Migratory movements and wintering areas of Leach's Storm-Petrels tracked using geolocators

Ingrid L. Pollet,^{1,2,4} April Hedd,³ Philip D. Taylor,¹ William A. Montevecchi,³ and Dave Shutler¹

¹Department of Biology, Acadia University, Wolfville, Nova Scotia, B4P 2R6 Canada ²Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4R2 Canada ³Cognitive and Behavioural Ecology, Departments of Psychology and Biology, Memorial University of Newfoundland, St John's, Newfoundland, A1B 3X9 Canada

Received 25 February 2014; accepted 2 June 2014

ABSTRACT. Accumulating evidence suggests that Atlantic populations of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) are experiencing significant declines. To better understand possible causes of these declines, we used geolocators to document movements of these small (~50-g) pelagic seabirds during migration and the non-breeding period. During 2012 and 2013, movement tracks were obtained from two birds that traveled in a clock-wise direction from two breeding colonies in eastern Canada (Bon Portage Island, Nova Scotia, and Gull Island, Newfoundland) to winter in tropical waters. The bird from Bon Portage Island started its migration back to Nova Scotia in April. The bird from Gull Island staged off Newfoundland in November and then again off Cape Verde in January before its geolocator stopped working. Movements of Leach's Storm-Petrels in our study and those of several other procellariiforms during the non-breeding period are likely facilitated by the prevailing easterly trade winds and the Antilles and Gulf Stream currents. Although staging and wintering areas used by Leach's Storm-Petrels in our study were characterized by low productivity, the West Africa and northeastern Brazilian waters are actively used by fisheries and discards can attract Leach's Storm-Petrels. Our results provide an initial step towards understanding movements of their migratory routes, staging areas, and wintering ranges.

RESUMEN. Movimientos migratorios y áreas invernales de Oceanodroma leucorboa seguidos utilizando geolocaliza-dores

La evidencia acumulada sugiere que las poblaciones del atlántico de *Oceanodroma leucorhoa* están experimentando una disminución significativa. En un esfuerzo para entender mejor las posibles causas de esta disminución, usamos geolocaliza-dores para documentar los movimientos de esta pequeña (~50-g) ave marina pelágica durante la migración y el periodo no reproductivo. Durante el 2012 y 2013, trayectorias de los movimiento fueron obtenidas basada en dos aves que viajaron en la dirección del reloj desde dos colonias al este de Canadá (isla Bon Portage, Nova Scotia, e isla Gull, Newfoundland) a pasar el invierno en aguas tropicales. El ave de la isla Bon Portage empezó su migración hacia cabo Verde en octubre, arribó a su área invernal en las afueras de la costa al este de Brasil en enero, y comenzó la migración de regreso a Nova Scotia en abril. El ave de la isla Gull salió de Newfoundland en noviembre y de nuevo desde cabo verde en enero antes de que su geolocaliza-dores dejada de funcionar. Los movimientos de *O. leucorhoa* en nuestro estudio y los de muchos otros procellariiformes durante los periodos no reproductivos están probablemente facilitados por la prevalencia de los vientos alisios del este y las corrientes de las Antillas y el golfo. Aunque *O. leucorhoa* utilizó áreas estacionarias y de invierno en nuestro estudio, estas se caracterizaron por tener una baja productividad, pero las aguas del oeste Africano y el noreste Brasilero son utilizadas activamente por pescadores y los desechos pueden atraer a *O. leucorhoa*. Nuestros resultados proveen un paso inicial hacia el entendimiento de los movimientos de *O. leucorhoa* durante el periodo no reproductivo, pero futuros rastreos son requeridos para confirmar la generalidad de sus rutas migratorias, áreas estacionarias y rangos de invierno.

Key words: archival light logger, migration, Oceanodroma leucorhoa, seabird tracking

Seabirds are the most wide-ranging marine animals (Egevang et al. 2010), but, until recently, detailed information about movements of individual birds at sea remained scarce, particularly for smaller species. Even now, nonbreeding movements of small pelagic seabirds are poorly understood. Historically, banding programs provided the only information about migratory connectivity (e.g., Imber 1982, Gaston et al. 2008). More recently, stable isotopes have provided information about connections between breeding and non-breeding areas (Cherel et al. 2006, Hedd and Montevecchi 2006, Philips et al. 2009, Bicknell et al. 2014),

⁴Corresponding author. Email: ipollet@yahoo.com

^{© 2014} Association of Field Ornithologists

but resolution of these data limits their utility. Recent advances in technology have, however, made it possible to deploy smaller, longer-lasting tracking units on birds (Bridge et al. 2011) that provide information on travel routes, staging areas, and non-breeding locations.

Leach's Storm-Petrels (Oceanodroma leu*corhoa*) are small burrow-nesting pelagic seabirds that breed in the Northern Hemisphere (Huntington et al. 1996). Over 67,000 have been banded in Canada, but only six bands (0.01%) have been recovered outside of North America (Gaston et al. 2008). These recoveries provide limited information about banding and recovery sites, and no information on intervening movements. Winter surveys at sea and stable isotope data indicate that Leach's Storm-Petrels that breed in colonies in Newfoundland winter in tropical waters, but greater resolution of where birds from specific colonies travel is not possible with these data (Harrison 1985, Hedd and Montevecchi 2006, Onley and Scofield 2007). Thus, our objective was to use lightlevel geolocators to improve our knowledge of migration routes and wintering areas of Leach's Storm-Petrels.

METHODS

Study species and study sites. Leach's Storm-Petrels are sexually monomorphic procellariiforms that arrive at breeding colonies in eastern North America in early May. A single egg is laid in June or July and incubated \sim 45 d, with duties shared between parents on a 3- to 5-d rotation. Newly hatched chicks are brooded for several days, after which they are left alone. Parents return independently to feed their nestling at night. The nestling stage lasts \sim 65 d (Huntington et al. 1996).

Bon Portage Island ($43^{\circ}28'N$, $65^{\circ}44'W$) is located 4 km off the southern tip of Nova Scotia, Canada. Gull Island ($47^{\circ}57'N$, $53^{\circ}02'W$) is located in the Witless Bay Seabird Ecological Reserve on the east coast of Newfoundland, Canada. At each of these colonies, we monitor ~300 to 400 burrows and attempt to capture breeding adults each year.

Geolocator attachment. On Bon Portage Island, geolocators (MK5740, Biotrack, Cambridge, UK) were deployed between 22 and 26 September 2012. Geolocators weighed 0.9 g and were $21.9 \times 7.9 \times 3.8$ mm with a 6.8-mm lightsensor stalk. These geolocators had a tube at the front end for suture attachment, and we epoxied a small bead on the back of the device to attach a rear suture. Total mass with attaching material was 1.3 g, which was <3% of the average mass (46.3 \pm 4.4 [SD] g, range = 38–65 g, N = 116) of adult Leach's Storm-Petrels on Bon Portage Island in 2012.

One-way traps were set in entrances of active burrows to catch adults returning to the colony to feed their chicks. Geolocators were attached to birds during daylight hours, so that when returned to nest burrows, they spent several hours before departing to sea after dark. Sixteen geolocators were deployed on the backs of breeding adults (sexes unknown) using subdermal sutures (Ethicon Prolene 4-0, FS-2 19 mm; MacLeod et al. 2008). Suture sites were sterilized with 70% ethanol and feathers were parted to expose the skin at the center of the back. Skin was lifted to thread sutures between the scapulae for the front end of the geolocator and 2 cm behind that for the back end. Using clamp forceps, ≥ 3 double square knots were used to tie each suture. The procedure took < 10 min and birds were returned to their burrows immediately afterwards.

On Gull Island, geolocators (MK5040, Biotrack; 0.75 g, $20 \times 8 \times 3$ mm) were deployed between 18 and 20 September 2012 on the left legs of five adults (sexes unknown) attending chicks. Geolocators were mounted on two soft metal leg bands, each with two drilled holes, using fine-gauge wire twisted and secured at the ends with epoxy. Geolocators plus attachments weighed 1.1 g, or $\sim 2.2\%$ of the average mass $(51.1 \pm 4.2 \text{ [SD] g, range} = 39-61.5 \text{ g}, N =$ 176) of adult Leach's Storm-Petrels on Gull Island in 2012. Devices were deployed at night on adults that returned to feed chicks. Attachment took < 5 min and this method was similar to that used on larger seabirds (Hedd et al. 2012, Quillfeldt et al. 2012).

Data processing. Geolocators had an internal clock and battery, measured light levels every 60 sec, and recorded maximum light levels at 2-min intervals (Afanasyev 2004). Data from geolocators were decompressed using BAS Track software (Biotrack, Dorset, UK), and times of sunrise and sunset were determined from light curves using MultiTrace Geolocation (Jensen Software Systems, Laboe, Germany). Data were processed at a light-level threshold of 10 and an Vol. 85, No. 3

angle of elevation of -4.0° and -3.0° for Bon Portage and Gull Island, respectively. These parameters produced the greatest correspondence with, and least variation from, ground-truth locations for each site. Day/night length was used to provide an estimate of latitude, and Julian date plus the time of local midday/midnight relative to GMT was used to estimate longitude. This procedure produces two locations per day, with a mean positional error of 186 ± 114 (SD) km and 202 \pm 171 km (Phillips et al. 2004, Shaffer et al. 2005) outside equinoxes. Because day length is similar around the globe during equinox, latitude cannot be accurately estimated from light levels during these times. Using a Geographic Information Systems database, lightbased latitudes that were affected by proximity to equinox were excluded (N = 31 and 40 positions during fall equinox for Bon Portage and Gull Island birds, respectively, and N = 49 positions for spring equinox for the Bon Portage bird). Clearly erroneous positions derived from light curves associated with interference around sunrise and sunset (N = 10 and 35 positions for Bon Portage and Gull Island birds, respectively) were also excluded. Resulting validated spatial data were smoothed twice, with raw positions maintained at the start and end of records (Phillips et al. 2004). Traveling speed during migration was calculated by dividing the distance between start and end points of the migration by the number of days required to travel that distance. Because birds do not travel in a straight line, this necessarily underestimates true speeds and distances traveled.

Sea surface temperature (SST Habitat use. in °C), and chlorophyll-a concentration (Chl-a in mg/m³) data were obtained from the National Oceanic and Atmospheric Administration Coast Watch website (http://coastwatch. pfeg.noaa.gov/erddap/index.html; accessed 7 December 2013). Monthly composites (October 2012-May 2013) of Chl-a concentration and SST were obtained through the Moderate Resolution Imaging Spectroradiometer sensor located on NASA's Aqua satellite. Data had a resolution of 0.04 degrees latitude by 0.04 degrees longitude. Bathymetry data (m) were obtained from the National Oceanic and Atmospheric Administration National Geophysical Data Center website (http://www.ngdc. noaa.gov/mgg/image/2minrelief.html; accessed 7 December 2013). Data had a resolution of 0.0167 degrees latitude and 0.0167 degrees longitude. We overlaid geolocator locations for each month with corresponding monthly environmental layers in ArcMap 10.0 (ESRI), and extracted and averaged values of environmental layers at each geolocator point.

Band recoveries. We used Web of Science (Thomson Reuters, New York, NY) to search for studies where either band recoveries or sightings of Leach's Storm-Petrels were reported during the non-breeding season. We also obtained the full record of band recoveries away from colonies from the North American Band Recovery database housed with Environment Canada (data obtained for 1921 to 2013).

RESULTS

Of 16 individuals fitted with Return rate. back-sutured geolocators on Bon Portage Island in 2012, nine (56%) were recaptured in the same burrow in 2013 and one still carried a geolocator. Birds that had been fitted with geolocators showed no signs of infection or injury at suture sites; we suspect devices were lost as sutures worked their way through the skin. At Gull Island, three of five (60%) individuals with geolocators returned in 2013, and all still had their geolocators. These three devices failed prematurely (6, 16, and 130 d after initialization), providing long-term information on movements of only a single bird from 12 October 2012 to 25 January 2013. We found no difference in return rates of birds with (N =9/16 and 3/5 for Bon Portage and Gull Islands, respectively) and without (N = 196/448 and 89/178) geolocators (Bon Portage: $\chi_1^2 = 0.1$, P = 0.79; Gull Island: $\chi_1^2 = 0.2$, P = 0.66), and masses of birds fitted with geolocators were similar to those of non-geolocator birds when recaptured on Bon Portage (ANOVA, $F_{1,462}$ < 0.1, P = 0.87) and Gull Island ($F_{1,158} = 1.3$, P = 0.26).

At-sea movements and habitat use. The bird from Bon Portage Island stopped returning to feed its chick in early October, shortly after geolocator deployment, and began outward migration soon after. Active migration from the Newfoundland Basin to the Cape Verde Islands occurred over five days from 19 to 23 October, with the bird traveling at an average speed of 255 km/d. From the end of outward migration, the bird traveled slowly south between longitude 29°W and 33°W to reach the eastern tip of



Fig. 1. Month by month migration tracks of Leach's Storm-Petrels from (A) Bon Portage Island and (B) Gull Island. Dots represent noon and midnight locations.

Table 1. Mean (\pm SD) oceanographic variables, including bathymetry, sea-surface temperature (SST), and chlorophyll a (Chl-a) concentration, for each month of tracking of two Leach's Storm-Petrels. *N* is the number of locations, and NA denotes Not Available because the geolocator stopped recording the bird's location.

	Breeding colony						
	Bon Portage Island				Gull Island		
Month	Bathymetry (m)	SST (°C)	Chl-a (mg/m ³)	N	Bathymetry (m)	SST (°C)	Chl-a (mg/m ³) N
October	4843 ± 635	27.0 ± 1.5	0.12 ± 0.10	26	4501 ± 516	18.8 ± 3.1	0.26 ± 0.13 22
November	5387 ± 446	28.3 ± 0.3	0.11 ± 0.03	37	4427 ± 501	14.8 ± 3.5	$0.28 \pm 0.11 48$
December	4392 ± 652	27.3 ± 0.3	0.10 ± 0.03	62	4387 ± 748	22.0 ± 4.6	$0.25 \pm 0.23 57$
January	4935 ± 391	27.6 ± 0.2	0.04 ± 0.01	62	4692 ± 396	24.9 ± 1.2	$0.14 \pm 0.04 33$
February	4721 ± 321	$28.1~\pm~0.2$	0.04 ± 0.02	51	NA	NA	NA
March	4783 ± 271	28.4 ± 0.2	0.04 ± 0.01	21	NA	NA	NA
April	4619 ± 855	16.5 ± 7.7	0.70 ± 0.79	58	NA	NA	NA
Ŵay	1403 ± 1913	$8.7~\pm~3.1$	$1.13~\pm~1.01$	56	NA	NA	NA

Brazil in early January. Movements were more localized later in winter (January to mid-March), bounding the equator between $\sim 5^{\circ}$ N and 12°S. Spring migration began about 1 April and lasted ~ 15 d, with the bird moving at an average speed of 375 km/d (Fig. 1A). From the oceanographic parameters analyzed, the bird stayed over deep water (≥ 4000 m), characterized by high temperatures and low Chl-a concentration (Table 1). The bird returned to within 500 km of Bon Portage Island by mid-April and returned to its burrow on 29 May when we captured it and removed its geolocator. An egg was found in the burrow on 19 July, and was estimated by candling (Weller 1956) to have been laid 8–10 d earlier. The egg did not hatch.

Vol. 85, No. 3

Although both the trajectory and the area occupied at the end of the outward migration were comparable between the Bon Portage and Gull Island birds, the timing of migration differed. Based on longitude (because deployment occurred during fall equinox), the bird from Gull Island did not return to its burrow following device attachment on 18 September 2012. It moved quickly offshore to deep (4500 m) and cool (15°C; Table 1) waters in the Newfoundland Basin (~600 km from the colony) where it staged until early December. Movements were within an area $\sim 500 \times 900$ km during this time. Outward migration occurred from 8 to 19 December 2012, with the bird settling at $\sim 17^{\circ}$ N in deep (4692 \pm 396 m), warm (24.9 \pm 1.2°C) waters off West Africa, southwest of the Cape Verde Islands (Fig. 1B). The bird traveled an average of 420 km/d during migration, and then remained near the Cape Verde Islands until its record ended on 25 January 2013. Movements through January were within a ~ 500 \times 1000 km area associated with the upwelling ecosystem of the Canary Current (Arístegui et al. 2009). The date of return to the breeding colony was unknown, but this bird was recaptured in its burrow incubating an egg on 17 June 2013. The burrow was left undisturbed after the device was retrieved, so the breeding outcome was unknown. Although no useful locations were obtained from the other two geolocators (because they were deployed and failed during the fall equinox), consistent longitudinal displacement for the longest of these records (16 d) also suggests that this bird did not return to the colony following geolocator attachment. Brevity of the other record (6 d) was inconclusive, but suggested the same outcome.

Band recoveries and sightings. From the band-recovery database, we found evidence of six recoveries of Leach's Storm-Petrels banded in Atlantic Canadian colonies and recaptured outside North America (Fig. 2); records occurred throughout the eastern North Atlantic during winter (January and February), and throughout the western North Atlantic between 55°N and 10°N during migration (March and October). Sightings of Leach's Storm-Petrels outside of their described winter range (Fig. 2) have been reported in Antarctic waters in February and March (Griffiths and Sinclair 1982, Veit et al. 1996, Hahn and Quillfeldt 1998). Those



Fig. 2. Winter range of Leach's Storm-Petrels (dark gray) based on Harrison (1985) and Onley and Scofield (2007), recovery records of Leach's Storm-Petrels banded in Canadian colonies and captured at locations outside North America (filled circles), and reported bird sightings outside the winter range (open circles).

birds may have been blown off course by severe weather (Hahn and Quillfeldt 1998).

DISCUSSION

Based on the two tracks we obtained, Leach's Storm-Petrels breeding in Atlantic Canada have a clock-wise migration, following the Gulf Stream and Canary Currents across the North Atlantic from October to December to winter in tropical waters in the eastern and western Atlantic, then moving northward in the midand western Atlantic back to breeding areas. This migration movement is facilitated by the prevailing easterly trade winds and the Antilles and Gulf Stream currents. Using stable isotope analysis, Hedd and Montevecchi (2006) also suggested that Leach's Storm-Petrels occupied tropical waters during the non-breeding season. The apparent clock-wise migration of Leach's Storm-Petrels through the North Atlantic is similar to that of several other procellariiforms (González-Solís et al. 2007, Guilford et al. 2009, Egevang et al. 2010, Kopp et al. 2011, Hedd et al. 2012), suggesting that such large scale movements are facilitated by global wind circulation patterns (Felicísimo et al. 2008, González-Solís et al. 2009). Travel speeds during migration (255 km/d for outward migration and 375 km/d for inward migration) were somewhat lower than those reported for other procellariids, but data are available only for species larger than Leach's Storm-Petrels, e.g., Spectacled Petrels (Procellaria conspicillata, 400 km/d, Bugoni et al. 2009), Manx Shearwaters (Puffinus puffinus, 1320 km/d, Guilford et al. 2009), Westland Petrels (Procellaria westlandica, 1350 km/d, Landers et al. 2011), and Sooty Shearwaters (Puffinus griseus, 750 km/d, Hedd et al. 2012).

Interestingly, areas surrounding the Cape Verde archipelago and the eastern tip of Brazil used by the Leach's Storm-Petrels in our study are also used by non-breeding Bugio Petrels (*Pterodroma deserta*, Ramírez et al. 2013), suggesting that these areas may be important for surface-feeding seabirds in winter. Cape Verde is an area of important coastal upwellings influenced by the Canary Current and trade winds, an ideal stopover site for migrating seabirds (Stenhouse et al. 2012). The eastern tip of Brazil does not have major upwelling and Ramirez et al. (2013) found that the main oceanographic characteristic of this location was a steep bathymetric slope.

The two individuals we tracked did not travel south of 15°S during migration. Both the staging areas used by birds during outward migration and the wintering areas were characterized by low productivity ($\leq 0.28 \pm 0.11 \text{ mg/m}^3$). Possible reasons for the choice of wintering area include avoidance of competitors and predators via spatial segregation. In addition, however, the West Africa and northeastern Brazilian waters are actively used by fisheries (Camphuysen and van der Meer 2005, Bugoni et al. 2008), and discards (especially livers) can attract Leach's Storm-Petrels. The bird from Bon Portage returned to near its breeding colony, where productivity in spring was higher, weeks before the start of the breeding season. These limited observations suggest that Leach's Storm-Petrels are income breeders, with resources required for breeding acquired mainly on the breeding grounds. Bond and Diamond (2010) classified Leach's Storm-Petrels as intermediate between income and capital breeders.

Sutures have been used successfully to attach devices to a number of seabird species, e.g., Grey-faced Petrels (Pteodroma macroptera gouldi, MacLeod et al. 2008), Sooty Shearwaters (Puffinus griseus, Adams et al. 2009), and Spectacled Petrels (Reid et al. 2014), including for short-term deployment (up to 5 weeks) on Leach's Storm-Petrels (Pollet et al. 2014). However, we found that suturing geolocators to the backs of Leach's Storm-Petrels was not as effective as leg-band attachment for long-term deployment. Leg-band attachment is commonly used with seabirds (Hedd et al. 2012, Quillfeldt et al. 2012). This attachment method has little effect on breeding success and recovery rates are high, but this method can result in birds with increased levels of corticosterone (Elliott et al. 2012, Quillfeldt et al. 2012). Neither attachment method reduced over-winter return rates or body masses of Leach's Storm-Petrels in our study, but, when deployed late in the chick-rearing period, appeared to cause adults to abandon chicks. Effects on chicks, however, may have been negligible because they had reached asymptotic body mass by that time and were within 7–10 d of fledging. Despite the potential for parents to abandon their chick, this may be the most appropriate time to deploy such devices because abandonment this late may not compromise chick survival. At this stage, adults are already feeding their chicks less frequently than earlier in the season, and catching adults later in the season would be difficult.

Recoveries of Leach's Storm-Petrels banded in eastern North America indicate their presence throughout the North Atlantic during the nonbreeding season, from England to Senegal (West Africa) in the east and from Trinidad to the northeastern United States in the west, consistent with the geolocator tracks in our study. The eBird database also reports sightings of Leach's Storm-Petrels off the Canary Island in November and February (eBird 2014). In addition, Leach's Storm-Petrels are observed every year in the Bay of Biscay, France, from September to February (with peak numbers in November and December) in numbers that cannot be explained by the European population alone (Hémery Vol. 85, No. 3

and Jouanin 1988). The geolocator tracks in our study were consistent with these banding and sighting records.

Our findings that some North Atlantic Leach's Storm-Petrels have a staging area off Cape Verde and winter off the coast of Brazil are also consistent with stable isotope analysis of Leach's Storm-Petrels from Atlantic colonies (Hedd and Montevecchi 2006) and at-sea observations (Harrison 1985, Onley and Scofield 2007). More importantly, we have provided an initial step toward understanding individual migratory movements that will be useful in the conservation and management of this species. Further tracking will be required to confirm migratory routes and wintering areas, information that will help identify potential threats to Leach's Storm-Petrel populations in the Northwest Atlantic Ocean, where most breeding colonies are located.

ACKNOWLEDGMENTS

We thank R. Ronconi, Z. Crysler, E. Holland, M. Sutton, D. Fife, C. Burke, and S. Bennett for assistance in the field. Station manager L. Adams provided logistical support getting to and while on Bon Portage Island. We also thank L. Laurin from the Canadian Banding Office for providing information on band recoveries. We are grateful to G. Ritchison, M. Leonard, and three anonymous reviewers for constructive comments on the manuscript. Funding was provided through an NSERC PGS to I. L. Pollet, the Encana Corporation, the Nova Scotia Habitat Conservation Fund (contributions from hunters and trappers), an NSERC Collaborative Research and Development grant, and through NSERC and Environment Canada grants to the Montevecchi lab. All animal handling procedures were approved by our respective Animal Care Committees (Acadia Protocol 06-09; Memorial Protocol 12-01 WM and 13-01 WM).

LITERATURE CITED

- ADAMS, J., D. SCOTT, S. MCKECHNIE, G. BLACKWELL, S. A. SHAFFER, AND H. MOLLER. 2009. Effects of geolocation archival tags on reproduction and adult body mass of Sooty Shearwaters (*Puffinus* griseus). New Zealand Journal of Zoology 36: 355– 366.
- AFANASYEV, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. Memoirs of the National Institute for Polar Research 58: 227–233.
- ARÍSTEGUI, J., E. D. BARTON, X. A. ÁLVAREZ-SALGADO, A. M. P. SANTOS, F. G. FIGUEIRAS, S. KIFANI, S. HERNÁNDEZ-LEÓN, E. MASON, E. MACHÚ, AND H. DEMARCQ. 2009. Sub-regional ecosystem variabil-

ity in the Canary Current upwelling. Progress in Oceanography 83: 33–48.

- BICKNELL, A. W. J., M. E. KNIGHT, D. T. BILTON, M. CAMPBELL, J. B. REID, J. NEWTON, AND S. C. VOTIER. 2014. Intercolony movement of prebreeding seabirds over oceanic scales: implications of cryptic age-classes for conservation and metapopulation dynamics. Diversity and Distributions 20: 160–168.
- BOND, A. L., AND A. W. DIAMOND. 2010. Nutrient allocation for egg production in six Atlantic seabirds. Canadian Journal of Zoology 88: 1095–1102.
- BRIDGE, E. S., K. THORUP, M. S. BOWLIN, P. B. CHILSON, R. H. DIEHL, R. W. FLÉRON, P. HARTL, R. KAYS, J. F. KELLY, W. D. ROBINSON, AND M. WIKELSKI. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61: 689–698.
- BUGONI, L., P. L. MANCINI, D. S. MONTEIRO, L. NASCI-MENTO, AND T. S. NEVES. 2008. Seabird bycatch in the Brazilian pelagic longline fishery and a review of capture rates in the southwestern Atlantic Ocean. Endangered Species Research 5: 137–147.
- —, L. D'ALBA, AND R. W. FURNESS. 2009. Marine habitat use of wintering Spectacled Petrels *Procellaria conspicillata*, and overlap with longline fishery. Marine Ecology Progress Series 374: 273–285. CAMPHUYSEN, C. J., AND J. VAN DER MEER. 2005. Win-
- CAMPHUYSEN, C. J., AND J. VAN DER MEER. 2005. Wintering seabirds in West Africa: foraging hotspots off Western Sahara and Mauritanis driven by upwelling and fisheries. African Journal of Marine Science 27: 427–437.
- CHEREL, Y., R. A. PHILLIPS, K. A. HOBSON, AND R. MCGILL. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. Biology Letters 2: 301–303.
- EBIRD [online]. 2014. eBird: an online database of bird distribution and abundance. eBird, Ithaca, NY. <http://www.ebird.org> (Accessed 26 May 2014).
- EGEVANG, C., I. J. STENHOUSE, R. A. PHILLIPS, A. PETERSEN, J. W. FOX, AND J. R. D. SILK. 2010. Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. Proceedings of the National Academy of Sciences USA 107: 2078–2081.
- ELLIOTT, K. H., L. MCFARLANE-TRANQUILLA, C. M. BURKE, A. HEDD, W. A. MONTEVECCHI, AND W. G. ANDERSON. 2012. Year-long deployments of small geolocators increase corticosterone levels in murres. Marine Ecology Progress Series 466: 1–7.
- FELICÍSIMO, A., J. MUÑOZ, AND J. GONZÁLEZ-SOLÍS. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. PLoS ONE 3: e2928.
- GASTON, A. J., A. D. BREWER, A. W. DIAMOND, E. J. WOODSWORTH, AND B. T. COLLINS. 2008. Canadian Atlas of bird banding, volume 2: Seabirds, 1921– 1995. Canadian Wildlife Service, Ottawa, Canada.
- GONZÁLEZ-SOLÍS, J., J. P. CROXALL. D. ORO, AND X. RUIZ. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Frontiers in Ecology and the Environment 5: 297–301.
- —, A. FELICÍSIMO, J. W. FOX, V. AFANASYEV, Y. KOLBEINSSON, AND J. MUÑOZ. 2009. Influence of sea surface winds on shearwater migration detours. Marine Ecology Progress Series 391: 221–230.

- GRIFFITHS, A. M., AND J. C. SINCLAIR. 1982. The occurrence of Holarctic seabirds in the African sector of the Southern Ocean. Cormorant 10: 35–44.
- GUILFORD, T., J. MEADE, 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.
- HAHN, S., AND P. QUILLFELDT. 1998. First record of Leach's Storm-Petrel *Oceanodroma leucorhoa* for King George Island, South Shetlands, Antarctica. Marine Ornithology 26: 80.
- HARRISON, P. 1985. Seabirds: an identification guide, revised edition. Houghton Mifflin, Boston, MA.
- HEDD, A., AND W. A. MONTEVECCHI. 2006. Diet and trophic position of Leach's Storm-Petrel during breeding and molt, inferred from stable isotope analysis of feathers. Marine Ecology Progress Series 322: 291–301.
 - —, —, H. OTLEY, R. PHILLIPS, AND D. A. FIFIELD. 2012. Trans-equatorial migration and habitat use by Sooty Shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. Marine Ecology Progress Series 449: 277–290.
- HÉMERY, G., AND C. JOUANIN. 1988. Status and geographical origin of Leach's Storm-Petrel Oceanodroma leucorhoa in the Bay of Biscay, France. Alauda 56: 238–245.
- HUNTINGTON, C. E., R. G. BUTLER, AND R. A. MAUCK. 1996. Leach's Storm-Petrel (*Oceanodroma leucorhoa*). In: Birds of North America, no. 233 (A. Poole and F. Gill, eds.). The Academy of National Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.
- IMBER, M. J. 1982. Migration of White-faced Storm-Petrels *Pelagodroma marina* in the South Pacific and the status of the Kermadec subspecies. Emu 84: 32–35.
- KOPP, M., H.-U. PETER, O. MUSTAFA, S. LISOVSKI, M. S. RITZ, R. A. PHILLIPS, AND S. HAAHN. 2011. South Polar Skuas from a single breeding population overwinter in different oceans though show similar migration patterns. Marine Ecology Progress Series 435: 263–267.
- LANDERS, T. J., M. J. RAYNER, R. A. PHILLIPS, AND M. E. HAUBER. 2011. Dynamics of seasonal movements by a trans-Pacific migrant, the Westland Petrel. Condor 113: 71–79.
- MACLEOD, C. J., J. ADAMS, AND P. LYVER. 2008. At-sea distribution of satellite-tracked Grey-faced Petrels,

Pteodroma macroptera gouldi, captured on the Ruamaahua (Aldermen) Islands, New Zealand. Papers and Proceedings of the Royal Society of Tasmania 142: 73–88.

- ONLEY, D., AND P. SCOFIELD. 2007. Albatross, petrels and shearwaters of the world. Princeton University Press, Princeton, NJ.
- PHILLIPS, R. A., J. R. D. SILK, J. P. CROXALL, V. AFANASYEV, AND D. R. BRIGGS. 2004. Accuracy of geolocation estimates for flying seabirds. Marine Ecology Progress Series 266: 265–272.
- ——, S. BEARHOP, R. A. R. MCGILL, AND D. A. DAW-SON. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecologia 160: 795–806.
- POLLET, I. L., R. A. RONCONI, I. D. JONSEN, M. L. LEONARD, P. D. TAYLOR, AND D. SHUTLER. 2014. Foraging movements of Leach's Storm-Petrels, *Oceanodroma leucorhoa*, during incubation. Journal of Avian Biology 45: 305–314.
- QUILLFELDT, P., 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.
- RAMÍREZ, I., V. H. PAIVA, D. MENEZES, I. SILVA, R. A. PHILLIPS, J. A. RAMOS, AND S. GARTHE. 2013. Yearround distribution and habitat preferences of the Bugio Petrel. Marine Ecology Progress Series 476: 269–284.
- REID, T. A., R. A. RONCONI, R. J. CUTHBERT, AND P. G. RYAN. 2014. The summer foraging ranges of adult Spectacled Petrels *Procellaria conspicillata*. Antarctic Science 26: 23–32.
- 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.
- STENHOUSE, I. J., C. EGEVANG, AND R. A. PHILLIPS. 2012. Trans-equatorial migration, staging sites and wintering area of Sabine's Gulls *Larus sabini* on the Atlantic Ocean. Ibis 154: 42–51.
- VEIT, R. R., M. J. WHITEHOUSE, AND P. A. PRINCE. 1996. Sighting of a Leach's Storm-Petrel Oceanodroma leucorhoa near the Antarctic Polar Front. Marine Ornithology 24: 41–42.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20: 111–113.

Note added in proof: As of 22 July 2014, five more birds have been recovered with geolocators they had carried over the 2013-4 winter, three from Bon Portage (BP) and two from another study site north of BP on the eastern coast of Nova Scotia. Those data have not yet been analyzed.