MIGRATION ROUTES AND STOPOVER AREAS OF LEACH'S STORM PETRELS *OCEANODROMA LEUCORHOA*

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ABSTRACT

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Little is known about the movements of small seabirds during migration, but such information is important for their conservation. Leach's Storm Petrel *Oceanodroma leucorhoa* is the most abundant seabird in Atlantic Canada, but its population has declined in recent years. Here, we describe trans-equatorial and trans-Atlantic migration movements of 13 Leach's Storm Petrels, which were tracked with geolocators from two breeding colonies in Nova Scotia, Canada: Bon Portage Island and Country Island. Our results indicate that Leach's Storm Petrels have low migratory connectivity and that they use multiple stopover areas and overwintering destinations. Birds with stopover areas at higher latitudes overwintered in the North Atlantic Ocean, either in areas associated with the North Equatorial Current or in waters off Newfoundland and Labrador. Birds with lower-latitude stopover areas overwintered in the South Atlantic Ocean, in areas associated with the Benguela Current off southwestern Africa. We observed greater $\delta^{15}N$ values (indicating higher trophic level) in feathers from birds that migrated south compared to birds that stayed in the Northern Hemisphere, but we observed no difference in $\delta^{13}C$ (which may be interpreted in multiple ways). Species distribution modelling using remotely sensed oceanographic data indicated that high sea surface temperatures and high chlorophyll *a* concentrations were important predictors of habitat use in winter.

Key words: geolocator, Leach's Storm Petrel, migration, *Oceanodroma leucorhoa*, seabird tracking, species distribution modelling, stable-isotope analysis

INTRODUCTION

Seabirds are exposed to threats both in their terrestrial nesting and marine foraging environments (Croxall *et al.* 2012). These threats can lead to lower breeding success, mortality, and, ultimately, population declines. Terrestrial threats, including the introduction of mammalian predators to remote breeding islands, habitat loss, and extreme climatic conditions during the breeding season (Regehr *et al.* 2007, Cadiou *et al.* 2010, Ratcliffe *et al.* 2010, Ropert-Coudert *et al.* 2015), are relatively easy to identify and monitor. In contrast, seabirds can face many at-sea threats that are more difficult to ascertain. Some of these threats include a limitation of food resources due to climate change (Jenouvrier *et al.* 2003, Grémillet & Boulinier 2009, Borstad *et al.* 2011), bycatch from and competition with fisheries (Tasker *et al.* 2000, Tuck *et al.* 2011), pollution (Provencher *et al.* 2015), and off-shore industries (Ronconi *et al.* 2015). Knowing how seabirds use their marine environment is vital for identifying important at-sea habitats and for understanding factors influencing population dynamics. For example, stopover areas are important because birds presumably use these areas to replenish body reserves after energetically demanding breeding seasons or to await favourable weather before moving to other locations (Murray *et al.* 2003, Guilford *et al.* 2009, Egevang *et al.* 2010, Jessopp *et al.* 2013). Therefore, it is essential to know a species' key marine regions to understand phenological threats and stressors and to develop effective conservation and management strategies.

Until recently, little was known about the at-sea habitat requirements of small seabirds (< 100 g) outside of the breeding season, because tracking devices were too large to be carried by these species. However, due to recent miniaturization of data loggers, it is now possible to track smaller species (van der Winden *et al.* 2014). Leach's Storm Petrels *Oceanodroma leucorhoa* are small seabirds (~ 45 g) 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, Wilhelm *et al.* 2015, BirdLife International 2016, Hedd *et al.* 2018). Despite extensive knowledge of the breeding biology and dietary requirements of Leach's Storm Petrels (Ricklefs *et al.* 1987, Stenhouse & Montevecchi 2000, Hedd *et al.* 2009), relatively little is known about 1) their at-sea movements, either during the breeding season or during migration to and from wintering areas (Gaston *et al.* 2008, Bicknell *et al.* 2014, Pollet *et al.* 2014a, c) and 2) whether their diet varies with latitude and wintering area. This information is crucial for understanding how year-round conditions influence the population dynamics of this species.

Banding recoveries of Leach's Storm Petrels from Atlantic Canada indicate that they spend time in the North Atlantic Ocean during the non-breeding season (Gaston *et al.* 2008, Pollet *et al.* 2014b), but at-sea sightings also indicate movement to waters of the Southern Hemisphere (Camphuysen 2007). These observations do not, however, provide information on stopover locations, specific wintering areas, migration routes, or provenance of birds observed at sea. A recent study using geolocators on two individuals provided preliminary information about Leach's Storm Petrel locations and habitat associations during migration (Pollet *et al.* 2014a).

This study confirmed the presence of Leach's Storm Petrels in the North Atlantic during the non-breeding season, over warm and deep waters. However, the study was limited by the small sample size, and it did not provide information on stopover areas. The objectives of the current study were 1) to define stopover locations and refine information on both timing of migration and overwintering destinations, 2) to determine if stable-isotope analysis can differentiate overwintering latitudes and trophic niche separation among migration strategies, and 3) to describe habitat characteristics on the wintering grounds and the resulting distribution of the species.

METHODS

Study species and sites

Leach's Storm Petrel is a small, sexually monomorphic procellariiform that breeds in the Northern Hemisphere (Huntington *et al.* 1996). In eastern North America, these birds arrive at breeding colonies in early May, and females lay a single egg in a burrow in June or July. Incubation lasts approximately 45 days and is performed by both parents, alternating duties every three to six days. After several days of brooding, chicks are fed by both parents for 50–60 days and fledge at about 65 days post-hatch; the adults depart the colony by end of September or early October (Huntington *et al.* 1996). Our study was conducted on Bon Portage Island, Nova Scotia (2012–2016) and on Country Island, Nova Scotia (2013–2014). Bon Portage Island (43°28′N, 065°44′W) is located off the southern tip of Nova Scotia and is the largest Leach's Storm Petrel colony in the province. The current estimate of 39 000 breeding pairs is based on a 2016 survey and represents a 20 % decline since the previous survey in 1998 (Oxley 1999, Pollet & Shutler in press). Country Island (45°06′N, 061°32′W) is located off the Eastern Shore region of Nova Scotia, and a 2013 survey estimated the breeding population at around 11 900 pairs (Environment and Climate Change Canada, unpubl. data). The population here is also in decline (Wilhelm 2017), but the reasons for this are still unclear.

Burrow monitoring

On Bon Portage Island, we annually monitored approximately 300 nest burrows that were marked with uniquely numbered metal tags. We captured breeding adults in their burrows, took morphometric measurements (mass, wing, culmen, and tarsus length), and, if not already ringed, banded them with uniquely numbered Canadian Wildlife Service metal leg rings. After processing the first adult and returning it to its burrow, a lattice of twigs or a curtain of ferns was placed at the burrow entrance

to detect a switch of partner without disturbing incubating adults that had already been processed. Thus, incubating pairs were not disturbed more than twice (Blackmer *et al.* 2004). After hatch and until fledging, chicks were measured weekly for weight, tarsus length, and wing chord.

On Country Island, we annually monitored 80 numbered burrows in a similar manner. Birds were banded, and we took morphometric measures as above. However, time constraints prevented us from measuring chicks on a regular basis, and second adults were captured and identified less frequently.

All animal handling procedures were approved by the Acadia University Animal Care Committee (Protocol #06-09).

Geolocator attachment

To track year-round movements, we deployed geolocators (Global Location Sensors, GLS) on randomly selected adults within our working plots during the late stages of incubation. Adults were of unknown sex and age, and we tagged only one adult per burrow. We deployed a total of 65 GLS on Bon Portage Island over four breeding seasons and 15 GLS on Country Island during the 2013 season (Table 1).

We used GLS tags (MK5740, Biotrack, Cambridge, UK) that weighed 0.9 g and measured 21.9 × 7.9 × 3.8 mm. Each tag was attached to the back of a bird with two subcutaneous sutures, as described in Pollet *et al.* (2014a); attachment took less than 10 minutes per bird, and adults were returned to their burrows immediately following attachment. The total mass of a tag with attaching material was 1.1 g, which is below the accepted 3 % rule (Phillips *et al.* 2003). The average mass (± standard deviation (SD)) 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 Islands, respectively.

Geolocator retrieval

During incubation in the year following GLS attachment, we surveyed burrows of birds that had been tagged the previous season. If an adult was present that had not received a GLS as above, we latticed burrow entrances and made daily checks until the lattice was disturbed, at which point we checked for the presence of a tagged bird. To remove the GLS, we cut the suture and removed the thread. At this point, we also collected the tip of the 10th primary for $\delta^{13}C$ and $\delta^{15}N$ stable-isotope analysis. By checking band numbers, we could also determine if birds had lost their tags.

TABLE 1
Summary of GLS tag deployments, return rates, and tag recoveries on Leach's Storm Petrels breeding on Bon Portage Island (BP) and Country Island (CI), as well as average body mass of tagged and untagged birds

Year	Island	# GLS deployed	# Birds returned	# GLS recovered	Return rate of control birds	Mass of tagged birds (g)	Mass of untagged birds (g)
2012	BP	16	10	1	200/267	46.3 ± 4.3	46.4 ± 4.2
2013	BP	22	15	3	227/416	48.1 ±3.9	46.5 ± 3.4
	CI	15	7	2	-	46.2 ± 3.3	47.2 ± 4.5
2014	BP	17	10	3	209/362	46.3 ± 4.2	47.6 ± 3.9
2015	BP	10	6	4	208/300	47.8 ± 3.0	46.4 ± 3.7

Tag effects

To determine if tags affected inter-annual return rates, we checked for returning adults in all burrows that were occupied in the previous year. We used the same monitoring procedure in each year, with equal effort devoted to finding GLS- and non-GLS birds. We used Fisher's exact tests to compare inter-annual return rates of tagged and untagged birds for Bon Portage Island only. Time restrictions and logistical constraints prevented us from thoroughly monitoring burrows on Country Island to compare return rate of tagged and untagged birds.

Data processing

The GLS tags measured light levels and recorded maximum levels at two-minute intervals. Data from the tags were decompressed, and times of sunrise and sunset were determined from light curves using BAS Track software (Biotrack, Dorset, UK). Data were processed at a light-level threshold of 16 and an angle of elevation of the sun of −4.0°. These settings produced the greatest correspondence with and least deviation from ground-truthed locations for each site. Within the program R (R Development Core Team 2011), we used the "rjags" package to run a Bayesian state-space model to account for errors in the light-level GLS data (Jonsen *et al.* 2013). The model is a modification of the first-difference correlated random walk model that accounts for light-level GLS data (Jonsen *et al.* 2005), and it is described in detail elsewhere (Pollet *et al.* 2014c). During equinox, day length is similar around the globe; hence, latitude cannot be estimated from light levels (Ekstrom 2004). We therefore removed 10 days of data on either side of equinox dates from analysis.

Migration movements

We defined the start of fall migration to be when a bird moved from its breeding colony by more than 600 km, which is the mean distance travelled during breeding seasons on Bon Portage Island (Pollet *et al.* 2014c), and did not return to its colony until the following spring. We defined a stopover area to be when a bird moved less than 0.8° in latitude per half-day for a minimum of 2.5 consecutive days. Due to the lack of accuracy in latitude around the equinoxes, longitude could be a preferred variable (Guilford *et al.* 2009); however, by excluding data around the equinoxes and filtering the data through a state-space model, we believe our method is appropriate to estimate stopover locations. We then took the mean latitude and longitude to determine the location of each stopover. We defined an overwintering location to be the southernmost location within which individuals moved less than 0.8° in latitude per half-day for a minimum of 2.5 consecutive days until locations moved in a northward direction. To determine the maximum distance between a colony and the furthest point reached by each bird, we used the *spDistsN1* function in the "sp" package in R. To illustrate distributions of birds during stopovers and overwintering periods, we determined the Kernel Utilization Distributions for each individual and for all individuals combined using the *kde2d* function from the "MASS" package in R, with a grid size of 0.05° longitude by 0.03° latitude. Bandwidths for latitude and longitude were chosen via Normal Reference Distributions, which account for variance and for the number of latitude and longitude values from which a kernel density is estimated. We set the raster resolution at 50 km and the search radius at 200 km to reflect error associated with GLS locations (Phillips *et al.* 2004).

Stable-isotope analysis

To determine if stable-isotope analysis could differentiate migratory strategies in Leach's Storm Petrels, we collected a flight feather grown during winter. In procellariformes, primary feathers are molted during the non-breeding season, starting distally from the first primary (Pyle 2008); hence, the 10th primary feather bears isotope signatures reflecting winter diet. Individual samples were kept in paper envelopes and shipped to the Stable Isotopes in Nature Laboratory at the University of New Brunswick (Fredericton, New Brunswick, Canada). Simultaneous determinations of carbon and nitrogen stable-isotope values were made through an elemental analyzer mass spectrometer. Stable isotopes were quantified as the deviation from a standard using the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X was ^{13}C or ^{15}N and $R_{sample}/R_{standard}$ was the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. Carbon signatures decrease as ones moves away from the equator and as one moves from a benthic to a pelagic environment, whereas $\delta^{15}N$ values increase in a stepwise manner with trophic level (Rubenstein and Hobson 2004).

Habitat preferences determined by SDM

To characterize habitat preferences of Leach's Storm Petrels during winter, predictive Species Distribution Models (SDMs) were developed using the maximum-entropy method (Phillips *et al.* 2006) with the software MaxEnt (version 3.3.3). This program models geographic distribution using presence-only species records and is better suited than other modeling methods for small sample sizes (Hernandez *et al.* 2006, Wisz *et al.* 2008). We set aside 25 % of the data, randomly chosen by the software, for spatial evaluation of models, and we used a bootstrap procedure to generate confidence intervals of estimates based on 10 replicates. Replicates were set with a convergence threshold of 1×10^{-5} with 500 iterations and 10 000 background points. To avoid bias from over-representation of points in the Northern Hemisphere due to incomplete tracks, only complete tracks were used in the final model. We used both static and dynamic environmental variables that were selected based on data availability and likely biological relevance for seabirds (Arcos *et al.* 2012, Watson *et al.* 2013). The static variables chosen were bathymetry (m below chart datum) and slope (degrees). The dynamic variables were winter sea surface temperature (SST, °C, November through April), winter chlorophyll *a* concentrations (chl *a*, mg·m^{-3}), and surface current speed (m·s^{-1}). All these variables are known to be strong predictors of seabird distributions (Pittman & Huettmann 2006). Data were downloaded from the Global Marine Environment Dataset website (Basher *et al.* 2014); they had a spatial resolution of 5 arcmin (equivalent to about 9 km at the Equator), which is more accurate than GLS data (~ 180 km resolution). In general, grain size and locational errors do not strongly affect predictions from SDMs (Guisan *et al.* 2007). We generated response curves of the environmental variables and performed a jackknife test to evaluate the relative contributions of each environmental variable to the model. Each MaxEnt predictive model was evaluated using the area under the curve (AUC) of the receiver operator characteristic, which evaluated how well model predictions discriminated among locations where observations were obtained versus random background data (pseudo-absence points). AUC statistics can range from 0 to 1, where an AUC of 0.5 indicates that model performance is equal to that of a random prediction and an AUC

of 1 indicates perfect discrimination between suitable and non-suitable habitat. However, for presence-only and pseudo-absence data, the maximum possible AUC is less than one (Phillips *et al.* 2006). The SDM returns two key results: a permutation importance and an AUC. The permutation importance for each variable is a measure of its contribution to the model; the permutation importance of all variables sums to 100. The AUC is the probability that a random-presence location will be ranked higher than a random-absence location, as an indication of how well a model performed. Means are expressed ± SD.

RESULTS

Across all years and both populations, 60 % (48 of 80) of tagged birds returned, of which 27.1 % (13 of 48) retained their tags (Table 1). Of the 13 GLS recovered, six worked until retrieval and the remaining seven stopped working at some time during migration (16 October to 07 February). Return rates did not differ significantly between tagged and untagged birds for any year (Fisher's exact tests, *P* = 0.83, 0.37, 0.99, and 0.99 for 2012/13, 2013/14, 2014/15, and 2015/16, respectively). On all tagged birds that returned with or without their GLS, skin at the suture sites appeared intact, and no scar tissue or infections were detected.

Fall migration

We obtained departure dates for four birds, each from a different pair, breeding on Bon Portage Island: three of these birds successfully fledged a chick and departed the colony between 14 and 23 October 2013 (Fig. 1A), while one failed breeder departed on 14 August 2013. The remaining birds from Bon Portage Island and those from Country Island all bred successfully, and they departed their colonies between 13 September and 02 October. Precise departure dates could not be determined because the dates coincided with the fall equinox, when location estimations from GLS are not
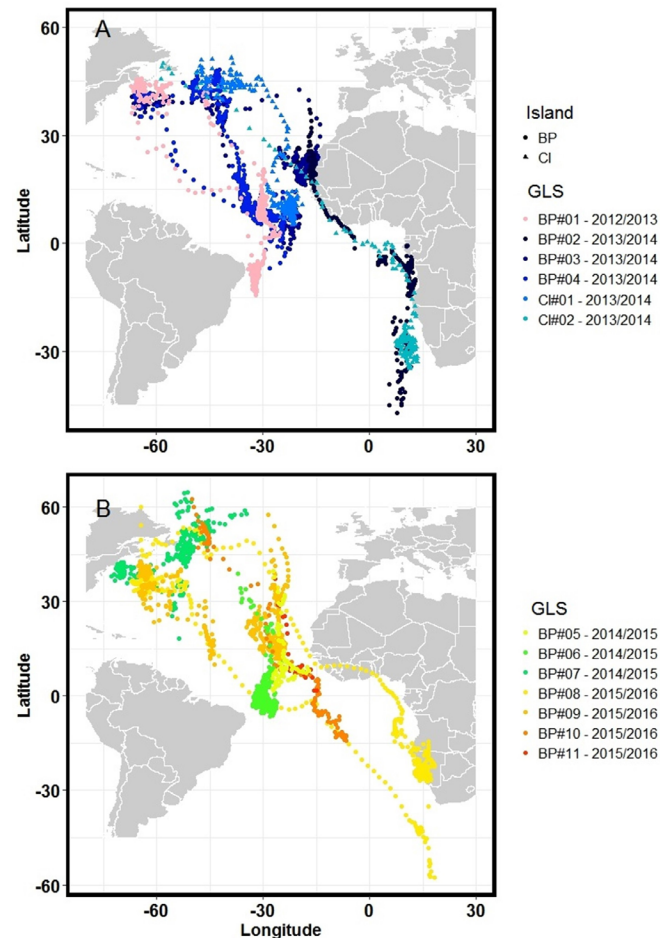

Fig. 1. Latitude of Leach's Storm Petrels tracked using geolocators (GLS) from Bon Portage Island (BP, circles) and Country Island (CI, triangles), Nova Scotia, Canada, relative to time of year (A = October, B = November–March, C = April–June). Horizontal lines represent the latitude for BP, CI, and the equator.

Fig. 2. Migration routes of Leach's Storm Petrels tracked using geolocators (GLS) from Bon Portage Island (BP, circles) and Country Island (CI, triangles), Nova Scotia, Canada in (A) 2012/13 and 2013/14; and (B) 2014/15 and 2015/16.

possible. All but one tagged bird (n = 12) started their migration by following a path southeast across the North Atlantic Ocean towards the Macaronesia archipelagos (Fig. 2). The remaining bird started its migration on 15 October by travelling north towards Greenland (Fig. 2); unlike the other tracked birds, it never travelled towards the Macaronesia archipelagos.

Stopover areas

We identified two stopover areas used by more than one tracked Leach's Storm Petrel (Fig. 3A). The first was used by birds from both Bon Portage Island (n = 5) and Country Island (n = 1) and was situated in the Western North Atlantic, southeast of the Grand Banks of Newfoundland and Labrador (40°N, 45°W; Fig. 3A), approximately 1 952 ± 254 km from breeding colonies. The mean time spent at this stopover area was 15.2 ± 8.1 d. The second area, also used by birds from both islands (Bon Portage Island n = 3, Country Island n = 1), was situated between the Macaronesia archipelagos and the North Equatorial Current (15°N, 20°W), approximately 5 128 ± 175 km from colonies. The

mean time spent at this stopover area was 13.4 ± 11.8 d, which was not significantly different from the amount of time spent in the Western North Atlantic ($F_{1,11} < 0.1$, $P = 0.77$). In addition, one bird made a four-day stopover in the Guinea Current, which is off the Ivory Coast, approximately 6 913 km from its colony. That same bird also made a nine-day stopover off Angola, 9 448 km from its colony.

Overwintering areas

Five of the six birds that made stopovers in the northwest Atlantic overwintered in the equatorial zone between Macaronesia and the northeast tip of Brazil, in areas associated with the Canary Current, the Guinea Current, the North Equatorial Current, and the South Equatorial Current (Fig. 3B). The sixth bird did not make a stopover and overwintered in the North Equatorial Current. All birds arrived at their overwintering areas between 06 and 27 December (Fig. 1B) and stayed for an average of 67.4 ± 15.3 d. The average distance between breeding colonies and this overwintering area was 6 600 ± 400 km. One bird from Bon Portage Island made a stopover off Newfoundland and Labrador then headed to waters off Greenland; it then travelled south again and spent the remainder of the winter in waters off Newfoundland and Labrador, only 1 300 km from its colony.

Two birds with stopover areas in the Macaronesia region and the one bird with stopover areas off the Ivory Coast and Angola overwintered in waters off southwestern Africa (Figs. 2 & 3). Birds arrived at their overwintering areas between 14 November and 5 January. The distance between breeding colonies and these overwintering areas was 12 000 ± 820 km. Birds stayed at their overwintering areas for an average of 44.0 ± 2.8 d, which is not significantly different from the times spent at overwintering areas in the Northern Hemisphere ($F_{1,5} = 4.1$, $P = 0.1$).

For the remaining birds (n = 4), their GLS stopped working during fall migration (30 December 2013, 16 November 2014, 16 October 2015, and 19 December 2015); therefore, their final winter destination could not be determined. Three of those birds were still in the Macaronesia region and one bird was farther south (15°S) when their GLS failed.

Spring migration

We obtained spring migration data for four birds that overwintered in the central Atlantic. Spring migration was initiated with birds heading northwest between 31 March and 23 May (Fig. 1C). Spring migration was rapid, lasting on average 14.7 ± 5.5 d (range: 10–22 d) with no stopovers. We also obtained spring migration data for one bird from Bon Portage Island that overwintered off southern Africa. Its spring migration began on 12 April, lasted 24 d, and did not contain a stopover. The GLS of the remaining birds stopped working before spring migration.

Stable-isotope analysis

Average stable-isotope values from the 10th primary feathers (n = 13) were 12.41 ± 1.20 ‰ for $\delta^{15}N$ and −17.92 ± 0.79 ‰ for $\delta^{13}C$. Values of $\delta^{15}N$ for birds migrating to the Southern Hemisphere were higher than the average (ANOVA $F_{1,11} = 17.9$, $P = 0.001$), which suggests that these birds spend time at a higher trophic level than those remaining in the Northern Hemisphere.
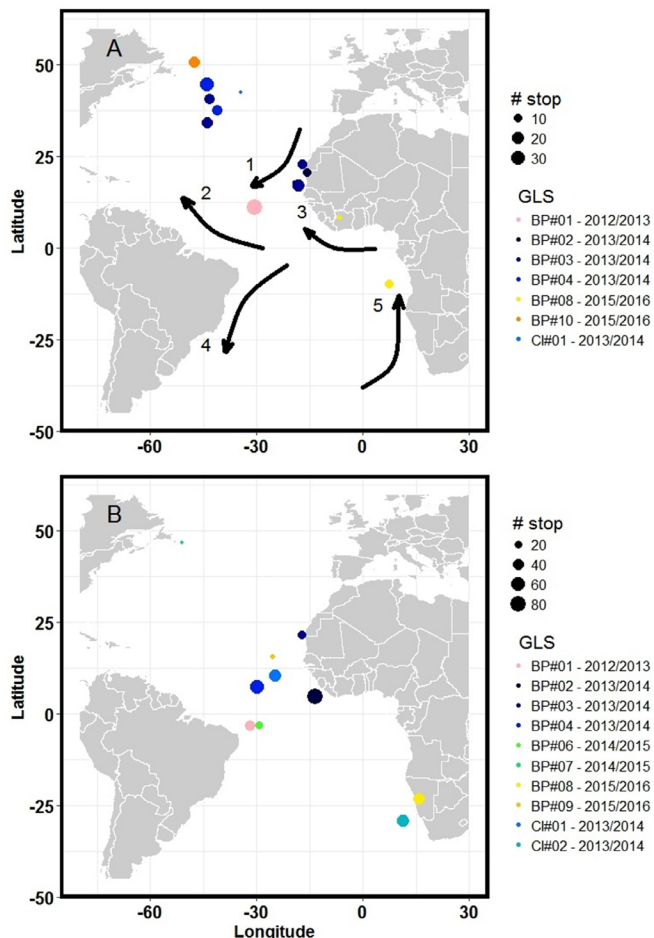

Fig. 3. Locations of stopover (A) and overwinter (B) areas for Leach's Storm Petrels from Bon Portage Island and Country Island, Nova Scotia, Canada. For each panel, point sizes are proportional to the length of stopovers, in days. Locations of major currents mentioned in the text are shown: 1—Canary Current; 2—North Equatorial Current; 3—Guinea Current; 4—South Equatorial Current; 5—Benguela Current.

There was no difference in $\delta^{13}C$ between the two hemispheres ($F_{1,11}$ = 1.8, P = 0.20, Fig. 4).

Habitat use determined by SDM

In the full model, the slope variable had a very low permutation importance, and the AUC was lower than in the model without the slope. This variable, therefore, was removed from the final model. Overwintering habitat for our tagged birds was best characterized by SST and chl *a*, which had permutation importance values of 50.10 and 29.95, respectively. The probability of presence of Leach's Storm Petrel was greater with higher SST and higher chl *a* values (Figs. 5A & 5B). Depth and surface currents had low permutation importance values (11.24 and 8.71, respectively). The model had a high performance (AUC = 0.84 ± 0.01), and it predicted all the wintering areas where tracked birds were located; waters associated with the Equatorial and Guinea currents had the highest probabilities of occurrence (Fig. 6C).

DISCUSSION

In this study we obtained full or partial migration tracks from 13 Leach's Storm Petrels breeding at two colonies in Nova Scotia. Our data provided new insights into migration patterns and habitat use in the Atlantic Ocean. Whereas some birds remained in the North Atlantic, as previously described (Pollet *et al.* 2014a), others travelled farther and overwintered off South Africa. One bird remained closer to its colony and overwintered off Newfoundland after a stopover near Greenland. At this point, it would be premature to estimate the proportions of birds from these colonies that perform each type of migration, due to our low GLS tag recovery rate.

We found no difference in return rates of tagged versus untagged birds, but over 70 % of the birds did not retain their GLS tag. We detected no signs of scarring or infection at tag attachment sites, and

we presumed that the non-absorbable suture worked its way through the skin, which is relatively thin in birds (Bennett & Harrison 1994). External devices may have effects on the birds in addition to return rate, such as stress levels, body condition, or offspring condition (Barron *et al.* 2010, Elliott *et al.* 2012). Thus, we chose to deploy GLS tags via sutures to the back rather than a ring on the leg to keep the extra weight close to the birds' centre of gravity (Lameris & Kleyheeg 2017). Tracking devices are getting smaller and deploying them for long periods on the legs of storm petrels might soon become the norm. Despite the potential effects of the tags, individuals in this study had widely variable migration patterns, and those movements agreed with at-sea observations of storm petrel concentrations (Huntington *et al.* 1996, Camphuysen 2007).

Like Arctic Terns *Sterna paradisaea* and Sooty Shearwaters *Ardenna grisea*, for example (Egevang *et al.* 2010, Hedd *et al.* 2012), tracked Leach's Storm Petrels migrated in a general clockwise pattern around the North Atlantic Gyre, which is associated with global wind patterns. Stopovers are thought to be a time of intense foraging that serves a refuelling function (Guilford *et al.* 2009; Dias *et al.* 2011). Birds tracked in this study made stopovers and/or overwintered in the northwest Atlantic (i.e., southeast of the Grand Banks), the Northern and Southern Equatorial currents, and the Canary and Guinea currents; they also used waters associated with the Benguela Current for an overwintering area.

Waters southeast of the Grand Banks are nutrient-rich and thus abundant in prey items, due to the mixing of cold water from the Labrador Current and warm water from the Gulf Stream. This
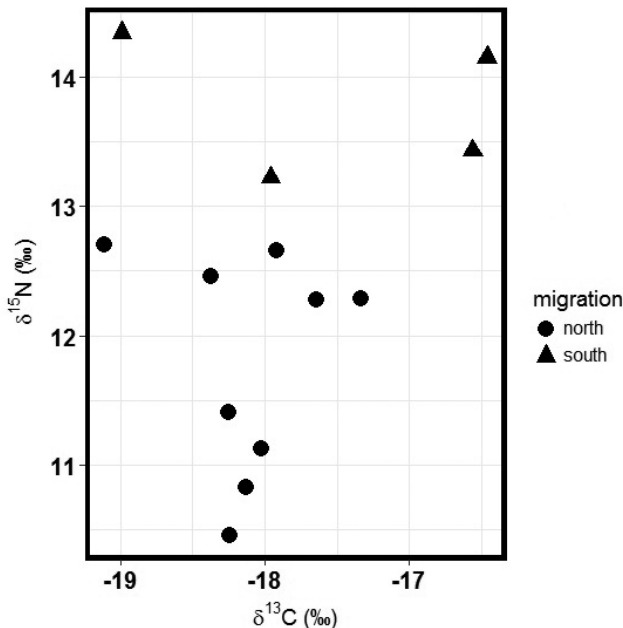

Fig. 4. Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in the 10th primaries of Leach's Storm Petrels migrating to the Southern (triangles) or Northern hemisphere (circles).
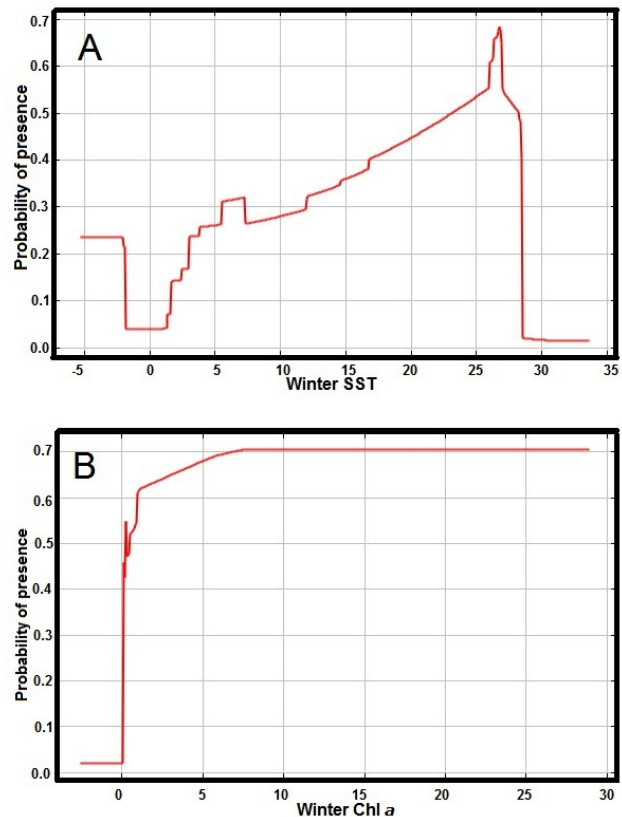

Fig. 5. Response curve of Leach's Storm Petrels to (A) winter sea surface temperature (SST, °C) and to (B) winter chlorophyll *a* (Chl *a*, log scale) concentration from our Species Distribution Model.

area is used as a stopover by other seabirds, including Long-tailed Jaeger *Stercorarius longicaudus*, Manx Shearwater *Puffinus puffinus*, and Sabine's Gull *Xema sabini* (Guilford *et al.* 2009, Stenhouse *et al.* 2012, Gilg *et al.* 2013), and as an overwintering area by species such as Great Skua *Stercorarius skua*, Little Auk *Alle alle*, Thick-billed Murre *Uria lomvia*, and Common Murre (*U. aalge*; Magnusdottir *et al.* 2012, Mosbech *et al.* 2012, McFarlane Tranquilla *et al.* 2015).

Waters associated with the Northern and Southern Equatorial currents have high SST and high productivity (Christian & Murtugudde 2003). These waters are used as overwintering areas by Zino's Petrel *Pterodroma madeira* and Desertas Petrel *P. deserta* (Ramos *et al.* 2016).

Like the Grand Banks, waters associated with the Canary Current have nutrient-rich upwelling (Barton *et al.* 1998), which likely explains the presence of several migrating seabird species (Grecian *et al.* 2016). Waters associated with the Guinea Current are also highly productive, thanks to strong tidal current and river runoff (Stobberup *et al.* 2005). Like other currents mentioned in our study, the Guinea Current is an area where many seabird species overwinter (Brown 1979).

Waters associated with the Benguela Current are areas of high productivity used by many overwintering seabird species from the Northern Hemisphere and species breeding in the Southern Hemisphere (González-Solís *et al.* 2007, Grémillet *et al.* 2008, Pichegru *et al.* 2009, Péron *et al.* 2010, Ronconi *et al.* 2018). This area benefits from strong winds and a narrow continental shelf, which create strong marine upwellings and productive ecosystems that are beneficial for marine species (Shannon & Field 1985, Heileman & O'Toole 2008).

Our results indicated that Leach's Storm Petrels from two Nova Scotian colonies had several different migratory strategies. Some birds undertook longer migrations to waters off southern Africa and spent less time at their overwintering areas (albeit not significantly so), while others stayed in the northern Atlantic Ocean during winter. This difference in strategies for trans-equatorial migrants is not unique. For example, González-Solís *et al.* (2007) tracked Cory's Shearwaters *Calonectris borealis* from three different colonies and noted that they used widely separated wintering areas within the Atlantic Ocean; Kopp *et al.* (2011) found that South Polar Skuas *Stercorarius maccormicki* breeding in the same colony can spend their winter in two different oceans. Results from our δ^{15}N analysis suggested that birds overwintering off southern Africa fed at a higher trophic level than storm petrels wintering elsewhere. However, the stable-isotope analysis did not detect a difference in δ^{13}C between individuals migrating south and those staying in the northern Atlantic Ocean, which suggests that δ^{15}N is a better predictor of migration strategies. This capacity to detect differences in migration patterns through stable-isotope analysis has been previously evaluated in Bulwer's Petrel *Bulweria bulwerii*, Sooty Shearwater, and Cory's Shearwater (Ramos *et al.* 2009, Thompson *et al.* 2015, Cruz-Flores *et al.* 2018). Our results must be viewed with caution, given our small sample size. In any case, based on information acquired through GLS, we suggest that individual Leach's Storm Petrels may use different migratory strategies, with birds from the same colony migrating to different areas.

Fig. 6. Overwintering home range (50 %) Kernel Utilization Distributions of combined data for Leach's Storm Petrels tracked from Bon Portage Island and Country Island, Nova Scotia, Canada. Data are laid over A) sea surface temperature (SST, °C); B) chlorophyll *a* concentration (Chl *a*, log scale); and C) probability of occurrence, from low (pink) to high (green), based on the environmental variables used in a maximum-entropy Species Distribution Model.

The SDM indicated high probabilities of presence around the Northern and Southern Equatorial currents, as well as the Canary, Guinea, and Benguela currents. This pattern matched the observed overwintering distributions of most individuals, despite our low sample size. SDMs based on GLS tracks, which have low accuracy, tended to have similar AUC values to models run with Platform Terminal Transmitters, which are known to have a much higher
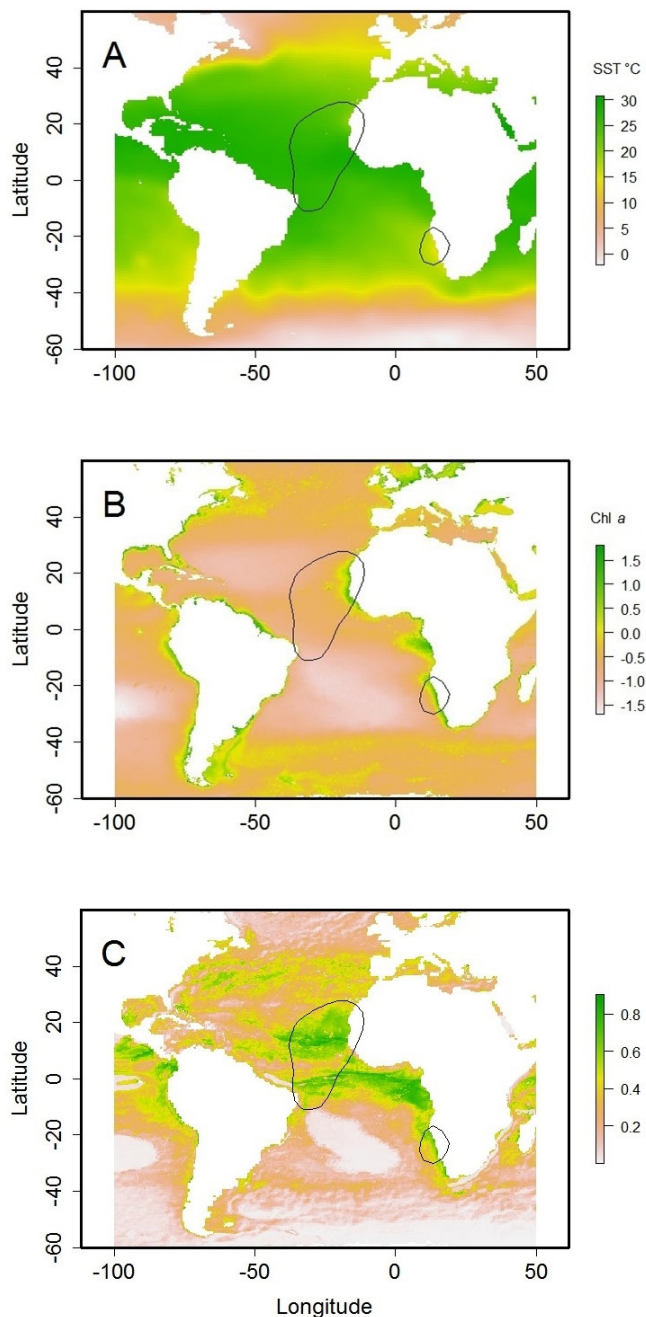
accuracy (Quillfeldt *et al.* 2017); hence, discrepancies between the SDM and our results may have resulted from our choice of environmental variables rather than the type or accuracy of the devices used. A larger sample size is required for more accurate modelling, because there appears to be low migratory connectivity within our small sample and because wide distributions tend to overinflate the performance of these models (Bean *et al.* 2012, van Proosdij *et al.* 2016). Other environmental variables, such as surface current, eddy kinetic energy, and distance to seamount might have improved the model. To evaluate the generality of this model to other Leach's Storm Petrel colonies, we need to validate it with tracking data from other North Atlantic colonies. However, we note that generalizing the results of our SDM should be treated with caution, because a recent study extrapolating an SDM obtained from two seabird colonies had poor transferability to a third colony (Torres *et al.* 2015).

Despite the potential for inter-colony biases (Torres *et al.* 2015), we found that individuals from different colonies overwintered in the same area and that individuals from the same colonies overwintered in different areas. Among seabirds, Cory's and Sooty Shearwaters provide similar examples of individuals from one colony using multiple overwintering locations (Shaffer *et al.* 2006, González-Solís *et al.* 2007). Previous researchers have suggested that an individual's overwintering location is heritable (Kopp *et al.* 2011), and Bicknell *et al.* (2014) documented inter-population connectivity and prebreeding movements among Leach's Storm Petrel colonies spanning the North Atlantic. Hence, variation in overwintering areas from birds originating from the same colony could be the result of historical movement among colonies. Age, sex, and experience also influence migration movements and overwintering areas, but in our study, we were unable to determine the age or experience of tracked individuals (see Weimerskirch *et al.* 2014, Haug *et al.* 2015, Phillips *et al.* 2017).

Our findings indicate the potential importance of the North Equatorial Current for Leach's Storm Petrels as both a stopover and an overwintering location, although this conclusion must be viewed with caution, given that our observations are limited to a small number of birds. Nonetheless, our results suggest that Leach's Storm Petrels may have a range of migration strategies. If this is true, this variability might make the species more adaptable to broad-scale climate change or spatially restrictive threats (Catry *et al.* 2011, Raine *et al.* 2013), but it would not explain the observed declines in populations. More tagging of other breeding populations and tagging of the same individuals over several winters could help us get a better sense of migration and overwintering habitat requirements.

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