


Year-round movements of sympatric Fork-tailed (*Oceanodroma furcata*) and Leach's (*O. leucorhoa*) storm-petrels

Luke R. Halpin,^{1,6,7}  Ingrid L. Pollet,² Christopher Lee,³ Ken H. Morgan,⁴ and Harry R. Carter⁵

¹Halpin Wildlife Research, Vancouver, British Columbia V6G 1J3, Canada

²Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada

³Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

⁴Canadian Wildlife Service, Environment and Climate Change Canada, Sidney, British Columbia V8L 4B2, Canada

⁵Carter Biological Consulting, Victoria, British Columbia V8S 4S8, Canada

Received 25 March 2018; accepted 28 May 2018

ABSTRACT. Long-distance movements are characteristic of most seabirds in the order Procellariiformes. However, little is known about the migration and foraging ranges of many of the smaller species in this order, especially storm-petrels (Hydrobatidae). We used Global Location Sensors to document the year-round movements of sympatrically breeding Fork-tailed Storm-Petrels (*Oceanodroma furcata*) and Leach's Storm-Petrels (*O. leucorhoa*) from the Gillam Islands located northwest of Vancouver Island, British Columbia, Canada. In 2016, breeding Fork-tailed ($N = 5$) and Leach's ($N = 2$) storm-petrels traveled maximum distances of ~1550–1600 km from their colony to a region that has a wide shelf with major canyons creating a highly productive foraging area. After the breeding season, Fork-tailed Storm-Petrels ($N = 2$) traveled to similar areas west of the Gillam Islands, a maximum distance of ~3600 km from the breeding colony, and remained in the North Pacific Ocean and north of the Subarctic Boundary for an average of 5.4 mo. Post-breeding Leach's Storm-Petrels ($N = 2$) moved south to the Eastern Tropical Pacific, west of central Mexico, Ecuador, and northern Peru, an estimated maximum distance of ~6700 km from their breeding colony, and remained there for an average of 7.2 mo. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analyses of feathers revealed niche separation between Fork-tailed ($N = 21$) and Leach's ($N = 53$) storm-petrels. The wide range of $\delta^{15}\text{N}$ values in the feathers of Leach's Storm-Petrels ($N = 53$) suggests that they foraged at a variety of trophic levels during the non-breeding season. Our results demonstrate that storm-petrels have large core foraging areas and occupy vast oceanic areas in the Pacific during their annual cycle. However, given the coarse precision of Global Location Sensors, additional study is needed to identify the specific areas used by each species during both breeding and non-breeding periods.

RESUMEN. Movimientos anuales de los simpátricos Paíño rabihorcado (*Oceanodroma furcata*) y Paíño boreal (*O. leucorhoa*)

Los movimientos a larga distancia son característicos de la mayoría de las aves marinas del orden Procellariiformes. Aun así, poco se sabe de la migración y los rangos de forrajeo de las especies más pequeñas del orden, especialmente los petreles de las tormentas o paíños (Hydrobatidae). Usamos Sensores de Ubicación Global para documentar los movimientos durante todo el año de dos especies que crían simpátricamente, el Paíño rabihorcado (*Oceanodroma furcata*) y el Paíño boreal (*O. leucorhoa*), desde las Islas Gillam ubicadas al noroeste de la Isla de Vancouver, Columbia Británica, Canadá. En 2016, los paíños rabihorcados ($N = 5$) y boreales ($N = 2$) reproductivamente activos viajaron distancias máximas de ~1550–1600 km desde su colonia a una región que tiene una placa ancha con grandes cañones que crean un área de forrajeo altamente productiva. Luego de la temporada reproductiva, los paíño rabihorcados ($N = 2$) viajaron a áreas similares al oeste de las Islas Gillam, una distancia máxima de ~3600 km desde la colonia reproductiva, y se mantuvieron en el Océano Pacífico Norte y al norte del Límite Subártico por un promedio de 5.4 meses. Los paíño boreales ($N = 2$) post reproductivos se movieron al sur al Pacífico Tropical del Este, al oeste de México central, Ecuador, y el norte de Perú, una distancia estimada de ~6700 km desde de su colonia reproductiva, y se quedaron ahí por un promedio de 7.2 meses. Los análisis de isótopos estables de carbono ($\delta^{13}\text{C}$) y nitrógeno ($\delta^{15}\text{N}$) en plumas revelaron una separación de nichos entre los paíños rabihorcados ($N = 21$) y boreales ($N = 53$). El amplio rango de valores de $\delta^{15}\text{N}$ en las plumas de los paíños boreales ($N = 53$) sugiere que forrajearon en una variedad de niveles tróficos durante la temporada no reproductiva. Nuestros resultados demostraron que los paíños tienen áreas de forrajeo amplias y que ocupan vastas áreas oceánicas en el Pacífico

⁶Corresponding author. Email: lukehalpin@gmail.com

⁷School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

durante su ciclo anual. Sin embargo, dada la precisión poco fina de los Sensores de Ubicación Global, estudios adicionales son necesarios para identificar las áreas específicas usadas por cada especie tanto durante los periodos reproductivos como los no reproductivos.

Key words: geolocation, migration, pelagic seabirds, seabird distribution, stable isotopes

Tube-nosed seabirds in the order Procellariiformes are well-known as central place foragers with large ranges during the breeding season and even longer distance movements when not breeding (Shaffer et al. 2006, Rayner et al. 2016, Clay et al. 2017). However, we lack information about the foraging ranges and migratory movements of many seabirds in the order, particularly the smaller species. As highly pelagic long-distance migrants, many seabirds embark on extended migratory journeys, including trans-hemispheric movements to marine regions far removed from breeding areas. Conditions in these distant marine regions during the non-breeding period may influence their survival and reproductive performance in subsequent breeding seasons (Sorensen et al. 2009, Harrison et al. 2011). Therefore, additional study of migration routes, non-breeding areas, and foraging ranges is needed for a more complete understanding of life histories and behavior (Nathan et al. 2008).

In many parts of the world, storm-petrel populations are reported to be declining (Robertson et al. 2006, Newson et al. 2008, Fife et al. 2015). In the northeast Pacific Ocean, the number of storm-petrels is estimated to be in the millions (Harris 1974, SOWLS et al. 1978, Rodway 1991, Briggs et al. 1992, Boersma and Groom 1993), but information about their breeding-season foraging distributions and wintering areas is limited (Huntington et al. 1996, Boersma and Silva 2001). The year-round range of Fork-tailed Storm-Petrels (*Oceanodroma furcata*) is thought to be limited to the North Pacific Ocean, the Bering Sea, and the Sea of Okhotsk (Boersma and Silva 2001, Kenyon et al. 2009). Their breeding colonies are located on islands throughout the eastern North Pacific, ranging from northern California to Alaska and, in the northwest Pacific, in Russia (Boersma et al. 1980, Boersma and Groom 1993). In Pacific Canada, large breeding colonies are located in the Haida Gwaii archipelago, British Columbia, and along the northwest coast of Vancouver Island, British

Columbia (Rodway 1991). An estimated 300,000–1.3 million individuals nest in British Columbia (Rodway 1991, Boersma and Groom 1993), with a global population estimate of 5–10 million birds (Boersma and Groom 1993, Boersma and Silva 2001).

Leach's Storm-Petrels (*O. leucorhoa*) range widely throughout the Pacific and Atlantic oceans, breeding in sympatry with Fork-tailed Storm-Petrels in the north and northeast Pacific (Huntington et al. 1996). Breeding colonies are located on islands throughout the Northern Hemisphere (Huntington et al. 1996). British Columbia supports a breeding population of Leach's Storm-Petrels estimated to exceed 1 million birds (Rodway 1991). The global breeding population was estimated to exceed 10 million individuals (Boersma and Groom 1993, Huntington et al. 1996), but recent information indicates that numbers are declining in many parts of the world (Robertson et al. 2006, Newson et al. 2008, Fife et al. 2015).

After breeding, storm-petrels need to replenish body reserves and replace worn plumage in preparation for the next breeding season. Analysis of stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) in feathers grown during the non-breeding period is frequently used to infer trophic level, latitude, or relative reliance on inshore vs. offshore habitats (Furness et al. 2006, Inger and Bearhop 2008, Quillfeldt et al. 2010). Isotopic values of feathers are metabolically inert and primary feathers of storm-petrels grown during the non-breeding season (Ainley et al. 1976) maintain isotopic signatures as a record of diet composition during this period (Bearhop et al. 2002). The heavy isotope of nitrogen (^{15}N) is incorporated into the tissues of a consumer from its diet, resulting in stepwise enrichment (or depletion) in ^{15}N at each trophic level (Kelly 2000). Conversely, $\delta^{13}\text{C}$ is linked to primary productivity, with trophic fractionation increasing the $\delta^{13}\text{C}$ in a consumer's tissues by 0.5–1‰ relative to its trophic level (Michener and Kaufman 2007).

Therefore, $\delta^{13}\text{C}$ is typically used to infer either foraging in nearshore vs. offshore waters (Hobson et al. 1995) or latitude (Cherel and Hobson 2007).

We combined Global Location Sensor tracking and stable isotope analysis to examine the year-round movements of Fork-tailed and Leach's storm-petrels from populations in the North Pacific Ocean. Our main objectives were to: (i) identify the marine foraging ranges and core-use areas of birds tracked during the breeding season from a mixed-species colony on Gillam Island ($50^{\circ}26'\text{N}$ $127^{\circ}58'\text{W}$) in Quatsino Sound, northwest of Vancouver Island, British Columbia, Canada, and (ii) describe the migratory movements and identify non-breeding core-use areas of Fork-tailed and Leach's storm-petrels.

METHODS

Geolocator programming and deployment. We used Intigeo-P65A11-7-sea Global Location Sensors (Migrate Technology Ltd., Cambridge, UK) to estimate the year-round movements of Fork-tailed and Leach's storm-petrels. Global Location Sensors (hereafter, GLS tags) record changes in ambient light-levels over time that are used to estimate locations. Mean estimates (\pm SD) of spatial error of positions derived from GLS data in temperate polar regions have ranged from 186 ± 114 km (Phillips et al. 2004) to 202 ± 171 km (Shaffer et al. 2005). Despite their coarse precision relative to positions derived from devices using the global positioning system (GPS, $< 10 \pm 5$ m, Hulbert and French 2001) and ARGOS satellites ($\sim 1\text{--}3$ km, Burger and Shaffer 2008), GLS tags are nonetheless considered suitable for assessing the at-sea distribution and movements of seabirds (Phillips et al. 2004, Quillfeldt et al. 2017).

Each GLS tag used in our study had a protruding 7-mm light pipe to prevent plumage-shading of the light sensor, and two plastic tubes (1-mm-diameter) at each end for suture attachment. Prior to GLS deployment, we calibrated GLS tags by activating them at a known location in an area free of artificial light, and within 10 km of the study colony for a minimum of 4 d. GLS tags retrieved in 2017 were re-calibrated in the same location for at least 2 d to account for changes in

opacity of the GLS light sensors between deployment and recapture.

Storm-petrels were captured in their nests and fit with GLS tags during daylight hours. We fit 11 incubating Fork-tailed Storm-Petrels and 30 incubating Leach's Storm-Petrels with GLS tags between 19 and 22 May and between 27 June and 1 July 2016, respectively. GLS tags were attached to the back of each bird (between the scapulae) using sutures (Ethicon Prolene 4-0, FS-2.19 mm, Ethicon US LLC, Cincinnati, OH, USA). We sterilized skin at suture sites beneath contour feathers between scapulae with Povidone-iodine, followed by 70% ethanol to remove residual iodine solution. We then lifted the skin between the scapulae and threaded sutures at the front and rear ends of the GLS tags at 1.5-cm distance between sutures. A small strip of Tesa[®] tape (4651, Tesa Tape Inc., Charlotte, NC, USA) was cut to fit the length of the underside of the GLS tags to facilitate straightforward removal of the device should the need occur. One drop of glue (LePage[®] Gel Control, Henkel, Rocky Hill, CT, USA) was placed on the taped underside of the GLS tags, which were then placed on contour feathers before we tied sutures. Each suture was tied with a surgical knot followed by ≥ 3 double square knots. Birds were then returned to their nests. The entire procedure took < 10 min.

Weighing 0.8 g, GLS tags represented $\sim 1.5\%$ of the mean body mass of adult Fork-tailed Storm-Petrels (55.1 ± 3.8 [SD] g; $N = 12$), and $\sim 1.9\%$ of adult Leach's Storm-Petrels (41.9 ± 3.9 [SD] g; $N = 35$), consistent with guidelines for reducing deleterious effects of telemetric devices on birds ($\sim 3\text{--}5\%$) (Phillips et al. 2003, Barron et al. 2010). To reduce risk of nest abandonment, we only selected birds that had begun incubation and had eggs with an embryonic development age of at least 4 d determined by candling (Weller 1956). Prior to GLS attachment, we weighed (with a 100-g Pesola scale, ± 1 g) each bird. A uniquely identified stainless steel band was also attached to the right leg of each bird.

To explore the possible effect of GLS tag attachment on annual return rate and changes in body mass, we included a control cohort of 29 breeding Leach's Storm-Petrels. We randomly selected birds in the control group

and matched the selection process for GLS-tagged birds. Controls were captured and restrained for the same duration as GLS-tagged birds (i.e., ≤ 10 min). We did not include a control group for Fork-tailed Storm-Petrels because we were unable to locate enough individuals of the species during allotted field time. Due to limited field time in 2016, we did not band the mates of GLS-tagged and control birds so we were unable to determine return rates of the mates of birds in those groups.

Geolocator retrieval. Between 27 June and 1 July 2016, we recaptured five Fork-tailed Storm-Petrels for download of mid-season GLS data during the chick-provisioning phase. This was timed to coincide with GLS deployment on Leach's Storm-Petrels. Because Fork-tailed Storm-Petrels were provisioning nestlings at this time, we used one-way wire traps at nest entrances to facilitate capture. Nests were checked each morning, and chicks were weighed to determine if they had been fed, concurrently determining if parent birds had escaped the traps. The one-way traps were removed if mates of the tagged birds had been captured, and were not replaced until the non-tagged mate had departed. In 2017, after a ~ 1 -yr deployment, we recaptured Fork-tailed Storm-Petrels (between 19 and 24 May) and Leach's Storm-Petrels (between 24 June and 1 July) during their incubation periods.

Analysis of geolocator data. Data were downloaded from GLS tags using IntiGeo software (Migrate Technology Ltd.). We imported raw light-level GLS data into R v3.4.1 (R Core Team 2010) and defined twilight events (i.e., sunrise and sunset) using the "twilightCalc" function in the package "GeoLight" (Lisovski et al. 2012) using a threshold level of 1.5 to automatically delimit sunrises and sunsets. Light intensity levels that pass over the specified threshold level are automatically identified as twilight events (Lisovski and Hahn 2012). A threshold level of 1.5 was above ambient nighttime light in our data. However, twilights can sometimes be erroneously demarcated by the automated process when artificial shading of a GLS sensor occurs (e.g., weather events and feathers obscuring the sensor). Therefore, we conducted a visual inspection of all twilights generated by GeoLight and removed any false

twilight demarcation. Processed light-level data were analyzed in the FLIGHTR package (Rakhimberdiev et al. 2015) and included calibration light-level data recorded by GLS tags before deployment and after recapture. We used FLIGHTR to estimate the spatial likelihood of occurrence for all processed twilights using a template-fit method (Ekstrom 2004, Rakhimberdiev et al. 2015). We chose FLIGHTR over traditional threshold methods because it has been demonstrated to produce locations with lower spatial errors, can estimate locations during the equinoxes when global day length is uniform, is less sensitive to potential error from light-sensor shading, and provides estimates of spatial uncertainty (Ekstrom 2007, Rakhimberdiev et al. 2016). However, location estimates during equinox periods remain susceptible to error and should be treated with caution (Rakhimberdiev et al. 2015). We did not exclude locations around the equinoxes from analyses, but provide estimates of spatial uncertainty in Figure S1. We used a spatial mask to restrict locations more than 1 km inland and restricted maximum flight distance between twilights to 1500 km (Rakhimberdiev et al. 2016), using a large 50-km spatial grid that encompassed the entire Pacific Ocean. Last, to calculate year-round storm-petrel locations, we ran the FLIGHTR particle filter with one million particles produced over the spatial grid, and used the median of the posterior probability distribution as the estimates of storm-petrel locations for further spatial analysis in ArcGIS v. 10.2 (ESRI 2013).

Spatial analysis. Following the FLIGHTR analysis, we projected storm-petrel locations in the World Geodetic System (WGS) 1984 in ArcGIS (ESRI, v. 10.2, Redlands, CA) and exported shape files for subsequent kernel density estimation. We generated kernel densities using the "kde" tool in Geospatial Modeling Environment (GME) Version 0.7.3 (Beyer 2012) with a raster resolution of 50 km and a search radius of 200 km to reflect average reported error of GLS locations in kilometers (Phillips et al. 2006). We used the "iso" tool in GME to calculate utilization distributions (UD) representing areas of use at different densities (30, 50, 70, and 90%).

We focused on the 50% UD to define core-use areas of foraging ranges. Some estimated locations were over land (i.e., within

the 1-km inland restriction) and, although those were almost certainly erroneous, they were not removed to avoid biasing overall centers of storm-petrel distribution (Guilford et al. 2009). We report the duration of tracking for each storm-petrel and used ArcGIS 10.2 for Desktop (ESRI 2013) to calculate estimated spatio-temporal characteristics of storm-petrel movements including: (i) average great-circle distance from the colony during breeding (km \pm SD), (ii) total distance traveled (km) during the breeding period, (iii) post-breeding departure date, (iv) maximum foraging range (furthest great-circle distance from the colony) during migration (km), (v) total distance traveled (km) during the post-breeding period, and (vi) date of return to the breeding area. Distances are rounded to the nearest 50 km to account for error associated with GLS locations. All reported distances are orthodromic (great-circle distance) measurements.

Breeding and non-breeding season distributions. We grouped estimated locations of tracked storm-petrels into categories based on whether positions were associated with breeding or non-breeding movements and calculated UDs using these two categories. We used GLS locations that indicated obvious southward or westward movements away from the general breeding area to define the onset of fall migration. To identify implausibly early departures by adults relative to projected chick fledging dates and to concurrently infer if GLS-tagged birds likely bred successfully, we estimated egg development stage at time of capture to approximate hatching dates and subsequent dates when nestlings likely fledged and compared these to the date of the onset of fall migration.

To estimate the stage of embryonic development on a scale of 0–44 d, we used criteria adapted from Weller (1956) that were used successfully with Leach's Storm-Petrels nesting in Nova Scotia and Newfoundland, Canada (Pollet et al. 2014a). We selected this metric for estimating breeding stage rather than day of the year because neither species breeds synchronously (Boersma et al. 1980, Huntington et al. 1996).

To delineate the at-sea movements of the storm-petrels during the breeding season, we used all available GLS locations preceding the estimated post-breeding departure date for each individual. Non-breeding season

distributions included all locations from the date of an individual's departure from the breeding area to the first date when it was detected in its nest burrow the following breeding season.

Stable isotope analysis and molecular sexing. For analysis of stable carbon and stable nitrogen isotope values representing diet during the non-breeding period, we sampled the tips of the tenth primary feathers (P10) grown during the non-breeding period ($N = 21$ and 53 for Fork-tailed and Leach's storm-petrels, respectively). We collected blood and feather samples from all tagged storm-petrels recaptured in their nest burrows in 2017. We also sampled additional Fork-tailed ($N = 12$) and Leach's ($N = 30$) storm-petrels inferred to be mates of individuals from GLS-tagged or control groups, but could not eliminate the possibility that some were new nest occupants. To determine the sex of each bird, we took 1–2 μ l of blood from the brachial vein using a 26-gauge needle and stored the sample on FTA classic cards (Whatman International Ltd., Maidstone, UK). Sex of birds was determined by PCR reactions using the Z43B molecular marker identified by Dawson et al. (2016).

Stable isotope analysis was conducted at the University of Waterloo Environmental Isotope Laboratory in Waterloo, ON, Canada. Isotope ratios are expressed as δ values in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000,$$

where X is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ and R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, according to the corresponding primary reference scales: R_{standard} is Vienna Pee Dee Belemnite (VPDB) Atmospheric Nitrogen (AIR) for ^{13}C and ^{15}N , respectively. Replicate runs indicated measurement errors of $\pm 0.2\text{‰}$ for carbon and $\pm 0.3\text{‰}$ for nitrogen analyses.

Statistical analysis. To test for possible effects of carrying GLS tags, we conducted two-sample t -tests to compare the mean body mass of returning Leach's Storm-Petrels with and without GLS tags. Because we did not have a control group of Fork-tailed Storm-Petrels to compare recapture rates, we performed a paired t -test to compare body mass of Fork-tailed Storm-Petrels before and after

they had carried GLS tags. We used one-way ANOVAs to test effects of species and sex on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained from P10 feathers. Results of statistical tests were considered significant if $P < 0.05$. Statistical analyses were run in program R v3.4.1 (R Core Team 2010), and values are presented as means \pm 1 SD.

RESULTS

Geolocator retrieval and device effects. We recaptured five of 11 GLS-tagged Fork-tailed Storm-Petrels halfway through the 2016 breeding season and downloaded the data stored on the GLS. Three of these appeared to have healthy chicks, one was incubating an egg, and one had neither an egg nor a chick, indicating nest failure. Of the six Fork-tailed Storm-Petrels that were not recaptured, two had apparently healthy chicks, two had empty nests, one had a nest with a dead chick, and one had a nest with one cold egg and an adult Leach's Storm-Petrel incubating its own egg. Mean body mass of Fork-tailed Storm-Petrels recaptured halfway through breeding did not change significantly between when they were first captured (55.9 ± 4.9 g, $N = 5$) and when recaptured (60 ± 3.6 g, $t_4 = 1.1$, $P = 0.32$).

Recapture rates of birds with GLS tags for part or all of the previous year were 82% (9 of 11 birds) and 33% (10 of 30 birds) for Fork-tailed and Leach's storm-petrels, respectively. However, retention rates of GLS tags were low, with only 22% of Fork-tailed and 20% of Leach's storm-petrels retaining GLS tags after 1 yr. The recapture rate of Leach's Storm-Petrels in the control group was 45% (13 of 29 birds). Mean body mass of Fork-tailed Storm-Petrels before (54.9 ± 4.2 g) and 1 yr after tagging (57 ± 2.9 g, $N = 9$) did not differ ($t_8 = -1.1$, $P = 0.30$). In addition, mean body mass of Leach's Storm-Petrels in the control group (43.5 ± 5.1 g, $N = 12$) did not differ ($t_{20} = 0.7$, $P = 0.74$) from that of those fit with GLS tags the previous year (42.3 ± 3.2 g, $N = 10$).

Both recaptured Fork-tailed Storm-Petrels with GLS tags were incubating eggs, as were all recaptured Fork-tailed Storm-Petrels that had lost their GLS tags (identified by band numbers). Both Leach's Storm-Petrels recaptured with GLS tags still attached had brood

patches and one was incubating a 24-d-old egg. One bird (x863) had retained its GLS tag and was recaptured in the same nest where first captured, but was sharing a nest with a Fork-tailed Storm-Petrel chick estimated to be 5–10 d old. All recaptured birds appeared to be in good condition, and suture sites of birds that either retained or lost GLS tags showed no signs of infection or scar tissue. In 2017, 12% of the nest sites occupied by Leach's Storm-Petrels in 2016 were occupied by Fork-tailed Storm-Petrels in 2017; no nest sites occupied by Fork-tailed Storm-Petrels in 2016 were occupied by Leach's Storm-Petrels in 2017.

Breeding-season distribution. Mean maximum great-circle distances traveled from the colony during incubation and chick provisioning were 1550 ± 250 km for Fork-tailed Storm-Petrels and 1600 ± 300 km for Leach's Storm-Petrels (Table 1). Estimated foraging ranges of both species extended beyond the Canadian Exclusive Economic Zone (EEZ; 370 km from British Columbia) into the United States EEZ and international waters (Fig. 1). The centroids of core UD were located 50 and 177 km from the colony for Fork-tailed and Leach's storm-petrels, respectively (Fig. 1). During the 2016 breeding season, the core UD of Fork-tailed Storm-Petrels encompassed an area of 114 km^2 confined to Canada's EEZ (Fig. 1). In contrast, the core UD of Leach's Storm-Petrels encompassed an area of 232 km^2 that extended beyond Canada's EEZ and included waters in the United States EEZ as well as international waters. In calculating UD of breeding Fork-tailed Storm-Petrels, we excluded data from one individual (x889; Table 1) because its nest had failed and the average distance of estimated positions from the colony of this individual was far greater than those of breeding individuals (Table 1).

Non-breeding-season distribution. Fork-tailed Storm-Petrels foraged over a greater longitudinal area than Leach's Storm-Petrels during the non-breeding season, but remained in the North Pacific Ocean, generally north of the Subarctic Boundary (Kanaji et al. 2016, Fig. 2). Credible intervals associated with storm-petrel positions estimated by FLIGHTR were greater around the vernal and autumnal equinoxes. We provide estimates of spatial uncertainty for storm-petrels tracked

Table 1. Sex, tracking dates and duration, and estimated movement distances and foraging ranges of GLS-tracked Fork-tailed and Leach's storm-petrels during the 2016 breeding season.

Bird	Species	Sex	Start of tracking	End of tracking	Tracking duration (d)	Average distance from colony (km \pm SD)	Maximum foraging range (km)
x883	Fork-tailed Storm-Petrel	M	20 May 2016	27 June 2016	38	150 \pm 150	500
x889 ^a	Fork-tailed Storm-Petrel	F	21 May 2016	27 June 2016	37	900 \pm 550	2250
x892	Fork-tailed Storm-Petrel	M	19 May 2016	31 July 2016	73	200 \pm 200	600
x894	Fork-tailed Storm-Petrel	M	23 May 2016	23 August 2016	92	100 \pm 50	200
x898	Fork-tailed Storm-Petrel	M	20 May 2016	26 June 2016	37	50 \pm 0.5	50
x899	Fork-tailed Storm-Petrel	M	21 May 2016	24 June 2016	34	600 \pm 450	1550
x900	Leach's Storm-Petrel	F	2 July 2016	29 September 2016	89	550 \pm 350	900
x863	Leach's Storm-Petrel	M	1 July 2016	24 October 2016	115	350 \pm 200	1600

^aFailed breeder (excluded from calculation of Utilization Distributions).

year-round in Figure S1. Analysis of the post-breeding movements of one Fork-tailed Storm-Petrel (x894) revealed five core UD areas (Fig. 2). Although the geometric center of the five core UD areas was \sim 1050 km northwest of Gillam Island, this bird traveled a maximum great-circle distance $>$ 3500 km from the colony during the non-breeding period (Table 2), and its non-breeding season core UD encompassed an area of 542 km² of North Pacific waters. The core UD of the other tracked Fork-tailed Storm-Petrel (x892) included two areas encompassing 447 km², with the geometric center located \sim 700 km great-circle distance west of the colony (Fig. 2). Determination of egg stage was useful for estimating departure dates and related well to GLS positions that indicated obvious movements away from the breeding colony (Table 2).

Leach's Storm-Petrels began their southward migrations at the end of the 2016 breeding season, with bird x900 departing on 30 September and bird x863 on 25 October (Table 2). The centroid of bird x863's (Fig. 2) single-core UD was south of the equator at \sim 6450 km great-circle distance from the colony. The core UD encompassed 308 km² and was centered over an area associated with the South Equatorial Current, the Peru-Chile Undercurrent, and the Humboldt Current (Kessler 2006) west of Peru and Ecuador. Throughout the non-breeding period, including its return to British Columbia, x863 traveled over the EEZs of Canada, the United States, Mexico, Colombia, Ecuador, Chile, and France (Île de Clipperton). This individual remained in the breeding core UD for approximately 1 mo after the estimated date that its chick would have fledged (Table 2) before beginning southward migration.

The other Leach's Storm-Petrel (x900; Fig. 2) also had a single wintering area, but it was centered farther north to the west of central Mexico over the Tehuantepec Bowl and associated with the California Current and the West Mexican Current (Kessler 2006). The centroid of x900's core UD was \sim 3400 km great-circle distance from the breeding colony (Table 2) and encompassed an area of 344 km². During its migration, x900 traveled through the EEZs of Canada, the United States, Mexico, and France.

Stable isotope analysis. We found significantly lower values of $\delta^{13}\text{C}$ in the P10

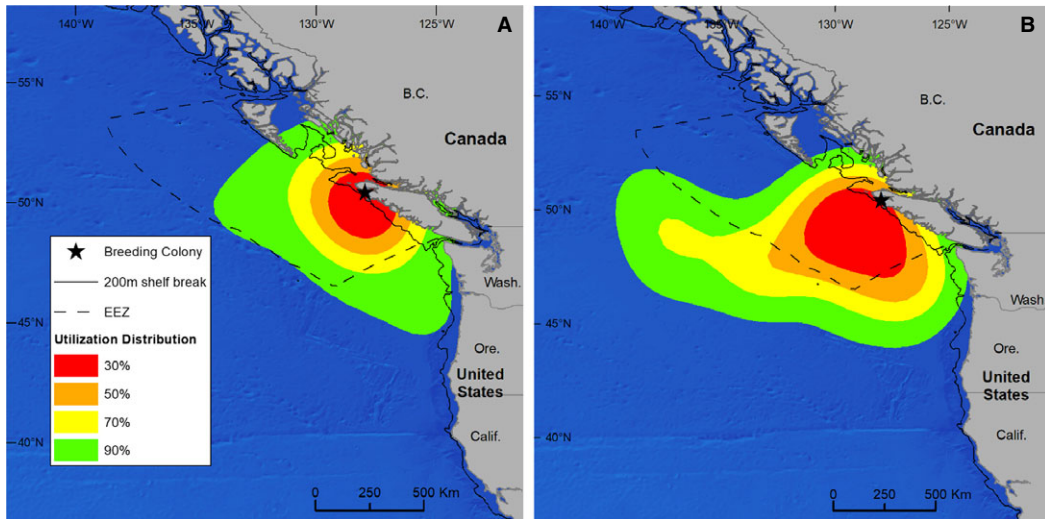


Fig. 1. At-sea distribution of storm-petrels during the 2016 breeding season expressed as utilization distributions calculated from combined estimated locations of Fork-tailed Storm-Petrels (A, $N = 5$, May–August) and combined estimated locations of Leach’s Storm-Petrels (B, $N = 2$, July–October). The location of Gillam Island is indicated by a black star. [Color figure can be viewed at wileyonlinelibrary.com]

feathers of Fork-tailed Storm-Petrels than in those of Leach’s Storm-Petrels (ANOVA $F_{1,72} = 99.5$, $P < 0.0001$; Fig. 3, Table 3) and higher values of $\delta^{15}\text{N}$ in the P10 feathers of Fork-tailed Storm-Petrels than those of Leach’s Storm-Petrels (ANOVA $F_{1,72} = 10.1$, $P = 0.002$; Fig. 3). We found no differences in values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of males and females for either Leach’s Storm-Petrels (ANOVA for $\delta^{13}\text{C}$: $F_{1,51} = 3.4$, $P = 0.071$; ANOVA for $\delta^{15}\text{N}$: $F_{1,51} = 1.7$, $P = 0.20$) or Fork-tailed Storm-Petrels (ANOVA for $\delta^{13}\text{C}$: $F_{1,19} = 2.3$, $P = 0.15$; ANOVA for $\delta^{15}\text{N}$: $F_{1,19} = 0.1$, $P = 0.82$).

DISCUSSION

Both species of storm-petrels in our study had large foraging ranges during the breeding season and extensive post-breeding migrations. During incubation and chick provisioning, estimated maximum foraging ranges of storm-petrels were up to 1600 km from the breeding colony. In comparison, Hedd et al. (2018) reported that Leach’s Storm-Petrels in the Atlantic Ocean ranged up to 830 km from breeding colonies during incubation. Other small Procellariiform seabirds are also known to forage over large areas when

breeding (Pollet et al. 2014a), including Murphy’s Petrels (*Pterodroma ultima*) that range up to 4800 km from breeding colonies (Clay et al. 2017) and Chatham Petrels (*Pterodroma axillaris*) that range up to 2095 km from breeding colonies (Rayner et al. 2012).

Our results for the breeding distribution of Fork-tailed and Leach’s storm-petrels align with observations reported in other studies. For example, ship-based surveys in the region have shown that the distribution of both species tends to be concentrated seaward of the continental shelf break (> 200 m isobath, Kenyon et al. 2009), and other investigators have reported that Leach’s Storm-Petrels forage further offshore than Fork-tailed Storm-Petrels (Vermeer and Rankin 1984, Briggs et al. 1987, Hoefler 2000, Yen et al. 2005). Kenyon et al. (2009) noted that, during spring (16 March–15 June), both Fork-tailed and Leach’s storm-petrels were widely distributed west of Vancouver Island, including the outer shelf, the continental slope, and farther offshore.

The region where breeding birds in our study foraged has a wide shelf with major canyons creating a highly productive foraging area (Burger et al. 2004) known to be important for several migratory seabird species,

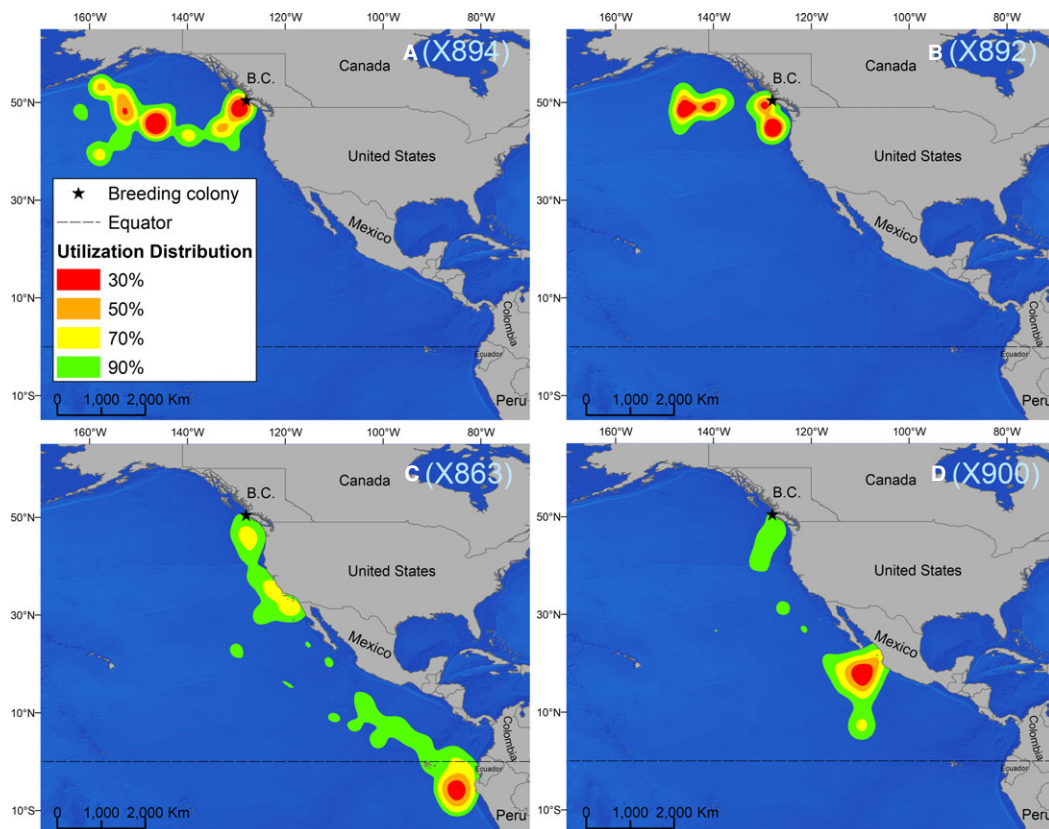


Fig. 2. At-sea distribution of storm-petrels (individual bird IDs in parentheses) during the non-breeding season expressed as utilization distributions calculated from estimated locations of Fork-tailed Storm-Petrels (A, August 2016–January 2017, B, August 2016–January 2017) and Leach's Storm-Petrels (C, October 2016–May 2017, D, September 2016–May 2017). The location of Gillam Island is indicated by a black star. Estimates of spatial uncertainty of storm-petrels tracked year-round are provided in Figure S1. [Color figure can be viewed at wileyonlinelibrary.com]

including Sooty Shearwaters (*Ardenna grisea*), Black-footed Albatrosses (*Phoebastria nigripes*), and Cassin's Auklets (*Ptychoramphus aleuticus*) (Kenyon et al. 2009). Suryan et al. (2012) identified an area that roughly approximated the 50% UD in our study as one location with elevated chlorophyll *a* persistence, and suggested that large areas with similar characteristics might attract abundant mid- to upper-trophic-level consumers (e.g., seabirds) over large temporal scales.

Our tracking results during the non-breeding season aligned well with results of long-term ship-based surveys in the North Pacific. For example, Kenyon et al. (2009) demonstrated that, during fall and winter, Fork-tailed Storm-Petrels were relatively abundant, whereas Leach's Storm-Petrels were nearly

absent from British Columbia waters. During the 2016–2017 non-breeding period, Fork-tailed Storm-Petrels in our study remained in the northeast Pacific Ocean, primarily north of the Subarctic Boundary and closely matched areas identified by Sydeman et al. (2012) as hotspots for the species. In contrast, Leach's Storm-Petrels in our study moved to disparate highly productive areas in the Eastern Tropical Pacific, with one bird (x900) spending most of the non-breeding period in the Tehuantepec Bowl that is associated with the California Current and the West Mexican Current. The other bird (x863) spent most of the non-breeding period in the productive waters of the South Equatorial Current, the Peru-Chile Undercurrent, and the Humboldt Current, primarily west of Peru and Ecuador.

Table 2. Summary of estimated post-breeding movements and breeding phenology of GLS-tracked Fork-tailed (FTSP) and Leach's (LSPE) storm-petrels in relation to date of post-breeding dispersal in 2016.

Bird	Species	Sex	Capture date	Estimated		Estimated laying date	Estimated hatching date	Estimated fledging date	Departure from breeding area	Return date	Tracking duration (d)	Maximum foraging range (km)	Total distance traveled (km)
				egg age at capture (d)	egg age at capture (d)								
x892	FTSP	M	20 May 2016	32	18 April 2016	3 June 2016	31 July 2016	1 Aug 2016	25 Jan 2017	177	2200	9300	
x894	FTSP	M	21 May 2016	8	13 May 2016	28 June 2016	25 Aug 2016	24 Aug 2016	24 Jan 2017	153	3600	17,200	
x900	LSPE	F	29 June 2016	24	5 June 2016	20 July 2016	23 Sep 2016	30 Sep 2016	18 May 2017	230	4650	18,700	
x863	LSPE	M	28 June 2016	24	4 June 2016	19 July 2016	22 Sep 2016	25 Oct 2016	22 May 2017	209	6700	19,750	

Other investigators have also reported high numbers of Leach's Storm-Petrels in the Eastern Tropical Pacific Ocean during the non-breeding season (King 1974, Ribic et al. 1997, Spear et al. 2001, Spear and Ainley 2007). Similarly, post-breeding Leach's Storm-Petrels tracked from colonies in Newfoundland and Nova Scotia, Canada, spent their non-breeding period at tropical latitudes in the South Atlantic (Pollet et al. 2014b) in approximately the area where the Atlantic South Equatorial Current splits into the southward flowing Brazil Current and northward flowing North Brazil Current (Peterson and Stramma 1991).

After breeding, one Leach's Storm-Petrel (x863) in our study remained in an area that approximated its breeding core UD for almost a month before embarking on its southward migration. Few data exist on post-breeding movements of Leach's Storm-Petrels in the Pacific, but we hypothesize that this bird likely remained in the area due to high prey abundance. High abundance of near-surface prey (i.e., euphausiids and other zooplankton) accompanied by mixed-species flocks of seabirds are known to occur in this region in the fall (Burger et al. 2004).

Our stable isotope analyses revealed differences in isotope ratios from which we inferred niche separation of Fork-tailed and Leach's storm-petrels during the non-breeding period. We demonstrated wider ranges of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios in Leach's Storm-Petrel tissues than those of Fork-tailed Storm-Petrels. The observed differences in ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ may be because Leach's Storm-Petrels occupied a wider range of trophic levels during the non-breeding season (Hedd and Montecchi 2006), or reflect more extensive latitudinal movement. Individuals from Canadian Atlantic colonies have been observed to spend non-breeding periods in South African waters (Pollet et al., unpubl. data), suggesting wide latitudinal variation in the non-breeding areas of Leach's Storm-Petrels in the Atlantic Ocean.

Although we found no measureable effect of carrying GLS tags on annual recapture rates, many recaptured individuals returned without GLS tags. We are unaware of how long these individuals retained GLS tags and our ability to measure device effects is

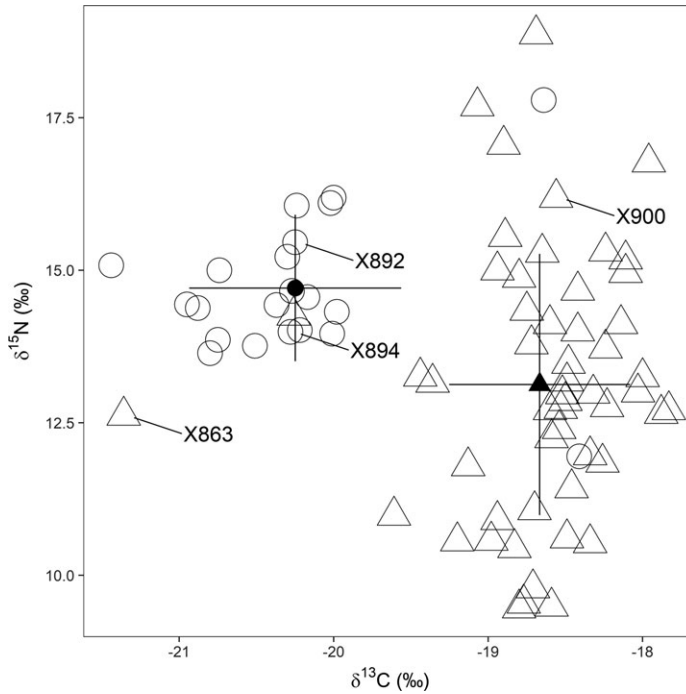


Fig. 3. Variation in the stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in feathers of Fork-tailed Storm-Petrels (●) and Leach's Storm-Petrels (Δ) grown during the 2016-2017 post-breeding period. Solid black shapes indicate the species means with 95% CI. Values for tracked birds are labeled.

Table 3. Stable isotope ratios and descriptive statistics of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in P10 feathers of Fork-tailed and Leach's storm-petrels grown during the 2016/2017 non-breeding period.

Species	Group	N	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
			Mean $\delta^{13}\text{C}$ (‰)	SD	Range	Mean $\delta^{15}\text{N}$ (‰)	SD	Range
Fork-tailed Storm-Petrels	All birds	21	-20.2	0.7	-21.4 to -18.4	14.7	1.2	12.0-17.8
	Males	14	-20.1	0.7	-21.0 to -18.4	14.8	1.4	12.0-17.8
	Females	7	-20.6	0.5	-21.4 to -20.0	14.6	0.5	13.6-15.2
Leach's Storm-Petrels	All birds	53	-18.7	0.6	-21.4 to -17.8	13.1	2.1	9.5-18.9
	Males	29	-18.8	0.7	-21.4 to -18.0	13.5	2.0	9.5-18.9
	Females	24	-18.5	0.4	-19.2 to -17.8	12.7	2.2	9.5-17.1

consequently limited. Because the GLS tags we used represented > 1% of storm-petrel body mass, they may have affected survival rates (Bodey et al. 2017). Even devices < 1% of a bird's body mass have been found to cause elevated stress levels and associated physiological effects in some small seabirds (Quillfeldt et al. 2012).

The population status of storm-petrels in British Columbia is currently unclear, but,

given the declining populations of Leach's Storm-Petrels reported elsewhere (Robertson et al. 2006, Newson et al. 2008, Fife et al. 2015), identifying factors that may influence survival during the breeding and non-breeding seasons may be key for future conservation efforts for both species. Additional study is also needed to identify the specific areas used by each species during both breeding and non-breeding periods. A better

understanding of the year-round distribution of North Pacific storm-petrels will make it possible to identify potential threats to their survival at sea.

ACKNOWLEDGMENTS

Our research was supported by Environment & Climate Change Canada (ECCC) and the James L. Baillie Memorial Fund of Bird Studies Canada. We thank E. Carter, J. Whitton, and P. Hebert for providing valuable field assistance, P. and P. Wainwright for logistical assistance, E. Lok for assistance with project planning, M. Thies for analytical advice, and R. H. Clarke and three anonymous reviewers for comments that greatly improved an early version of the manuscript. Fieldwork was authorized under ECCC Western and Northern Animal Care Committee permit #16LH01 and Canadian Wildlife Service bird banding permits 10695H and 10695N. We thank the Quatsino First Nation for granting permission to conduct our research on their traditional territory.

LITERATURE CITED

- AINLEY, D. G., T. J. LEWIS, AND S. MORRELL. 1976. Molt in Leach's and Ashy storm-petrels. *Wilson Bulletin* 88: 76–95.
- BARRON, D. G., J. D. BRAWN, AND P. J. WEATHERHEAD. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1: 180–187.
- BEARHOP, S., S. WALDRON, S. C. VOTIER, AND R. W. FURNESS. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* 75: 451–458.
- BEYER, H. L. [online]. 2012. Geospatial modelling environment. <<http://www spatialecology.com/gme>> (Accessed 18 January 2018).
- BODEY, T. W., I. R. CLEASBY, F. BELL, N. PARR, A. SCHULTZ, S. VOTIER, AND S. BEARHOP. 2017. A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. *Methods in Ecology and Evolution* 9: 946–955.
- BOERSMA, P. D., N. T. WHEELWRIGHT, M. K. NERINI, AND E. S. WHEELWRIGHT. 1980. The Breeding Biology of the Fork-tailed Storm-Petrel (*Oceanodroma furcata*). *Auk* 97: 268–282.
- , AND M. J. GROOM. 1993. Conservation of storm-petrels in the North Pacific. In: The status, ecology, and conservation of marine birds of the North Pacific (K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey, eds.), pp. 112–121. Canadian Wildlife Service, Ottawa, ON.
- , AND M. C. SILVA. 2001. Fork-tailed Storm-Petrel (*Oceanodroma furcata*). In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- BRIGGS, K. T., W. M. B. TYLER, D. B. LEWIS, AND D. R. CARLSON. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology* 11: 1–74.
- , D. H. VAROUJEAN, W. W. WILLIAMS, R. G. FORD, M. L. BONNELL, AND J. L. CASEY. 1992. Seabirds of the Oregon and Washington OCS, 1989–1990: Oregon and Washington marine mammal and seabird surveys. Ecological Consulting, Inc., Portland, OR.
- BURGER, A. E., C. L. HITCHCOCK, AND G. K. DAVOREN. 2004. Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. *Marine Ecology Progress Series* 283: 279–292.
- , AND S. A. SHAFFER. 2008. Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125: 253–264.
- CHEREL, Y., AND K. A. HOBSON. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series* 329: 281–287.
- CLAY, T., R. PHILLIPS, A. MANICA, H. JACKSON, AND M. BROOKE. 2017. Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's Petrels. *Marine Ecology Progress Series* 579: 139–155.
- DAWSON, D. A., N. DOS REMEDIOS, AND G. J. HORSBURGH. 2016. A new marker based on the avian spindlin gene that is able to sex most birds, including species problematic to sex with CHD markers. *Zoo Biology* 35: 533–545.
- EKSTROM, P. A. 2004. An advance in geolocation by light. *Memoirs of National Institute of Polar Research, Special Issue* 58: 210–226.
- . 2007. Error measures for template-fit geolocation based on light. *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 392–403.
- ESRI 2013. ArcGIS v. 10.2. Environmental Systems Research Institute, Redlands, CA.
- FIFE, D. T., I. L. POLLET, G. J. ROBERTSON, M. L. MALLORY, AND D. SHUTLER. 2015. Apparent survival of adult Leach's Storm-Petrels (*Oceanodroma leucorhoa*) breeding on Bon Portage Island, Nova Scotia. *Avian Conservation and Ecology* 10: 1.
- FURNESS, R. W., J. E. CRANE, S. BEARHOP, S. GARTHE, A. KÄKELÄ, R. KÄKELÄ, A. KELLY, U. KUBETZKI, S. C. VOTIER, AND S. WALDRON. 2006. Techniques to link individual migration patterns of seabirds with diet specialization, condition and breeding performance. *Ardea* 94: 631–638.
- GUILFORD, T., J. MEADE, J. WILLIS, R. A. PHILLIPS, D. BOYLE, S. ROBERTS, M. COLLETT, R. FREEMAN, AND C. M. PERRINS. 2009. Migration and stopover in a small pelagic seabird, the Manx Shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B* 276: 1215–1223.

- HARRIS, S. W. 1974. Status, chronology, and ecology of nesting storm petrels in northwestern California. *Condor* 76: 249–261.
- HARRISON, X. A., J. D. BLOUNT, R. INGER, D. R. NORRIS, AND S. BEARHOP. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80: 4–18.
- HEDD, A., AND W. A. MONTEVECCHI. 2006. Diet and trophic position of Leach's Storm-Petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. *Marine Ecology Progress Series* 322: 291–301.
- , I. L. POLLET, R. A. MAUCK, C. M. BURKE, M. L. MALLORY, L. A. M. TRANQUILLA, W. A. MONTEVECCHI, G. J. ROBERTSON, R. A. RONCONI, D. SHUTLER, AND S. I. WILHELM. 2018. Foraging areas, offshore habitat use, and colony overlap by incubating Leach's Storm-Petrels *Oceanodroma leucorhoa* in the Northwest Atlantic. *PLoS ONE* 13: e0194389.
- HOBSON, K. A., W. G. AMBROSE, JR., AND P. E. RENAUD. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 128: 1–10.
- HOEFER, C. J. 2000. Marine bird attraction to thermal fronts in the California Current System. *Condor* 102: 423–427.
- HULBERT, I. A., AND J. FRENCH. 2001. The accuracy of GPS for wildlife telemetry and habitat mapping. *Journal of Applied Ecology* 38: 869–878.
- HUNTINGTON, C. E., R. G. BUTLER, AND R. A. MAUCK. 1996. Leach's Storm-Petrel (*Oceanodroma leucorhoa*). In: *The Birds of North America* (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- INGER, R., AND S. BEARHOP. 2008. Applications of stable isotope analyses to avian ecology. *Ibis* 150: 447–461.
- KANAJI, Y., M. OKAZAKI, H. WATANABE, AND T. MIYAHITA. 2016. Biogeography of small odontocetes in relation to wide-scale oceanographic structure in the North Pacific Ocean. *Fisheries Oceanography* 25: 119–132.
- KELLY, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78: 1–27.
- KENYON, J. K., K. H. MORGAN, M. D. BENTLEY, L. A. MCFARLANE-TRANQUILLA, AND K. E. MOORE. 2009. Atlas of pelagic seabirds off the west coast of Canada and adjacent areas. Technical Report Series No. 499, Canadian Wildlife Service, Pacific and Yukon Region, Delta, BC, Canada.
- KESSLER, W. S. 2006. The circulation of the eastern tropical Pacific: a review. *Progress in Oceanography* 69: 181–217.
- KING, W. B. 1974. Pelagic studies of sea birds in the central and eastern Pacific Ocean. *Smithsonian Contributions to Zoology* 158: 1–277.
- LISOVSKI, S., AND S. HAHN. 2012. GeoLight – processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution* 3: 1055–1059.
- , C. M. HEWSON, R. H. G. KLAASSEN, F. KORNER-NIEVERGELT, M. W. KRISTENSEN, AND S. HAHN. 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution* 3: 603–612.
- MICHENER, R. H., AND L. KAUFMAN. 2007. Stable isotope ratios as tracers in marine food webs: an update. In: *Stable isotopes in ecology and environmental science* (R. H. Michener and K. Lajtha, eds.), pp. 238–282. Blackwell, London, UK.
- NATHAN, R., W. M. GETZ, E. REVILLA, M. HOLYOAK, R. KADMON, D. SALTZ, AND P. E. SMOUSE. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA* 105: 19052–19059.
- NEWSON, S. E., P. I. MITCHELL, M. PARSONS, S. H. O'BRIEN, G. E. AUSTIN, S. BENN, J. BLACK, J. BLACKBURN, B. BRODIE, E. HUMPHREYS, AND D. LEECH. 2008. Population decline of Leach's Storm-Petrel *Oceanodroma leucorhoa* within the largest colony in Britain and Ireland. *Seabird* 21: 77–84.
- PETERSON, R. G., AND L. STRAMMA. 1991. Upper-level circulation in the South Atlantic Ocean. *Progress in Oceanography* 26: 1–73.
- PHILLIPS, R. A., J. R. D. SILK, J. P. CROXALL, AND V. AFANASYEV. 2006. Year-round distribution of White-chinned Petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation* 129: 336–347.
- , ———, ———, AND D. R. BRIGGS. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266: 265–272.
- , J. C. XAVIER, J. P. CROXALL, AND A. E. BURGER. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* 120: 1082–1090.
- POLLET, I. L., A. HEDD, P. D. TAYLOR, W. A. MONTEVECCHI, AND D. SHUTLER. 2014b. Migratory movements and wintering areas of Leach's Storm-Petrels tracked using geolocators. *Journal of Field Ornithology* 85: 321–328.
- , R. A. RONCONI, I. D. JONSEN, M. L. LEONARD, P. D. TAYLOR, AND D. SHUTLER. 2014a. Foraging movements of Leach's Storm-Petrels *Oceanodroma leucorhoa* during incubation. *Journal of Avian Biology* 45: 305–314.
- QUILLFELDT, P., J. O. ENGLER, J. R. D. SILK, AND R. A. PHILLIPS. 2017. Influence of device accuracy and choice of algorithm for species distribution modelling of seabirds: a case study using Black-browed Albatrosses. *Journal of Avian Biology* 48: 1549–1555.
- , R. A. R. MCGILL, R. W. FURNESS, E. MÖSTL, K. LUDYNIA, AND J. F. MASELLO. 2012. Impact of miniature geolocation loggers on a small petrel, the Thin-billed Prion *Pachyptila belcheri*. *Marine Biology* 159: 1809–1816.
- , C. C. VOIGT, AND J. F. MASELLO. 2010. Plasticity versus repeatability in seabird migratory

- behavior. *Behavioral Ecology and Sociobiology* 64: 1157–1164.
- R CORE TEAM. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RAKHIMBERDIEV, E., N. R. SENNER, M. A. VERHOEVEN, D. W. WINKLER, W. BOUTEN, AND T. PIERSMA. 2016. Comparing inferences of solar geolocation data against high-precision GPS data: annual movements of a double-tagged Black-tailed Godwit. *Journal of Avian Biology* 47: 589–596.
- , D. W. WINKLER, E. BRIDGE, N. E. SEAVY, D. SHELDON, T. PIERSMA, AND A. SAVELIEV. 2015. A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Movement Ecology* 3: 25.
- RAYNER, M. J., N. CARLILE, D. PRIDDEL, V. BRETAGNOLLE, M. G. R. MILLER, R. A. PHILLIPS, L. RANJARD, S. J. BURY, AND L. G. TORRES. 2016. Niche partitioning by three *Pterodroma* petrel species during non-breeding in the equatorial Pacific Ocean. *Marine Ecology Progress Series* 549: 217–229.
- RAYNER, M., G. TAYLOR, R. A. PHILLIPS, AND P. SAGAR. 2012. The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). *Emu* 112: 107–116.
- RIBIC, C. A., D. G. AINLEY, AND L. B. SPEAR. 1997. Seabird associations in Pacific equatorial waters. *Ibis* 139: 482–487.
- ROBERTSON, G. J., J. RUSSELL, R. BRYANT, D. A. FIFIELD, AND I. J. STENHOUSE. 2006. Size and trends of Leach's Storm-Petrel *Oceanodroma leucorhoa* breeding populations in Newfoundland. *Atlantic Seabirds* 8: 41–50.
- RODWAY, M. 1991. Status and conservation of breeding seabirds in British Columbia. In: Seabird status and conservation: a supplement (J. P. Croxall, ed.), pp. 43–102. International Council for Bird Preservation Technical Publication No. 11, Cambridge, UK.
- SHAFFER, S. A., Y. TREMBLAY, J. A. AWKERMAN, R. W. HENRY, S. L. H. TEO, D. J. ANDERSON, D. A. CROLL, B. A. BLOCK, AND D. P. COSTA. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147: 833–843.
- , ———, H. WEIMERSKIRCH, D. SCOTT, D. R. THOMPSON, P. M. SAGAR, H. MOLLER, G. A. TAYLOR, D. G. FOLEY, B. A. BLOCK, AND D. P. COSTA. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences USA* 103: 12799–12802.
- SORENSEN, M. C., J. M. HIPFNER, T. K. KYSER, AND D. R. NORRIS. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology* 78: 460–467.
- SOWLS, A. L., S. A. HATCH, AND C. J. LEN-SINK. 1978. Catalog of Alaskan seabird colonies. U.S. Fish and Wildlife Service FWS/OBS 78/78, Anchorage, AK.
- SPEAR, L. B., AND D. G. AINLEY. 2007. Storm-petrels of the Eastern Pacific Ocean: species assembly and diversity along marine habitat gradients. *Ornithological Monographs* 62: 1–77.
- , L. T. BALLANCE, AND D. G. AINLEY. 2001. Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Marine Ecology Progress Series* 219: 275–289.
- SURYAN, R. M., J. A. SANTORA, AND W. J. SYDEMAN. 2012. New approach for using remotely sensed chlorophyll *a* to identify seabird hotspots. *Marine Ecology Progress Series* 451: 213–225.
- SYDEMAN, W. J., M. LOSEKOOT, J. A. SANTORA, S. A. THOMPSON, K. H. MORGAN, T. DISTLER, A. WEINSTEIN, M. A. SMITH, AND N. WALKER. 2012. Hotspots of seabird abundance in the California Current: implications for important bird areas. Audubon California, Petaluma, CA.
- VERMEER, K., AND L. RANKIN. 1984. Pelagic seabird populations in Hecate Strait and Queen Charlotte Sound: comparison with the west coast of the Queen Charlotte Islands. Canadian Technical Report of Hydrography and Ocean Sciences No. 52, Ottawa, Canada.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20: 111–113.
- YEN, P. P. W., W. J. SYDEMAN, K. H. MORGAN, AND F. A. WHITNEY. 2005. Top predator distribution and abundance across the eastern Gulf of Alaska: temporal variability and ocean habitat associations. *Deep-Sea Research II* 52: 799–822.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Fig. S1. Uncertainty associated with location estimates of two Fork-tailed Storm-Petrels (FTSP) and two Leach's Storm-Petrels (LSPE) from the Gillam Islands, British Columbia, Canada, tracked year-round with geolocators.