



Marine distribution and foraging habitat highlight potential threats at sea for the Endangered Bermuda petrel *Pterodroma cahow*

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ABSTRACT: Marine spatial planning relies on detailed spatial information of marine areas to ensure effective conservation of species. To enhance our understanding of marine habitat use by the highly pelagic Bermuda petrel *Pterodroma cahow*, we deployed GPS tags on 6 chick-rearing adults in April 2019 and constructed a habitat suitability model using locations classified as foraging to explore functional responses to a selection of marine environmental variables. We defined 15 trips for 5 individuals, ranging from 1–6 trips per bird, that included both short and long foraging excursions indicative of a dual foraging strategy that optimizes chick feeding and self maintenance. The maximum distance birds flew from Bermuda during foraging trips ranged from 61 to 2513 km (total trip lengths: 186–14 051 km). Behaviourally deduced foraging habitat was best predicted at shorter distances from the colony, under warmer sea surface temperature, greater sea surface height, and in deeper water compared to transiting locations; our model results indicated that suitable foraging habitat exists beyond the core home range of the population, as far north as the highly productive Gulf Stream frontal system, and within the territorial waters of both the USA and Canada. Our results are crucial to inform management decisions and international conservation efforts by better identifying potential threats encountered at sea by this globally rare seabird and highlighting jurisdictions potentially responsible for mitigating those threats.

KEY WORDS: *Pterodroma cahow* · Foraging behaviour · Marine habitat suitability · GPS tracking · Marine threats · Marine conservation

1. INTRODUCTION

Gadfly petrels (*Pterodroma* spp.) are among the most threatened group of seabirds (Croxall et al. 2012, Rodríguez et al. 2019), with limited available habitat on land, very small population sizes, and threats at colonies that require intensive management and conservation efforts (e.g. Carlile et al. 2003). Limiting the impacts of invasive alien species (Jones et al. 2016, Brooke et al. 2018, Raine et al. 2020b) and protecting and enhancing nest sites (Madeiros et al.

2014, Gummer et al. 2015) have addressed direct threats at colonies and have helped stabilize population trends. However, detailed information is limited for many of these species at sea (Grémillet & Boulinier 2009), where additional threats have yet to be identified. To be effective, conservation planning directed at these pelagic seabirds with extensive at-sea distributions extending beyond national boundaries, requires a better understanding of their spatial and temporal use of marine areas (Hays et al. 2019, Beal et al. 2021).

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Publisher: Inter-Research · www.int-res.com

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Several recent studies have deployed tracking devices on gadfly petrels in the Atlantic Ocean to help address gaps in our understanding of their marine habitat use. Year-round distributions of the Bermuda *Pterodroma cahow*, Zino's *P. madeira*, Deserta's *P. deserta*, and Cape Verde *P. feae* petrels have been described using data collected from global location sensor (GLS) tags (Madeiros et al. 2012, Ramirez et al. 2016, Ramos et al. 2016). Platform terminal transmitters (PTTs) have been used to define marine-use areas and movement patterns of black-capped petrels *P. hasitata* (Jodice et al. 2015). More recently, Ventura et al. (2020) described flight behaviour and foraging strategies of breeding Deserta's petrels using global positioning system (GPS) tags, which provided greater spatial resolution and accuracy than both GLS and PTT technologies (Heylen & Nachtsheim 2018). The resulting analyses that integrated results among species or across multiple years (Madeiros et al. 2012, Ramirez et al. 2016, Ramos et al. 2016, 2017) identified several important marine areas for far-ranging petrels, including the waters located along the east coast of North America (Ramos et al. 2017).

These marine areas also support industrial fisheries (Guiet et al. 2019) where interactions with the birds and competition for small pelagic fish or larger, obligate predatory fishes (that drive prey to the surface) may have negative impacts on petrel populations (Ramos et al. 2017). Additionally, these areas broadly overlap with major shipping lanes (Halpern et al. 2015, Pirotta et al. 2019), potentially increasing risks from chemical inputs, including hydrocarbon spills. Brightly illuminated vessels at sea (Black 2005, Merkel & Johansen 2011) and offshore oil and gas platforms off the coast of eastern Canada present other potential risks (Ronconi et al. 2015, Lieske et al. 2019), particularly for the nocturnally phototactic Bermuda petrel (BirdLife International 2018) during the breeding season (Ramos et al. 2017). Furthermore, ocean waters off the US east coast, from Maine through the Carolinas, have recently been proposed or developed to support renewable energy sources in the form of offshore wind power (<https://www.boem.gov/renewable-energy/renewable-energy-path-forward-atlantic>; accessed 2 November 2020). Offshore wind-energy facilities pose a collision risk to birds, and may lead to habitat loss and degradation through displacement from feeding areas (Desholm & Kahlert 2005, Dierschke et al. 2016).

As recently as 2005, the pelagic range and foraging behaviour of the Bermuda petrel remained almost

completely unknown (Madeiros 2005), and our understanding was limited to a small number of observations at sea in the waters around Bermuda and along the eastern seaboard of the US (www.GBIF.org (accessed 9 June 2020) GBIF Occurrence Download <https://doi.org/10.15468/dl.2ut9pu>); only 2 credible sightings were documented in Canadian waters (McLaren 2012). Increased understanding of Bermuda petrel marine habitat use came from GLS dataloggers deployed during 2009–2012 that revealed 3 primary areas used by adults during the chick-rearing period: the central Atlantic Ocean (northeast of Bermuda), waters off North Carolina, USA, and an area southeast of Nova Scotia, Canada (Madeiros et al. 2014, Ramos et al. 2017). Distinct broad-scale habitat use areas identified during the nonbreeding season included waters near the Azores in the eastern Atlantic, and northwest of Bermuda within 1500 km of the breeding colony (Madeiros et al. 2014, Ramos et al. 2017). However, the spatial accuracy of GLS data (estimated at ca. 180 km; Phillips et al. 2004) and relatively low temporal resolution (daily positions) permitted only broad-scale habitat descriptions with limited ability to classify movement-based behaviours, define important mesoscale foraging habitat use, assess risks at sea for the species, and define the jurisdictions potentially responsible for mitigating threats.

The Bermuda petrel is listed as Endangered on the IUCN Red List due to its small population size, restricted breeding range, and ongoing threats at the colony (BirdLife International 2018). It is also listed as endangered by the US Endangered Species Act 1973 (USFWS 2009) and in Bermuda, by the Protected Species Act 2003. In Canada, the Bermuda petrel is protected under the Migratory Bird Convention Act, 1994 (SC1994, c 22), which prohibits the killing or disturbance of the Bermuda petrel and the deposition of any substance that is harmful to the bird in waters frequented by the species. However, none of the current legislation provides broad protection for the marine habitat of this species, which would be deemed essential for the survival and recovery of the species. Our goals were to use high-resolution GPS tags to (1) quantify distribution and behaviour of adults at sea during the chick-rearing period, and (2) use an environmentally informed modelling approach to define foraging habitat. We hypothesized that chick-provisioning adults would forage well beyond the territorial waters of Bermuda, into both the USA and Canada, where they would potentially be exposed to offshore energy infrastructure and development.

2. MATERIALS AND METHODS

2.1. Study species

The breeding population of the Bermuda petrel was estimated at half a million pairs when Bermuda was first discovered by Portuguese and Spanish mariners in the early 1500s (Lefroy 1981). This was later substantiated by the presence of numerous sub-fossil bones in caves and sandy deposits throughout Bermuda (Shufeldt 1916, 1922, Olson et al. 2005). The population was rapidly decimated by introduced mammalian predators and intensive hunting for food by passing mariners and early human colonists. The population collapsed so rapidly that despite protective legislation passed in 1616, the Bermuda petrel seemingly disappeared by the early 1620s (Lefroy 1981, Madeiros 2005). For more than 300 yr, the Bermuda petrel was believed extinct, until 1951, when a small population was discovered on a few rocky islands in northeast Bermuda (Brinkley & Sutherland 2020). Through intensive management efforts that addressed land-based threats such as predation by introduced rats *Rattus rattus*, nest competition with the native white-tailed tropicbird *Phaethon lepturus catsbyii*, and a lack of suitable nesting sites (Wingate 1977, Carlile et al. 2012), the population has grown from 18 breeding pairs in 1961 (Madeiros et al. 2012) to 134 breeding pairs in 2019–20 (J. Madeiros unpubl. data).

The Bermuda petrel is a medium-sized petrel; adults range in mass from 285 to 590 g, with a wingspan of 890–920 mm (Madeiros 2005). Adults first return to breeding islands in Bermuda in late October to engage in courtship behaviour, mating, and nest maintenance (76% of the breeding population now nests within artificial burrows; J. Madeiros unpubl. data). Breeding adults depart for a 5 to 6 wk long, pre-egg-laying exodus during which they forage extensively in preparation for egg-laying and incubation (Madeiros et al. 2012). They arrive back on the breeding grounds in early January and incubation of a single egg lasts up to 55 d and is shared by the male and female. Chicks hatch from late February through March and are fed by both parents during short nocturnal visits to the burrow. Typical among petrels, including *Pterodroma* spp., provisioning parents engage in a dual-foraging strategy (Weimerskirch et al. 1994) where short trips with provisioning on successive nights alternate with extended, long-duration foraging trips lasting as long as 14 d (Madeiros 2005). Chicks fledge between mid-May and mid-June at ca. 88–100 d after hatch, and may not return to the colony for 5 or more years (Madeiros 2005). Little is

known about their diet, but Bermuda petrels are assumed to feed mainly on small squid, fish, and crustaceans either on the wing (typical among other *Pterodroma* spp.) or while surface-skimming and during shallow dives (Madeiros 2005).

2.2. Study site

Nonsuch Island (32.348° N, 64.663° W) and Horn Rock (32.343° N, 64.666° W) are located on the eastern side of Castle Harbour, Bermuda (Madeiros et al. 2012). Nonsuch Island (6 ha) is a recently re-established colony for Bermuda petrels (eradicated by the 1620s; Carlile et al. 2012) with a breeding population of 24 pairs (J. Madeiros unpubl. data); the re-establishment of the colony on Nonsuch was in part a response to tackling the issue of sea level rise and increased storm surge due to climate change, which has been identified as a major threat to remaining Bermuda petrel colonies located on small, low-lying islets (Wingate & Talbot 2003, Carlile et al. 2012). Birds on this island nest exclusively in artificial burrows (Madeiros et al. 2014) located on a south-facing slope surrounded by native vegetation (Carlile et al. 2012). Horn Rock (0.3 ha) is located ca. 300 m southwest of Nonsuch Island and is occupied by 47 pairs, of which 38 nest in artificial burrows (J. Madeiros unpubl. data); Horn Rock is a low-lying (10 m), sparsely vegetated limestone islet frequently inundated by storms and threatened with erosion (Madeiros et al. 2014).

2.3. GPS tag deployment

On successive nights from 9 to 13 April 2019, we visited active burrows just before sunset and placed a row of small sticks across the opening of each burrow to provide us with an indication of the arrival of adult birds at the burrow ($n = 9$ on Nonsuch, 9–11 April; $n = 8$ on Horn Rock, 12–13 April). We visited burrows every hour until dawn and if the sticks were knocked down, we examined the burrow chamber. If a breeding adult was found, we blocked the entrance of the burrow with a stone and the adult was left for 1 h to allow the chick to be fed before the adult was removed and the tag attached. Chicks were left undisturbed.

We deployed GPS tags (e-Obs Bird Solar, 10 g) to 6 chick-rearing adults (mean \pm SD chick age at time of deployment was 39.7 ± 5.4 d; range 34–49 d) located on both islands ($n = 2$ on Nonsuch; $n = 4$ on Horn

Rock). We chose the eObs tags as they were the lightest depth-reinforced GPS tags that would give us the highest-resolution data over multiple foraging trips for the study. Obtaining high-resolution data was a critical element to assess where Bermuda petrels were foraging and whether they were entering oil and gas exploration lease areas or associating with oil and gas platforms, all of which are issues crucial for the conservation of the species. Furthermore, the fact that data from tags could remotely download to a base station meant further handling (and associated stress) would not be necessary. We opted for attachment techniques that were previously successful on other similar *Pterodroma* species (MacLeod et al. 2008, Jodice et al. 2015, Ventura et al. 2020) and thought to be less intrusive than harnessing or subcutaneous wire anchors (Barron et al. 2010). Sutures are not a permanent attachment method (unlike harnesses, for example), with the sutures breaking and the tag falling off after 3–4 mo. This ensured that we would obtain multiple tracks for each bird during this key period of the breeding season (important for understanding whether individual tracks were indicative of the main foraging areas) but not burden the bird with the tag beyond the study period.

Based on information from previous limited tracking of *Pterodroma* petrels, we alternated tag attachment location to either the back ($n = 3$; cf. Jodice et al. 2015) or tail ($n = 3$; cf. Ventura et al. 2020) in an effort to minimize the potential effects of increased drag. For back-mounted tags, we used a modified suture-tape-glue attachment technique (MacLeod et al. 2008, Jodice et al. 2015, Raine et al. 2020a) to attach a 3D-printed plastic platform using 4 surgical sutures and then mounted the tag to the platform with 3 cable ties. For tail-mounted tags (Ventura et al. 2020), the 3D printed platforms were attached to 4 central tail feathers with tape (Tesa 4651). The tag

was then cable-tied to the plate through holes located at the front and sides. Total handling time during tagging was 15–35 min per bird, and tag mass (including plastic platform and ties) was 3.6–4.4% of adult body mass (body mass of tagged birds: 303.3 ± 16.6 g [SD]; Table 1).

We programmed tags to record locations every 2 min, 24 h per day at full battery power and every 8 or 10 min (3 tags at each) when battery power was depleted (low power mode). We set tags to timeout if they did not obtain a GPS fix after 2 min. We set the tag transmitting radio interval (how often they attempted to transmit to any nearby base station) to 5 s. We weighed each adult before attaching GPS tags. We also weighed chicks from burrows with a tagged adult ($n = 6$) and from burrows where no adult was tagged ($n = 14$) weekly through to fledging. As per existing protocols already in place for this species, if chick mass fell below 250 g during their final stage of development (6–10 weeks old), they were hand-fed supplemental fish (*Sardinella anchovia*) to increase their chance of fledging (Carlile et al. 2012).

To test whether tagging the adult had an effect on chick mass gain, we fitted a linear mixed model with an interaction term between chick age and treatment (control vs. GPS) as predictive terms for 2 different chick age groups: between age 10 and 40 d, and post tag-deployment between age 40 and 100 d. We included individual chick as a random effect to account for successive measurements carried out on the same chick, and did not include mass if the chick was receiving supplemental food. We tested for the significance of the interaction using a likelihood ratio test comparing our initial model, which included age and treatment in interaction, to a second model that only included age and treatment as fixed additive terms.

We deployed 2 base stations for remote data downloading: one each on Nonsuch Island and Horn Rock,

Table 1. Summary table describing tag deployment metrics and tag performance from 6 adult Bermuda petrels tagged during the 2018–19 breeding season, and date on which breeding status was confirmed in the year following deployments (2019–20). DNR: did not return to the colony in the following year to breed. Dashes indicate no data transmitted

Tag ID	Sex	Bird weight (g)	Mount position	Tag weight as percentage of total bird mass	No. fixes attempted by tag	Proportion (%) of attempts with locations	Days tracked	Chick fledge mass (g)	2019–20 Breeding confirmed
E0002	Male	290	Tail	4.3	1415	52	37.7	306 ^a	DNR
E0029	Male	310	Back	3.8	21495	87	51.9	258	31 Jan 20
E0204	Male	330	Back	3.6	2263	86	6 Feb	308 ^a	5 Nov 19
E0208	Male	285	Tail	4.4	–	–	–	222	DNR
E0258	Female	310	Back	3.8	10546	85	28.0	260	DNR
E0400	Female	295	Tail	4.2	2766	58	27.0	214 ^a	8 Nov 19

^aChick taken into care during its final stage of development (6–10 wk old) and fed until fledged

where stations had a clear, unobstructed view of the sea and sufficient exposure to sunlight for solar charging. Data from tags automatically downloaded to a base station when birds returned, allowing for continuous data collection until tags presumably detached from individuals or adults no longer visited their colony. These base stations had the additional benefit that there was no need to recapture the adult birds, thus preventing repeated handling stress.

2.4. Data processing and analyses

2.4.1. Data processing and evaluation

We archived and uploaded all data files stored on base stations to Movebank.org (Wikelski et al. 2020) to synthesize tracking data from all birds into a single database. We evaluated the performance of each tag by quantifying the total number of days tracked (as measured by last communication of the tag with the base station), number of locational fixes attempted by the tag, and number of successful locational fixes recorded (i.e. the GPS could get a fix and did not time out). We manually identified the start and end times of unique foraging trips from the colony by visually inspecting mapped tracks and addressed any ambiguities (due to lack of GPS locational fixes) by inspecting tag–base station communication and downloading records (recorded by e-obs programming) to determine when birds visited the colony when gaps in locational fixes existed.

2.4.2. Spatial analyses

For each Bermuda petrel foraging trip identified, we calculated the trip duration, distance travelled, mean and maximum distance from the colony, time (absolute and proportion of trip) spent in territorial and international waters, distance to nearest oil and gas exploration areas, and production platforms (<https://www.cnlopb.ca/information/shapefiles/> and <https://www.cnsopb.ns.ca/resource-library/maps-and-coordinates>; accessed 26 October 2020), and the distance to the nearest, designated US wind energy area (<https://www.boem.gov/oil-gas-energy/boem-renewable-energy-geodatabase>; accessed 2 November 2020). We also described the diel patterns of occupancy by individual petrels within territorial and international waters by annotating GPS locations with 'day' (solar angle $> -6^\circ$, encompassing daytime and civil twilight) or 'night' (solar angle $\leq -6^\circ$) based

on location and time. All calculations were conducted in R (R Core Team 2020) and ArcGIS (ESRI). We further estimated Bermuda petrel spatial utilization using a kernel density estimator using the 'ade-habitatHR' package (Calenge & Dufour 2006) in R. We tested different smoothing parameter values (h) at 5 km increments until results formed a contiguous polygon at the 95% probability contour level when considering all locations (final $h = 65$ km) (Kie 2013). We used the utilization distribution (UD) polygons to describe the core area (50% UD) and the overall home range (95% UD) for each petrel and calculated the proportion of the population (UD for all individuals pooled) and proportion of the individual home ranges that overlapped with the exclusive economic zones (EEZs) of the USA and Canada.

2.4.3. Behavioural classification

To further detail the spatial ecology of the species at sea, we classified behaviours of Bermuda petrels tracked at sea using the 'Expectation Maximization binary Clustering' method ('EMbC' Package in R; Garriga et al. 2016, 2019, Mendez et al. 2020). The EMbC method is a general purpose, unsupervised multivariate data-clustering algorithm based on maximum likelihood estimation of a Gaussian mixture model (Garriga et al. 2016). The EMbC classification method requires location data collected at a uniform sampling interval for meaningful output and interpretation. Because our tracking data were collected at multiple sampling intervals (2, 8, and 10 min) and because of variable gaps caused by GPS functionality, we interpolated track segments of sufficient duration to a fixed interval prior to behavioural classification. We identified distinct sequences of locations for which the time between successive points was < 30 min and then linearly interpolated points in each sequence to a 10 min interval to standardize sampling rate and prevent fabrication of locations across longer tracking gaps. We pooled locations from all interpolated track sequences that had ≥ 3 locations (e.g. the minimum required to behaviourally classify at least 1 point) and processed them using the EMbC behavioural classification algorithm. Locations classified using this method fall into 4 categories: low-speed-low-angle (LL), interpreted as sitting on the water; low-speed-high-angle (LH) represented foraging at a small scale; high-speed-high-angle (HH) represented sinuous, exploratory movements at a larger scale; and high-speed-low-angle (HL) represented directional movements associated with transiting and commut-

ing. We considered the locations classified as LL and LH to represent foraging, and those classified HH and HL to represent transiting.

2.4.4. Environmental data

To build our habitat suitability model (see Section 2.4.5), we first extracted environmental variables (Table S1 in the Supplement at www.int-res.com/articles/suppl/n045p337_supp.pdf) restricted to the study period (11 April to 4 June 2019) from a domain considered representative of foraging Bermuda petrels (as represented by our data). The limits of this domain were as follows; to the east the maximum range reached by an individual during a foraging trip multiplied by 1.1 (Wakefield et al. 2017, Baylis et al. 2019); to the north by that same distance excluding the Gulf of St Lawrence and the Bay of Fundy; to the west by the North American continent; and to the south by the latitude corresponding to the limit of the EEZ of Bermuda (Fig. 1). From this domain, we extracted a suite of dynamic variables including daily sea surface temperature (SST, °C), daily sea surface height (SSH, m), finite-size Lyapunov exponent (FSLE, d^{-1} ; indicative of water stirring), daily eastward (u) and northward (v) water velocity components ($m\ s^{-1}$) (based on altimetry), 8 d composite of

chlorophyll *a* concentration (chl *a*, $mg\ m^{-3}$), and weekly ocean surface winds ($m\ s^{-1}$). Given persistent cloud cover, we used an 8 d chl *a* composite and filled missing values for each weekly layer by nearest-neighbour interpolation. We used the u and v water velocity component to calculate daily eddy kinetic energy (EKE, $m\ s^{-1}$; Table S1) indicative of mesoscale circulation patterns. Surface EKE quantifies the energy associated with water displacement, with higher values corresponding to higher velocity and lower values indicating lower flow energy.

As indices of mesoscale fronts, we also calculated spatially discrete, scale-dependent differences among values for SST, chl *a*, and SSH; high values correspond with greater differences in values at a given location. Specifically, we used a moving window function to estimate the range in SST, chl *a*, and SSH within neighbourhood cells associated with focal locations. We considered 2 scales for the moving window function: 3×3 and 15×15 grid cells (function: $\max[\text{value}] - \min[\text{value}]$). The size of the moving window was chosen to capture mesoscale (~60–120 km) frontal features. Each cell of the moving window corresponded to the spatial resolution of the projected layers (~8 km for SST and SSH, ~4 km for chl *a*; Table S1).

We also considered static variables including distance to the colony (km; great circle distance), water

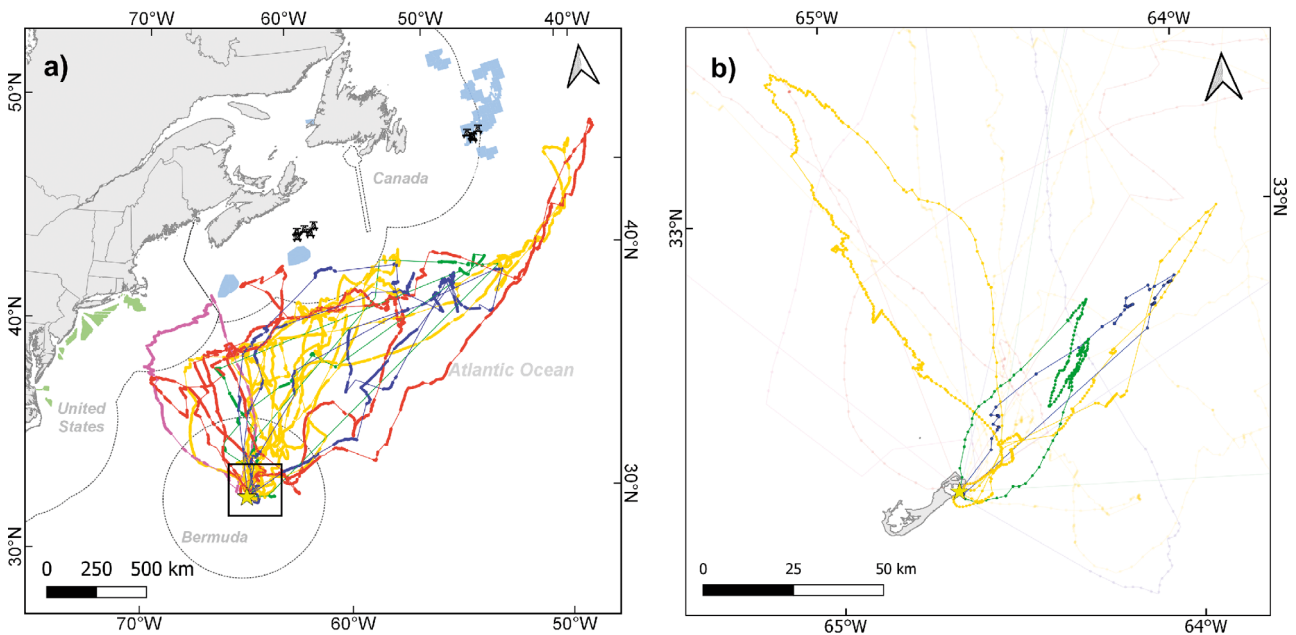


Fig. 1. (a) Foraging trips of individual Bermuda petrels (different colours, $n = 5$) GPS-tracked during the chick-rearing period from 19 April to 6 June 2019 in Bermuda (colony shown as a yellow star). (b) Although long foraging trips were the norm ($n = 11$), the birds also took short trips within Bermudian waters ($n = 4$). Exclusive economic zones for Canada, the USA, and Bermuda are presented (dotted lines), as well as active oil and gas exploration licence areas (blue polygons) and production platforms (black crosses) in Canada and wind energy areas (green polygons) in the USA. Projection is Quebec Lambert EPSG:6622

depth (m), and the frequency of chlorophyll peak index (FCPI). We calculated FCPI based on monthly chl *a* values from 2002 through 2019 (Suryan et al. 2012). FCPI provides a measure of long-term deviation from the temporal trend in surface chl *a* (9 km pixel resolution) at each measurement location.

2.4.5. Habitat suitability model

To investigate the functional response of Bermuda petrels to their environment, we used the foraging locations (LL and LH) identified using EMbC ($n = 2449$) to produce a habitat suitability model during the study period (11 April to 4 June 2019) within their defined foraging domain (see Section 2.4.4). Within this defined domain, we randomly sampled 3 background locations (hereafter, pseudo-absences) for each foraging location (i.e. presence; Aarts et al. 2008) after first excluding an area of 1 km radius around each presence location, and randomly assigned a date to each of those pseudo-absence locations within the study period. Habitat variables were then extracted at each presence and pseudo-absence location at corresponding dates using the R package 'raster' (Hijmans & van Etten 2012).

To determine which covariates to include in our final predictive model, we fit a logistic regression with binomial distribution to each covariate separately using generalized additive models with the R package 'mgcv' (Wood 2019). To account for the latitudinal gradient in SST across our study area, we also considered a bivariate smoother with SST evaluated by latitude (Forney 2000, Becker et al. 2019). Each model was fit using cubic regression splines with the number of knots initially set to 3 and increased to a maximum of 5 to minimize overfitting and to facilitate interpretation of the response curves. We selected the best model as indicated by the greatest area under the receiver operating curve (AUC) after 10-fold cross validation. Cross validation can mitigate inherent autocorrelation that exists within tracking data (Wood 2006). We further ranked univariate models by AUC. AUC values range from 0.5 (the model is no better than random) to 1 (perfect model fit). To avoid including collinear covariates, we calculated Spearman rank correlations (ρ) for each pairwise comparison of covariates and excluded the covariate with absolute $\rho \geq 0.7$ that also correlated with one other covariate, or we kept the covariate with the greatest AUC (if no other correlation was detected). We then followed a step-forward selection,

adding covariates one by one based on AUC rank, retaining additional covariates if inclusion increased model AUC and decreased Akaike's information criterion (AIC) of the model by ≥ 4 .

We predicted the probability of occurrence of foraging Bermuda petrels at sea within their domain using a grid corresponding to the lowest resolution of our final environmental layers (0.08°). We extracted values from the selected covariates of our final model at the centroid of each daily grid cell. We used the function 'predict.gam' ('mgcv' package) to predict the probability of occurrence of foraging for each of the 55 d of the tracking study (daily habitat suitability index [HSI]). We averaged the resulting 55 HSI raster layers to generate a final, predictive map corresponding to the average daily probability of occurrence of foraging Bermuda petrels and summarized the error of the spatial prediction by calculating the pixel-specific standard deviation.

3. RESULTS

3.1. Tagging

We obtained locational data from 5 of 6 tags; birds were tracked for 6.2–51.9 d (729–18 780 GPS locations). The tags obtained GPS locations during 85–87 % of fix attempts when mounted on the back of the bird compared with 52–58 % when mounted on the tail (Table 1).

All 6 chicks of tagged adults fledged, although 3 chicks received supplemental fish (*Sardinella anchovia*) in their final stage of development (mean \pm SD age when supplemental feeding started: 93 ± 7 d) to maintain growth rates and increase their likelihood of survival. An additional 3 chicks of adults not used in our study also received supplemental fish; of these, 1 died before fledging (J. Madeiros unpubl. data). Mean fledging mass of the chicks with a tagged parent (without supplementary feeding) was significantly lower compared to chicks with untagged parents (Welch 2-sample *t*-test: $t_{5,4} = -3.10$, $p = 0.02$). The effect of age on chick mass between age 10 and 40 d did not differ between control and tagged burrows ($\chi^2 = 3.04$, $p = 0.08$), i.e. the interaction between age and treatment was not significant. However, the interaction between chick age and treatment group (i.e. tagged parent or control) on chick mass post-tagging (between age 40 and 100 d) was significant ($\chi^2 = 34.08$, $p < 0.001$); chicks from burrows with a tagged parent had a lower mass at a given age than chicks from control burrows.

Monitoring in 2019–20 revealed that 3 of 6 tagged adults did not return to breed during the following year and their untagged partners returned and paired with alternate mates (Table 1). All untagged adults ($n = 14$) returned to breed in 2019–20, although 1 untagged male was replaced at its burrow prior to egg-laying by a younger male.

3.2. Foraging trips and marine distribution

We identified 15 trips for 5 individuals (Fig. 1), ranging from 1–6 trips per bird, including both short trips (≤ 24 h in duration, departing the colony one night and returning the next; $n = 4$) and long trips (> 24 h, $n = 11$; Table 2). Short trips averaged (\pm SD) 242.0 ± 63.6 km in total distance travelled (range 186–328 km) and reached an average distance of 47.5 ± 15.6 km (range 27–62 km) from the colony; maximum distances reached during short trips ranged from 61 to 121 km from the colony (Table 2, Fig. 1b). On

average, birds on long trips were absent from the colony for 13.4 ± 7.2 d (range 4.2–25.9 d) and travelled a total distance of 6248.0 ± 3443.9 km (range 2740–14 051 km; Table 2). Birds on long trips flew an average of 739.4 ± 247.3 km from the colony (range 436–1132 km), travelling to a maximum distance from the colony of 1497.7 ± 577.1 km (range 774–2513 km; Table 2, Fig. 1a). In general, birds on long trips travelled in a clockwise direction; they headed north after departing from the colony, remained in deeper water (> 1000 m depth) off the continental shelf, and returned to the colony from the northeast (Fig. 1a). Three of the 4 longest trips (Table 2) were comprised of shorter ‘sub-trips’, where birds returned to within ca. 250 km of the colony after 10.3–12.5 d, then headed out on a second (or third) sub-trip before finally returning to the colony (Table 2, Fig. 2).

In addition to Bermudian waters, GPS locations for tagged Bermuda petrels fell within the EEZs of both the USA and Canada, and within international ‘high-seas’ waters (Fig. 1a). Only 1 of 5 (20.0%) birds (dur-

Table 2. Summary of foraging trip durations, distances travelled, and mean and maximum distances from colony for 5 adult Bermuda petrels GPS-tracked during the chick-rearing period in April–May 2019. The nearest distances to oil and gas exploration areas (EL), production platforms, and wind energy areas are indicated. Dashes indicate no data transmitted

Individual	Trip metrics			Distance from colony (km)			Nearest distance (km)		
	No.	Type	Duration (d)	Total distance travelled ^a (km)	Mean	Max	Active EL	Oil/gas platform	US wind energy area
E0002	1	Short	0.7	203	44	61	1176.2	1587.9	1254.6
E0002	2	Long	24.8 ^b	7801	674	1675	453.9	770.8	588.4
E0002 ^c	3	Long	12.2	–	–	–	–	–	–
E0029	1	Long	25.9 ^d	14051	999	2369	248.4	436.9	674.7
E0029	2	Long	10.9	5296	493	1255	256.2	365.0	425.7
E0029	3	Long	4.2	2740	506	1012	368.7	543.0	853.8
E0029	4	Short	0.8	328	62	121	1095.5	1542.5	1151.9
E0029	5	Short	1.0	251	27	102	1154.8	1552.3	1258.8
E0029	6	Long	9.2	3147	436	774	379.8	701.1	636.1
E0204	1	Long	6.2	2893	699	1001	31.8	700.6	165.2
E0258	1	Long	11.1	7077	1132	2513	276.4	503.6	461.8
E0258	2	Long	16.9 ^e	8680	710	1215	16.1	220.3	427.5
E0400	1	Long	8.0	4587	673	1491	364.5	586.5	754.3
E0400	2	Short	0.8	186	57	81	1173.8	1576.5	1260.3
E0400	3	Long	18.2 ^f	6208	1072	1672	99.5	255.2	688.2

^aDue to some gaps in GPS tracking (GPS timeout issues or battery depletion), trip distance travelled should be interpreted as a minimum

^bAfter 10.3 d from initial departure from the colony, bird returned to within 166 km of the colony but departed for a second sub-trip lasting 14.5 d before finally returning to the colony. Trip end time determined from base station download record

^cTrip start and end times determined from base station download record, but no locational information was recorded

^dAfter 12.5 d from its initial departure from the colony, the bird returned to within 247 km of the colony but departed for a second sub-trip lasting 6.8 d before returning to the same area (within 254 km of colony) without visiting the colony. Bird departed again for a third sub-trip lasting 5.2 d before finally returning to the colony

^eAfter 11.7 d from its initial departure from colony, the bird returned to within 202 km of colony but departed for a second sub-trip lasting 4.8 d before finally returning to the colony

^fTrip end time determined from base station download record

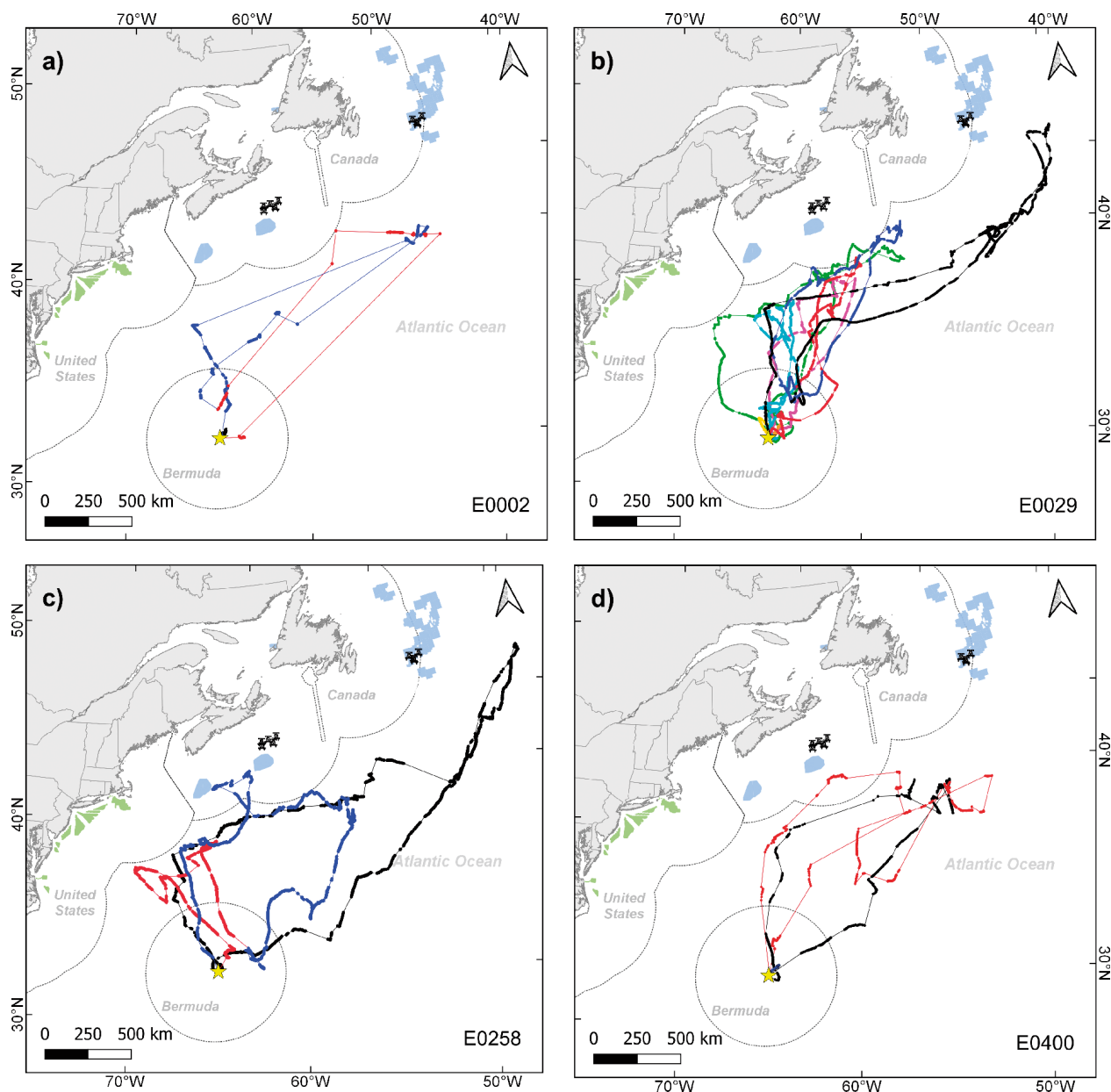


Fig. 2. Successive tracks (different colours) of chick-rearing Bermuda petrels tracked for at least 2 trips (or sub-trips, when birds returned to within ca. 250 km of colony then returned to the high seas without first returning to the colony; Table 2) within the 2018–19 breeding season. Panels correspond to individual birds: (a) E0002, (b) E0029, (c) E0258, (d) E0400. Other details as in Fig. 1

ing a single trip) entered US territorial waters (Fig. 1a). In comparison, 4 of 5 (80.0%) birds (and 5 of 14 [35.7%] trips with location information) entered Canadian territorial waters (Fig. 1), and included night-time locations (46.8% of the GPS locations obtained from the birds while in Canadian waters occurred at night). Within these waters, the closest a tagged bird came to an oil or gas platform was 220.3 km, and that same individual ventured to within 16.1 km of an active exploratory licence area (Table 2, Fig. 2c). Within the USA, the closest a tagged bird

came to a designated wind energy area was 165.2 km (Table 2, Fig. 1).

The home range (95% UD) estimated for all individuals combined spanned ca. 2.5 million km², with 24.9% of their area overlapping territorial waters of Bermuda, the USA, or Canada and the remainder within international waters (Fig. 3a). Bermuda accounted for the most territorial overlap (13.5%), followed by the USA (6.6%) and Canada (4.8%); the areas of overlap were 354 000, 172 000, and 126 000 km², respectively (Fig. 3a). Canadian waters

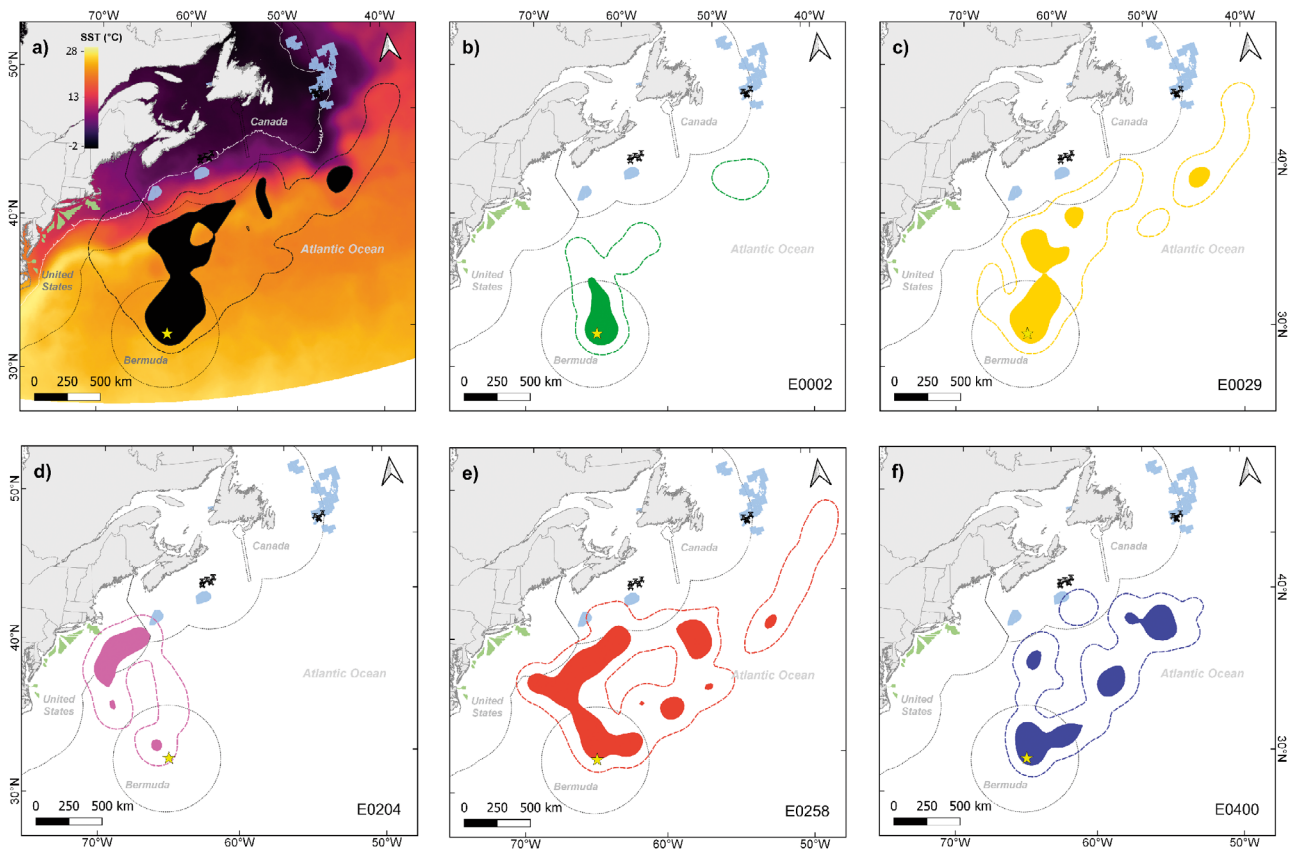


Fig. 3. Estimated kernel utilization distribution (UD; $h = 65$ km) for the 5 Bermuda petrels tracked during the chick-rearing period in 2019 showing 95 % UD (dashed coloured lines in panels b–f; black dashed line in panel a) and 50 % UD (solid coloured patches in panels b–f, black patches in panel a) of all locations obtained for (a) all 5 individuals pooled with daily sea surface temperature (SST, °C); SST averaged over the study period (11 April to 4 June 2019; warmer colours represent warmer temperatures), and (b–f) for each of the individual birds tracked (E0002, E0029, E0204, E0258, and E0400, respectively). The 500 m isobath is included in panel a (white line) to represent the approximate location of the shelf break. Other details as in Fig. 1

were included within the 95 % UD estimated for 4 of the 5 birds and within the core area (50 % UD) estimated for 2 birds (Fig. 3b–f).

3.3. Behavioural classification

We classified a total of 10 542 interpolated 10 min locations into 4 behavioural classes (Table 3): HH ($n = 2460$), HL ($n = 5633$), LH ($n = 718$), and LL ($n = 1731$). The proportions of location classes were similar for day (26% HH, 52% HL, 8% LH, 15% LL) and night (19% HH, 56% HL, 5% LH, 20% LL), with high-speed behaviours (HH, HL) combined accounting for the majority of locations in both diel periods.

3.4. Habitat suitability model

Based on AUC, the final model predicting probability of occurrence of foraging (based on LH and LL

vs. random) included 4 covariates: distance to colony (Dist2col), SST smoothed by latitude (SST:lat), water depth (Depth), and SSH (Table 4). Following a step-forward procedure, this model explained 53.2% of the deviance (Table 5). Within the Bermuda petrel domain, the relative habitat suitability for foraging Bermuda petrels was mostly influenced by distance

Table 3. Number of GPS locations from 5 adult Bermuda petrels tracked during the chick-rearing period in April–May 2019 classified into behavioural classes. HH: high speed, high turning angle; HL: high speed, low turning angle; LH: low speed, high turning angle; LL: low speed, low turning angle. Mean \pm SD speed and turning angle are also shown

Behavioural classification	No. GPS locations	Speed (km h ⁻¹)	Turning angle (rad)
HH	2460	5.01 \pm 3.02	1.07 \pm 0.74
HL	5633	7.78 \pm 3.45	0.09 \pm 0.09
LH	718	0.39 \pm 0.24	1.27 \pm 0.81
LL	1731	0.48 \pm 0.29	0.08 \pm 0.09

Table 4. Summary of generalized additive model built with single covariates. Shown are the number of knots used in the smooth function (k), percentage of model deviance explained (% dev.), and the area under the receiver operative curve (AUC) calculated for each model following 10-fold cross-validation. Covariates in **bold** were kept in the final model in the order of their AUC score rank. We present estimates for range in sea surface temperature (SST), chlorophyll a , and sea surface height (SSH) from a 15×15 grid cell moving window function. Dist2col: distance to colony; SST:lat: SST smoothed by latitude; FCPI: frequency of chlorophyll peak index; EKE: eddy kinetic energy; FSLE: finite-size Lyapunov exponent

Covariate	k	% dev.	AUC
Dist2col	3	29.9	0.85
SST:lat	5	16.1	0.74
Depth	5	13.5	0.74
SSH	3	8.4	0.70
FCPI	3	6.4	0.69
SST ₀	5	13.9	0.69
Chl a range	5	6.6	0.65
EKE ₀	4	2.6	0.63
SST range	5	1.8	0.62
SSH range	4	3.2	0.60
Wind speed	5	0.9	0.60
Chl a	3	3.4	0.58
FSLE	5	2.1	0.57

to the colony, which was negatively related to the probability of occurrence of foraging (Fig. 4a). Foraging Bermuda petrel locations were more likely associated with warmer SST within the domain (Fig. 4b), deeper waters off the North American shelf-break (Fig. 4c), and greater SSH (Fig. 4d). Despite the absence of any association with the continental shelf (<500 m depth) off eastern North America, modelled habitat suitability was greatest around the colony and extended far into the oceanic zone to the limit of the continental shelf break and into both US and Canadian waters (Fig. 5a), although the probability

Table 5. Model selection following step-forward procedure. The model in **bold** is the final model selected based on increase in the area under the receiver operative curve (AUC) score, decrease in Akaike's information criterion (AIC) score ($\Delta AIC \geq 4$), and increase in deviance explained (% dev) following the successive addition of covariates (defined in Table 4)

Model	AUC	AIC	% dev
presence ~ s(Dist2col)	0.8614	7731	29.9
presence ~ s(Dist2col) + s(SST:lat)	0.9372	5395	51.2
presence ~ s(Dist2col) + s(SST:lat) + s(Depth)	0.9391	5262	52.4
presence ~ s(Dist2col) + s(SST:lat) + s(Depth) + s(SSH)	0.9399	5184	53.2
presence ~ s(Dist2col) + s(SST:lat) + s(Depth) + s(SSH) + s(FCPI)	0.9398	5182	53.1

of occurrence of foraging was most variable at the northern limits of suitable habitat (Fig. 5b).

4. DISCUSSION

4.1. Marine distribution and behaviour

Our study provides the first fine-scale distribution data at sea for Bermuda petrels during the breeding season. We tracked 5 birds for an average of 30 d and obtained 32 055 locations. Chick-rearing adults used an extensive area in the western North Atlantic (ca. 2.5 million km²) north of Bermuda. Some birds travelled in a clockwise direction as far as the edge of the Canadian continental shelf before returning to Bermuda, presumably following a flyway with favourable wind direction (Adams et al. 2010, Ventura et al. 2020). Gadfly petrels are known for undertaking remarkably long foraging trips (Ramirez et al. 2016, Ramos et al. 2017, Raine & Driskill 2019) and for using persistent winds to efficiently travel thousands of kilometres at sea (Ventura et al. 2020). Previously, the waters located along the east coast of North America were described as key habitat for breeding Bermuda petrels (Madeiros et al. 2014), but also for other globally threatened *Pterodroma* species including black-capped and Deserta's petrels during breeding (Ramos et al. 2017), and Trindade petrels *P. arminjoniana* during their non-breeding season (Krüger et al. 2016). In general, the western North Atlantic supports a diversity of marine predators year-round (Barrett et al. 2006, Hedd et al. 2012, 2018, Gaube et al. 2018, Davis et al. 2020) where warm, salty surface waters are transported northwards within the Gulf Stream to mix with cool, fresh, nutrient-rich deep waters flowing southward within the Deep Western Boundary Current (Puerta et al. 2020).

Our tracking data indicated that Bermuda petrels performed both short (~1 d duration) and long (>4 d duration) foraging excursions, indicative of a dual foraging strategy (Weimerskirch et al. 1994), although 97.7% of their time at sea was spent on long trips. Birds on short trips remained within Bermudian waters, perhaps to increase the feeding frequency of the chick (Weimerskirch et al. 1994). In contrast, birds on long trips travelled to more distant regions far beyond Bermudian territorial waters, a strategy consistent with previous studies of

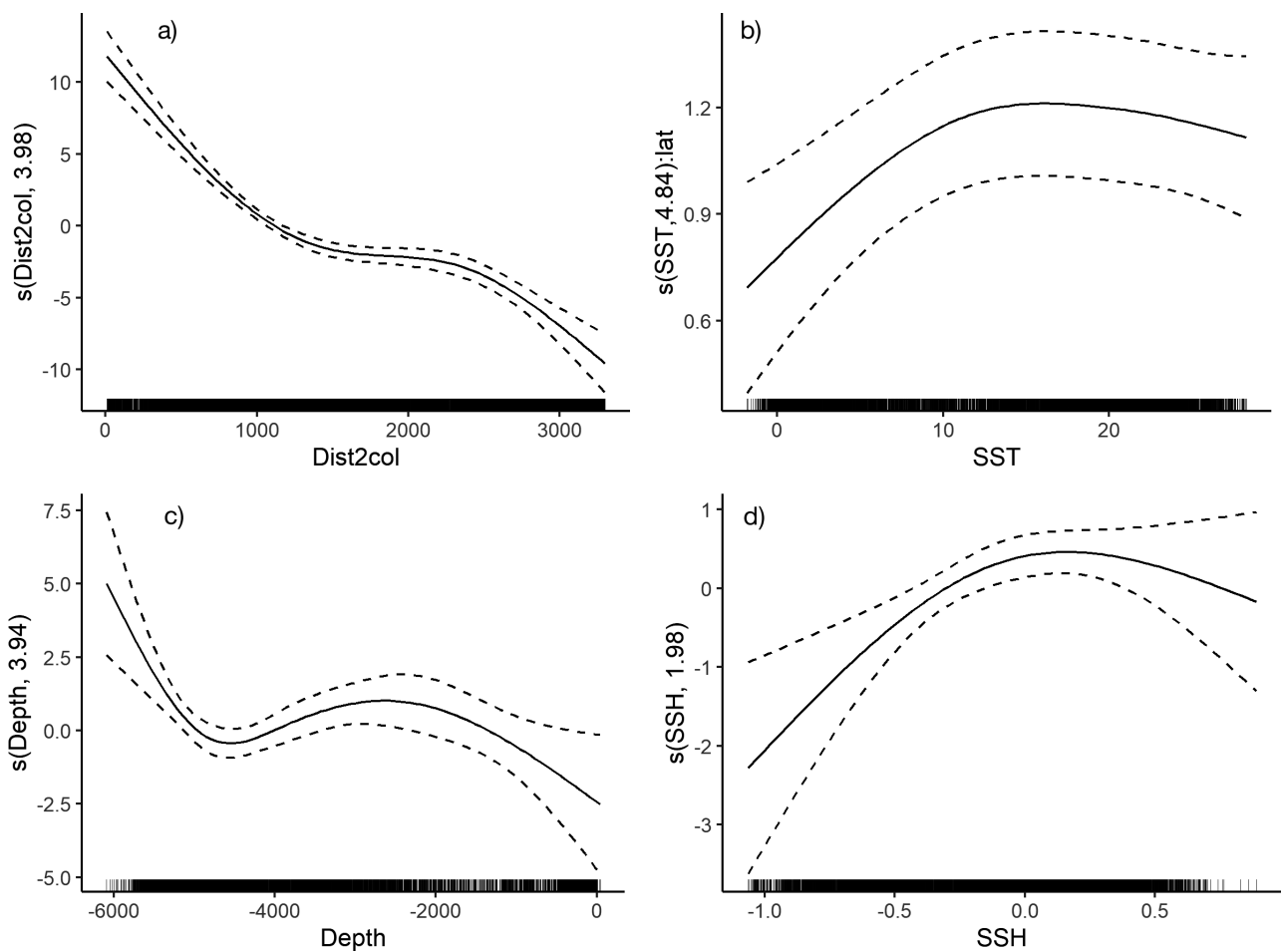


Fig. 4. Model terms for estimated probability of occurrence of foraging Bermuda petrels tracked during the breeding season 2018–19. The y-axis represents the function of each term with the effective degrees of freedom (edf) of the smooth term in brackets. 0 on the y-axis corresponds to absence of an effect of the predictor variable on the estimated probability of occurrence. Terms included in the generalized additive model were (a) distance to colony (Dist2col; km), (b) daily sea surface temperature smoothed by latitude (SST:lat; °C), (c) bathymetry (depth; m), and (d) sea surface height (SSH; m); the y-axis scale varies to emphasise model fit. The confidence intervals (dashed lines) are shown at 5 standard errors above and below the estimate of the smooth

procellariids (Chaurand & Weimerskirch 1994, Paiva et al. 2010, Jodice et al. 2015, Shoji et al. 2015) that may provide them access to large-scale, predictable, and potentially richer foraging areas associated with the Gulf Stream. Three of 10 (30%) long trips showed birds returning to Bermudian waters, but not to their colony to provision chicks, before initiating another long trip to the high seas. It is unknown if such interrupted trips were anomalous, perhaps indicating behavioural alterations resulting from tagging (see Section 4.3). Alternatively, such trips may have resulted from poor flying or feeding conditions (i.e. insufficient wind, insufficient food load), making the trip back to the home colony too costly. Long-term observations at the colony indicate decreased bird activity during nights with relatively little wind (J. Madeiros

unpubl. data). Satellite tracking of Hawaiian petrels *P. sandwichensis* indicated that similar, incomplete long trips also do occur (J. Adams unpubl. data).

The behaviour of Bermuda petrels at sea mostly comprised transiting (high speed) movements, and proportions did not vary markedly between day and night, indicating that foraging, as classified here, might occur at any time. Little is known about the diet of Bermuda petrels, but similar to other *Pterodroma* species (Imber 1973, Klages & Cooper 1997, Bester et al. 2010, Rayner et al. 2016, Leal et al. 2017), they likely feed on mesopelagic prey including small squid, fish, and crustaceans, and perhaps bioluminescent species that perform diel vertical migrations to the surface at night when they would become more available to the petrels.

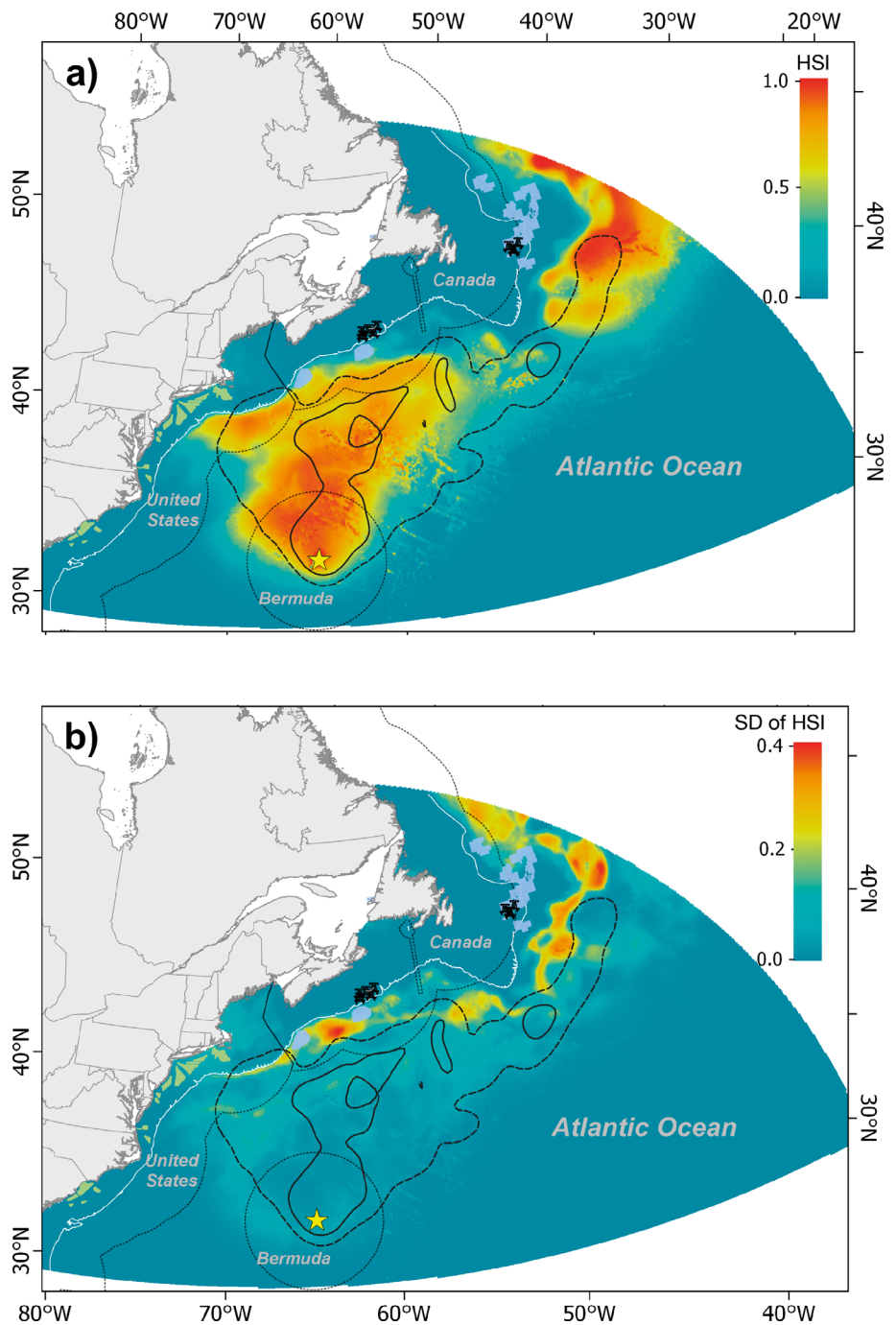


Fig. 5. Spatial habitat predictions of foraging Bermuda petrels tracked from Bermuda (yellow star) during the chick-rearing period (11 April to 4 June 2019; 55 d). (a) Average of daily habitat suitability index (HSI) scaled from 0 (unsuitable) to 1 (highly suitable), and (b) standard deviation of daily HSI. The spatial resolution of the prediction was set to the lowest resolution of our environmental layers (sea surface height, SSH, at 0.08°). The 500 m isobath (white line) represents the approximate location of the shelf break. The thick black lines depict the 50% (solid) and 95% (dashed) utilization distributions (see also Fig. 2) of the population. Other details as in Fig. 1

4.2. Foraging habitat suitability

Our habitat suitability model highlighted the pelagic distribution of Bermuda petrels during chick-rearing; the continental shelf did not appear to be important foraging habitat for the species during this time of the year (Fig. 5a). Model results indicated that the northern limit of foraging roughly corresponded with the Gulf Stream frontal system mark-

ing the limit between subtropical and subpolar gyres in the North Atlantic where a sharp temperature front known as the Gulf Stream North Wall (Chi et al. 2019) occurs (Fig. S1). This area of convergence is a dynamic and productive zone (Wenegrat et al. 2020) used by multiple marine predators and consumers, including seabirds (Haney 1986, De Monte et al. 2012), sharks (Gaube et al. 2018, Braun et al. 2019), and neonate sea turtles (Chambault et al. 2017). The

importance of persistent frontal zones for multiple marine vertebrates makes these regions good candidates for marine conservation areas (Scales et al. 2014).

Despite being a persistent, large-scale oceanographic feature located between Cape Hatteras and the Grand Banks (Seidov et al. 2019), the Gulf Stream trajectory and the latitude of its North Wall front are dynamic, fluctuating in velocity and turbulence and shifting latitudinally among years (McCarthy et al. 2018, Seidov et al. 2019). Dynamic mesoscale features including eddies and meanders shift through space following horizontal water displacement and currents that characterize this region (Kang & Curchitser 2013, Gaube & McGillicuddy 2017), and can influence aggregation of foraging marine vertebrates (Cotté et al. 2015, Braun et al. 2019) including seabirds (Hyrenbach et al. 2006, Oliver et al. 2019). This spatiotemporal variability may help explain why we also observed greater variability in our predictions of foraging occurrence in this area, and why our habitat suitability model did not retain covariates that represented mesoscale features (FSLE or EKE) associated with the Gulf Stream, nor covariates that index frontal zones (SST range, chl *a* range, and SSH range) despite evaluation at multiple scales (results at the sub-mesoscale [~12–24 km] are not presented herein). Alternatively, the large percentage of locations within homeothermic warm Bermudan waters classified as ‘foraging’ may have masked finer-scale relationships strictly associated with the frontal domain. This might be better resolved in the future with a larger sample size that would allow for modelling short trips separately from long trips, or by evaluating habitat associations within a more focussed domain encapsulating the Gulf Stream frontal area. Nonetheless, the Gulf Stream did appear to be the northern boundary for Bermuda petrel foraging (Fig. S1), and warmer relative SST in particular was an important predictor of foraging occurrence in the final habitat suitability model. Other *Pterodroma* petrels showed an affinity for warmer SST (Ramos et al. 2016, Krüger et al. 2018); however, the opposite trend (positive association with cooler waters) was observed in albatrosses foraging within the North Pacific Transition Zone (Kappes et al. 2015, Thorne et al. 2015).

In our study, predicted foraging occurrence was most influenced by distance to the colony, which is typical and expected among central-place foragers obligated to return frequently to their breeding colony during the chick-rearing season, and especially for long-ranging seabirds with dual short-trip

long-trip strategies. While depth and SSH only explained a small fraction of the deviance in our model, the addition of these variables improved overall model fit. Although seamounts in pelagic areas have been identified as important foraging areas for other marine predators (Morato et al. 2008, Wong & Whitehead 2014, Kokubun et al. 2015), we have found little support so far for seamounts influencing foraging behaviour among petrels in this study.

Our model indicated that suitable habitat exists beyond the pooled core range (50% UD), in international waters far from the colonies, but also within the territorial waters of the USA and Canada. However, these areas revealed greater variability in probability of foraging occurrence. Furthermore, our model only explained 53.2% of the deviance; although not atypical for habitat surface modelling among marine vertebrates (Scales et al. 2014, Virgili et al. 2017, Briscoe et al. 2018, Chavez-Rosales et al. 2019), other unidentified factors such as prevailing wind direction and speed (Ventura et al. 2020), and distribution of prey or obligate predators (e.g. tuna; see Miller et al. 2018) may enhance our ability to define foraging habitat.

4.3. Potential tag effects

It is important to address the degree to which our results could have been influenced by tagging effects and to acknowledge that carrying tags may have imposed burdens (Kay et al. 2019) on the petrels in this study. We suspect that tags may have caused decreased food delivery to chicks, and for 3 adult birds it may have suspended breeding in the following year. However, the precise cause of potential impacts (i.e. handling time and disturbance, device effects, timing or length of deployment) is difficult to accurately determine because of the very small sample size. The tags used in this study weighed 3.6–4.4% of adult body mass, below the 5% threshold expected to have negative effects on birds (Kenward 2001, Barron et al. 2010), but exceeding the 3% threshold often adopted for tracking procellariiform seabirds (Phillips et al. 2003). Seabirds typically experience large variations in body mass during the breeding period, particularly during chick-rearing, because birds must adjust wing-loading and work harder to supply both themselves and their chicks with enough food (Weimerskirch & Lys 2000, O'Dwyer et al. 2006, Robertson et al. 2014). Bermuda petrel adult mass decreases up to 29% from beginning of egg incubation to chick-rearing (J. Madeiros

unpubl. data), and presumably also within chick-feeding visits when they deliver meals weighing 40–60 g (Carlile et al. 2012). The tag effect results were potentially confounded by the fact that foraging conditions were poor during the 2018–19 breeding season compared with previous years, as indicated by overall lower than average adult and chick weights (J. Madeiros unpubl. data), potentially amplifying any effects of the tags.

In this study, we considered tag positioning in relation to the potential effects of increased drag. From a hydrodynamic perspective, modelling results on seals have shown that tag position can cause variation in drag by up to 11% and that tag shape is also important (Kay et al. 2019). Conversely, a study on little penguins *Eudyptula minor* found that tag placement had little effect on diving performance compared with effects of tag size (Ropert-Coudert et al. 2007). As petrels rely on long-distance flights, tag placement presents complex trade-offs regarding drag, weight burden, and balance (see also Vandenabeele et al. 2012, 2014). Bermuda petrels had not previously been tagged with these tags, and in anticipation of potentially long-distance flights, we centred the tags either on the back or the base of the tail to minimize interference with flight, balance, and behaviour (Healy et al. 2004, Vandenabeele et al. 2014). Both positions had been used successfully with the same tags on structurally similar Hawaiian petrels (Raine et al. 2018).

The longer deployments with remote data capture minimized handling time and potentially provided more insight into individual foraging behaviour and habitat use than shorter deployments (Felis et al. 2019, Raine et al. 2020a). However, short-term deployments for sensitive species may minimize energy expenditure associated with carrying tags and have fewer cumulative costs to the study birds (Adams et al. 2009, Barron et al. 2010). We therefore suggest that future efforts to track similar-sized *Pterodroma* petrels using GPS should not only opt for the smallest tags available, but also minimize tracking durations to decrease cumulative impacts to individuals (Adams et al. 2009). For the Bermuda petrels involved in this study, monitoring for the return of tagged birds in future breeding seasons is also important to determine whether these individuals remain missing (and thus presumed dead), or whether they had taken a breeding season off, something that has been recorded in this species, typically after a pair has successfully fledged chicks throughout several successive years and adult body mass drops below average (J. Madeiros unpubl. data).

4.4. Conservation implications

Our study provides new information on the spatial distribution of Bermuda petrels during breeding, where threats related to offshore oil and gas activities or offshore wind-energy infrastructure (OWEI) may co-occur. Gadfly petrels, including Bermuda petrels, are susceptible to disorientation and grounding due to light attraction (Le Corre et al. 2002, Rodríguez et al. 2017, Brinkley & Sutherland 2020). Offshore oil and gas production platforms and support vessels use artificial lights to illuminate working and living areas, and some installations flare excess gas, which increases the mortality risk to birds that fly near or into the flare (Ronconi et al. 2015, Fraser & Carter 2018). Accidental oil spills and regular discharges of produced water increase the birds' exposure to oil, often with lethal effects (Wiese et al. 2001, Fraser et al. 2006).

Although there are currently no active oil and gas leases in Atlantic waters off the US coast where Bermuda petrels are known to occur, 4 oil production facilities operate offshore Newfoundland and Labrador (NL), and 32 areas are licensed for exploration (Fig. 1a; <https://www.cnlopbc.ca/>; accessed 2 November 2020). At the time of this study, 6 platforms (2 gas production platforms and 4 satellite, unstaffed platforms) were also located ca. 250 km from Halifax, Nova Scotia (NS), on the continental shelf (Fig. 1a); however, decommissioning and removal of these platforms is now underway (<https://www.cnsopb.ns.ca/offshore-activity/current-activity>; accessed 2 November 2020). Two exploration licences remain active in NS waters beyond the shelf break (Fig. 1a), and a moratorium on oil and gas activities on the Canadian portion of Georges Bank, located along the Canada–US maritime boundary off the coast of southwest NS, is set to expire in 2022 (<https://www.cnsopb.ns.ca/what-we-do/environmental-protection/special-designated-areas>; accessed 23 November 2020). None of the birds we tracked approached the platforms in either NL or NS; however, the home range (95% UD) for 3 of the 5 birds overlapped with at least 1 of the active exploration licence areas in NS waters (Fig. 3). In addition, we predicted that suitable foraging habitat exists within these licensed areas where exploration, and any future production activities, could pose a risk to Bermuda petrels. Fishing vessels, container ships, oil and gas industry support vessels, and cruise ships also add light to the offshore environment in areas where birds may encounter them (Merkel & Johansen 2011, Ronconi et al. 2015, Krüger et al. 2017), contributing to a cumulative-risk-land-

scape at sea that includes fishing activity, ship-sourced oil pollution, plastic pollution, and OWEI (Van Sebille et al. 2015, Lieske et al. 2019, 2020).

When considering vulnerability to OWEI in the Atlantic Outer Continental Shelf region of the USA, Bermuda petrels (along with black-capped petrels) were ranked as having the greatest 'population sensitivity' score among all marine birds, had the eighth highest 'collision sensitivity' score, and a medium 'displacement sensitivity' score (Robinson-Willmott et al. 2013). In 2020, active offshore wind energy leases located from the Carolinas through the New York Bight and Gulf of Maine totalled 3652 km² (Fig. 1a; <https://www.boem.gov/renewable-energy/>; accessed 2 November 2020). With increasing renewable energy goals among states in this area, impacts to Bermuda petrels could be anticipated during the chick-provisioning period, especially if individuals shift their foraging substantially toward the northeast of Bermuda and inshore from the 500 m isobath. Such displacement was documented for black-capped petrels, which can be steered across the shelf waters, and even inland, during hurricanes, which are predicted to increase in both frequency and magnitude in the future (see Hass et al. 2012). More information at appropriate spatial scales is needed to comprehensively evaluate sensitivity to OWEI and offshore oil and gas activities during the non-breeding and pre-breeding periods.

Intensive management and conservation efforts have limited the impacts of colony-based threats for Bermuda petrels, but currently there is no protection for this species at sea. In Bermuda, the species is listed as endangered under the Protected Species Act 2003 and the Protected Species Order 2012 (Bermuda BR 7/2012), which grant both the bird and its nesting habitat full protection. Further protection is legislated under the US Endangered Species Act of 1973 (USFWS 2009), which prohibits the killing or capturing of the petrels, but critical habitat has not been defined nor has a recovery plan been implemented (USFWS 2019). Bermuda petrels are not presently listed as at-risk in Canada; detections of individuals in Canadian waters were considered accidental, although data from adults fitted with GLS tracking devices indicated that birds may occur in Canada, as far north as NL (Madeiros et al. 2014, Ramos et al. 2017). Our results identify important marine habitat in Canada used by Bermuda petrels for foraging during the breeding season, and confirm the species' eligibility for assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; www.cosewic.ca/index.php/en-

[ca/assessment-process/](#); accessed on 20 October 2020), an independent body of experts that assesses wildlife according to a broad range of scientific data. If assessed, a decision whether to list the species under the Species at Risk Act (SARA; S.C. 2002, c. 29) will be made by the federal Cabinet. Recovery strategies and action plans would then be required, which must identify critical habitat and protect it from destruction. Additional high-resolution (i.e. GPS) tracking studies during several years that include birds during other phases of the annual cycle (i.e. pre-laying exodus, incubation, migration, and wintering) would add significant information to improve our understanding of the petrels' range at sea, verify factors we identified as important predictors of distribution, and help define Canada's role in the conservation of this species. Ultimately, how this information is applied to conservation, marine spatial planning, and management interventions will also benefit by considering the impacts of climate change on the spatial ecology of the species (Grémillet & Boulinier 2009, Hass et al. 2012).

Acknowledgements. All work was authorized under the Research Permit (Licence no. 19-03-19-81) provided by the Government of Bermuda, Ministry of Home Affairs, Department of Environment and Natural Resources. Financial support was provided by the Canadian Wildlife Service, Environment and Climate Change Canada. J.A. and J.J.F. were supported in part by the US Geological Survey Ecosystems Mission Area. We thank Karel Allard for the inspiration to conduct this research, and for valuable discussion and advice during project development and manuscript review; Jennifer Schullien (USGS) for calculating FCPI using code kindly provided by Rob Suryan; Dave Fifield for additional analytical support; Jill Raine for support during the field season; Andrew Boyne for informative discussions pertaining to the protection of birds in Canada; and Morgan Gilmour and Tom Kimball (USGS) and 3 anonymous reviewers who improved this paper. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US Government.

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*Editorial responsibility: Rory Wilson,
Swansea, UK*
Reviewed by: 3 anonymous referees

Submitted: November 26, 2020
Accepted: June 3, 2021
Proofs received from author(s): August 16, 2021