used to track animals in the 1960s (Cochran and Rexford 1963). Each tag has a uniquely identifiable pulse, allowing detection of multiple tags on the same frequency. VHF tags have a limited detection range (< 40 km) and require data to be collected at stations composed of antennas and receivers. VHF tags can be used to infer presence/absence of birds near receiver stations, or further afield by triangulation techniques if several receiver stations are used simultaneously (Wilson et al. 2009).

VHF tags used for this dissertation were NanoTag NTQB-1 (Lotek Wireless, Newmarket, Ontario, Canada). Tags were programmed with a burst rate of 5 sec that allowed for a battery life of at least 21 d. Tags measured 10 × 4 × 2 mm with an external aerial measuring 180 × 0.2 mm, and weighed 0.29 g, which is less than 1% of an adult Leach's storm-petrel's body mass (average adult mass on Bon Portage Island in 2010 was 46.1 ± 4.4 g, *n* = 98). Tags were attached to birds with two small strips of Tesa tape® under them. The underside of the tape was glued to the backs of birds. Tape was then wrapped around tags and the first set of contour feathers, while a second set of contour feathers covered the entire device. This setup was designed to fall off birds during the following molt, which would occur during fall migration.

1.8.2 Geolocator Tags

Geolocator (GLS) tags collect light intensity data and have a built-in clock and were first used in the 1990s (Wilson et al. 1992). Using light intensity and time of day, one is able to estimate time of sunset and sunrise for each day. The duration of a day indicates latitude whereas the start of the day indicates the longitude of a bird's location. These data have an error of approximately 200-km radius (Bridge et al. 2011, Phillips et al 2004). GLS tags must be retrieved to acquire stored information.

GLS tags used in this dissertation were Mk5740 (BAS, Cambridge, UK). GLS tags had enough battery longevity to collect data for one year and store data for an additional year. Tags weighed 0.9 g and measured 21.9 × 7.9 × 3.8 mm which is less than 3% of Leach's storm-petrel body mass (average adult mass on Bon Portage Island in 2012 was 46.1 ± 4.3 g, *n* = 95). GLS tags were initially attached to birds using the same technique as for VHF tags for summer deployment, but later loggers were attached with subdermal sutures

(MacLeod et al. 2008). The suture attachment method allowed recovery of GLS tags the following breeding season after they had collected data during the non-breeding period. Suture areas were sterilized with 70% ethanol at the center of a bird's back, between the scapulae. The front end of the GLS tags was positioned between the scapulae, and attached at the front and back ends of the tags with subdermal sutures (Ethicon Prolene 4-0 FS-2 19 mm). Each suture was tied by performing one surgical knot followed by two square knots with clamp forceps.

1.9 Dissertation Outline

The central aim of this thesis was to evaluate how different extrinsic factors influence movements and reproductive success of a small long-lived seabird, Leach's storm-petrel. Specifically, the main goals of this thesis were to determine:

1) how ocean conditions during the breeding season, when Leach`s storm-petrels are central-place foragers, affect foraging movements, incubation routine, and reproductive success, and determine how conditions associated with the NAO index affect reproductive success,

2) winter positional data to estimate the migration routes of Leach's storm-petrels, to identify extrinsic factors they face during the non-breeding season, and

3) the effects of mercury levels, a neurotoxin extrinsic factor, on the reproductive success of Leach's storm-petrels.

To evaluate how ocean conditions affect foraging movements, and reproductive success of Leach's storm-petrels during the breeding season, I first needed to determine what marine habitats they used during that time. Therefore, in Chapter 2, I used GLS to track Leach's storm-petrels during the incubation period, from the two breeding colonies described above, over two consecutive years. I determined their foraging range, and compared foraging movements between colonies and among years.

To determine how ocean conditions affect foraging movement, incubation routine, and reproductive success and how conditions associated with the NAO index affect reproductive success, in Chapter 3 I used VHF telemetry to assess foraging movement, and monitored reproductive success of Leach's storm-petrels on Bon Portage Island. I also determined how the oceanographic conditions within the foraging ranges identified in Chapter 2 influenced foraging movement. Finally, I explored the relationship between the NAO index and reproductive success.

To identify how ocean conditions during the non-breeding season affect migration movement, in Chapter 4 I used GLS over three consecutive years, to identify migration routes, stopover locations, and wintering locations of Leach's storm-petrels. I then used a Species Distribution Modelling program to assess which oceanographic conditions were most important in determining the species' home range during the non-breeding season.

To evaluate effects of a pollutant on Leach's storm-petrel reproductive success, in Chapter 5 I evaluated the effects of adult blood mercury levels on several Leach's storm-petrel reproductive parameters over four consecutive years.

Finally, in Chapter 6, I summarize the results of my dissertation and their implications at a broader scale, and discuss future research priorities.

Chapter 2 - Foraging Movements of Leach's Storm-Petrels, *Oceanodroma leucorhoa*, During Incubation

2.1 Abstract

Knowledge of foraging movements during the breeding season is key to understanding energetic stresses faced by seabirds. Using geolocators, a Bayesian state-space model, and stable isotope analysis, I compared foraging movements and trophic positions of Leach's storm-petrels (*Oceanodroma leucorhoa,* hereafter storm-petrels) during incubation in 2012 and 2013. Data were collected from two colonies, Country Island and Bon Portage Island, Nova Scotia, Canada. The allometric relationship between body mass and foraging distance for procellariiforms suggests that storm-petrels should forage approximately 200 km from their breeding colonies; however, the maximum distances recorded in my study were 3 to 5 times that. Storm-petrels from Country Island travelled 1,015 ± 238 km south-east to the Laurentian fan and south of the Grand Banks, whereas storm-petrels from Bon Portage Island travelled 613 ± 167 km south-east, beyond the continental slope, east of Georges Bank. The average distance travelled in a return trip was 2,287 ± 603 km and 1,303 ± 351 km for Country Island and Bon Portage Island, respectively. Although round-trip distances did not differ with year, overall foraging trip duration was less in 2013 (4.7 ± 1.5 d) than in 2012 (6.2 ± 2.1 d). Stable isotope analyses indicated that during the incubation period, prey items from Country Island were from

higher trophic levels and possibly had higher energy content than those from Bon Portage Island, perhaps explaining why Country Island birds foraged over longer distances.

2.2 Introduction

Pelagic seabirds spend most of their time at sea (Warham 1990). Determining how marine habitat is used is key to understanding many of the threats they face (Weimerskirch et al. 1997a). Knowing at-sea distributions of seabirds is also critical for understanding their role in ocean ecosystems and for identifying sites for the establishment of marine protected areas that are vital to population persistence (Ronconi et al. 2012, Maxwell and Morgan 2013, McGowan et al. 2013). At-sea distributions for most seabirds are strongly linked to the distribution of their prey, which in turn are influenced by physical characteristics of the ocean such as temperature, wind, currents, and salinity (Franks 1992, Nogueira et al. 2012). Those characteristics are heterogeneous both spatially and temporally (Hunt and Schneider 1987, Donaghay et al. 1991, Mahadevan and Campbell 2002), which means that prey distribution varies accordingly, and seabirds must adjust their foraging movements daily, seasonally, and annually (Weimerskirch et al. 1993, Quillfeldt et al. 2010a, Garthe et al. 2011).

Until recently, seabird movements have been difficult to track on open oceans. The earliest studies of at-sea distribution consisted of observations carried out from ships that could identify birds to species (Brown 1979, Griffiths and Sinclair 1982), but usually provided little information on breeding status, sex, age, foraging behavior, or distance from a colony (Burger and Shaffer 2008). In recent years, development of electronic tracking devices has made it possible to track some bird species at sea (Weimerskirch et al. 2005, Shaffer et al. 2006, Egevang et al. 2010, Harris et al. 2010, Bridge et al. 2011, Guilford et al. 2012). Tracking devices have provided information about sex-specific foraging behavior (Pinet et al. 2012), intraspecific avoidance of competition (Grémillet et al. 2004), and migration routes (Egevang et al. 2010) that was previously impossible to gather. Miniaturization of archival light loggers (geolocators) has enabled researchers to gain valuable knowledge about foraging and migratory movements of an increasing number of seabird species that weigh less than 500 g (Rayner et al. 2012, Navarro et al. 2013).

Stable isotope analysis has also been used to study geographic movements (Cherel et al. 2000) and changes in diet associated with movements for many birds, including seabirds (Mallory et al. 2010, González-Solís et al. 2011). For instance, ^{13}C tends to be depleted towards the poles (Cherel and Hobson 2007, Quillfeldt et al. 2010b), so differences in carbon signature can provide information about north-south movement. Similarly, stable isotopes of carbon have lower proportions of ^{13}C in oceanic particulate organic matter compared to benthic environments, indicating whether a bird has foraged closer to shore versus in more pelagic waters (Rubenstein and Hobson 2004). Finally, proportions of $\delta^{15}N$ increase in a stepwise manner at each trophic level (Kelly 2000) and so can be used to infer trophic position at which birds feed. Stable isotope analysis can provide information on movements on a coarse scale, but because most small seabird species have yet to be tracked, we have a knowledge gap in the fine scale movements of many species.

Leach's storm-petrels (*Oceanodroma leucorhoa,* hereafter storm-petrels) are small, abundant seabirds of the western North Atlantic. Populations at many surveyed breeding colonies have declined in the past 50 years, and some colonies have been abandoned (Robertson et al. 2006). Several processes are thought to be related to these declines including mammalian and avian predation at breeding colonies (Bicknell et al. 2009), collisions with large man-made offshore structures (Wiese et al. 2001), and exposure to oil contamination (Leighton 1993). The probability of encountering offshore structures and oil during breeding may increase with increasing foraging range. However, limited information on storm-petrel movement during the breeding season makes it difficult to assess the impact of those threats.

Based on allometry for other procellariiforms, storm-petrels are expected to forage within 200 km of their colony during the breeding season (Ricklefs and Schew 1994, Huntington et al. 1996, Thaxter et al. 2012) but there are no empirical data to evaluate this expectation. The goals of my study were to determine at-sea distributions and movements of storm-petrels during their incubation period, when foraging trip duration is longer than during the chick-rearing period (Huntington et al. 1996), and relate those movements to stable isotope signatures. Here, I used geolocators (GLS) to map foraging ranges of incubating storm-petrels in two different breeding seasons, at two geographically separated breeding colonies in Nova Scotia, Canada. I compared foraging movements from the two colonies to determine if there were colony-specific differences in foraging duration and distance, and if so, whether these differences were reflected in trophic position, as determined by stable-isotope signatures.

2.3 Methods

2.3.1 Study Sites

This study was conducted during the summers of 2012 and 2013 on Country Island and Bon Portage Island in Nova Scotia, Canada. On Country Island, my study plot consisted of 62 randomly selected nesting burrows and on Bon Portage Island, I monitored ~250 burrows, distributed among twelve 12- x 12-m plots. On both islands, occupied burrows were labelled with uniquely numbered metal tags. Burrows were visited no more than twice during incubation to reduce desertion (Blackmer et al. 2003). When first handled, adults were fitted with a uniquely numbered Canadian Wildlife Service metal band. The Acadia University Animal Care Committee approved all animal handling procedures (Protocol # 06-09).

2.3.2 GLS Deployment and Nest Monitoring

I used MK5740, British Antarctic Survey (BAS) GLS, which weighed 0.9 g and measured 21.9 × 7.9 × 3.8 mm with a light sensor stalk of 6.8 mm. GLS and attaching materials weighed 1.3 g, which represents less than 3% of an average adult storm-petrel’s mass (e.g. average adult mass on Bon Portage Island in 2012 was 46.1 g). GLS were equipped with an internal clock and battery, measured light levels every 60 sec, and recorded maximum levels in 10-min intervals.

To determine foraging locations in 2012, I deployed 21 GLS during the day on storm-petrels on Country Island between 8 and 9 July, during early stages of incubation. I also deployed 17 GLS during the day on storm-petrels on Bon Portage Island between 19 July and 22 August, during late stages of incubation. Storm-petrels were randomly selected to be fitted with GLS on Country Island and distributed (1 or 2 per plot) amongst the twelve plots on Bon Portage Island. Only one adult per pair was tagged.

On Country Island, nine of the 21 GLS were deployed using a modified leg-loop harness following Haramis and Kearns (2000). Of those nine storm-petrels, only one bird was recovered and it had lost the GLS. None of those birds was relocated in 2013. The remaining GLS (n = 12) on Country Island and all GLS on Bon Portage Island were deployed using a combination of tape and glue, as described in Chapter 1. Individuals were returned to their burrows immediately after GLS were affixed. Of the 29 storm-petrels fitted with GLS using the tape and glue technique, 17 were recaptured during the same breeding season using one-way traps (Mauck and Grubb 1995). Five GLS (total of 9 foraging tracks) were recovered from Country Island and another 5 GLS (total of 6 foraging tracks) were recovered from Bon Portage Island. The remaining seven birds were recaptured without a GLS. All individuals from which I recovered GLS were still incubating at the time of recovery.

To determine foraging locations in 2013, I deployed 15 GLS on storm-petrels on Country Island between 3 and 4 July, and 15 GLS on Bon Portage Island between 6 and 10 July, during early stages of incubation. Another 5 GLS on Bon Portage Island were deployed on 2 August, during late stages of incubation. All GLS deployed in 2013 were attached with sub-dermal sutures (Ethicon Prolene 4-0, FS-2 19 mm) to the backs of birds (MacLeod et al. 2008) as described in Chapter 1. Storm-petrels were returned to their burrows immediately after GLS were affixed, usually within 10 min. Eleven individuals were recovered from Country Island (total of 21 foraging tracks) and 14 individuals were recovered from Bon Portage Island (total of 32 foraging tracks). The remaining 4 individuals on Country Island and 6 individuals on Bon Portage Island were not recaptured within the breeding season. Upon GLS recovery, storm-petrels from both islands and in each year were weighed.

To test for changes in foraging duration relative to stage of incubation, on the day of the GLS deployment, I candled eggs to estimate stage of development on a scale of 0 to 22 using Weller's criteria (1956). Stage 0 corresponds to a freshly laid egg; stage 22 corresponds to day 45 of incubation, when the bill of the chick is pressed against the inner shell membrane; chicks at the latter stage hatch within 24 h.

To determine hatching rate and fledging rate, I monitored burrows. Hatching rate was defined as the percent of eggs that hatched and fledging rate was defined as the percent of chicks that fledged. Chicks were weighed on a weekly basis and chick growth rate was measured by the slope of mass gain between days 5 and 30.

2.3.3 Data Processing

Data obtained from GLS were decompressed using BAS Trak software (Biotrack, Dorset, UK). From pre-deployment calibration on Acadia University Campus, I chose the threshold that led to the location closest to the calibration location with the least variation. Times of sunrise and sunset, used to determine the longitude and latitude, were determined from light curves using TransEdit2 software (Biotrack 2010).

I used a light level threshold of 12 and calculated a sun elevation of -3.7° for Country Island and -4.0° for Bon Portage Island (angle corresponding to sunrise and sunset based on pre-deployment calibration). Accuracy, calculated from the calibration period, was 170 ± 88 km, with a magnitude of 1.06 ± 1.16° for latitude and 0.86 ± 0.47° for longitude.

I then obtained latitude and longitude using Locator software (BAS; Ekstrom 2004). This method gave me two locations per day (midnight and noon). I excluded positions associated with storm-petrels being in burrows where they spent several days in complete darkness. Light-level based locations can have high errors due to effects of cloud cover, feather or body shading of the light sensor, and high daily travel rates, all of which interfere with recording of local sunrise and sunset events (Phillips et al. 2004, Block et al. 2011). I used a Bayesian state-space model to filter location data (Jonsen et al. 2013), accounting for location errors and yielding sets of locations at regular 12-h time intervals. The model is a modification of the first-difference correlated random walk model described in Jonsen et al. (2005) to account for light-level GLS data (as per Winship et al. 2012), with the following process equation:

$$\mathbf{d}_t = \gamma \mathbf{T} \mathbf{d}_{t-1} + \eta_t \tag{1}$$

where $\mathbf{d}_t = \mathbf{x}_t - \mathbf{x}_{t-1}$ and $\mathbf{x}_t$ is a vector of length 2 representing the true longitude and latitude of a storm-petrel at time t. The transition matrix $\mathbf{T}$ is parameterized by the mean turning angle θ and gives the average change in direction between movements $\mathbf{d}_t$ and $\mathbf{d}_{t-1}$. The degree of correlation or persistence in movements is controlled by γ, where values approaching 1 imply highly correlated, straight-line movements, and values approaching 0 imply uncorrelated, tortuous movements. Stochastic deviations in movement η_t are assumed to be normally distributed with mean 0 and variance-covariance Σ.

True locations $\mathbf{x}_t$ were linked to GLS data via the following observation equation:

$$\mathbf{y}_i = \mu_i + \varepsilon_t \tag{2}$$

where $\mathbf{y}_i$ is the i^{th} pair of longitude and latitude observations, μ_i is the corresponding true longitude and latitude, and ε_i are normally distributed, serially independent observation errors in longitude and latitude. True locations μ_i were derived from estimated states $\mathbf{x}_t$ that were regular in time according to the following interpolation:

$$\mu_i = (1 - j_i)\mathbf{x}_{t-1} + j_i \mathbf{x}_t \text{ for I} \in I_t \tag{3}$$

where I_t is the set of observations that occurs between times t-1 and t, and the scalar j_i is the proportion of this time step that elapsed prior to μ_i. See Winship et al. (2012) for further details.

Because foraging trips were relatively short, I used a hierarchical state-space formulation that facilitated improved location estimates by simultaneously fitting to multiple track datasets (Jonsen et al. 2003). The model described in equations (1) through (3) was fit hierarchically by estimating movement parameters γ, θ, and Σ across all tracks rather than individually (e.g. Block et al. 2011). Models were fit to tracking data using open source JAGS software (version 3.3.0; Plummer 2003). A total of 100,000 samples was taken as an adaptive sampling and burn-in phase and an additional 100,000 joint posterior samples in each of two Markov Chain Monte Carlo chains were generated after convergence was assumed. These latter samples were thinned by a factor of 100 to reduce sample autocorrelation, yielding a final set of 2000 joint posterior samples. Convergence was assessed visually by examining: (1) trace plots of model parameters for signs of non-stationarity and poor mixing of the chains; (2) density plots of the chains overlaid to ensure posterior distributions were unimodal; (3) autocorrelation function plots of each chain to ensure that sample autocorrelation was not unduly large after thinning. I used program R (version 2.15.2 2; R Development Core Team 2012) for all subsequent analyses.

2.3.4 Foraging Movement During Incubation

To study the distribution of foraging positions during the incubation period, I created a kernel density map using the kde2d function in R. Coordinates representing track start and endpoints (i.e., colony locations) were removed to avoid over-representation of those areas. I defined: 1) foraging trip duration as the number of days an individual was at sea,

2) maximum distance as the farthest point from the colony during a foraging trip, and 3) cumulative distance as the total distance travelled during a foraging trip. Maximum distance from a colony and cumulative distance travelled for each foraging trip were calculated from the set of locations produced by the state-space model, using the package 'sp'. I calculated distances from colonies to the maxima of their respective kernel density surface.

To test for seasonal, inter-annual, and island differences in foraging movements, I fit a linear mixed-effects model to each foraging measure (foraging trip duration, maximum distance from colony, and cumulative distance) using 'lmer' in the package 'lme4'. Egg stage (a continuous variable), island, and year were explanatory variables in all models, and birds were treated as random effects. I used likelihood ratio tests to assess effects of each of the remaining terms in the set of nested models.

2.3.5 Impacts of Geolocators on Leach's Storm-Petrels

To test for potential impacts of GLS on adults and reproductive success, I compared changes in adult mass between GLS deployment and recapture, hatching rate and fledging rate, and chick growth rate between GLS-birds (tape and glue method, and suture methods) and a random set of control birds that did not receive tags (n = 15 on Country Island and n = 100 on Bon Portage Island). Chi-square tests were used to compare hatching rate and fledging rate between GLS birds tagged with tape and glue method and suture method separately, versus control birds; ANOVAs were used to compare mass change and chick growth between GLS birds (tape and glue method, and suture method) and control birds. I could not determine how long adults had been incubating on a given incubation bout at the time that they were weighed. Weight can decrease up to 3 g per day throughout the incubation bout (Ricklefs et al. 1986), so some variation in weight could simply be due to how long an adult had been incubating. This should not, however, affect my results because I treated control birds and GLS birds in the same manner.

2.3.6 Trophic Level Inferred from Stable Isotopes

To test for differences in trophic level between individuals from each island, ~100 µl of blood was drawn from a subset of incubating storm-petrels in 2012 ($n = 15$ and $n = 10$ for Country Island and Bon Portage Island, respectively) for carbon and nitrogen stable isotope analysis. I used a drop of 10% ethanol to mat feathers over the brachial veins, and then punctured the vein with a 26-gauge needle. I collected the blood with capillary tubes and stored it in centrifuge tubes. I kept samples on ice for < 2 h in the field before transferring blood to liquid nitrogen. Every 7 to 14 d, I transferred samples to a -80°C freezer. Blood samples were dried at 60°C for 3 d, then ground up using a metal probe. Samples were analysed at the Stable Isotopes in Nature Laboratory at the University of New Brunswick, Fredericton, New Brunswick, Canada for simultaneous determination of carbon and nitrogen stable isotope values. Stable isotopes are quantified as the deviation from a standard following the equation: $\delta X = [(R_{sample}/R_{standard})-1] \times 1000$, with X being either ^{13}C or ^{15}N and R being the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. Stable isotope data were compared between islands using ANOVA.

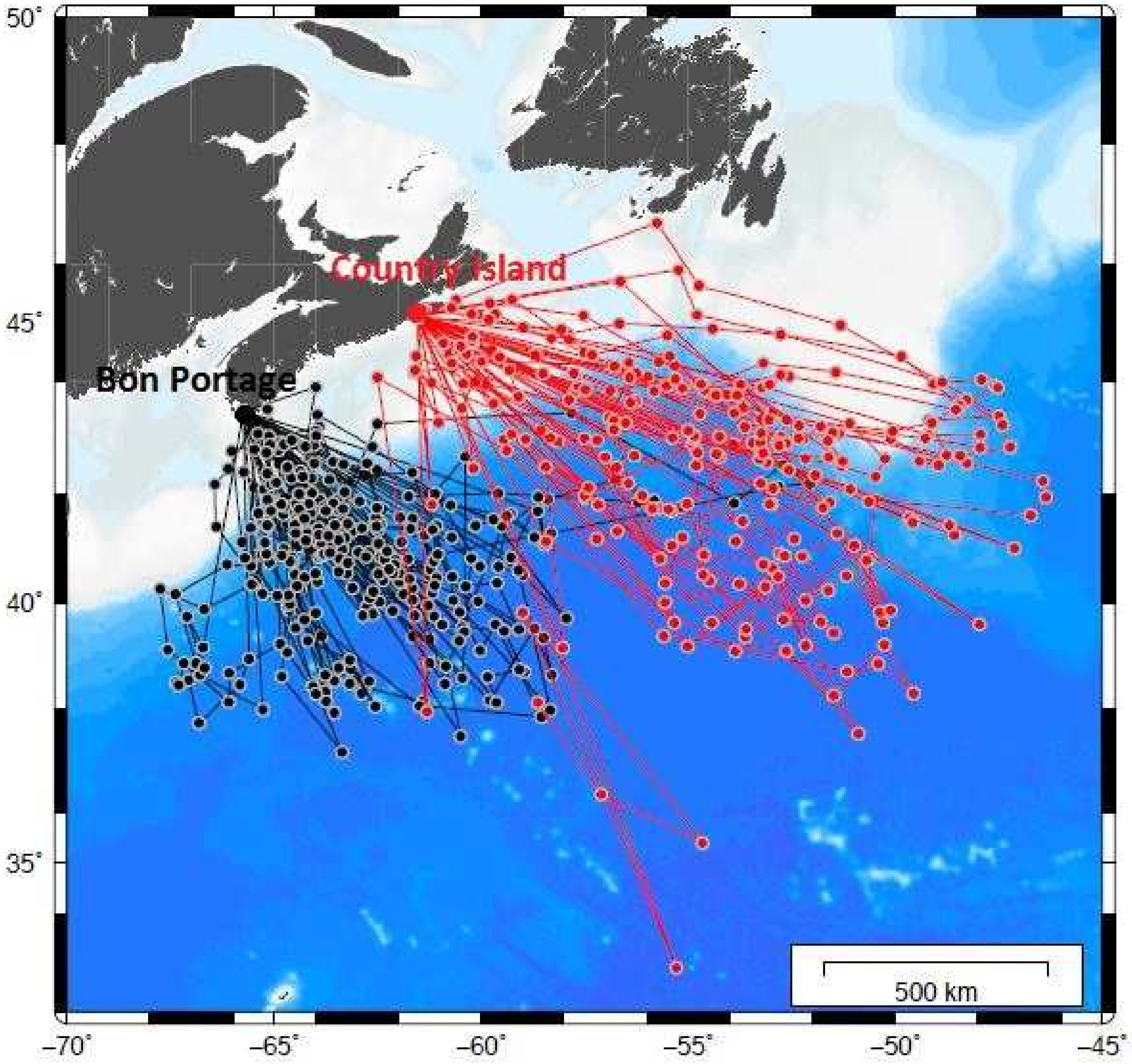

Figure 2.1 Tracks of Leach's storm-petrels with noon and midnight locations from Bon Portage (black dots) and Country Island (red dots).

2.4 Results

2.4.1 Foraging Movements During Incubation

The mean deployment duration was 17 ± 6 d and 20 ± 12 d on Country Island for 2012 and 2013, respectively, corresponding to 1.8 ± 0.4 and 1.9 ± 0.3 foraging trips per GLS, for 2012 and 2013, respectively. Foraging trips initiated on Country Island tracked south-east, on or past the continental shelf. The mean deployment duration was 9 ± 4 d and 31 ± 17 d on Bon Portage Island for 2012 and 2013, respectively, corresponding to 1.2 ± 0.4 and 2.3 ± 0.8 foraging trips per GLS, for 2012 and 2013, respectively. Foraging trips initiated on Bon Portage Island also tracked south-east, usually past the continental shelf (Figure 2.1). There was little geographical overlap in foraging range between the two colonies (Figure 2.1).

Foraging trip duration did not vary significantly with incubation stage ($\chi^2_1 = 0.7$, $p = 0.41$), so differences between islands could not be attributed to differences in timing of tag deployment between islands. Foraging trip duration varied between years, with birds making significantly shorter trips in 2013 than 2012 ($\chi^2_1 = 6.8$, $p = 0.009$, Tables 2.1 and 2.2). The mean distance from colonies to the maximum of each bird's respective kernel density surface was 699.3 km and 249.5 km for Country Island and Bon Portage Island, respectively (Figure 2.2). Maximum distance ($\chi^2_1 = 0.5$, $p = 0.48$) and cumulative distance ($\chi^2_1 = 0.8$, $p = 0.37$) did not differ significantly between the two years. Individuals on Country Island did, however, have significantly greater maximum distances ($\chi^2_1 = 26.8$, $p < 0.001$, Tables 2.1 and 2.2) and significantly greater cumulative distance ($\chi^2_1 = 15.7$, $p < 0.001$, Tables 2.1 and 2.2) than individuals from Bon Portage Island. During GLS deployment, adults from Country Island gained significantly more mass/day (+ 0.23 ± 0.18 g/day) than did individuals from Bon Portage Island (+ 0.02 ± 0.21 g/day; $F_{1,26} = 6.7$, $p = 0.02$).

Table 2.1 Summary of foraging trip characteristics of Leach's storm-petrels from Country Island (CI) and Bon Portage Island (BP) during 2012 and 2013 incubation periods.

	Year			
	2012		2013	
Metric	CI	BP	CI	BP
Foraging trip duration (d)	6.2 ± 0.5	6.3 ± 1.2	4.9 ± 0.3	4.6 ± 0.3
Maximum distance from colony (km)	1086 ± 220	684 ± 209	983 ± 249	587 ± 149
Cumulative distance (km)	2659 ± 615	1013 ± 159	2117 ± 541	1371 ± 379

Table 2.2 Fixed effects means and standard errors of linear mixed effect models, with foraging duration, maximum distance from colony, and cumulative distance, as response variables for Leach's storm-petrels from Bon Portage and Country Island. Variables with no value had no significant effect in models.

Model	Egg stage	Island	Year
Foraging distance ~egg +island + year + 1|Bird			-1.38 ± 0.53
Maximum ~ egg +island + year + 1|Bird		368.0 ± 63.5	
Cumulative ~ egg +island + year + 1|Bird		729.0 ± 174.4	

2.4.2 Impacts of Geolocators

Adult mass change did not differ significantly between control birds and those with GLS affixed with tape ($F_{1,5} = 0.4$, $p = 0.56$), or between control birds and those with sutured GLS ($F_{1,80} = 0.8$, $p = 0.36$). Fledging rate was low on Country Island for both GLS (7%) and control birds (15%), likely because of predation by meadow voles (*Microtus pennsylvanicus*), so only results from Bon Portage Island are presented here. Hatching rate did not differ significantly between control birds and those with GLS affixed with tape ($\chi^2_1 = 1.7$, $p = 0.19$), or between control birds and those with sutured GLS ($\chi^2_1 = 1.4$, $p = 0.23$). Similarly, fledging rate did not differ significantly between control birds and those with GLS affixed with tape ($\chi^2_1 = 0.1$, $p = 0.73$) or between control birds and those with sutured GLS ($\chi^2_1 = 0.6$, $p = 0.44$). Chick growth also did not differ significantly between control birds (1.67 ± 0.57 g/day) and those with GLS affixed with tape (1.30 ±

0.44 g/day, $F_{1,54} = 3.0$, $p = 0.08$); however, chick growth was significantly higher for control birds (1.57 ± 0.59 g/day) than for those with sutured GLS (1.19 ± 0.63 g/day, $F_{1,128} = 5.0$, $p = 0.03$).

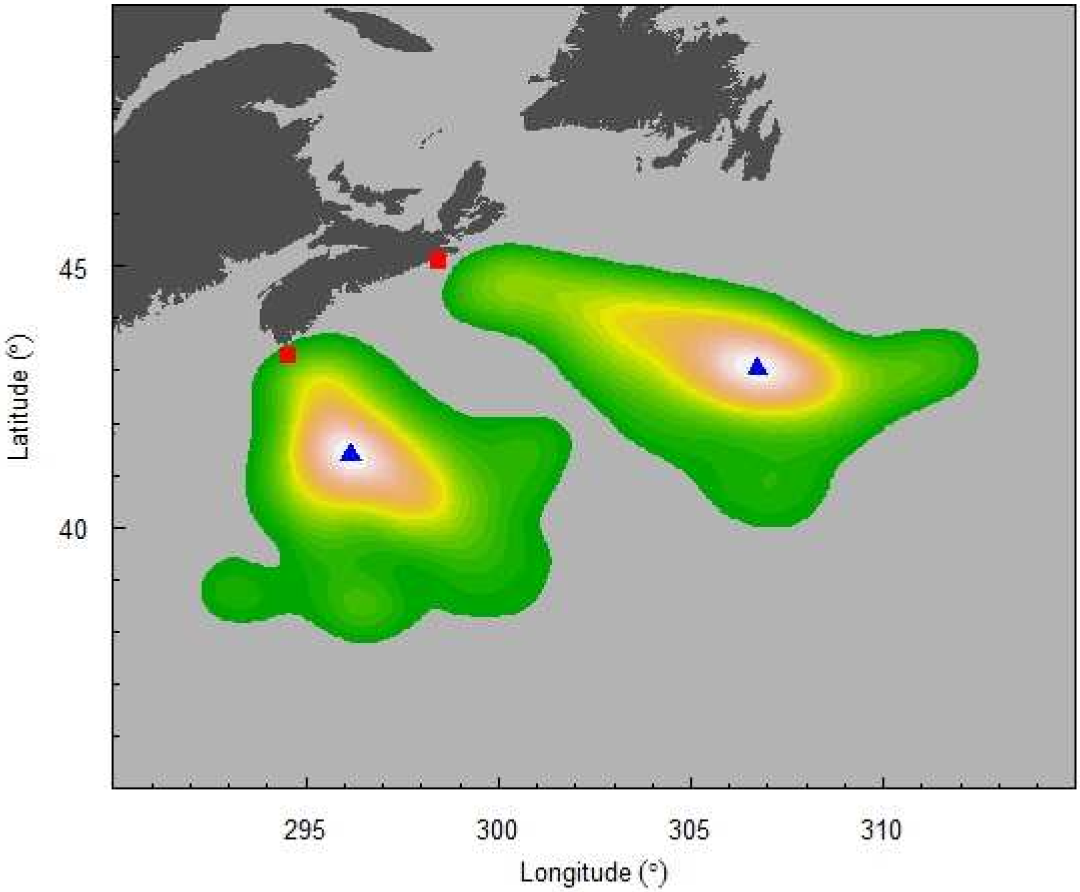

Figure 2.2 Map showing colour gradient of the upper 0.90 quantile of the kernel density surface for each island, with maximum kernel density (blue triangles) and source islands (red squares).

2.4.3 Trophic Level Inferred from Stable Isotopes

Blood samples of storm-petrels on Country Island were significantly more depleted in ^{13}C than samples from birds on Bon Portage Island (Country Island: -19.5 ± 0.2, Bon Portage Island: -19.1 ± 0.2; $F_{1,23} = 20.7$, $p < 0.001$, Figure 2.3), suggesting that birds from Country Island foraged further north, and/or in more pelagic waters than birds from Bon Portage Island, which is in line with the GLS tracking data. Blood samples of storm-petrels on Country Island were significantly more enriched in ^{15}N than samples from storm-petrels on Bon Portage Island (Country Island: 13.8 ± 0.3, Bon Portage Island: 12.6 ± 0.3; $F_{1,23} = 86.3$, $p < 0.001$, Figure 2.3), indicating that birds from Country Island fed at a higher trophic level.

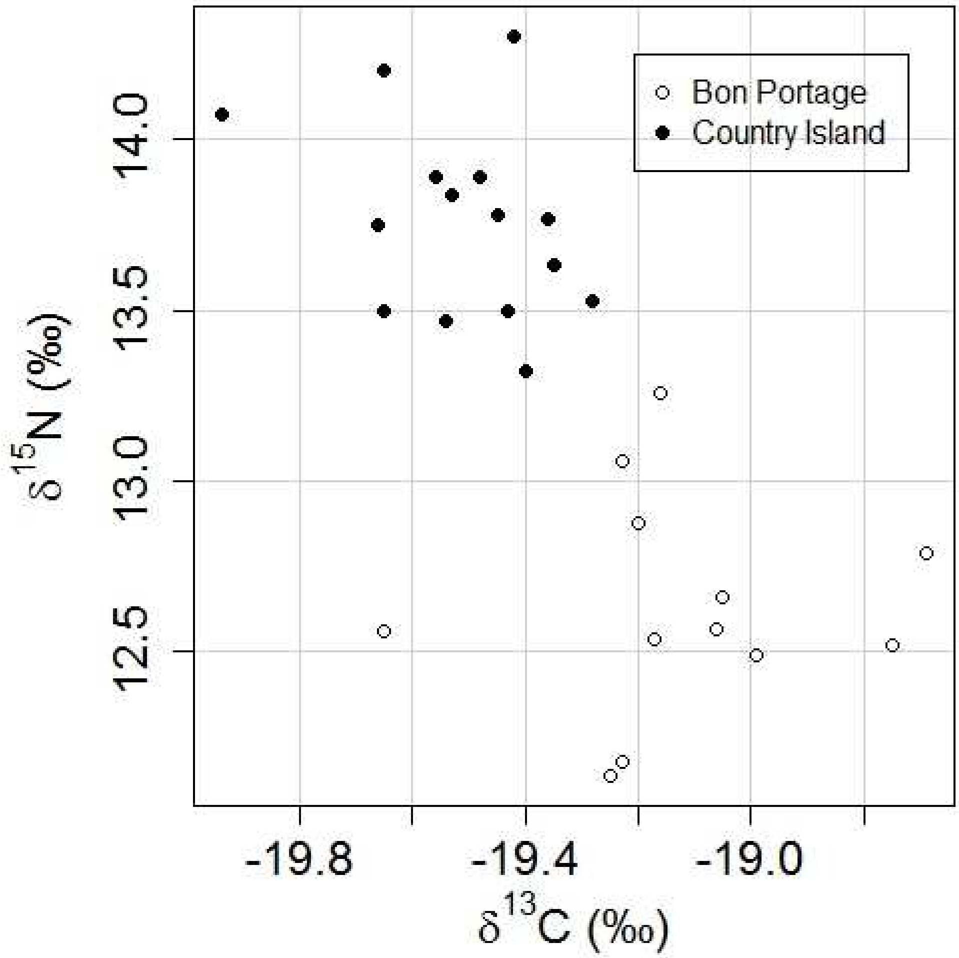

Figure 2.3 Blood $\delta^{13}C$ and $\delta^{15}N$ from Leach's storm-petrels from Bon Portage (open circles) and Country Island (solid circles).

2.5 Discussion

My data show that storm-petrels from colonies 380 km apart have distinct foraging locations. Storm-petrels from Country Island travelled ~1,000 km, with a maximum kernel density 700 km from the colony. They travelled south-east to the Laurentian fan and deep waters beyond, south of the Grand Banks of Newfoundland. From a conservation point of view, these long-distance foraging trips are of concern for the Country Island colony as the home range overlaps with gas and oil offshore platforms, which can be a threat to seabirds (Ronconi et al. 2015), including Leach's storm-petrels (Baillie et al. 2005). In contrast, storm-petrels from Bon Portage Island travelled ~500 km south-east, with a maximum kernel density 250 km from the colony. They travelled east of Georges Bank and into areas of deep water beyond the continental slope, including western portions of the New England Seamount chain. Given this range, they should not come close to existing offshore platforms.

It is not clear what drives the segregation of foraging grounds for storm-petrels at my study sites, but a recent multi-colony study, including these two islands, also suggest some at-sea segregation (Hedd et al. 2016). This work, based on 7 colonies, suggests that the average foraging range varies from 400 ± 129 km to 833 ± 163 km depending on the colony, and for 4 of those colonies, foraging ranges overlapped with offshore platforms. Colony-specific segregation of foraging areas has been observed in other seabirds with neighboring colonies, and they may be influenced by regional wind patterns and foraging site fidelity (Grémillet et al. 2004), as well as intra-specific competition among colonies (Wakefield et al. 2013, Ceia et al. 2015).

I found that some storm-petrels at my study sites travelled from 600 to over 1000 km from their breeding colonies to forage. These distances are 3 to 5 times higher than previous estimates for storm-petrels (Ricklefs and Schew 1994, Huntington et al. 1996, Thaxter et al. 2012). To compare the foraging range for these studied populations, based on the size of the birds, with other procellariiforms, I did a post-hoc test, using the ISI Web of Knowledge (© Thomson Reuters 2013). I compared foraging distance (in km per trip) to the foraging distance: mass (in g) index from procellariiform species (Table 2.3) during incubation (i.e., I excluded studies that provided results for the nestling stage). The index for other procellariiform species ranged from 0.1 for black-browed albatrosses (*Thalassarche melanophrys*) to 10.5 for Chatham petrels (*Pterodroma axillaris*); the index for storm-petrels was 24.1. Foraging range for species similar in size to storm-petrels have yet to be published and might provide similar ratios.

The long trips observed in this study may only be possible during incubation when parents do not have to make frequent trips back to the colony to feed their chick. During chick-rearing, foraging must provide both chicks' and adults' energy requirements, and adults reduce trip lengths to meet demands of rearing young (Huntington et al. 1996). Many procellariiforms accommodate this demand by alternating long foraging trips when individuals build up their own body reserves with shorter foraging trips used to provision chicks (Weimerskirch 1998). Foraging seabirds may travel for many days during incubation and some species decrease the duration of foraging trips towards the end of incubation periods (Weimerskirch et al. 1986, 1993, González-Solís 2004). This behavior ensures that chicks can be fed soon after hatching. In this study, I could not confirm this behavior, partly because tracking ended before the end of incubation for most individuals. It could also be that foraging trip durations are not variable enough in this species to detect decreases during incubation.

Despite travelling longer distances during the incubation period, individuals from Country Island gained more weight during GLS deployment than those from Bon Portage Island. Differences in geographic locations and ocean depth at their foraging areas likely have important implications for food availability. Hedd et al. (2009) estimated that storm-petrel diets in Newfoundland consisted mainly of fish with high energy content, including mature lanternfish (myctophids; *Benthosema glaciale*, *Protomyctophum arcticum*) and sand lance (genus *Ammodytes*), with hyperiid and euphausiid crustaceans, of lower energy content than fish, accounting for a smaller proportion. My data suggest that prey items of storm-petrels from Country Island are at a higher trophic level (more fish and fewer crustaceans) than they are for storm-petrels from Bon Portage Island. There is evidence that concentrations of some essential fatty acids may be positively correlated with trophic level in marine food webs (Connelly et al. 2013) so that foraging at higher trophic levels may be associated with higher quality prey, but this hypothesis requires further evaluation. This would perhaps indicate that birds from Country Island forage further to reach higher quality prey.

Despite not observing a seasonal change in foraging distance, I observed an inter-annual decrease in foraging duration between 2012 and 2013 for individuals from both islands. This difference could be the result of better foraging conditions in 2013, because seabirds can adjust characteristics of their foraging, taking shorter foraging trips to capture high trophic level prey during favorable foraging conditions (Quillfeldt et al. 2010b).

To my knowledge, this study is the first to successfully deploy GLS on a seabird as small as storm-petrels (45 g). I used three different attachment techniques. At this point, I discourage researchers from using the leg-loop harness method on storm-petrels (0% recovery rate). The tape and glue method (34% recovery rate) is quick and could be improved by inserting a layer of chiffon material between GLS and the tape (R. Mauck, pers. comm.). Sub-dermal suturing gave me the best GLS recovery rate (71%) but previous experience with suturing and very steady hands are mandatory to work on such a small bird. Neither the tape and glue method nor the suture method had an impact on hatching rate or fledging rate. However, chicks with one GLS-sutured parent had lower growth rates than chicks with neither parent tagged. The impact of GLS on chick growth has previously been observed in other seabird species, and is thought to be the result of adults adjusting chick-provisioning to maintain their own condition (Adams et al. 2009). At this point, I cannot evaluate the long-term impact of such devices and attachment methods on the physiology and survival of storm-petrels, but I recognize there may be potential consequences (Barron et al. 2010, Quillfeldt et al. 2012).

Table 2.3 Maximum distance, mass, and the ratio of foraging range to mass from published data (ISI web of Knowledge (© Thomson Reuters 2013)) for species of procellariiforms during the incubation period. Methods include geolocators (GLS), platform terminal transmitters (PTT), global positioning systems (GPS), or a combination of tracking devices (Various).

Species	Mass (g)	Range (km)	Range:Mass index	Method	Reference
Leach's storm-petrel (*Oceanodroma leucorhoa*)	45	1086	24.13	GLS	This study
Chatham petrel (*Pterodroma axillaris*)	200	2095	10.47	GLS	Rayner et al. 2012
Barau's petrel (*Pterodroma baraui*)	375	2336	6.23	GLS	Pinet et al. 2012
Thin-billed prion (*Pachyptila belcheri*)	130	670	5.15	GLS	Quillfeldt et al. 2013
Antarctic prion (*Pachyptila desolata*)	163	824	5.05	GLS	Navarro et al. 2013
Blue petrel (*Halobaena caerulea*)	187	834	4.46	GLS	Navarro et al. 2013
Short-tailed shearwater (*Puffinus tenuirostris*)	600	2877	4.80	PTT	Einoder et al. 2011
Great shearwater (*Puffinus gravis*)	850	3813	4.49	PTT	Ronconi et al. 2010
Grey-faced petrel (*Ptoma macroptera*)	572	2208	3.86	PTT	MacLeod et al. 2008

Cory’s shearwater (*Calonectris diomedea*)	535	1819	3.40	PTT	Magalhães et al. 2008
Manx shearwater (*Puffinus puffinus*)	450	1191	2.65	GPS	Dean et al. 2012
South Georgian diving petrel (*Pelecanoides georgicus*)	124	240	1.93	GLS	Navarro et al. 2013
Common diving petrel (*Pelecanoides urinatrix*)	147	261	1.77	GLS	Navarro et al. 2013
White-chinned petrel (*Procellaria aequinoctialis*)	1279	2100	1.64	GLS	Phillips et al. 2006
Streaked shearwater (*Calonectris leucomelas*)	500	645	1.29	GLS	Yamamoto et al. 2012
Laysan albatross (*Phoebastria immutabilis*)	2780	2356	0.84	PTT	Kappes et al. 2010
Westland petrel (*Procellaria westlandica*)	1200	961	0.80	GLS	Landers et al. 2011
Northern fulmar (*Fulmarus glacialis*)	600	400	0.67	Various	Thaxter et al. 2012
Black-footed albatross (*Phoebastria nigripes*)	3150	1782	0.56	PTT	Kappes et al. 2010
Black petrel (*Procellaria parkinsoni*)	700	332	0.47	GLS	Freeman et al. 2010
Grey-headed albatross (*Thalassarche chrysostoma*)	3507	1211	0.34	Various	Phalan et al. 2007
Northern giant petrel (*Macronectes halli*)	3700	1226	0.33	PTT	Gonzáles-Solís et al. 2000
Wandering albatross (*Diomedea exulans*)	7650	1483	0.19	Various	Phalan et al. 2007
Black-browed albatross (*Thalassarche melanophrys*)	3800	474	0.12	Various	Phalan et al. 2007

Chapter 3 - Breeding Success of Leach's Storm-Petrels, *Oceanodroma leucorhoa,* in Relation to Movements Around Breeding Colonies and Ocean Conditions

3.1 Abstract

Ocean conditions can be measured at global or local scales, and have immediate or delayed effects on the movements of seabirds, and ultimately on their reproductive success. In this 4-year study, I related global and local ocean conditions to the movements of Leach's storm-petrels at a breeding colony in Nova Scotia and related those movements to reproductive success. During incubation, unsuccessful adults (i.e. those whose egg did not hatch) had shorter incubation bouts and longer foraging trip durations than successful adults. During the chick-rearing period, unsuccessful adults (i.e. those whose chick did not fledge) had shorter foraging trips than successful adults. Sea-surface temperature anomalies and chlorophyll-a concentration averaged over the foraging range influenced hatching and fledgling success. There was also a negative relationship between the North Atlantic Oscillation (NAO) index, but not the Atlantic Multidecadal Oscillation (AMO) index and reproductive success. Warming of the Scotian shelf due to climate change, combined with positive NAO values, appears to correlate with movements of Leach's storm-petrel and is a concern for the reproductive success of the species in the future.

3.2 Introduction

Seabirds are ocean wanderers for most of their annual cycle, and bound to their breeding colony for the remainder of the year. Therefore, they are confronted through much of their life-cycle with ocean conditions such as ocean temperature and primary productivity that vary at different spatial scales. Ocean conditions observed at either global or local scales around a breeding colony affect the adult survival and productivity of many seabird species (Frederiksen et al. 2004, Quillfeldt and Masello 2013, Russell et al. 2015).

At a global scale, ocean conditions can be described by the Southern Oscillation Index (SOI) in the Pacific Ocean and the North Atlantic Oscillation index (NAO) in the Atlantic Ocean. The SOI measures the seesaw variation in surface pressure anomalies between the Indian Ocean - Australian region and the southeastern tropical Pacific Ocean, usually Darwin, Australia, and Tahiti, French Polynesia (Nicholls 2008). The NAO refers to similar seesaw variation in the surface pressure anomalies between Stykkisholmur, Iceland and Lisbon, Portugal (Hurrell 1995). These indices are strongly associated with sea surface temperatures (SST) and precipitation patterns (Forchhammer et al. 2002, Frederiksen et al. 2004), which in turn affect each level of the ocean food web starting with plankton. In the Northwest Atlantic Ocean, positive NAO values are associated with more storms, wetter conditions and warmer SST than during phases of negative NAO (Greene and Pershing 2000). In the North Atlantic basin, SST anomalies (SST-a, the difference between the SST at a given time and the normal SST for that time of the year) tend to follow a 60-80 year cycle defined as the Atlantic Multi-decadal Oscillation (AMO, Sutton and Hodson 2005).

The effects associated with these indices affect the marine environment at different levels. For example, the timing, location, and quantity of zooplankton and fish, the major prey items of seabirds, are associated with both SOI and NAO (Planque and Taylor 1998, Pennington and Chavez 2000). As such, these global weather patterns can influence the timing of migration, onset of reproduction, body condition upon arrival at a breeding colony, productivity, and survival of many seabird species (Thompson and Ollason 2001, Sandvik et al. 2005, Ancona et al. 2011). The relationship between ocean conditions measured by the NAO and seabird productivity can be lagged by one or more years, if the NAO is associated with availability of prey at hatching, and if prey is mainly composed of 1 or 2-year-old fish (Ottersen et al. 2001, Gaston et al. 2009). As for the AMO's effects on the marine environment, they are noticeable at the plankton level, with cascading effects on the fish community, and potentially the seabirds (Edwards et al. 2013).

At a local scale, ocean conditions are described in terms of SST, SST-a, and chlorophyll-a concentration (Chl-a). Higher SST and SST-a are associated with poorer body condition and lower reproductive success in many seabirds (Ainley et al. 1995, Veit et al. 1997, Guinet et al. 1998), or with even total breeding failure (Sydeman et al. 2006). Higher Chl-a concentrations are often linked with greater reproductive success (Monticelli et al. 2007, Devney et al. 2009). However, this trend is not true for all seabirds. In some cases, this difference in response to SSTs can be attributed to diet (e.g. planktivorous versus piscivorous) of different species (Kitaysky and Goluba 2000).

Ocean conditions prior to or during the breeding season affect the quality and quantity of prey available, and in turn affect foraging trip characteristics such as distance travelled from a colony or trip duration (Durant et al. 2006, McLeay et al. 2010). For example, in Europeans colonies, the timing and location of the spring phytoplankton bloom may dictate the growth of sandeels (*Ammodytes marinus*), which are critical prey for common murres (*Uria aalge*), and black-legged kittiwakes (*Rissa tridactyla*) during chick-rearing (Harris and Wanless 1985, Lewis et al. 2001). The location of their main prey may affect the foraging distance of these birds from their colonies. Foraging distance is often positively related to foraging duration (Boersma and Rebstock 2009), and both foraging distance and foraging duration can be negatively related to reproductive success (Suryan et al. 2000, Boersma and Rebstock 2009). As such, ocean conditions, by affecting the timing of phytoplankton blooms and ocean temperatures, can affect reproductive success of seabirds. Information on how ocean conditions relate to foraging trip characteristics, incubation routine, and reproductive success can be used to model population dynamics and better predict seabird population trends (Wolf et al. 2010, Sandvik et al. 2012), which can be challenging to measure, especially for burrow-nesting species that are difficult to survey (Oppel et al. 2014, Rexer-Hubert et al. 2014).

Leach's storm-petrels (*Oceanodroma leucorhoa*, hereafter storm-petrels) are small burrow-nesting seabirds that breed in the northern hemisphere, with highly variable reproductive success from year to year (Huntington et al. 1996). The causes of this variation in reproductive success are probably complex and the result of associations among multiple factors, of which ocean conditions probably plays a role. For example, in the California Current System, storm-petrels tend to be in warmer, less saline waters than most seabirds and in waters with lower chlorophyll content (Ainley et al. 2005). However, we do not know the foraging preferences of storm-petrels in the Northwest Atlantic, where they are an important species of the seabird community, representing up to 80% by number and 20% by biomass in the Newfoundland and Labrador region (Barrett et al. 2006).

The overarching goal of this chapter was to determine how ocean conditions in the Northwest Atlantic influenced storm-petrel foraging during both incubation and chick-rearing, and reproductive success over a four-year period. To determine how ocean conditions influenced reproductive success, I compared incubation routines (which includes the duration of incubation bouts, and duration of foraging trips during incubation (Table 3.1)), and the duration of foraging trips during chick-provisioning, between successful and unsuccessful breeders. To determine the influence of local ocean conditions on incubation routines and chick-provisioning movements, I then tested for associations between local ocean conditions (SST, SST-a, and chl-a) and foraging trips during both incubation and chick-rearing. Finally, I established how the conditions related to the NAO and the AMO indices affected the annual productivity of storm-petrels.

Table 3.1 Definition of the variables, estimated through telemetry, that define incubation routine.

Name of variable	Definition
Incubation bout	Continuous time spent on a nest by an adult during incubation, begins when an adult enters the nest burrow and ends when they leave
Recess	Time spent off a nest by an adult. I divided recess bouts during the incubation into two categories: short recesses < 36 h, where a bird left the island but was not replaced by its partner, and long recesses > 36 h (i.e. foraging trip) that corresponded to a foraging trip, when the other adult was assumed to be incubating.
Incubation shift	Total time between when an adult arrived to relieve its partner to the time it was relieved. It includes incubation bouts and short recesses during that time.

3.3 Methods

3.3.1 Study Site

This study was conducted during summers of 2010 through 2013 on Bon Portage Island, Nova Scotia, Canada. I monitored ~300 burrows, distributed among twelve, 12 x 12 m plots (see Chapter 1). Occupied burrows were labeled with uniquely numbered metal tags. A random subset of these burrows was used for VHF tag deployment, and the remaining occupied burrows were used as controls to investigate potential effects of these tags.

Adult storm-petrels were caught either during incubation or during chick-provisioning using one way traps (Mauck and Grubb 1995). The traps were 10 cm long wire cylinders with a thin metal flap, that allow adults to enter their burrow, but prevented them from leaving. When first handled, adults were fitted with a uniquely numbered Canadian Wildlife Service metal band. Burrows were visited no more than twice during incubation to reduce desertion (Blackmer et al. 2003) and eggs were examined for embryonic development by placing them at the end of a tube facing the sun (i.e. candling) to estimate the stage of development using Weller (1956) criteria. Two visits were occasionally not enough to catch both adults. Hatching success was defined as the percent of eggs laid that produced a chick. Chicks were weighed on a weekly basis to monitor growth. Reproductive success was defined for each nest as the successful fledgling of a chick, and was determined for the tagged birds and a set of control birds. I considered fledging to have occurred if at 60 days post-hatch a burrow was empty and during the previous visit the nestling had reached its asymptotic mass and weighed $\leq$ 60 g and had a wing chord $\geq$ 120 mm. Annual productivity was defined as the percent of eggs laid that produced a fledgling in the study area. To determine if tags affected adult return rates, control and tagged burrows, as well as adjacent burrows, were visited the following year, because storm-petrels have high burrow fidelity (Morse and Kress 1984), and if they switch burrows, it is usually within half a meter of their previous burrow.

3.3.2 VHF Transmitters

Transmitters weighed 0.29 g and measured 10 x 4 x 2 mm with an external aerial measuring 180 x 0.2 mm. To mount transmitters, I used a combination of tape and glue (methods described in Chapter 1). Storm-petrels were returned to their burrows immediately after transmitters were affixed. The entire procedure took less than 4 min. Once activated, transmitters had a life expectancy of about 3 weeks and pulsed every 5 sec with a unique ID associated with a specific frequency.

A total of 107 transmitters (Lotek Wireless, Newmarket, Ontario, Canada) was deployed over the 4 years. In 2010, 32 transmitters were deployed on a random subset of active breeders during incubation, with one adult tagged per burrow. The return rate after that first year was not significantly different between tagged (n = 32) and untagged birds (n = 273; $\chi^2_1 \leq 01$, $P = 0.99$), so for the following years, whenever possible, I deployed tags on both adults from the same burrow, taking care not to use the same burrows (or adults) in multiple years. As such, in 2011, 30 transmitters were deployed (12 pairs and 6 individuals). In 2012, 20 transmitters were deployed (9 pairs and 2 individuals). Finally, in 2013, 25 transmitters were deployed (3 pairs and 19 individuals).

3.3.3 Telemetry Data

A tower supporting four 9-element Yagi antennae was erected on the balcony of the lighthouse, the highest structure on the island, 700 m from the colony. Another tower supporting four 9-element Yagi antennae in 2010 and 2011 and an omnidirectional antenna in 2012 and 2013 were erected on top of a small building, 200 m from the area of the colony in which I worked. Each tower was linked to a scanning receiver (SRX600, Lotek wireless) programmed to obtain information from one antenna at a time, switching antenna every 7 sec.

Data recorded for each detection included the unique transmitter number, date, time, antenna, and signal strength (an indication of how close the bird was to a receiver). Receivers were synchronized for time using the built-in GPS system. Transmitters pulsed a signal every 5 sec. so consecutive detections of one transmitter by the same antenna could indicate the direction of the tagged bird if the new signal strength was stronger or weaker than the previous one. Detection of transmitters could be achieved for more than several kilometers over water. Data from receivers were converted into text files and analyzed in R version 3.0.2 (R Development Core Team 2013). In addition to the automated telemetry array, I also used a handheld receiver with a five-element Yagi antenna. This allowed me to confirm presence or absence of the birds in their burrow during the day. Plots of signal strength detection of all antennae against time were generated for each tagged individual for each week, by zooming in on the time of detection, I could assign times of departures from or arrivals at the colony (Figure 3.1).

The duration of an incubation bout was determined by subtracting departure times from arrival times. I considered absences from the nests of < 36 h to be short recesses, when the focal bird left the nest, but their partner was not incubating. I assumed birds were not foraging in their usual foraging areas during this time because they would not have time to reach regular foraging areas and return in < 36 h (Chapter 2). Short recesses were thus included as part of the incubation shift. Absences longer than 36 h were considered to be foraging trips. Some seabirds desert their nests when their body mass drops below a threshold (Ancel et al. 1988, Chaurand and Weimerskirch 1994a, Ronconi and Hipfner 2009), so incubation bout and foraging trip duration may not be correlated. I determined foraging trip duration during the chick-rearing-stage, by subtracting arrival time at the nest from the last recorded departure time.

3.3.4 Environmental Data

Local ocean conditions, SST (°C), SST-a (°C), and Chl-a (mg/m^3), were obtained from the National Oceanic and Atmospheric Administration Coast Watch website (http://coastwatch.pfeg.noaa.gov/erddap/index.html) in raster format for each year and each week that birds were foraging from the National Oceanic and Atmospheric Administration Coast Watch website. In ArcMap 10.1 (ESRI 2012), raster data were averaged over 1) the area covered by foraging storm-petrels from Bon Portage during incubation, defined by GLS tracking (see Pollet et al. 2014a, and Chapter 2), and 2) the area covered by foraging storm-petrels from Bon Portage during chick-rearing, defined by GLS tracking (unpublished data). There was a strong collinearity between SST and SSTa therefore SST was removed from the models.

Global environmental data were collected from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based (accessed 13 September 2014) for the yearly and winter (December through March) NAO index values, and from https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/AMO (accessed 08 February 2017) for the AMO values. In some cases, winter NAO is known to be a better predictor than annual NAO for the timing of breeding, such as in common murre and Atlantic puffin (*Fratercula arctica*, Durant et al. 2004, Votier et al. 2009), so I have included both in my study.

3.3.5 Statistical Analyses

To check for independence of variables, I first evaluated the correlation between incubation shift duration and subsequent foraging trip duration for each bird, and also the correlation between incubation shift duration of one bird and foraging trip duration of its partner during that time, if both individuals were tagged.

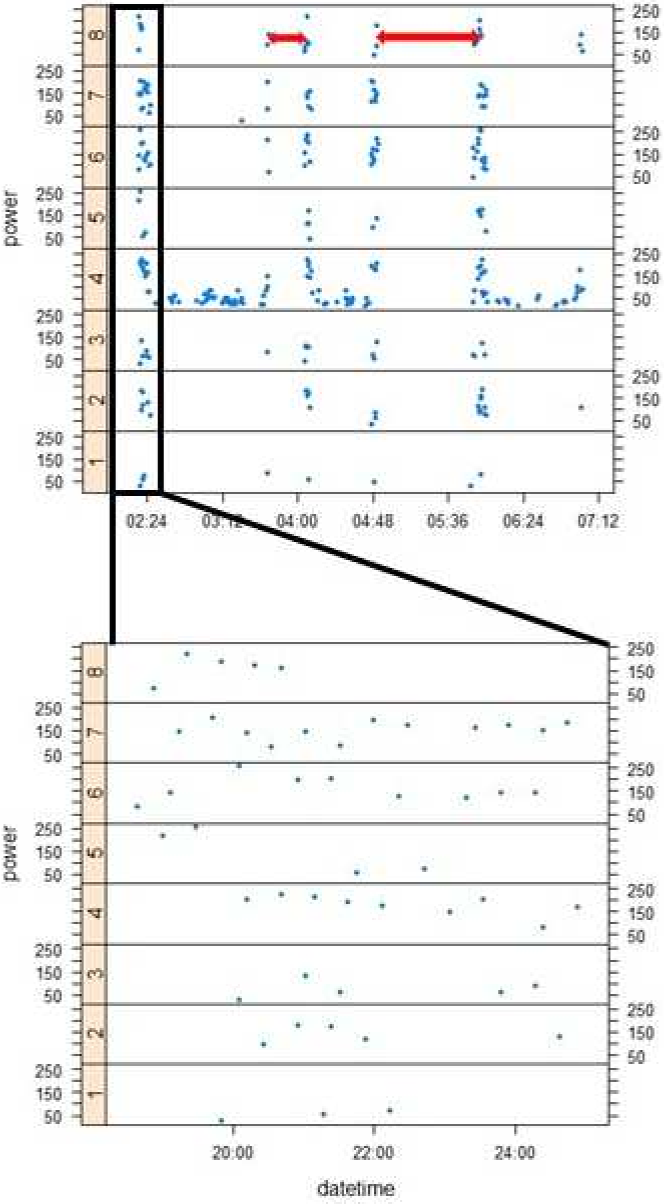

Figure 3.1 Example of data obtained from a single representative transmitter for 8 August 2010, from 0210 until 0720 GMT (= AST +3h). Y axis shows separate signal intensities for 8 antennae (Channels 1 through 4: antennae close to the colony, channels 5 through 8: antennae by the light house). Top panel: red arrows indicate incubation recesses. Bottom panel: zoom in on arrival data to determine time of arrival (2:19 am).

To assess how incubation routine and local ocean conditions during the incubation period affect hatching success, I used mixed effects logistic regression models to determine the effect of incubation duration, foraging trip duration, SST-a, and Chl-a during each foraging trip, year, and all possible interactions on hatching success (0 = unsuccessful, 1 = successful individuals). Individuals,and burrows (to take into account when both adults were tagged) were treated as random effects. Similarly, to assess how foraging trip duration and local ocean conditions during the chick-rearing stage affect fledgling success, I used mixed effects logistic regression models in relation to foraging trip duration, SST-a, and Chl-a during each foraging trip during chick-rearing, year, and all possible interactions on fledgling success (0 = unsuccessful, 1 = successful individuals). Individuals, and burrows were treated as random effects. Models were then compared using Akaike's Information Criterion for small numbers (AICc). As a rule of thumb, a difference in AICc values < 2 between the top performing model and another model suggests that both models a have substantial level of empirical support (Burnham and Anderson 2002).

NAO and AMO indices are related to the ocean conditions at a global level, and it is not possible to relate individual foraging movements or individual reproductive success to NAO and AMO. Therefore, I determined the correlation of NAO and AMO on overall annual productivity on Bon Portage Island, using a generalized linear model with either the annual NAO index, the winter NAO index, or the AMO index with time lags from 0 to 3 years, to account for potential time-lag effects. For this series of tests, I did not require information collected via telemetry, so in addition to the annual productivity data of the four years of this study, I also included productivity data available for other years (namely 2014 and 2015).

To determine transmitter effects, I used Fisher's exact test to compare hatching success (the percentage of eggs hatched), and fledging success (the percentage of chicks fledged) of tagged to untagged birds. I also compared the return rate of tagged and untagged birds between seasons.

3.4 Results

3.4.1 Factors Influencing Hatching Success

Incubation bouts varied in length between 3 min and 6.2 days, as some storm-petrels had short recesses during their incubation shift (Figure 3.1). The average duration of short recesses was 13.9 ± 9.6 h (range: 8 min to 29 h). Foraging trip duration during incubation varied between 41.7 and 239.4 h, with an average of 111.1 ± 49.0 h/trip.

Incubation bout, and foraging trip durations, SST-a, Chl-a, were significant predictors of hatching success (Table 3.2), with year always present in the models. The probability of hatching increased with higher incubation bout duration and shorter foraging trip duration, lower SST-a, higher Chl-a. However, it should be noted that none of the models had very strong support (Table 3.2).

Table 3.2. Summary of the best AICc models (ΔAICc: difference in AICc values with the best performing model, ω_i: weight of the model) for the logistic regression of hatching success. In all models, transmitters and burrows were treated as random effects. Incubation: incubation bout duration. Foraging: Foraging trip duration. None of the interaction terms made it to the top models.

Statistical model	AICc	ΔAICc	ω_i
SST-a + Year	53.35	0.00	0.19
Chl-a + Year	53.43	0.08	0.18
Incubation + Year	53.45	0.10	0.18
Foraging + Year	53.45	0.10	0.17
SST-a + Foraging + Year	55.77	2.42	0.06
SST-a + Chl-a + Year	55.77	2.42	0.06
SST-a + Incubation + Year	55.77	2.42	0.05
Chl-a + Foraging + Year	55.86	2.51	0.05
Incubation + Foraging + Year	55.88	2.53	0.05
SSTa- + Chl-a + Foraging + Year	58.27	4.92	0.01

3.4.2 Factors Influencing Fledgling Success

During chick-rearing, adults returned to their nests only at night to provision chicks, and time spent at the nest lasted between 3 min and 29.1 h (average: 4.0 ± 4.6 h per visit).

Foraging trip duration, SST-a, and Chl-a were significant predictors of fledgling success (Table 3.3), with the probability of fledging increasing with shorter foraging trip durations, lower SST-a, and higher Chl-a. The variable year is not present in the best performing models. It should be noted that the top three models have very similar support (Table 3.3).

3.4.3 Global Climate Indices and Reproductive Success

At the global scale, there was a negative correlation between the annual NAO index and average annual productivity with no lag effect (Figure 3.2). All other combinations (annual NAO or winter NAO, with or without lag) showed no significant correlation with reproductive success (all *Ps* > 0.51). There was no correlation between the annual AMO index and average annual productivity, with or without a lag effect. All combinations showed no significant correlation with reproductive success (all *Ps* > 0.51).

3.4.4 Transmitter Effect

Hatching success was significantly higher in burrows with single tagged birds (68.7%) or both tagged birds (74.5%) versus control burrows (58.9% Fisher's exact $P = 0.05$, and $P = 0.03$, respectively), but there was no significant difference in fledging success between single tagged birds (54.7%), both tagged birds (66.7%) and control birds (53.6%, Fisher's exact $P = 0.88$, and $P = 0.21$, respectively). Furthermore, tagged storm-petrels and control birds did not have significantly different return rates (Fisher's exact $P = 0.49$).

Table 3.3. Summary of the best AICc models (ΔAICc : difference in AICc values with the best performing model, ω_i: weight of the model) for the logistic regression of fledgling success. In all models, transmitters and burrows were treated as random effects. Foraging: Foraging trip duration.

Statistical model	AICc	ΔAICc	ω_i
Foraging	22.30	0.00	0.28
Chl-a	22.42	0.12	0.21
SST-a	22.43	0.13	0.20
Foraging + Chl-a	24.36	2.03	0.08
Chl-a + SST-a	24.49	2.19	0.07
Foraging + SST-a	24.58	2.28	0.06
Foraging + Chl-a +Foraging * Chl-a	26.36	4.05	0.03
Foraging + SST-a +Foraging * SST-a	26.40	4.10	0.03
Foraging + Chl-a + SST-a	26.49	4.18	0.02
Chl-a + SST-a + Chl-a* SST-a	26.52	4.22	0.02

3.5 Discussion

The overarching goal of this chapter was to determine how movements of storm-petrels during incubation and chick-rearing, as well as ocean conditions are influencing the reproductive success of storm-petrels. The results show that in general, greater SST-a, lower Chl-a, and longer foraging trips were related to both lower hatching and lower fledgling success. In addition, a higher NAO index, but not AMO index was correlated to lower reproductive success. These results suggest that warmer ocean conditions during the breeding season could have a negative impact on the reproductive success of storm-petrels on Bon Portage.

My results revealed considerable individual variability in incubation routine and foraging patterns during chick-rearing of storm-petrels around the colony, but also variability among years. Variation in reproductive success may reflect differences in individual quality. That is, successful birds had longer incubation bouts and shorter foraging trips than unsuccessful birds. Some of the individual variation could also be explained by adult experience or body condition (Weimerskirch et al. 1995, Welcker et al. 2009), but neither of those factors were included in this study. Variability among years could be in response to ocean conditions in the foraging areas, especially SST and SSTa.

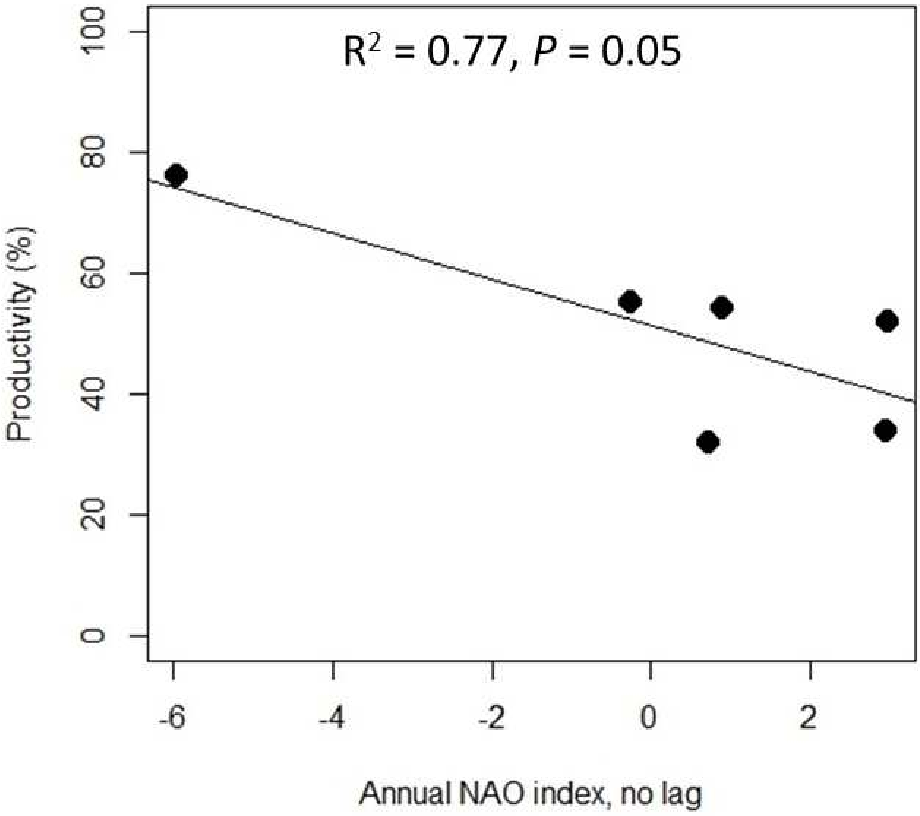

Figure 3.2 Relationship between annual productivity of Leach's storm-petrels on Bon Portage Island and annual NAO index.

3.5.1 Incubation Routine, Foraging Movements During Chick Rearing, and Reproductive Success

To my knowledge, this is the first record of Leach's storm-petrels performing a recess during incubation (i.e. leaving and returning to the burrow before their mate returns), rather than egg neglect (i.e. leaving the burrow before their mate took over incubation duties). A similar phenomenon, where eggs were left unattended for at least one day, was reported for Leach's storm-petrels in a previous study (Zangmeister et al. 2009).

However, it was not clear if the next adult that returned to the nest was the same individual or its partner. These short recesses were probably not long enough for storm-petrels at my study site to reach their usual feeding areas off the continental shelf (Wilbur 1969, Steele and Montevecchi 1994, Pollet et al. 2014a, Chapter 2). This suggests that the decision to leave the nest is probably the consequence of the incubating adult reaching a threshold body mass where it needs to forage to survive (Chaurand and Weimerskirch 1994a, Gaston and Hipfner 2006); although my results suggest that this foraging stint does not happen in their regular foraging grounds. Presumably, the benefits associated with short recesses (foraging) outweigh costs (energy flying to and from foraging areas, risk of predation departing from and returning to the colony, and leaving the egg unattended). Although eggs of procellariiforms nesting inside burrows are resilient to cold, and continue development when unattended (Boersma and Wheelwright. 1979) prolonged or frequent egg neglect could ultimately result in reduced reproductive success.

The inter-annual differences in the duration of incubation bouts that I observed in this study could reflect differences in food availability across years. In years of reduced food availability, adults may need to forage further from the colony and or for longer periods, resulting in shorter incubation bouts. This pattern has been observed in other seabirds, such as common murres (Monaghan et al. 1994), or northern gannets (*Morus bassanus*, Warwick-Evans et al. 2016). In my study, shorter incubation bouts were related to lower reproductive success.

During the chick-rearing period, frequent provisioning to the chick will increase the chance of the survival of the chick and reproductive success. Reproductive success can also be related to factors beyond the scope of this study, such as age, and therefore experience, and duration of pair-bond (Bradley et al. 1995, Nisbet and Dann 2009).

Foraging trip duration is usually related to distance travelled, and chick feeding frequency is reduced when foraging trip duration increases (Shaffer et al. 2003, Boersma et al. 2007). Therefore, it comes as no surprise that unsuccessful breeders had longer foraging trips, while still caring for a chick. Similar associations of longer foraging trips leading to slower chick growth, lower fledgling weight, or chick starvation has been observed in other seabird species, such as common murre (Davoren and Montevecchi 2003), Magellanic penguins (*Spheniscus magellanicus*, Boersma and Rebstock 2009), and black-legged kittiwake (*Rissa tridactyla*, Chiver et al. 2012). Foraging trips of greater duration, most often associated with greater distance from the colony, is a common behavior for some seabirds during years of lower food availability than average (Burger and Piatt1990, Monaghan et al. 1994).

3.5.2 Ocean Conditions and Foraging Movements

Both local and global ocean conditions had an effect on storm-petrel reproductive success. At a local scale, SST-a varied across years, and I detected an increase in foraging trip duration during both incubation and chick-rearing, and lower reproductive success in years with higher SST-a. However, these results have to be carefully considered, as no model stood out strongly from the other ones.

Ocean conditions during the breeding season affect reproductive success of marine central place foragers, such as seabirds and pinnipeds, by affecting the location and density of prey (Simmonds and Isaac 2007, Grémillet and Boulinier 2009, Stenson et al. 2016). Different species will adapt their resource allocation differently when faced with a change in food abundance. For example, during a year of food shortage, some species (e.g. black-legged kittiwake, common murre) will increase their energy expenditure to provision their chick by foraging further from the colony (Burger and Piatt 1990, Kitaysky et al. 2000), while other species (e.g. thick-billed murre, *Uria lomvia*, wedge-tailed shearwater, *Puffinus pacificus*) will not change their energy expenditure at the expense of chick growth (Monaghan et al. 1994, Smithers et al. 2003). Results of my study suggests that storm-petrels increase their foraging trips when food abundance is likely to be low, but this increase is not always enough to successfully raise a chick.

However, effects of higher SST levels are not consistent across species. For example, tufted puffins (*Fratercula cirrhata*), and horned puffins (*F. corniculata*) showed an increase in reproductive success with increasing SST (Kitaysky and Golubova 2000), while at the same time crested auklets (*Aethia cristatella*) and parakeet auklets (*A. psittacula*) showed a decrease (Kitaysky and Golubova 2000). This difference in response to ocean conditions may be attributed to their different diet characteristics. The puffins are piscivorous and their prey eat mesoplankton that thrive during warm periods. In contrast, auklets, like storm-petrels, are planktivorous and their prey do better during cold periods, resulting in a decrease in reproductive success, due in part to a shortage in food availability during warmer periods (Kitaysky and Golubova 2000).

Global climate indices, such as NAO or SOI can be predictors of reproductive success for some seabird species around the globe (Ancona et al. 2011, Catry et al. 2013). Variation in the NAO index has cascading effects, first on SST, SSTa, Chl-a, then on zooplankton and fish abundance, and ultimately on seabird population dynamics (Thompson and Ollason 2001, Descamps et al. 2010). As such, reproductive success of top predators is affected indirectly by the NAO index via prey availability (Thompson and Ollason 2001, Smith and Gaston 2012). I observed a negative relationship between the NAO index and annual productivity. During the year of the highest NAO index (2012), productivity was 34%, and during the year of the lowest NAO index (2011), productivity was 76%. The NAO index has been mostly positive in the last 40 years, with a potential for cumulative years of low reproductive success. This could have a negative impact on recruitment to populations of Leach's storm-petrels, and some colonies are already showing a decline in the North Atlantic (Robertson et al. 2006, Newson et al. 2008, Wilhelm et al. 2016). With the recent listing of Leach’s storm-petrel as vulnerable by the International Union for the Conservation of Nature, long-term monitoring of adult survival and reproductive success, and up to date colony censuses will be put in place in all major breeding colonies. The NAO index is expected to stay mostly positive in the future, whereas the AMO is expected to enter a cooling phase (Chylek et al. 2014). In any case, predictions suggest that the SST of the Scotian shelf, where these birds forage, will keep increasing (Khan et al. 2013).

3.5.4 Transmitter Effect

In general, radio-tag deployment or the attachment of any type of tag on birds may impact their behavior, physiology, or survival (reviewed by Calvo and Furness 1992, Barron et al. 2010). In seabirds, tag deployment has resulted in various effects on seabirds. These effects can be behavioral, with tagged birds having longer foraging trips and less chick-provisioning effort (Hamel et al. 2004, Heggøy et al. 2015). Effects can also be physiological, with an increase in the avian stress hormone corticosterone (CORT) in tagged birds (Quillfeldt et al. 2012, Heggøy et al. 2015). Potential reasons for these effects are the extra weight of external devices may increase the cost of flight and reduce foraging efficiency, especially on small species (Passos et al. 2010, Vandenabeele et al. 2011, 2012). The different effects are probably the result of several factors: differences in the weight of the device compared to the body mass of the bird (Phillips et al. 2003, Vandenabeele et al. 2012), the invasiveness of attachment method and the position of the device on the bird's body (Wanless et al. 1998, Vandenabeele et al. 2014), the duration of the attachment, and the factors used to determine a potential impact (Wanless et al. 1998, Söhle et al. 2000). As such, the weight, position on the body, and duration of the study should all be carefully considered prior to the deployment of any devices.

In my study, I found that hatching success was greater in tagged birds (probably an artifact due to the timing of tagging), but overall reproductive success did not differ between tagged and untagged birds and, the return rate of the tagged birds was not significantly different than the control birds, despite similar search effort. Although my results suggest that the tags had no effect on the measured variables, I did not examine the long term effect of tags on reproductive success, nor did I determine if there were differences in CORT levels between tagged and untagged birds. Researchers should continue to monitor potential effects, and keep in mind that tags may have behavioral and physiological consequences, both on the short-term and long-term. As the tags get smaller, they will represent a smaller percent of the bird’s body weight, but will also be used more often in the future to determine movement ecology for small seabirds, or any other bird species for which we have so far limited information.

Chapter 4 - Migration Routes and Stop-Over Sites of Leach's Storm-Petrels

4.1 Abstract

Movements of small seabirds during migration are poorly known. Such information is important for conservation, especially for species in decline. Leach's storm-petrels, *Oceanodroma leucorhoa*, are the most abundant seabird in Atlantic Canada but have been in decline in recent years, so determining movements to identify important habitat is key to their conservation. Here, I describe migration movements of this species tracked with geolocators from two colonies: Bon Portage and Country Island, in Nova Scotia, Canada. In addition to the tracking data, I carried out species distribution modeling using remotely-sensing oceanographic data to quantify habitat use and identify regions important for this species. My results indicate that Leach's storm-petrels used multiple stop-over sites and over-winter destinations. Birds from both colonies used one of two main stop-over sites during fall migration: an area centered around 40° latitude, and an equatorial area. The birds used three main over-wintering sites: birds with stop-over sites at higher latitudes over-wintered either in a North Atlantic Ocean area associated with the North Equatorial Current or in waters off Newfoundland, whereas birds with lower latitude stop-over sites over-wintered in a South Atlantic Ocean area associated with the Benguela Current. All over-wintering sites were in areas used by other seabird species. The distribution model over- or under-estimated some regions, probably due to the low sample size available.

4.2 Introduction

Declines in seabird populations can be caused by a variety of threats that occur in both their terrestrial and marine environments (Croxall et al. 2012). Terrestrial threats, which include introduction of mammalian predators to remote breeding islands and habitat loss (Regehr et al. 2007, Ratcliffe et al. 2009, Cadiou et al. 2010), are relatively easy to identify and monitor. At-sea threats can, however, be challenging to monitor. These threats include changes in ocean conditions due to climate change (Jenouvrier et al. 2008, Grémillet and Boulinier 2009, Borstad et al. 2011), bycatch from and competition with fisheries (Tasker et al. 2000, Tuck et al. 2011), pollution (Provencher et al. 2014), and off-shore development (Ronconi et al. 2015). Knowledge of how seabirds use their marine environment is vital for identifying important at-sea habitats and for understanding threats influencing population dynamics. The environments seabirds use vary through their life-cycle, from their foraging grounds during the breeding season, to stop-over sites during migration, to over-wintering grounds during the non-breeding season. For example, stop-over sites are important, because birds presumably refuel after energetically demanding breeding seasons or wait for favorable weather conditions to move to other locations (Murray et al. 2003, Guilford et al. 2009, Egevang et al. 2010, Jessop et al. 2013). Therefore, it is essential to know the locations of those key marine regions, for effective management of declining species.

Until recently, little was known about the habitat requirements of small (< 100-g) seabird species outside of the breeding season because of technological limitations on the size of tracking devices. However, due to recent miniaturisation of loggers, it is now possible to track smaller species (van der Winden et al. 2014).

Leach's storm-petrels (*Oceanodroma leucorhoa*), hereafter storm-petrels, are small seabirds that breed throughout temperate zones in the northern hemisphere. Populations at many colonies in the western North Atlantic have declined in the past 50 years, and some colonies have been abandoned (Robertson et al. 2006, Fife et al. 2015, Wilhelm et al. 2015). Much is known about the breeding biology and dietary requirements of storm-petrels (Ricklefs et al. 1987, Stenhouse and Montevecchi, 2000, Hedd et al. 2009), but relatively little is known about their at-sea movements either during the breeding season or during migration to and from wintering sites (Gaston et al. 2008, Bicknell et al. 2014, Pollet et al. 2014a, b). This information is crucial for understanding year-round environmental conditions that may influence the population dynamics of this species.

Band recoveries of storm-petrels from the Canadian Atlantic have indicated they spend time in the North Atlantic Ocean during the non-breeding season (Gaston et al. 2008, Pollet et al. 2014c). These findings complemented at-sea surveys off Senegal indicating the presence of storm-petrels in the winter (Brown 1979). These observations do not, however, provide information on stop-over locations, specific wintering areas, or migration routes. A recent study using geolocators provided preliminary information about locations and habitat associations of two storm-petrels during migration (Pollet et al. 2014b). This study confirmed the presence of storm-petrels over warm and deep waters in the North Atlantic during the non-breeding season. However, this study was limited by the very small sample size and it did not provide information on stop-over sites. The intent of the current study was therefore to extend the results of the previous study by examining stop-over locations, timing of migration, migration routes, over-winter destinations, and habitat associations on the wintering grounds for storm-petrels breeding at two colonies in Nova Scotia, Canada.

4.3 Methods

4.3.1 Study Species and Study Sites

Storm-petrels are small, ~ 45-g, sexually monomorphic procellariiforms that breed in the northern hemisphere (see specifics about species in Chapter 1). My study was conducted between 2013 and 2015 at two breeding colonies in Nova Scotia, Canada: Bon Portage and Country Islands located off the eastern shore of Nova Scotia (see Chapter 1).

I monitored annually 300 and 80 burrows on Bon Portage and Country Island, respectively, and captured breeding adults that were ringed with uniquely numbered metal leg bands when first encountered. Burrows were marked with uniquely numbered metal tags within my study plots. Additional details are provided in Chapter 1 and in Pollet et al. (2014a, b).

4.3.2 Geolocator Attachment

To track year-round movements, I deployed geolocators (also called Global Location Sensors, GLS) during late stages of incubation on randomly selected adults of unknown sex that were present in burrows (only one adult per burrow was tagged). On Bon

Portage, I deployed 22 GLS between 5 and 10 July 2013 and another 17 GLS on 12 July 2014. On Country Island, I deployed 15 GLS on 3 July 2013.

I used GLS (MK5740, Biotrack, Cambridge, UK) that weighed 0.9 g and were 21.9 × 7.9 × 3.8 mm. These GLS were attached on the back with two subcutaneous sutures, as described in Chapter 1 and in Pollet et al. (2014a). GLS attachment took < 10 min/bird and adults were returned to their burrows immediately following attachment. Total mass with attaching material was 1.1 g, which is below the accepted 3% recommendation (Phillips et al. 2003). The average mass of adult Leach's storm-petrels in 2013 was 46.5 ± 3.4 g, $N = 22$ and 46.7 ± 3.1 g, $N = 15$, for Bon Portage and Country Island, respectively.

4.3.3 Data-Processing

GLS measured light levels every 60 sec, and recorded maximum levels at 10-min intervals. Data from GLS tags were decompressed and times of sunrise and sunset were determined from light curves using BAS Track software (Biotrack, Dorset, UK). Data were processed with the same method described in Chapter 2.

4.3.4 Migration Movements

I considered fall migration to have started when a bird moved at least 600 km, in any direction, from its breeding colony and did not return to the colony until the following spring. I considered a bird to be at a stop-over site if it moved less than 0.8° in latitude per half-day for a minimum of 2.5 consecutive days (Guilford et al. 2009). I then took the mean latitude and longitude for each stop-over location. I defined an over-winter location as the southernmost location within which individuals moved less than 0.8° in latitude per half-day until locations moved in a northward direction. Distance between the colony and the furthest point was calculated using the great circle distance method (Bivand et al. 2013). To illustrate distributions of birds during stop-over and over-winter, I determined the kernel utilization distribution (KUD) for each individual using the kde2d function from the 'MASS' package in R, with a grid size of 0.05° longitude by 0.03° latitude.

4.3.5 Habitat Characteristics

To describe habitat characteristics for the species at their wintering locations, I employed species distribution modelling (SDM) using Maximum Entropy (MaxEnt) software version 3.3.3 (Phillips et al. 2006). This program models geographic distributions using presence-only species records, and is better suited than other modeling methods for small sample size (Herdandez et al. 2006, Wisz et al. 2008). Presence data implemented in my model were locations within the 50% KUD of each individual. I set aside 10% of the data, randomly chosen by the software, for spatial evaluation of models, and used a bootstrap procedure to generate confidence intervals of estimates based on 10 replicates. I used winter (November through April) sea surface temperature (SST in °C), winter chlorophyll-a concentration (Chl-a in mg m^{-3}), bathymetry (in m), and surface current (in m s^{-1}) data downloaded from the Global Marine Environment Dataset browser (Basher et al. 2014) as explanatory variables. These data had a spatial resolution of 5 arcmin (equivalent to about 9 km at the equator), which is more accurate than GLS data (~ 180 km), but grain size and locational errors do not strongly affect predictions from SDM (Guisan et al. 2007). The SDM returns a permutation importance for each variable, a measure (in percent) of contribution to the model, as well as an area under the receiver-operator curve (AUC), the probability that a random presence location ranked higher than a random absence location. This is an indication of how well a model performed. Means are presented ± standard deviation unless otherwise stated.

4.3.6 Tag Effects

To determine if tags affected return rates, I checked for returning adults in all burrows that were occupied in the previous year. I used the same monitoring procedure in each year, with equal effort devoted to finding GLS- and all non-GLS birds within marked burrows. I used Fisher's exact tests to compare return rates of tagged and untagged birds from 2013-2014 and again from 2014-2015 for Bon Portage Island only. Logistic limitations prevented me from thoroughly monitoring burrows on Country Island to compare return rates of tagged and untagged birds.

4.4 Results

Of 22 birds tagged on Bon Portage in 2013, 15 were observed the following season, three of which still had their GLS attached. Of 17 birds tagged on Bon Portage in 2014, 10 were observed the following season, three of which had their GLS attached. Of 15 birds tagged on Country Island in 2013, seven were observed the following season, two of which had their GLS attached. Of the eight GLS recovered, three had worked until retrieval and the remaining five had stopped working some time during migration (range 30 December - 7 February).

4.4.1 Migration Movements

Storm-petrels were asynchronous leaving their colony, and they either remained in the northern hemisphere, or travelled below 25° South (Figure 4.1). I obtained departure dates for four birds from Bon Portage; three successful birds departed the colony between 14 and 23 October, and one failed breeder left on 14 August. The remaining birds from Bon Portage and those from Country Island bred successfully but their departure dates could not be determined because they coincided with the fall equinox, a time of year when it is not possible to determine the birds' positions with GLS.

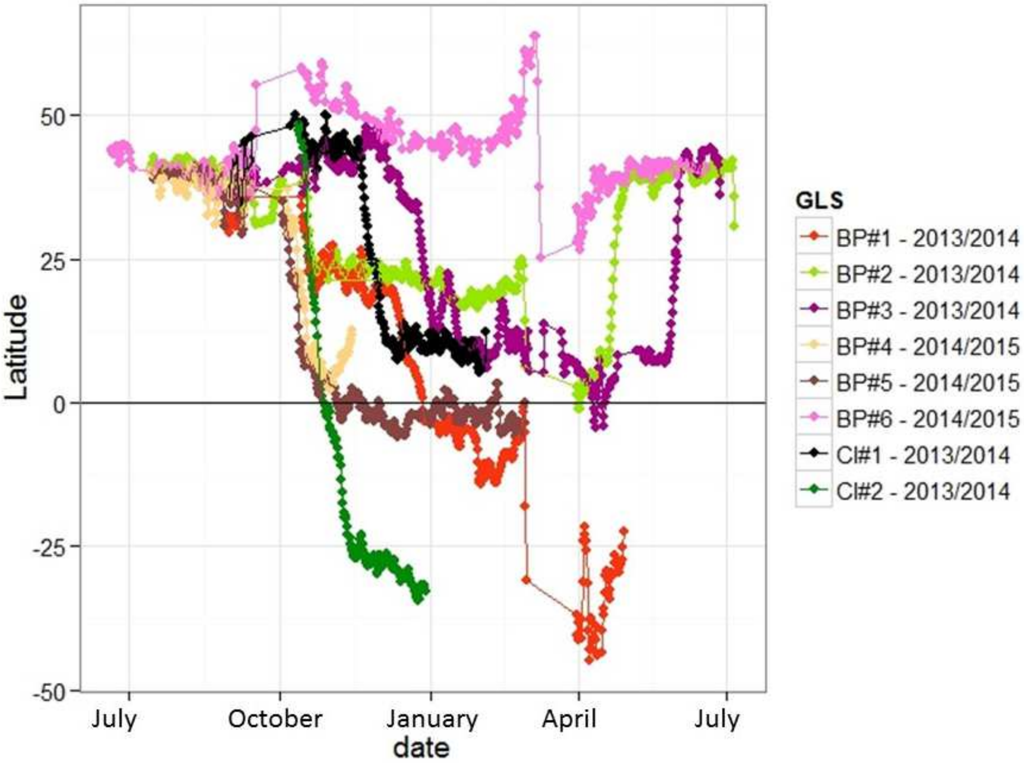

Figure 4.1 Latitude relative to time of year during the non-breeding period of Leach's storm-petrels tracked using geolocators (GLS) from Bon Portage Island (BP) and Country Island (CI), Nova Scotia, Canada.

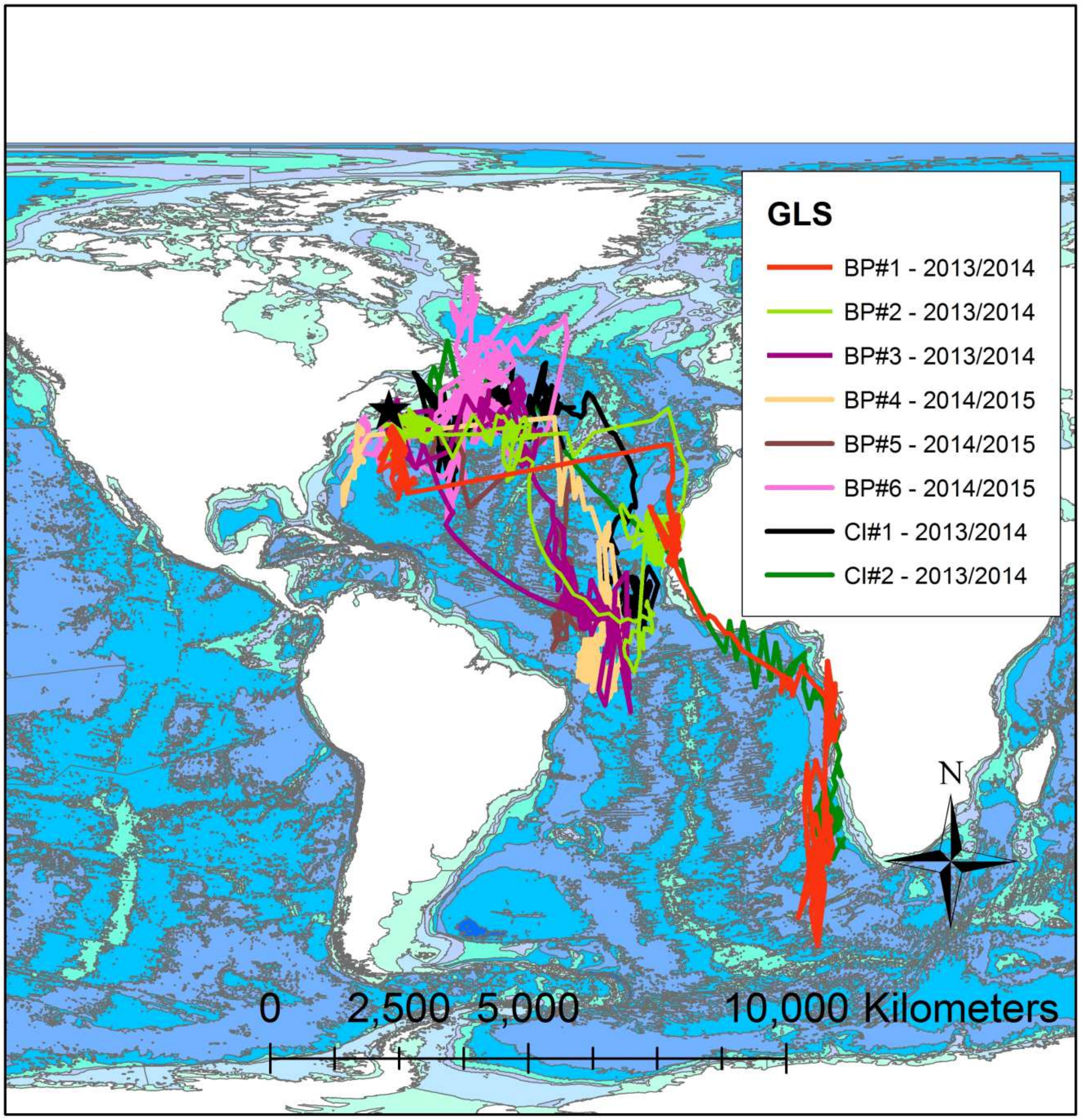

Figure 4.2 Migration routes of Leach's storm-petrels tracked using geolocators (GLS) from Bon Portage (BP) and Country Island (CI), Nova Scotia, Canada.

All but one tagged bird (n = 7) followed a southeast path across the North Atlantic Ocean towards the Canary Islands and Cape Verde (Figure 4.2). The remaining bird started its migration by travelling north towards Greenland (Figure 4.1).

Two major stop-over sites were identified for storm-petrels. The first stop-over site was used by birds from both Bon Portage (n = 5) and Country Island (n = 1), and was situated in the northwest Atlantic, southeast of the Grand Banks of Newfoundland (40° N and -45° W). The second stop-over site, also used by birds from both islands (one from Bon Portage, one from Country Island), was situated between the Cape Verde archipelago and the North Equatorial Currents (15° N and -20° W). Mean time spent at stop-over sites was 5.4 ± 3.5 d.

Five of the six birds with stop-over sites in the northwest Atlantic over-wintered in the equatorial zone between Cape Verde and the northeast tip of Brazil, in areas associated with the Canary and the North Equatorial Currents (Figures 4.2). They arrived at their wintering sites between 6 and 27 December and stayed for an average of 115.0 ± 14.0 days. The average distance between breeding colonies and this over-wintering site was 6,600 ± 400 km. The remaining bird, which was from Bon Portage started its migration on 15 October, made a stop-over off Newfoundland, and then headed to waters off Greenland. It travelled south again and spent the remainder of the winter in waters off Newfoundland, only 1,300 km from its colony.

The two birds with stop-over sites in the Cape Verde region over-wintered in waters adjacent to the southern part of the African continent (Figure 4.2). The two birds crossed the equator on 27 October and 1 January, and arrived at their wintering sites on 14 November and 5 January (Figure 4.1). They stayed at their over-winter sites for an average of 49.1 ± 22.2 days. The distance between the breeding colonies and the over-wintering sites was 12,000 ± 820 km.

I obtained spring migration data for three birds, none of which over-wintered off southern Africa. Spring migration was initiated with birds heading northwest around 28 March. Spring migration was rapid, lasting only 10 - 12 d, with no stop-overs.

4.4.2 Habitat Characteristics

The SDM determined that Leach's storm-petrels over-wintered in waters with high SST and low Chl-a (permutation importance values of 46.2 ± 1.6% and 37.1 ± 1.3%, respectively, Figures 4.3A and B). Depth and surface currents had low permutation importance values (8.8 ± 0.6% and 7.9 ± 1.2%, respectively). Although the model had a high performance (AUC = 0.903 ± 0.013), it predicted the presence of birds in areas not used by tracked birds, such as the Guineas Current and failed to predict the presence of the bird that wintered off Newfoundland (Figure 4.3C). Low sample size and wide distributions tend to over inflate the performance of the model, and a larger sample size would be required for more accurate modelling (Bean et al. 2012, van Proosdij et al. 2016).

4.4.3 Tag Effects

Return rates did not differ significantly between tagged and untagged birds for either year (Table 4.1). On all birds that returned with a GLS, either the anterior or posterior suture had worked its way through the skin, but birds still had one intact loop. Skin at suture sites appeared intact, and no scar tissue or infection was detected.

Table 4.1. Return rates for geolocator-tagged and untagged Leach's storm-petrels from Bon Portage Island, Nova Scotia, Canada, compared using Fisher's exact tests.

	Tagged (%)	Untagged (%)	*P*
2013 - 2014	15/22 (63.6)	112/301 (37.2)	0.09
2014 - 2015	10/17 (58.8)	199/345 (57.7)	> 0.99

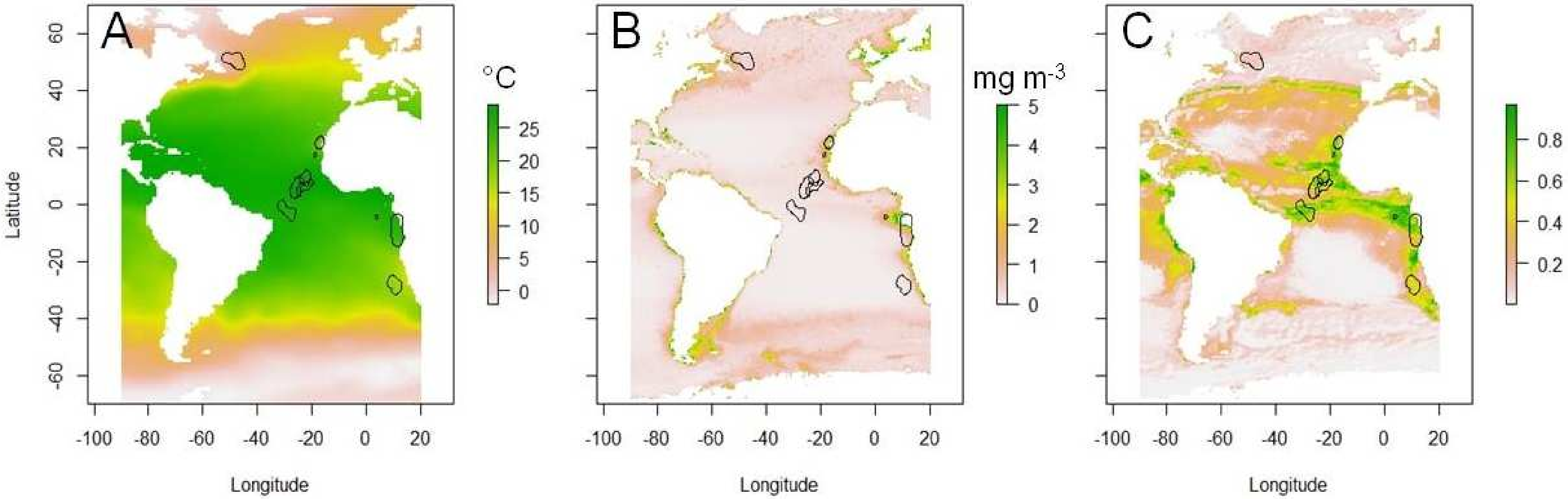

Figure 4.3 Over-winter home range (50%) Kernel Utilization Distributions of each Leach's storm-petrel tracked from Bon Portage and Country Island, Nova Scotia, Canada laid over A) Sea Surface Temperature (SST) in °C , B) Chlorophyll-a concentration in mg m^{-3}, and C) Probability of occurrence from pink (low) to green (high) based on environmental variables used in a Maximum Entropy Species Distribution Model.

4.5 Discussion

Tracked Leach's storm-petrels had different over-winter sites; however there was some level of migratory connectivity in the northern hemisphere. I found that tracked birds migrated in a general clockwise pattern around the North Atlantic gyre, which presumably followed global wind patterns (Egevang et al. 2010, Hedd et al. 2012). They made stop-overs in two geographically distinct areas: the northwest Atlantic, southeast of the Grand Banks of Newfoundland, and the Cape Verde archipelago and the North Equatorial Currents. Cape Verde region was also the over-wintering site of some birds, whereas other birds migrated to waters off South Africa, and one bird stayed in waters off Newfoundland. The species distribution modelling was efficient at selecting the first two areas, but failed to detect that last region as a potential over-wintering area. I observed no effect of GLS on return rates of Leach's storm-petrels. Birds that lost their tags showed no sign of scarring or infection at suture sites. I suspect that the skin of storm-petrels is thin and the non-absorbable suture slowly worked its way out.

Waters off Newfoundland, southeast of the Grand Banks, are used as a stop-over site by other seabirds including long-tailed skuas (*Stercorarius longicaudus*), Manx shearwaters (*Puffinus puffinus*), and Sabine's gulls (*Larus sabini*, Guilford et al. 2009, Stenhouse et al. 2012, Gilg et al. 2013). This area is also used as an over-wintering area by other species such as Great Skuas (*Stercorarius skua*), little auks (*Alle alle*), and thick-billed (*Uria lomvia*) and common murres (*U. aalge*, Magnusdottir et al. 2012, Mosbeck et al. 2012, McFarlane Tranquilla et al. 2015). It may be that Leach's storm-petrels use this area when they are going through some of their pre-basic moult. Ainley et al. (1976) suggested that in Leach's storm-petrels there was little overlap between wing feather moult and phases of reproduction, with primary and secondary feathers molting after the breeding season.

Waters associated with the North Equatorial currents are used by other seabirds including Cory's shearwaters (*Calonectris diomedea*) and northern gannets (*Morus bassanus*) as an over-wintering site (Ristow et al. 2000, Kubetzki et al. 2009). Finally, the Benguela Current is used by many over-wintering species that breed in the northern hemisphere such as Cory's shearwater (González-Solís et al. 2007) or Sabine's gull (*Larus sabini*, Stenhouse et al. 2012) and species that breed in the southern hemisphere such as white-chinned petrel (*Procellaria aequinoctialis*, Péron et al. 2010) and Cape gannet (*Morus capensis*, Grémillet et al. 2008). All these highly productive areas arise from either strong winds or narrow continental shelf, creating nutrient-rich upwelling waters (Shannon and Field 1985, Barton et al. 1998, Heileman and O'Toole 2008), favorable for seabirds, but also home of intense commercial fishery activities (Roux and Shannon 2004, Camphuysen and van der Meer 2005). Those areas are recognized as important hot spots for biodiversity (van der Lingen et al. 2006, Grecian et al. 2016); however, offshore platforms are present both off Mauritania (Coleman et al. 2005) and South Africa (Muntingh 1995).

The SDM suggested a high probability of presence around the North Equatorial Current, which matched the observed over-wintering distributions of the majority of tracked individuals, and the previous bands recoveries. However, the model over-predicted use of the Guinea Current, where no birds were observed, and under-predicted the use of the Benguela Current and the waters off Newfoundland. The small sample size of this study was probably a limiting factor for the model.

With such variability in over-wintering areas with so few birds, data from more birds are required to have a more robust SDM, and to detect the strength of the migratory connectivity in this population.

Interestingly, I found that individuals from different colonies over-wintered in the same area and that individuals from the same colonies over-wintered in different areas, suggesting low migratory connectivity. Again, this is based on a small sample size. Among seabirds, Cory's and sooty shearwaters (*Puffinus griseus*) provide similar examples of individuals from the same colonies using multiple over-winter locations (González-Solís et al. 2007, Shaffer et al. 2006). Population differentiation is thought to be influenced by non-breeding distributions (Friesen et al. 2007); thus the use of similar over-wintering areas by different populations is likely to increase inter-population connectivity. This inter-population connectivity was documented by Bicknell et al. (2014) who found that pre-breeding Leach's storm-petrels captured at colonies spanning the North Atlantic had isotope signatures that differed from breeders.

My findings indicate the potential importance of the North Equatorial Current for Leach's storm - petrels as both a stop-over and over-winter location, although this conclusion must be viewed with caution given that my observations are limited to only two years and a small number of birds. This area is a hot spot for migrating or over-wintering seabirds and conservation efforts in that region would benefit many species. More tracking is required to better understand how populations behave during migration and during the over-wintering period and to pinpoint major threats they are facing during such movement.

Chapter 5 - Relationships Among Blood Mercury Levels, Diet, Reproduction, and Return Rate in Leach's Storm-Petrel

5.1 Abstract

Mercury (Hg) is a ubiquitous heavy metal that occurs naturally in the environment, but its levels have been supplemented for decades by a variety of human activities. Mercury can have serious deleterious effects on a variety of organisms, with top predators being particularly susceptible because methylmercury bioaccumulates and biomagnifies in food webs. Among birds, seabirds can have especially high levels of Hg contamination and Leach's storm-petrels (*Oceanodroma leucorhoa*), in particular, have amongst the highest known levels. Several populations of Leach's storm-petrels have declined recently in the Northwest Atlantic. The causes of these declines remain uncertain, but the toxic effects of Hg could be a potential factor. Here, I tested for relationships between adult blood total Hg (THg) concentration and several reproductive parameters, and return rate of adult Leach's storm-petrels breeding on Bon Portage Island, Nova Scotia, Canada, between 2011 and 2015 (blood samples n = 20, 36, 6, 15, and 13 for each year, respectively). In 2013, I also compared Hg values between Bon Portage Island and Country Island, Nova Scotia, Canada. Overall, THg levels were high (0.78 ± 0.43 µg/g wet wt.) compared to other species of seabirds in this region, and varied significantly among years. However, I found no associations between reproductive parameters or, adult return rate and THg levels. Bon Portage levels were not significantly different than those from Country Island. Overall, my results indicate that the observed levels of mercury in Leach's storm-petrel blood,

although high, appear not to be adversely affecting their offspring's development or their survival at Bon Portage Island.

5.2 Introduction

Mercury (Hg) is a naturally occurring trace element that may leach from geological deposits into aquatic ecosystems, or be volatilized by volcanoes, hot springs, and forest fires (Mason and Sheu 2002, Fitzgerald et al. 2007, Wiedinmyer and Friedli 2007). Hg is also a by-product of human activities where the main sources are small-scale gold mining and burning of fossils fuels (Pacyna et al. 2006, UNEP 2013). Volatilized Hg can be transported through the atmosphere to reach locations far from sources in a short period of time, making Hg pollution a global issue (Fitzgerald et al. 2007, Cossa et al. 2011). Indeed, Hg levels in seabirds sampled at remote locations are not necessarily lower than closer to populated areas (Burger and Gochfeld 2002). While natural contributions of Hg to the atmosphere have stayed relatively stable over the last 150 years, anthropogenic contributions have increased dramatically, resulting in increased Hg loading, particularly in marine ecosystems (Thompson et al. 1992, Asmund and Nielsen 2002).

Hg is most toxic when it is transformed into methylmercury (MeHg), mostly by anaerobic bacteria in marine and freshwater ecosystems. MeHg bioaccumulates in tissues of organisms and biomagnifies from one trophic level to the next, resulting in top predators from aquatic food webs having high concentrations of MeHg in their bodies (Atwell et al. 1998, Campbell et al. 2005, Spencer et al. 2011). MeHg can cross the blood-brain barrier, causing negative neurological effects (Aschner and Aschner 1990). Moreover, Hg can affect the endocrine system, with higher levels of Hg correlated with lower levels of prolactin, a hormone involved in parental care behavior in birds. Lower levels of prolactin are associated with greater egg neglect and lower reproductive success (Tartu et al. 2015, 2016). Finally, MeHg is also responsible for reproductive effects, such has lower hatchability due to embryo malformation (Wolfe et al. 1998).

Foraging locations and diet types among species both have an effect on Hg levels. For example, off Midway Atoll in the northern Pacific Ocean, red-footed boobies (*Sula sula*) foraging further offshore than great frigatebirds (*Fregata minor*) had higher Hg levels (Burger and Gochfeld 2000). Beside the near- or off-shore foraging locations, the depth of the prey influences their Hg burdens, with deep, mesopelagic prey having higher Hg levels than surface prey (Choy et al. 2009). Piscivorous birds tends to have higher Hg levels than planktivorous birds, as a result of bioaccumulation (Goodale et al. 2008, Anderson et al. 2009).

Seabirds have been used as bioindicators of various contaminants in marine environments (Furness and Camphuisen 1997, Burger and Gochfeld 2004), including Hg (Kahle and Becker 1999, Goodale et al. 2008, Burgess et al. 2013). Although many studies monitored the levels of Hg in seabirds, few have determined their effects on seabirds (Braune et al. 2006). Nevertheless, high concentrations of Hg in seabird tissues have been associated with a variety of negative consequences, including direct effects such as decreased fitness through endocrine disruption, egg neglect and egg infertility, and indirect effects, such as increased numbers of parasitic helminths (Wayland et al. 2001, Dietz et al. 2013, Tartu et al. 2015). In seabirds, Hg has to reach higher levels than in humans to be toxic (Thompson 1990). Seabirds are capable of demethylating MeHg, especially in the liver, and storing it as less toxic inorganic Hg (Kim et al.

1996). They can also depurate MeHg through moulting, and to a lesser extent through guano and egg-laying (Monteiro and Furness 1995). Depuration through egg-laying may be minimal because no differences in blood MeHg levels were observed between males and females of several seabird species (Campbell et al. 2005). Presumably these mechanisms of depuration partly buffer the deleterious effects of Hg, yet other threats, such as global climate change could interact with Hg effects (Pinkney et al. 2015), and currently there are insufficient data to evaluate this assumption for many seabird populations. Associations between Hg and an organism's biology can vary among tissues. In wandering albatrosses (*Diomedea exulans*) sampled on Possession Island in the Crozet archipelago, Hg levels in blood were not associated with adult survival, but were associated with negative effects on hatching, fledgling, and breeding probability (Goutte et al. 2014a). However, Hg levels in feathers were not associated with survival, hatching, fledgling, or breeding probability (Bustamante et al. 2016). Whereas blood Hg levels inform us about a bird's recent exposure, feather Hg levels represent exposure when a bird grew that feather and remobilized Hg burdens (Wolfe et al. 1998, Evers et al. 2005).

Leach's storm-petrel (*Oceanodroma leucorhoa,* hereafter storm-petrel) is a small, abundant seabird of the northern hemisphere that feeds off the continental shelf during the breeding season (Pollet et al. 2014a) and over much of the Atlantic Ocean during the non-breeding season (Pollet et al. 2014b). Populations of this species in the North Atlantic have declined over the past 50 years (Robertson et al. 2006, Newson et al. 2008, Hedd et al. 2016). Several factors may be responsible for these declines including introductions of mammalian predators to breeding islands (Bicknell et al. 2009), increasing gull populations (Stenhouse and Montevecchi 2000, Sanz-Aguilar et al. 2009), and attraction to offshore structures with bright lights that lead to disorientation, and collisions with structures or incineration by gas flares (Wiese et al. 2001). Storm-petrels also have some of the highest reported concentrations of Hg amongst seabirds in the Gulf of Maine (Elliott et al. 1992, Goodale et al. 2008, Bond and Diamond 2009). It is not clear, however, whether these concentrations are contributing to population declines by reducing reproductive success or adult survival.

The main goals of this chapter were: 1) to assess the effects of Hg on reproductive success and return rate in storm-petrels. Specifically, I related blood Hg levels to egg-laying date, egg volume, nestling growth rate, hatching rate (defined as the percent of eggs that hatched) and fledging rate (defined as the percent of chicks that fledged), and adult return rate to the breeding colony (defined as the percent of adults seen in any subsequent season); and 2) to compare Hg levels between storm-petrels breeding on Bon Portage and those breeding on Country Island. My hypothesis was that Hg blood levels in storm-petrels from Country Island would be higher than those from Bon Portage, as they feed at a higher trophic level (see Chapter 2).

5.3 Materials and Methods

5.3.1 Study Sites

This study was conducted during summers of 2011 through 2015 on Bon Portage Island off the southwest coast of Nova Scotia, Canada. In addition, this study was also conducted on Country Island during summer 2013. Data from Chapter 2 indicate that storm-petrels from the two islands forage in different locations, determined from GLS, and have a different diet, inferred through stable isotope analysis.

5.3.2 Field Data Collection

On Bon Portage, I monitored and banded adults from ~250 uniquely numbered burrows, distributed among twelve 12- x 12-m plots. On Country Island, I monitored and banded adults of 80 uniquely numbered burrows, randomly distributed through the colony. I visited burrows up to two times during incubation to fit adults with uniquely numbered Canadian Wildlife Service metal bands, and to determine return rates of adults from previous years. Storm-petrels have high breeding site fidelity (Morse and Kress 1984, Huntington et al. 1996) so that return rate can be used as a proxy for over-winter survival. I limited visits during this time to reduce chances of nest desertion (Blackmer et al. 2003). If eggs were present in burrows, I measured their length and maximum width to the nearest 0.1 mm, and determined approximate laying and hatching date by candling following Weller's (1956) criteria. Egg volume (V, in mm^3) was estimated using Hoyt's (1979) formula: $V = 0.51 \times LW^2$, where L is length and W is width. I included these measures because in some seabird species reproductive success is positively related to early egg-laying dates (Wanless and Harris 1988, Sydeman et al. 1991) and egg volume (Thomas 1982, Croxall et al. 1992). I checked each burrow two days after the estimated hatching day to record hatching success. Once chicks hatched, I weighed them weekly to monitor their growth. For each chick, I calculated growth rate as mass gain per day ($g\ d^{-1}$) during the linear growth phase (between 5 and 30 d post-hatch; Huntington et al. 1986). I considered fledging to have occurred if at 60 days post-hatch a burrow was empty and during the previous visit the nestling had weighed $\geq$ 60 g and had a wing chord $\geq$ 120 mm.

To quantify Hg levels, I collected blood samples during the incubation period from 126 randomly selected adults. Compared to Hg concentrations in liver and feather that reflects long-term exposure, Hg concentrations in blood reflects short term exposure to Hg. Skin over the left brachial vein was wiped with ethanol and the vein was punctured with a 26-gauge needle. In 2011 – 2013, blood samples (maximum of 150 μL) were collected via hematocrit capillary tubes and transferred to centrifuge tubes that were then sealed. In 2014 and 2015, blood samples were collected in hematocrit capillary tubes, which were then sealed at both ends. In total, I collected blood samples from 126 different adult Leach's storm-petrels on Bon Portage between 2011 and 2015 (n = 20, 36, 42, 15, and 13 for each year, respectively), and collected an additional 10 samples on Country Island in 2013. However, for Bon Portage some samples (n = 29) for 2013 were not sealed properly and could not be used for the analysis, leaving n = 13 for that year. Samples were kept refrigerated for no more than a week until they were shipped on ice to the Environment Canada laboratory in Ottawa, at which point samples were frozen at - 20°C until processing. The Acadia University Animal Care Committee approved all animal handling procedures (Protocol # 06-09).

5.3.3 Mercury Speciation

I quantified MeHg and divalent mercury (Hg(II)) for the 2011-2013 samples using digestion in basic methanol (25% potassium hydroxide KOH) of dried and homogenized samples, followed by an ethylation purge and trap preconcentration and analysis using gas chromatography-atomic fluorescence spectrometry (Bloom and Fitzgerald 1988, Edmonds et al. 2010, 2012). Certified reference materials, including dogfish liver tissue (DOLT-4), and lobster hepatopancreas tissue (TORT-2), indicated good recovery of mercury with an overall mean recovery of 108 ± 2.4% for samples with known Hg concentration (n = 26). No samples were below the mean detection limit (3 times the standard deviation of blank concentrations) of 1.96 ng/g (based on a sample mass of 5 mg dry weight). For the 2011-2013 samples, total mercury (THg) was expressed as the sum of MeHg and Hg(II) species in digests. For the 2014 and 2015 samples, THg was quantified using a Direct Mercury Analyser-80 (Milestone Scientific). Samples were thermally and chemically decomposed under a continuous flow of ultra-pure oxygen. A gold amalgamator trapped mercury and realised mercury vapour under heat. Mercury was quantified with a single wavelength atomic absorption spectrometer. TORT-3 and DOLT-4 samples were used to evaluate accuracy. Recovery for samples with known Hg concentration was 111.1 ± 5.4% (n = 26).

5.3.4 Statistical Analyses

All data were tested for homogeneity of variance and residuals were tested for normality, and data that did not conform to the assumptions (blood THg concentrations and egg volume) were $\log_{10}$-transformed. I used analysis of variance (ANOVA) to test for differences in blood THg concentration (expressed in µg/g wet wt) across years, after ensuring that assumptions of normality and homogeneity of variance were met, followed by Tukey's multiple comparisons test. I used generalized linear regressions to test for correlations between laying date (day of year) based on candling, egg volume, and nestling growth rate, versus blood THg concentration, with year as a covariate. Finally, I used a logistic regression to test for associations between blood THg concentration and hatching success, fledging success, and adult return rate. Data were analyzed in R version 3.0.2 (R Development Core Team 2013).

5.4 Results

On Bon Portage, adult blood THg ranged from 0.24 to 2.33 µg/g (mean ± SD = 0.78 ± 0.42 µg/g) and differed significantly among years ($F_{4,85} = 6.94$, $P < 0.001$). Post hoc Tukey tests indicated that values for 2011 and 2015 were significantly lower than values for 2012 and 2013, and values for 2014 were intermediate (Figure 5.1). On Country Island, adult THg ranged from 0.49 to 1.79 µg/g (mean ± SD = 1.08 ± 0.32 µg/g). Country Island THg values for 2013 were not significantly different from Bon Portage values for 2013 ($F_{1,34} = 0.01$, $P = 0.93$). On Bon Portage, variation in THg was not associated with variation in laying date ($F_{1,69} \leq 0.01$, $P = 0.90$) and laying date did vary among years ($F_{1,69} = 0.56$, $P = 0.64$, Figure 2a, Table 5.1). Variation in THg was not associated with variation in egg volume ($F_{1,69} = 1.34$, $P = 0.26$) and egg volume did not vary among years ($F_{1,69} = 0.33$, $P = 0.57$, Figure 5.2b, Table 5.1). Variation in THg was also not associated with variation in chick growth ($F_{1,38} = 0.01$, $P = 0.9$) but chick growth did vary among years ($F_{1,38} = 3.89$, $P = 0.01$, Figure 5.2c, Table 5.1). Finally, there was no significant relationship between adult THg and hatching success, fledgling success, or return rate (Table 5.2).

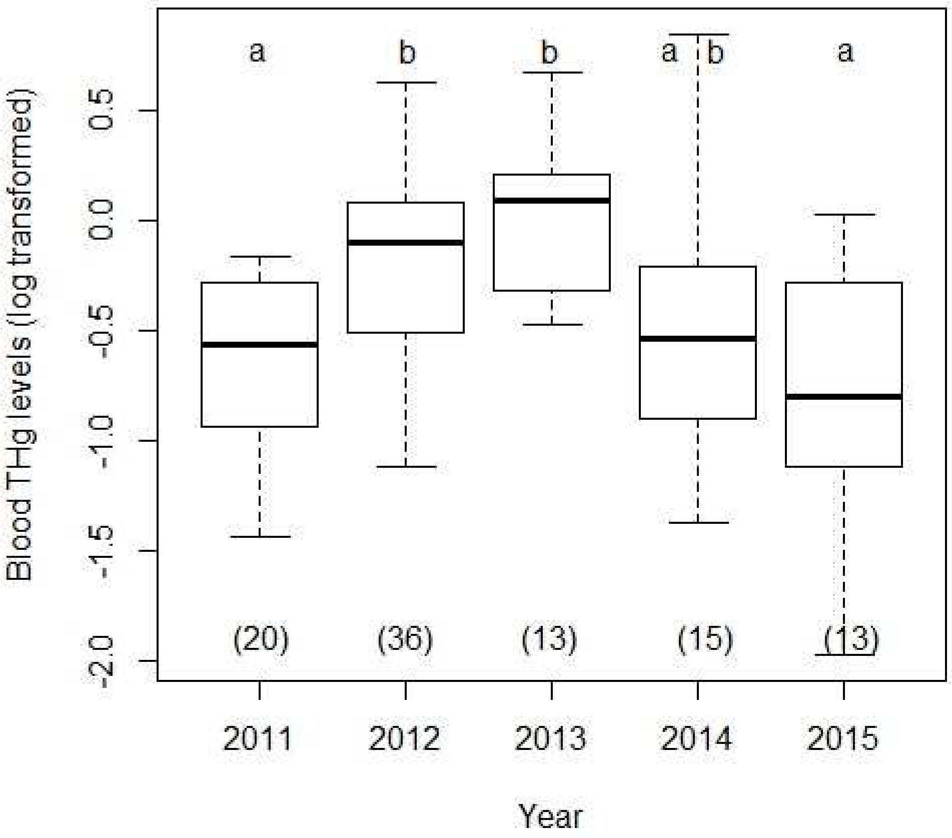

Figure 5.1 THg in blood of Leach's storm-petrels (log scale) by year on Bon Portage Island. Sample sizes are given in parentheses. Boxes sharing the same letter are not significantly different (*P* > 0.05). Middle line represents mean, box outlines ± 1 standard deviation, and whiskers are minimum and maximum values.

Table 5.1. Mean (± SD) adult blood total mercury (THg) and reproductive parameters in Leach's storm-petrels on Bon Portage for each year of this study.

Year	Blood THg (µg/g wet wt.)	Lay date (Day of year)	Egg volume (mm^3)	Chick growth ($g.day^{-1}$)
2011	0.54 ± 0.21	164.25 ± 10.54	8662.43 ± 537.34	1.08 ± 0.64
2012	0.91 ± 0.40	171.00 ± 8.31	8525.88 ± 641.61	1.86 ± 0.39
2013	1.51 ± 0.51	172.75 ± 5.31	9137.40 ± 1081.30	1.17 ± 0.63
2014	0.76 ± 0.57	166.00 ± 9.20	8937.87 ± 596.70	1.70 ± 0.51
2015	0.56 ± 0.31	161.85 ± 6.46	8791.63 ± 798.97	1.25 ± 0.52

Table 5.2 Results of logistic regressions of blood THg versus hatching success, fledging success, and return rates of Leach's storm-petrels on Bon Portage Island; n corresponds to the number of eggs monitored for hatching, the number of chicks monitored for fledgling, and the number of adults monitored for return rate.

Variable	n	Estimate	SE	z ratio	*P*
Hatching	90	0.11	0.89	0.13	0.90
Fledging	56	0.13	1.55	0.08	0.94
Return rate	97	0.85	0.98	0.87	0.38

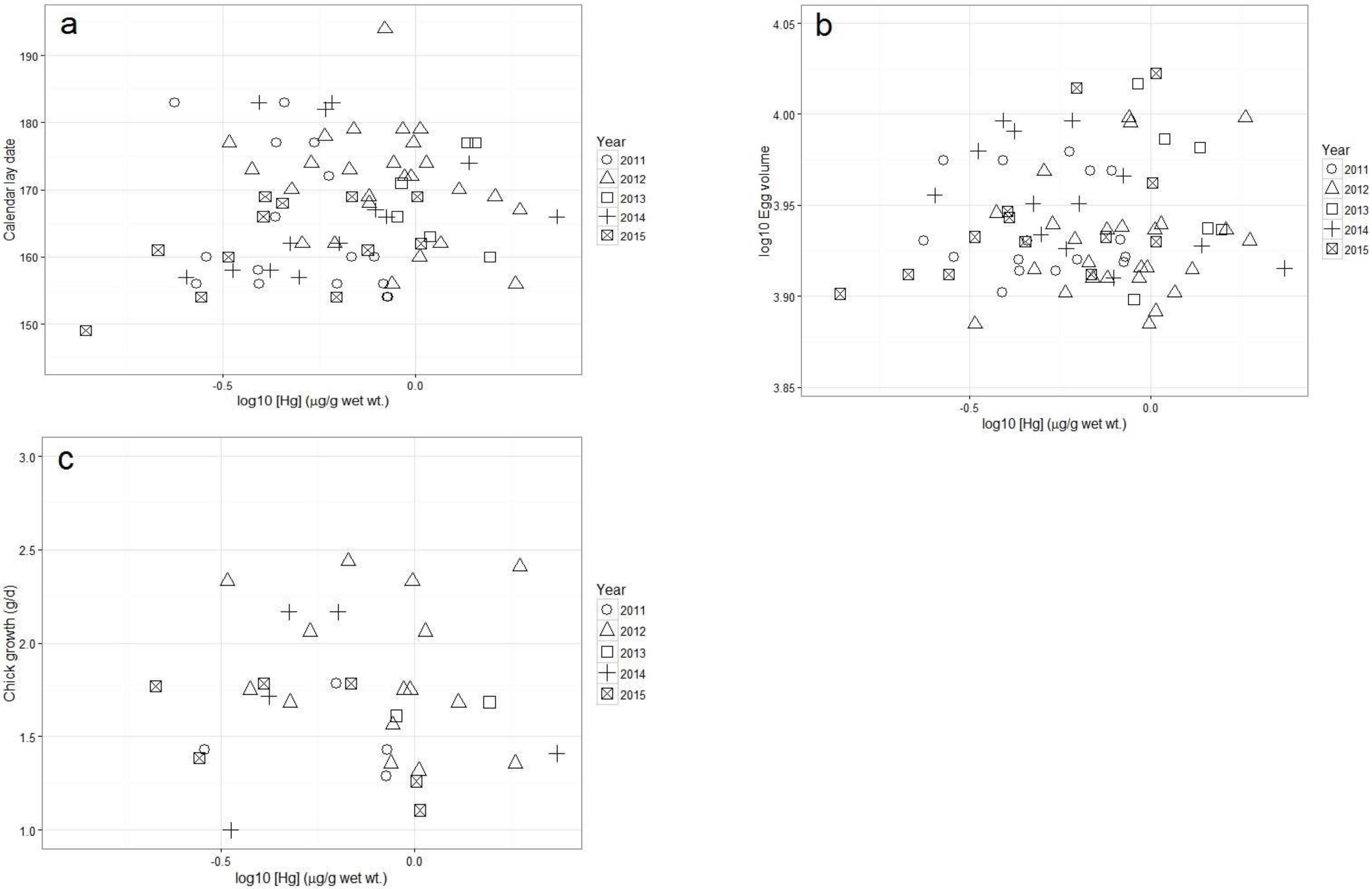

Figure 5.2 Relationships between blood THg concentration (log scale) and **a** egg-laying date, **b** egg volume (log scale), and **c** chick growth in Leach's storm-petrels from Bon Portage Island between 2011 and 2015.

5.5 Discussion

Adult Leach's storm-petrels at my study sites had blood concentrations of THg that are considered high, even for seabirds that often have higher blood Hg concentrations than other birds (Thompson et al. 1993). In addition, adult storm-petrels from Bon Portage and Country Island had higher average blood concentrations of THg than levels reported for storm-petrels from other islands in the Gulf of Maine (Table 5.3), but lower concentrations of THg than Leach's storm-petrels breeding further north (Burgess et al. 2016). During our 5-year study, I saw an increase in adult blood THg level concentrations, followed by a decrease. Whereas annual fluctuations in Hg are not atypical (Bond et al. 2015), in our case, higher values for 2013 could be explained by a handling issue. Sample storage issues in 2013 resulted in desiccation of a large number of samples and remaining samples (n = 13) might have suffered from partial desiccation; this could result in inflation of THg values. However, values from 2013 were not different than values from 2012. Data from Country Island were not different from those of Bon Portage, despite a difference in trophic level determined through stable isotope analysis (see Chapter 2), but THg values for islands near Newfoundland and New Brunswick suggest the presence of a THg gradient with foraging depth and foraging distance from colonies (Burgess et al. 2016, Hedd et al. 2016). Storm-petrels from New Brunswick forage over the continental shelf, whereas the remaining storm-petrels from the Atlantic region forage past the continental shelf on mesopelagic preys, which have a greater Hg burden (Choy et al. 2009).

Despite relatively high levels of adult blood THg, I found no negative associations between THg levels and egg-laying date, egg volume, nestling growth rate, hatching success, fledging success, or return rate. In some other seabirds, there is similarly no evidence of changes in reproductive success and survival in relation to Hg levels (Thompson et al. 1991, Mitro et al. 2008, Wayland et al. 2008), while in other seabirds reproductive success but not survival probability is reduced with higher Hg levels (Goutte et al. 2014a, b). In common loons (*Gavia immer*), for instance, Hg concentrations must reach 3 µg/g wet wt. to negatively affect reproductive outcomes (Burgess and Meyer 2008, Evers et al. 2008). In our study, despite high levels of Hg detected compared to other seabirds of the area, Leach's storm-petrel levels were well below this, so they may not reach a threshold where effects can be detected. In many species, including storm-petrels, high concentrations of Hg may be buffered in several ways. For instance, liver and to a lesser extent kidney and brain tissues have the capacity to demethylate and store Hg (Kim et al. 1996, Wolfe et al. 1998, Henny et al. 2002). In addition, although part of the Hg burden stays in bird tissue, a large portion of MeHg is depurated through feathers during molt (Braune and Gaskin 1987, Monteiro and Furness 1995), and a smaller fraction is excreted through guano or deposited in eggs (Burgess et al. 2013). Indeed, a multi-species, multi-organ study suggested that storm-petrels may be efficient at excreting mercury (Bond and Diamond 2009).

Mercury has the tendency to bioamplify through the food web, so I expect top predators to have higher levels of mercury than predators lower in the food web. However, Madeiran storm-petrels (*Oceanodroma castro*) and Bulwer's petrels (*Bulweria bulwerii*), both at the lower end of the food web spectrum within Procellariforms, had higher Hg values in the Azores than Cory's (*Calonectris diomeda*) or little shearwaters (*Puffinus assimilis*) both higher in the food chain (Monteiro et al. 1995). So, how high a species is in the food web is not always an indication of Hg level.

Global Hg emissions and atmospheric deposition have increased in the last century, and are predicted to continue to increase in the future (Streets et al. 2009, Pacyna et al. 2010, UNEP 2013). However, Hg concentrations have increased in some seabirds (Braune 2007, Bond et al. 2015) but not others (Burgess et al. 2013). Although I found high levels of THg in blood samples of Leach's storm-petrels in comparison to other seabirds from the Gulf of Maine (Goodale et al. 2008), I detected no relationship between THg and Leach's storm-petrel reproduction or survival. Results of my study suggest that Hg on its own is unlikely to explain low survival of Leach's storm-petrels recently observed on Bon Portage Island (Fife et al. 2015). It remains to be seen whether increases in Hg will lead to detectable detriments in survival or immunologic response via additive effects (Hawley et al. 2009). It is also possible that Hg had disruptive reproductive effects before laying (Evers et al. 2008), which I did not assess in this study.

Females have the potential to excrete mercury into an egg (Ackerman et al. 2016b), but past studies have failed to determine that seabird females necessarily have significantly lower levels of mercury than males. For example, in breeding northern and southern giant petrels (*Macronectes halli, M. giganteus,* respectively), females had higher levels of Hg than males, whereas in Forster's terns (*Sterna forsteri*) and gentoo penguins (*Pygoscelis papua*), males had higher levels of Hg than females (Becker et al. 2002, Ackerman et al. 2016a). These differences could arise from variation in niche use, such as sex-biased diets, or a number of other factors beyond the scope of this study. The small sample size of this study may reduce the likelihood of detecting a significant effect of Hg, and although this study presents an initial baseline for the effects of Hg on some offspring development, a follow-up study on the influence of mercury should include sex of the birds.

Table 5.3 Mean blood THg concentrations (µg/g wet weight) for adult Leach's storm-petrels breeding on several islands in the Gulf of Maine, Machias Seal Island (New Brunswick), and Bon Portage Island (Nova Scotia).

Location	Years	Hg (µg/g) SD, n	Analysis	Source
Gulf of Maine	2001-2006	0.54 ± 0.37, 28	Atomic absorption spectroscopy	Goodale et al. 2008
Machias Seal Island	2005-2006	0.40 ± 0.48, 16	Atomic absorption spectrophotometry	Bond and Diamond 2009
Bon Portage Island	2011-2015	0.78 ± 0.44, 90	Atomic fluorescence spectrometry	This study
Country Island	2013	1.08 ± 0.32, 23	Atomic fluorescence spectrometry	This study

Chapter 6 - General Discussion

The main goal of this thesis was to evaluate how extrinsic factors, such as environmental conditions and mercury pollution, influence movement and reproductive success of a small long-lived seabird. Below I summarize how my findings meet this goal, by (1) advancing our understanding of the movement ecology of Leach's storm-petrels in various environmental conditions; (2) identifying how environmental conditions affect reproductive success; and (3) determining whether mercury pollution affects reproductive success. In this final chapter, I provide a synthesis of the results of my thesis in those three areas, with some suggestions for future research.

Movement is an essential part of all seabirds' lives; they travel great distances from their breeding colonies to their pelagic foraging areas at sea, and to their non-breeding, wintering areas. Knowledge of how extrinsic factors influence large-scale movement and reproductive success is important for species conservation, because it helps predict seabird responses to environmental changes. Using various forms of tracking data collected over five breeding and three non-breeding seasons, my dissertation linked extrinsic factors to movements of Leach's storm-petrels at different spatial and temporal scales, and to reproductive success.

6.1 Advances in Movement Ecology

6.1.1 Movement During the Breeding Season

Previous observations of seabirds during incubation and allometric projections for other procellariiforms suggested a 200-km foraging range for seabirds the size of Leach's storm-petrels (Ricklefs and Schew 1994, Huntington et al. 1996, Thaxter et al. 2012). Results from Chapter 2 revealed that individuals forage beyond the continental shelf, 600 to 1,000 km from their colony depending on their source colony, exceeding allometric predictions by a factor of 3 to 5. The prediction was that storm-petrels forage just past the continental shelf, when indeed they forage in much more pelagic waters. As my work was some of the first tracking of small seabirds, we have few data from other storm-petrel species to compare my GLS results with, but tracking of fork-tailed storm-petrels (*Oceanodroma furcata*) in the Pacific Ocean suggest they forage 755 ± 389 km from their colony off British Columbia (Halpin et al. 2016). These remarkable foraging distances during incubation increase the area covered during the breeding season, and therefore increase potential encounters with threats thought to be beyond the species' reach. Indeed, collaborative work tracking Leach's storm-petrels from seven colonies in the North Atlantic, including those from Chapter 2, suggest foraging areas of four of the seven colonies overlapped with offshore oil and gas platforms (Hedd et al. 2016). These platforms are a serious hazard for seabirds in general (Wise et al. 2001, Ronconi et al. 2015), and specifically for these colonies. The wide foraging range of Leach's storm-petrels may also increase their encounter with other threats, such as vessels. Vessel traffic in the North Atlantic is abundant, and threats associated with this traffic come in the form of collisions with vessels through light attraction, and contamination through oil discharge (Wiese and Robertson 2004, Montevecchi 2006). In Atlantic Canada, 97% of the stranded birds on offshore platforms and vessels are storm-petrels (Environment Canada 2014).

In Chapter 3, I related ocean conditions during the breeding season to foraging movements of Leach's storm-petrels and reproductive success. I found that reproductive success was lower when longer foraging trips were performed during incubation. Additionally, foraging trips were longer with warmer SST. As central-place foragers, breeding seabirds are dependent on the resources available within the foraging range from the colony. Increases in SST could lead to a decrease in prey availability or a shift in prey location (Gjerdrum et al. 2003). As a result, adults possibly had to forage further away from the colony and stay at sea for longer intervals, hence reducing treproductive success (Hennicke and Culik 2005, Berlincourt and Arnould 2015). Predictions for future trends of the NAO suggest that NAO will stay positive (Visbeck et al. 2001, Folland et al. 2009), which is dire for the Leach’s storm-petrel population of the North Atlantic, as results from Chapter 3 suggest that positive NAO index is related to lower reproductive success.

6.1.2 Movement During the Non-Breeding Season

In Chapter 4, I found that Leach's storm-petrels showed variation in the timing of departure, stop-over locations, and wintering grounds. Despite this spatial and temporal variation, some areas of the Atlantic Ocean, such as waters off Newfoundland, and waters associated with the Canary and Benguela currents, appeared to be ecologically important. All these areas have high productivity with a large assembly of seabirds species during the Leach's storm-petrels' non-breeding period (González-Solís et al. 2007, Guilford et al. 2009, Péron et al. 2010, Magnusdottir et al. 2012, McFarlane Tranquilla et al. 2015). In addition, other species, such as humpback whales (*Megaptera novaeangliae*) and leatherback turtles (*Dermochelys coriacea*) also use those areas on a regular basis (Wenzel et al. 2009, Fossette et al. 2014). This suggest that theses areas have a rich biodiversity and should be protected from over-fishing. As it stands, the United Nations Development Program (UNDP) implemented the Benguela Current Large Marine Ecosystem (BCLME) to have sustainable management and use of resources in this region (Cochrana et al. 2009). Similarly, the Canary Current Large Marine Ecosystem (CCLME) created in 2010 has the long-tem goal of reversing the degradation of the CCLME created by over-fishing, to restore the habitat and water quality, and to adopt an ecosystem-based management approach (UNEP 2009).

Current management of pelagic seabirds uses foraging areas of larger seabird species to determine Marine Protected Areas (Le Corre et al. 2012, Young et al. 2015). In the Atlantic Ocean, the Canary Current and the Benguela Current areas were recognized as biodiversity hotspots (Sakko 1998, Grecian et al. 2016). Results of my thesis complement the at-sea surveys reporting the presence of Leach`s storm-petrels in these hotspots (Brown 1979, Camphuysen 2007). By having studies generating information about movement ecology for multiple species with a broad range of body size, and prey requirement, we can better delineate conservation areas.

6.1.3 Tag Deployment

Research presented in this thesis pushes the limits of seabird tracking, because it was the first time that a seabird weighing less than 100 g had been tracked. In turn, this opens up foraging movement research for many small seabird species for which there is a knowledge gap in their at-sea distribution. I deployed geolocators (GLS) to follow foraging (Chapter 2) and migratory movements (Chapter 4) of Leach's storm-petrels. Whereas most seabirds and waders are tracked by attaching devices to a leg band, in my opinion, this technique was not suitable for Leach's storm-petrels due to their long thin legs and their method of foraging, which includes pattering across the ocean surface. Another method commonly used to deploy electronic devices is a leg-loop harness, or backpack (Rappole and Tipton 1991). This method puts the device on the back of the bird, close to the center of gravity, but from my experience, the morphology of storm-petrels is not suited to this method. Indeed, storm-petrels lack strong thighs that keeps the harness in place. Therefore, I chose to suture GLS to the backs of the birds. While the technique is more invasive than a leg band, it allows for GLS to sit closer to a storm-petrel’s center of gravity and is less likely to impair their ability to fly. This technique has been used previously on ducks and large seabirds, with mixed results for retention periods of devices (Houston and Greenwood 1993, Rotella et al. 1993, MacLeod et al. 2008). This method, never used before on small seabirds, will enable researchers to track small seabird species for which little is known regarding their foraging movements. There are two issues with this technique. First, the growth rate of chicks belonging to a tagged adult was lower than control chicks (Chapter 2). Second, the retention through the winter is not optimal (Chapter 4). It appears that sutures worked their way through the thin skin of the storm-petrels, resulting in the loss of the device. Currently, another attachment method is being tested on similar storm-petrels using a modified harness (M. Bolton, pers. comm.). This technique would overcome the drawbacks associated with the suture technique (i.e. invasiveness and low retention rate over long periods), while keeping the GLS close to the center of gravity.

Early studies using tracking devices on birds seldom reported the impacts of such devices (Calvo and Furness 1992), but recently, impacts of tracking devices are commonly the main theme of published research (Adams et al. 2009, Quillfeldt et al. 2012, Jones et al. 2013, Kim et al. 2014, Scandolara et al. 2014). This demonstrates the importance researchers devote to animal welfare and the realization that when effects are detected, behavior acquired from tracking data may not represent that of the rest of the population (Barron et al. 2010).

6.2 Influence of Environmental Variables on Reproductive Success

Foraging areas used by adults and attendant oceanic conditions were determined in Chapter 2. I found that higher SSTa, and lower Chl-a were associated with longer foraging trips, and overall lower reproductive success (Chapter 3). Food availability has a major influence on foraging trip duration (Chaurand and Weimerskirch 1994b, Tveera et al. 1997, Quillfeldt et al. 2003). The main prey source of Leach’s storm-petrels, myctophids, has a restricted temperature tolerance (Suneetha and Salvanes 2001), so as SST increases, potentially resulting in higher SST-a, myctophids may migrate further from colonies. During the chick-rearing period, short foraging trips to access quality prey is key because it affects how often adults feed their chick, and hence chick growth and reproductive success (Quillfeldt et al. 2003). This explains why longer foraging trips, due to the potential changes in foraging locations, may lead to lower reproductive success in my study. When foraging locations are too far from the colony, prey become inaccessible or energetically too costly to reach (Inchausti et al. 2003, Weimerskirch et al. 2012). With increasing SSTs in the Scotian Shelf (Ting et al. 2009, Khan et al. 2013), we can expect a general trend for a decrease in reproductive success in Leach's storm-petrels, leading to a decrease in population size in the coming years. This trend is already noticeable in some Leach's storm-petrel colonies for which recent population estimates have been done (Wilhelm et al. 2015).

6.3 Effect of Mercury on Reproductive Success

Mercury is a highly toxic, non-essential metal, with negative effects on wildlife. In birds, effects include negative impacts on behavior, impaired neurological development, and lower reproductive success (review in Wolfe et al. 1998). With higher levels of mercury detected in Leach's storm-petrels compared to other seabirds (Goodale et al. 2008, Bond and Diamond 2009), it was important to investigate potential effects of mercury on this species. In Chapter 5, I found no correlation between several reproductive parameters and mercury levels, however the birds were not sexed and a potential difference could be observed between the sexes, with females having generally a lower burden than males. It is possible that by separating the sexes, I would have seen a correlation between some reproductive parameters and mercury levels. Birds in general have an effective mechanism of getting rid of mercury through depuration via their feathers. This might enable them to bear large quantities of mercury with limited negative effects from this toxic environmental factor. However, long-term monitoring of the effects of mercury levels, and additive effects of stressors in individuals is necessary, because it is possible that individuals with higher mercury burdens, are more prone to chronic disease (Wolfe et al. 1998).

6.4 Future Directions

Recent population declines at different Leach's storm-petrel colonies, both in the West and East side of the North Atlantic (Robertson et al. 2006, Newson et al. 2008, Murray et al. 2010, Wilhelm et al. 2015) highlight the need to better understand the causes of these declines and should be a priority research topic for this species. These declines resulted in the recent uplisting of Leach's storm-petrel from "least concern" to "vulnerable" by the International Union for the Conservation of Nature (IUCN) Red List (www.iucnredlist.org). Other species of storm-petrels are also in decline (Sydeman et al. 1998). Specifically, we should focus on determining if threats are mostly during the breeding, or the non-breeding season. As mentioned earlier, by their remarkable foraging range, off-shore platforms are within range of Leach's storm-petrels. Interactions with oil and gas off-shore platforms in the North Atlantic require monitoring to evaluate the risk they create for Leach's storm-petrels from many colonies.

Finally, miniaturization of electronic devices will allow tracking of small seabird species, for which there are still significant knowledge gaps regarding foraging movements. Specifically, smaller species in Antarctic regions will be of importance as effects of climate change observed in the polar regions induce broad-scale changes in marine ecosystems, creating new challenges for many organisms (Croxall et al. 2002). Now that tracking of small seabird species is achievable, we should aim to study movement at different life stages. For most seabird species, the movement of juveniles is poorly known, and is often referred to as the "lost years" (Péron and Grémillet 2013). During this juvenile stage, they build their flying and foraging skills. Yet, it is a critical life stage, with birds prone to high mortality and most individuals will not reach adult stage (Warham 1990). In addition, it will be important to determine if monomorphic species such as the Leach's storm-petrel, show sexual segregation in their foraging areas. In larger sexually monomorphic, or dimorphic species where it is well documented (Weimerskirch et al. 1997b, González-Solís et al. 2000, Hedd et al. 2014) sexual segregation is often coupled with a difference in diet. As intra-specific competition may lead to the evolution of sexual segregation of foraging area, and prey choice (Lewis et al. 2002, Thaxter et al. 2009), future research should investigate the sexual segregation of small sexually monomorphic seabird species, both during breeding and non-breeding season, as sexual segregation may have implication for conservation (Phillips et al. 2005).

By determining areas exploited by multiple species throughout the year, and integrating life stage parameters (i.e. age, breeding status, sex), we can develop better conservation approaches to protect marine biodiversity and ocean habitat effectively. Collaborative work to increase sample size of tracked birds, and pooling of information, such as the Seabird Tracking Database (BirdLife International 2004), will also enable policy-makers to make informed decisions that encompass spatial and temporal overlap of species from multiple guilds, as well as potential threats (Lascelles et al. 2016). Once published, all the GLS tracking data from this thesis will be added to the Seabird Tracking Database and contribute information currently lacking for small procellariforms.

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Appendix 1 - Co-authorship and Copyright Release.

Chapter 2 Foraging Movements of Leach's storm-petrels, *Oceanodroma leucorhoa*, During Incubation

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Ronconi, Taylor, and Shutler provided feedback on the study design. Ronconi helped with the field work. Jonsen build the space-state model. All co-authors provided editorial comments on the manuscript.

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Chapter 5 Relationships Among Blood Mercury Levels, Diet, Reproduction, and Return Rate in Leach's Storm-Petrel

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Burgess and Shutler provided feedback on the study design. O'Driscoll and Burgess provided help with interpretation of the results. All co-authors provided editorial comments on the manuscript.

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