Consistent foraging habitat use by a vulnerable breeding seabird highlights potential areas for protection in the mid-Atlantic Ocean

V. C. Neves[1,*,#], G. Carroll[2,#], W. C. Schäfer[3], H. F. R. Hereward[4,5], P. Quillfeldt[3]

[1]OKEANOS - Institute of Marine Sciences, University of the Azores, Horta, Portugal

[2]Environmental Defense Fund, 123 Mission St, San Francisco, CA, USA

[3]Department of Animal Ecology & Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany

[4]Cardiff School of Biosciences, Cardiff University, Cardiff, UK

[5]*Present address*: British Trust for Ornithology Cymru, Thoday Building, Deiniol Road, Bangor, Wales, UK

ABSTRACT: Identifying animal foraging habitat can help prioritise areas for conservation and enable better predictions of how populations respond to environmental change. Recent reductions in the size of biologging devices now enable fine-scale foraging habitat tracking for very small seabirds. We investigated the foraging distribution and habitat preferences of Monteiro's storm-petrel *Hydrobates monteiroi*, a tiny (<60 g), vulnerable seabird that is endemic to the Azores Archipelago. We tracked 67 storm-petrels with 108 GPS deployments across 4 consecutive breeding seasons (2018–2021) to identify important foraging areas and preferences for dynamic and static features of their mid-ocean environment. We found that static bathymetric features such as seafloor depth and distance from the nearest seamount were the most important predictors of foraging location, suggesting that topographic features may provide areas of enhanced biological productivity in the mid-Atlantic Ocean that are predictable across long timescales. Although dynamic oceanographic variables (sea surface temperature and chlorophyll *a*) also helped predict foraging activity, both the location and environmental characteristics of foraging habitat were relatively stable across 4 consecutive years. This suggests that meso-scale oceanographic dynamics do not drive strong interannual variation in foraging behaviour in this system. Currently, only 11.4% of Monteiro's storm-petrel foraging locations overlap with designated marine protected areas. A total of 95% of unprotected foraging locations fell within the Azores exclusive economic zone (EEZ), indicating a responsibility of the Portuguese government to increase habitat protection. Our findings suggest that more comprehensive at-sea conservation for this vulnerable species could be focused in predictable geographic areas over the mid-Atlantic ridge and seamounts.

KEY WORDS: Endangered seabird · Azores Archipelago · Storm-petrel · Habitat selection · Foraging ecology

1. INTRODUCTION

Seabirds are among the most threatened bird groups on the planet with an estimated 70% reduction in their total population since the 1950s (Pa-leczny et al. 2015, BirdLife International 2021). On land, seabirds face a host of intersecting challenges including predation, light pollution, habitat degradation and the impacts of increasingly extreme weather (Croxall et al. 2012, Rodríguez et al. 2017). At sea,

seabirds are exposed to risks such as climate-induced changes in habitat and prey availability, bycatch in fishing gear, competition with fisheries for scarce prey resources (e.g. Grémillet & Boulinier 2009, Dias et al. 2019), stranding due to artificial lights of coastal and offshore structures and drilling (Ronconi et al. 2015) and potentially by deep-sea mining. At-sea challenges for seabirds are exacerbated by the fact that during the breeding season they are constrained to return regularly to the nest for incubation shifts or to feed chicks. This constraint on their mobility makes them reliant on the predictability of productive foraging habitat within a specific distance from the breeding colony and increases their vulnerability to changes in local ocean conditions (Carroll et al. 2016) and reduced prey abundance within their foraging grounds (Boyd et al. 2017). It is therefore important to understand how seabirds use the limited area that is available to them during the breeding season (Sansom et al. 2018) and to understand which environmental conditions might promote or reduce foraging opportunities, potentially contributing to interannual variation in individual condition and reproductive success (Phillips et al. 2022).

Over the last few decades, tracking technologies have revolutionised the study of seabird movement ecology and magnified our understanding of the oceanographic conditions guiding seabird foraging behaviour (Bernard et al. 2021). Insights into the geographic location and habitat characteristics that are important for seabirds have been central to the proposal and classification of several marine protected areas (MPAs) to mitigate against at-sea threats (Oppel et al. 2018). For example, a meta-analysis of tracking studies recently revealed an oceanic area shared by over 20 seabird species breeding in 16 countries and accounting for 4.4–5 million individual birds every year (Davies et al. 2021). However, even in the best sampled regions our knowledge on the movements of seabirds remains incomplete, and we lack a strong understanding of how seabird foraging is mediated by dynamic and changing oceanographic environments (Bernard et al. 2021). Furthermore, the miniaturisation of biologging devices has only recently enabled us to begin tracking the very smallest seabird species, including the elusive storm-petrels (e.g. Pollet et al. 2014, Rotger et al. 2020, Bolton 2021, De Pascalis et al. 2021, 2022, Alho et al. 2022, Collins et al. 2022, Medrano et al. 2022, Mauck et al. 2023). The at-sea behaviour of these tiny birds remains poorly understood, and many species are vulnerable to extinction (Dias et al. 2019). Understanding their foraging distributions and habitat

preferences will enable a better understanding of their ecology and inform their at-sea conservation.

The summer-breeding Monteiro's storm-petrel *Hydrobates monteiroi* is part of the band-rumped storm-petrel complex in the northeast Atlantic and is endemic to the Azores, having recently been split from the winter-breeding band-rumped storm-petrel *H. castro* (Monteiro & Furness 1998, Bolton et al. 2008). The Monteiro's storm-petrel population is estimated at 328–378 breeding pairs (Oliveira et al. 2016), and the species is currently confirmed to breed on only 3 small islets: Praia, Baixo and Baleia, all off Graciosa Island in the Azores Archipelago. The species is classified as 'Vulnerable' by the IUCN (BirdLife International 2021). Although the species awaits classification in the new Portuguese Red Book, as the last one was published before the species split (Cabral et al. 2005), its small breeding population, reduced distribution and recent decline in breeding success mean that the Monteiro's storm-petrel is likely to meet the Portuguese Red Book's criteria for 'Endangered'. The causes of its reduced breeding range and low breeding success are thought to be low availability of introduced-mammal-free habitat, interspecific competition for nests with the band-rumped storm-petrel, predation of eggs and chicks by Madeiran wall lizards *Lacerta dugesii* (Neves et al. 2017, 2022) and potentially increased temperatures that also raise temperature in the nest. In recent years the number of breeding attempts in natural and artificial nests has also been decreasing (V. C. Neves pers. obs.).

The at-sea distribution of Monteiro's storm-petrel, and thus its overlap with at-sea threats, remains virtually unknown. For most storm-petrels, fisheries bycatch does not seem to present a major threat at the population level (Dias et al. 2019), but this group is among the most affected by bright lights at coastal and offshore industrial sites (Gjerdrum et al. 2021), strandings which may represent a significant source of mortality in some species. There is a pressing need to study the foraging ecology and spatial distribution of Monteiro's storm-petrel to identify possible at-sea threats and ensure its protection.

Here we studied the at-sea distribution, foraging trip characteristics, habitat selection and inter annual variability in foraging habitat selection of Monteiro's storm-petrel. We used miniaturised GPS data loggers to track the distribution and foraging movements of incubating (2018–2021) and chick-rearing (2018–2020) individuals of different sexes. We assessed the spatial and environmental niches of foraging birds to understand which geographic locations and oceano-

graphic features are important predictors of foraging activity and constructed generalised additive mixed models (GAMMs) to predict the distribution of suitable at-sea foraging habitat. Finally, we overlapped the species′ suitable habitat with current MPAs within the Azores Marine Park.

The main objectives of this work are therefore to (1) identify which places and features of the oceanic environment represent important foraging habitat for breeding Monteiro′s storm-petrels; (2) determine whether foraging distribution is consistent between years, and (3) assess the level of protection offered by existing MPAs to estimate the extent to which the Monteiro′s storm-petrel is currently protected from activities including fishing, drilling, and other industrial activities. By better understanding the foraging distribution of this vulnerable species, we hope to motivate efforts to increase conservation of important offshore habitat in the mid-Atlantic.

2. MATERIALS AND METHODS

2.1. Study site

Fieldwork was conducted at Praia Islet (39° 03′ N, 27° 57′ W, 0.12 km^2, 1650 m of coastline and max. altitude of 52 m), which is located about 1.3 km off Graciosa Island, one of the 9 main islands of the Azores Archipelago in the North Atlantic Ocean (Fig. 1A). All Azorean islands are of volcanic origin as the archipelago lies above the junction of 3 tectonic plates – the North American Plate, the Eurasian Plate and the African Plate. Oceanic waters are known to be of low productivity, but the tectonic arrangement around the Azores provides a high number of seamounts, which can promote upwelling (Whittaker & Likens 1973, Monteiro et al. 1996). Moreover, the Azorean oceanographic conditions are influenced by the Gulf Stream (Monteiro et al. 1996), which branches off below the Azores Archipelago as the Azores Current ~34° N (Juliano & Alves 2007) and passes above the archipelago as the North Atlantic Current at ~50–52° N (Rossby 1996). The Azorean climate is subtropical with only minor fluctuations in temperature, high precipitation rates and high humidity (Borges et al. 2010). Praia Islet has been designated as a Special Protection Area (SPA) under European legislation, as an Important Bird Area (IBA) by BirdLife and it is also classified as a Nature Reserve under the framework of Graciosa Natural Park (Azores Government).

2.2. Study species

The Monteiro′s storm-petrel *Hydrobates monteiroi* is a small seabird, endemic to the Azores Archipel-
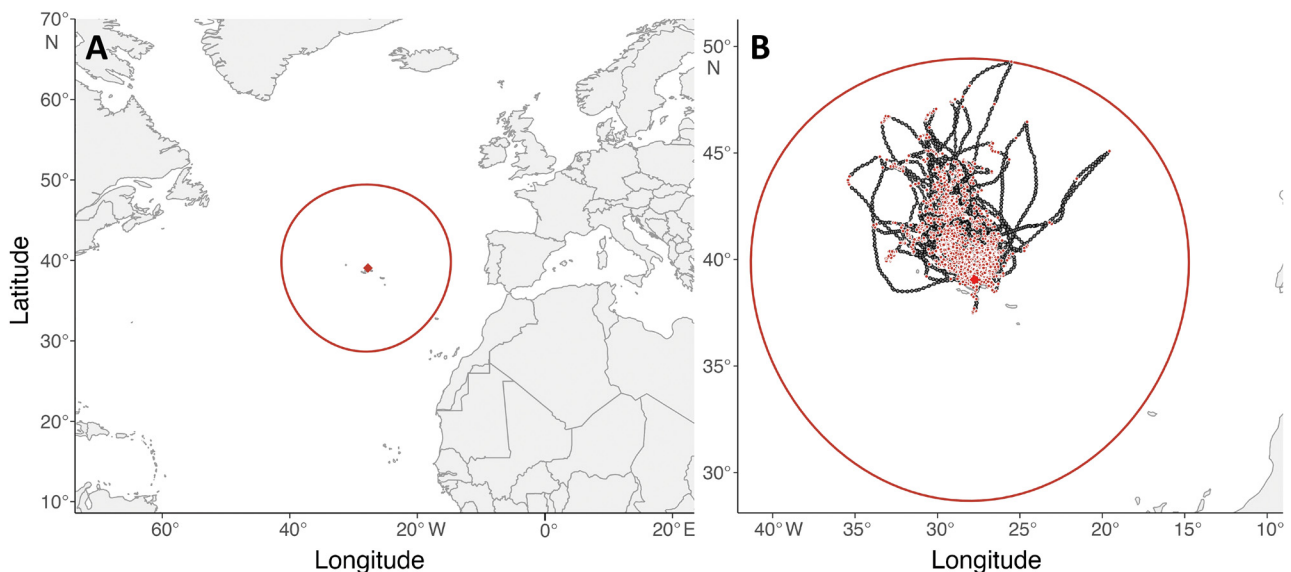

Fig. 1. (A) Study region, with a red diamond indicating the location of the colony where Monteiro's storm-petrels were tracked from Praia Islet, near Graciosa Island, in the Azores Archipelago. The red circle has a radius equal to the maximum distance travelled by a Monteiro's storm-petrel during this study (1154 km) and is the area considered in foraging habitat models. (B) All locations (black points) recorded by GPS units attached to foraging Monteiro's storm-petrels over 4 years (2018–2021). Red points highlight locations identified as 'foraging' by a 2-state hidden Markov model. Red diamond indicates the study colony at Praia Islet; the red circle is the same as in (A), indicating the foraging area considered in habitat models

ago, and breeds on only 3 small, mammal-free islets: Praia, Baixo and Baleia Islets, all off Graciosa Island, Azores Archipelago. Its population size is estimated at 328–378 breeding pairs, from which about half of the population (178 pairs) breed at Praia Islet (Oliveira et al. 2016). Around 164 artificial nest boxes have been installed at Praia Islet (Bolton et al. 2004: 150 nests, V. C. Neves unpubl.: 14 new nests installed in 2015), providing an ideal setting to investigate the ecology of this species. Like all procellariiforms, the Monteiro's storm-petrel is a long-lived seabird and is socially monogamous (Warham 1990). Between late April and early July females lay a single egg, and chicks hatch between late May and early August; the latest chicks fledge by early October (Bolton et al. 2008). Both parents participate in incubation and chick-rearing (Warham 1990). They come to the breeding colony at night either to undertake an incubation shift or to feed their chick.

2.3. Nest occupancy

Fieldwork was carried out between June and August during the years 2018–2020 and in June–July during 2021. At the start of each field season, all artificial nest boxes were checked to determine breeding attempts and to identify both breeding partners of each nest. The ring number of each adult was noted, and unmarked birds were ringed. In each nest, one of the birds was marked with a blue dot on its head using a waterproof Edding® marker (Edding GmbH) to make identification of the partners possible in subsequent nest visits without the need to remove the bird to check the ring number, thus reducing disturbance (Schäfer 2019). Occupied nests were monitored every other day to determine the length of incubation shifts, to predict the probability of a shift change for the following night and to determine the hatching date of the chicks.

2.4. GPS tracking

High accuracy GPS loggers (n = 36, model nanoFix®Geo Mini, Pathtrack) were used to determine the at-sea distribution during the incubation and chick-rearing portions of the breeding season. The devices weighed less than 1 g, which represents approximately 2.1% of the mean body mass of the Monteiro's storm-petrels (47.6 ± 3.8 g, n = 108), below the recommended 3% threshold (Kenward 2001, p. 9). The sampling interval of GPS devices was set between 30 min

and 3 h, with most tracks (90.2%) being recorded at ≤1 h intervals. Table S1 in the Supplement (www.int-res.com/articles/suppl/m716p107_supp.pdf) shows the percentage of deployments for each time resolution in different years. During incubation, birds with a higher probability of leaving the colony that night (i.e. had been incubating for 3 or more days) were captured at the nest during the day. During chick-rearing we targeted birds with a chick older than 10 d and captured them at night, when adults were coming to the colony to feed their chick. If necessary, we used door traps to catch the adult during their short night visits. After deployment, birds were returned to their nests immediately. Birds that were incubating an egg when the logger was attached but had a hatched chick when the logger was retrieved were classified as 'incubating'. The captured birds were equipped with the loggers attached to the 4 central tail feathers with waterproof TESA® tape (TESA SE), ~0.5 cm downwards from the uropygial gland. The first 9 deployments were made on the 2 central tail feathers only, but after the loss of 4 devices (44% loss rate) we attached all the following devices to the 4 central tail feathers to increase stability, and all the devices were retrieved except for one device. In that case the device was not lost, but it was not possible to retrieve the bird in the nest as the chick was close to fledging and the adult was visiting the nest rarely and for very short times. This individual was observed breeding in the colony in the following year. During tracking, nests were monitored daily, and devices were removed from the birds after a single foraging trip (incubation) and after a minimum of 4 d (chick-rearing). All birds were weighed upon GPS retrieval after the logger was removed.

Our data ensured both a high tracking effort (108 deployments on 67 individuals; see Table S2 for details on dates of deployment per year and per breeding stage) and a good coverage of the breeding population (50% of accessible colonies).

To determine the sex of birds where these were not known from previous studies, blood samples were taken by puncturing the brachial vein with a sterile disposable cannula tip (0.40 × 20 mm). The blood was either collected with a microhaematocrit capillary tube (75 mm, Hirschmann Laborgeräte) or collected directly on filter paper. After sampling, the puncture was shortly compressed with a piece of cottonwool to stop bleeding. Blood was stored in 100% ethanol or kept dry in filter paper. Sexing (n = 56 ind.: 33 in 2018, 5 in 2019, 14 in 2020 and 4 in 2021) was conducted using molecular methods, following Fridolfsson & Ellegren (1999).

2.5. GPS data processing

Raw GPS tracks were manually divided into unique foraging trips in cases where the bird performed more than one trip during a deployment (usually during chick-rearing). The start and end location of each trip was the midpoint of Praia Islet (39.056326° N, 27.955567° W). To account for different GPS sampling frequencies during device deployments, all tracks were regularised to 1 h intervals using linear interpolation (90.2% of tracks were recorded at intervals ≤1 h). Low quality tracks with few locations were removed after visual inspection, and all locations within 1 km of the colony were filtered from the dataset prior to analysis. To identify at-sea locations associated with foraging, a 2-state hidden Markov model was developed to classify locations into foraging-type movements (characterised by wide turning angles and small step lengths) and transiting-type movements (characterised by narrow turning angles and large step lengths). Step length frequency distributions were fitted using a gamma distribution, and relative turning angles were fit using a von Mises distribution in the R package *moveHMM* (Michelot et al. 2016). Only locations associated with foraging-type movements were used in further habitat selection analyses to focus on elucidating the locations and characteristics of important feeding areas at sea, rather than areas that the birds transited through.

2.6. Environmental data

A suite of environmental covariates was downloaded to assess the habitat preferences of foraging Monteiro's storm-petrels. Two dynamic oceanographic features were chosen that we hypothesised might influence the location and abundance of prey between years: sea surface temperature (SST; °C; UK Met Office Global Ocean OSTIA Sea Surface Temperature analysis product; native resolution 0.05° × 0.05° daily, downloaded from marine.copernicus.eu), and chlorophyll *a* (chl *a*; mg m^{-3}; Copernicus-GlobColour; native resolution 4 × 4 km daily, downloaded from marine.copernicus.eu). We also included 2 static environmental variables that we hypothesised might indicate relative productivity or prey accessibility on longer timescales: seafloor depth (m; ETOPO1 Global Relief Model, 1 arc-minute native resolution downloaded from www.ngdc.noaa.gov/mgg/global/), and distance from the nearest seamount (km; seamount coordinates downloaded from the GEBCO Undersea Feature Names Gazetteer www.ngdc.noaa.gov/gazetteer/).

2.7. Statistical analyses

All statistical analyses were conducted in R (R Core Team 2020). Significance of all statistical tests was determined at the p < 0.05 level and all values are mean ± standard error.

2.7.1. Foraging distribution

Due to the recent splitting of Monteiro's storm-petrel from the band-rumped storm-petrel, and the relatively recent ability to track tiny seabird species with small dataloggers, little is known about the basic foraging ecology of this species. For this reason, we describe the effects of breeding stage, sex and year on maximum straight-line distance from the colony (km), total distance covered on a foraging trip (km), and trip duration (d). Based on a previous study on Monteiro's storm-petrels, we expected a sexual foraging segregation during the breeding period, particularly during the incubation (Paiva et al. 2018). To explore these relationships, we used generalised estimating equations (GEEs) to analyse the population effects of breeding stage, sex and year while allowing for correlations among clusters of repeated samples of individual birds (Liang & Zeger 1986). Response variables were log-transformed and fit with Gaussian error structures. Because only 2 chick-rearing birds were tracked in 2020 and none were tracked in 2021, these 2 years were excluded from comparisons of foraging distribution during chick-rearing.

To assess consistency in the locations of core foraging areas between years, we estimated 75% kernel densities using the R package adehabitatHR (Calenge 2006) and calculated pairwise overlap between years.

2.7.2. Habitat models

To provide information on the full suite of environmental conditions available to foraging petrels, we generated 10 pseudo-absence points for every foraging location, matched to the dates and times of observed foraging locations. Pseudo-absence points were selected randomly from within 2 circular buffers around the colony corresponding to the max-

imum foraging displacements observed during each breeding stage (radius 1154 km during incubation and 611 km during chick-rearing). This 'background sampling' approach allows wide sampling across all habitat conditions theoretically available to foraging animals, given the constraints of breeding. This enables an understanding of the broad characteristics of preferred foraging habitat by this species and allows the development of high-performing models for prediction (Hazen et al. 2021). Observations of each environmental covariate were extracted at the locations and times of presences and pseudo-absences to assess how preferred foraging habitat differs from non-preferred habitat.

To explore the effects of non-environmental covariates on foraging location, we first built a 'null' model. We tested the inclusion of breeding stage and sex as categorical fixed effects, distance from colony as a continuous fixed effect, and year and individual ID (bird ring number) as random effects. The null model was compared with 6 candidate environmental models: 4 single covariate models testing the relative importance of (1) seafloor depth, (2) distance to the nearest seamount, (3) SST and (4) chl *a*, then 2 additional models: (5) seafloor depth and seamount distance, and (6) seafloor depth, seamount distance, SST and chl *a*. This final model configuration tested the combined importance of static environmental variables and had the additional benefit of including dynamic features that change through time.

All habitat models were built as binomial generalised additive mixed models (GAMMs) in the R package *mgcv* (Wood 2011). Models were compared using Akaike's information criterion (AIC), and model performance was assessed using adjusted R^2 and deviance explained. Estimates of the probability of storm-petrel presence from the best model were predicted onto a 0.1° × 0.1° grid encompassing the observed foraging range. We overlapped the locations of existing MPAs around the Azores Archipelago onto foraging locations to assess the current extent of protection of Monteiro's storm-petrels at sea both within and outside of the Azores exclusive economic zone (EEZ).

2.8. Data accessibility

Tracking data is stored both in Movebank Data Repository (Movebank.org, Monteiro's storm-petrel *H. monteiroi*, Hydrobatidae, Azores, study ID 1751846326) and in the Seabird Tracking Database managed by BirdLife International (www.seabirdtracking.org).

3. RESULTS

3.1. GPS retrieval

Our overall GPS recovery rate was 95%, and data was downloaded from 89% of retrieved devices (Table S2). A total of 84 foraging trips from 53 adults were recorded during the incubation period and 54 foraging trips from 21 adults during the chick-rearing period (Table S2). Out of the 108 deployments, 5 loggers were lost, and 11 deployments failed (loggers stopped working) or provided incomplete or low-quality tracks. A total of 142 foraging trips, from 94 deployments (70 during incubation and 24 during chick-rearing) on 61 birds, were included in analyses of foraging habitat selection after application of the Hidden Markov model (Fig. 1B). During incubation, birds gained on average 3.98 ± 3.15 g in body mass between logger deployment and retrieval (range: −5.1 to 11.6 g; n = 63); during chick-rearing the weight increment was lower at 0.68 ± 3.70 g (range: −7.0 to 6.3 g; n = 27). The lower mass gain during chick-rearing is likely due to adults having already fed the chick upon arrival at the nest, before logger retrieval and measurements of body mass were performed. We did not include weight measurements when adults were incubating an egg upon GPS deployment and had a small chick by the time the GPS unit was retrieved because in those cases, we only retrieved GPS units during the day, several hours after adults returned to the nest.

3.2. Foraging distribution

As expected, Monteiro's storm-petrels travelled greater distances on longer foraging trips during incubation compared to during chick-rearing (Fig. 2). GEEs showed that after accounting for the effects of sex, year, and individual, Monteiro's storm-petrels travelled approximately 1.94 times further from the colony during incubation than during chick-rearing (Table S2, incubating = 384.5 ± 28.9 km, chick-rearing = 156.56 ± 16.86 km; GEE coefficient = 1.94 ± 1.15, Wald test, W = 19.79, p < 0.001). Incubating birds also travelled 2.07 times greater total distances (incubating = 1095.0 ± 69.2 km, chick-rearing = 457.5 ± 45.6 km; 2.07 ± 1.11, W = 25.68, p < 0.001) and spent 1.97 times more days away from the colony on a trip (incubating = 4.10 ± 0.37 d; chick-rearing = 2.2 ± 0.3 d; GEE coefficient = 1.97 ± 1.13, W = 32.14, p < 0.001).

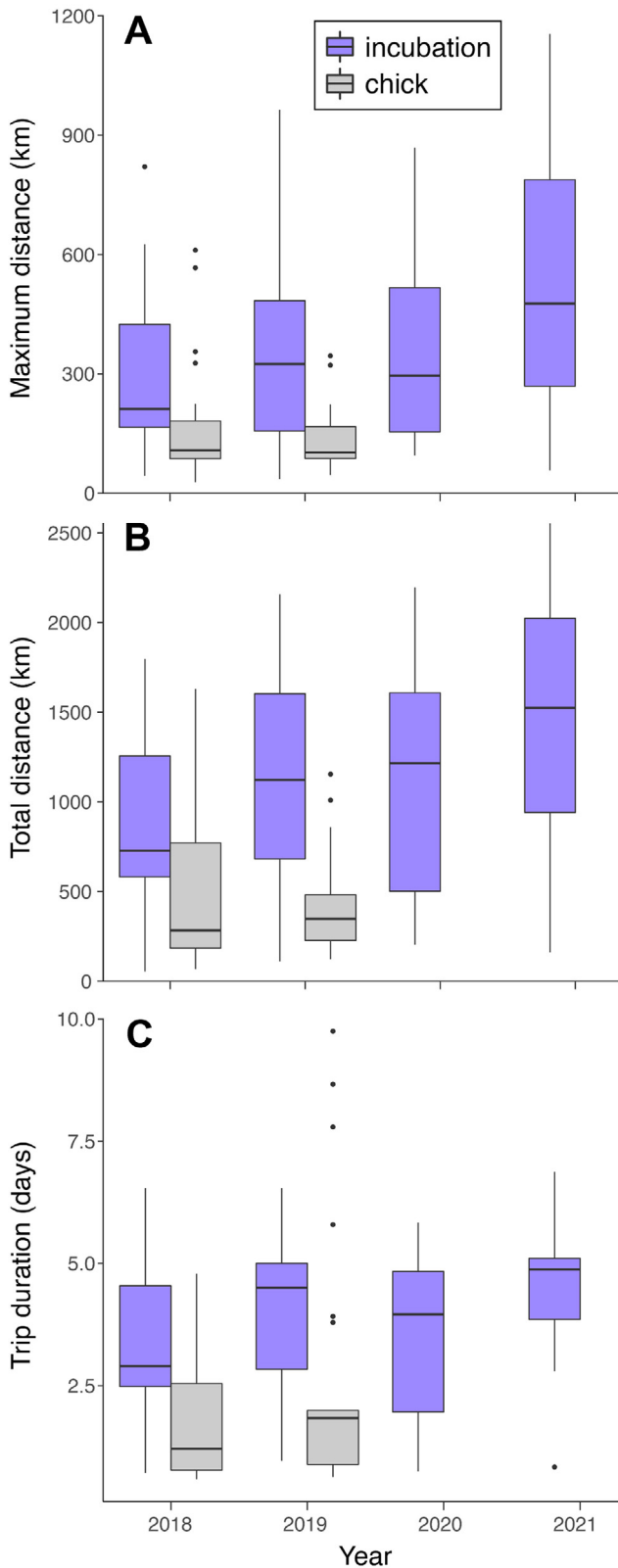Contrary to expectations there were no significant sex differences in maximum distance travelled from

Fig. 2. Differences in the (A) maximum distance from the colony (km); (B) total distance covered (km); and (C) trip duration (d) by foraging Monteiro's storm-petrels during the incubation and chick-rearing periods. Bar: median; box: interquartile range; whiskers: non-outlier range; points: outliers

the colony, (female = 324.5 ± 28.3 km; male = 262.1 ± 23.8 km; GEE coefficient = 0.95 ± 1.11, W = 0.211, p = 0.646), total distance covered (female = 901.9 ± 81.2 km; male = 772.9 ± 66.1 km; GEE coefficient = 0.91 ± 1.10, W = 0.88, p = 0.348) or trip duration (female = 3.3 ± 0.2 d; male = 3.39 ± 0.44 d; GEE coefficient = 0.93 ± 1.13, W = 0.54, p = 0.464).

Despite some variability in foraging location between years, there were no significant differences in trip distance or duration between years after accounting for breeding stage and sex, based on a multiple comparison of GEE estimates using Tukey tests with single-step adjusted p-values (Table S3).

Most birds foraged to the north of the Azores Archipelago during both incubation and chick-rearing. The core foraging area (75% kernel utilisation distribution [UD]) was similar in all 4 years, with birds concentrating foraging activity to the immediate northeast of the colony during chick-rearing (approximately 38–40° N and 26–28° W), and in 2 connected core foraging locations to both the northeast (approximately 38–42° N and 26–29° W; Fig. 3A), and northwest during incubation (approximately 40–43° N and 29–31° W; Fig. 3B). Kernel UD overlap values between years ranged from 47–92% during incubation (2018–2021; mean = 71.6 ± 3.7%) and 34–100% during chick-rearing (2018–2019; mean = 67 ± 33%; Table S4).

3.3. Habitat models

Monteiro's storm-petrels selected foraging habitat that was much shallower and closer to seamounts than would be expected if they used foraging habitat in proportion to its availability (Fig. 4A). Birds tended to forage along the relatively shallow waters of the mid-Atlantic ridge (mean depth = 1425.5 ± 9.1 m; Fig. 4B) within 100 km of the nearest seamount (mean distance = 98.1 ± 0.9 km; Fig. 4C). Monteiro's storm-petrels selected waters that were slightly more productive than mean available habitat in all years (Fig. S1; mean chl a = 0.11 ± 0.01 mg m^{-3}), and with slightly cooler temperatures than the mean available habitat in most years (Fig. S2; mean SST = 20.9 ± 0.1°C). These relationships with dynamic oceanographic features and the general locations of foraging activity did not change greatly across the 4 study years in response to different oceanographic conditions, indicating that birds had interannual fidelity to relatively stable foraging habitat at the population level.
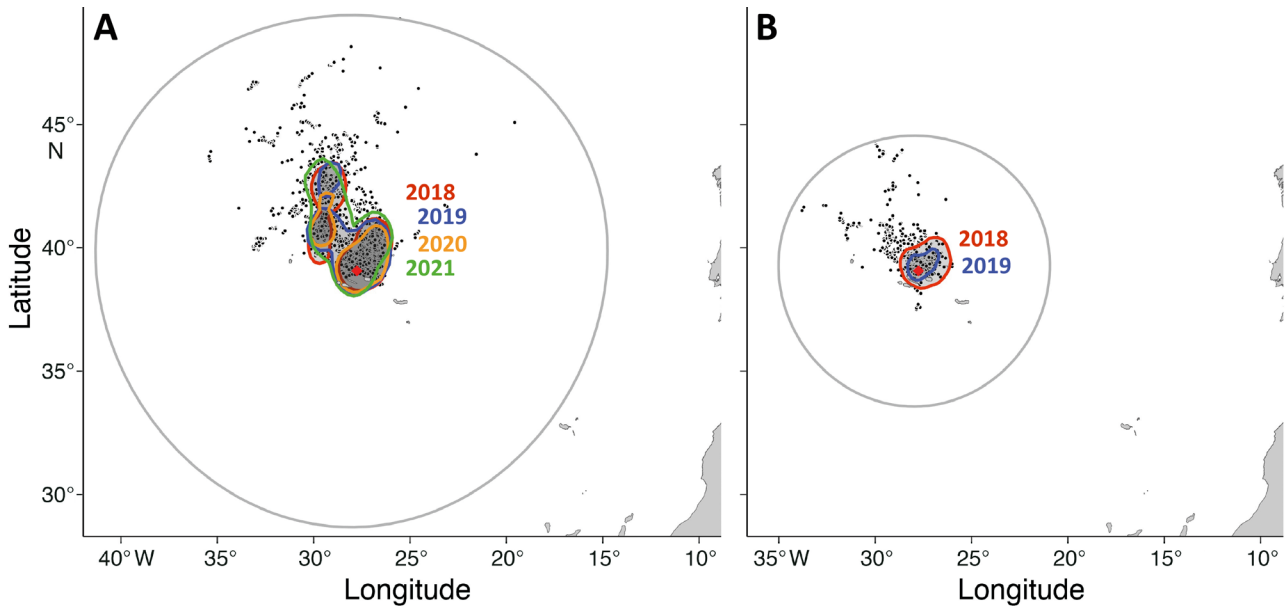
Fig. 3. Locations and 75% kernel utilisation distributions of foraging Monteiro's storm-petrels. (A) Overlap between distributions of incubating birds in each year. Grey circle is the maximum foraging range during incubation (radius 1154 km). (B) Overlap between distributions of chick-rearing birds. Grey circle is the maximum foraging range during chick-rearing (radius 610 km). Red diamond indicates study colony

GAMMs all included breeding stage, distance from colony, year and individual ID. The inclusion of sex led to lower parsimony according to AIC, and the term was therefore dropped from final models. GAMMs showed that seafloor depth was the most

important habitat attribute that influenced the location of foraging by Monteiro's storm-petrels (Table 1). The single covariate model (null model + depth) explained 51% of the variation in foraging location (ΔAIC from null model = 20610.29; Table 1),
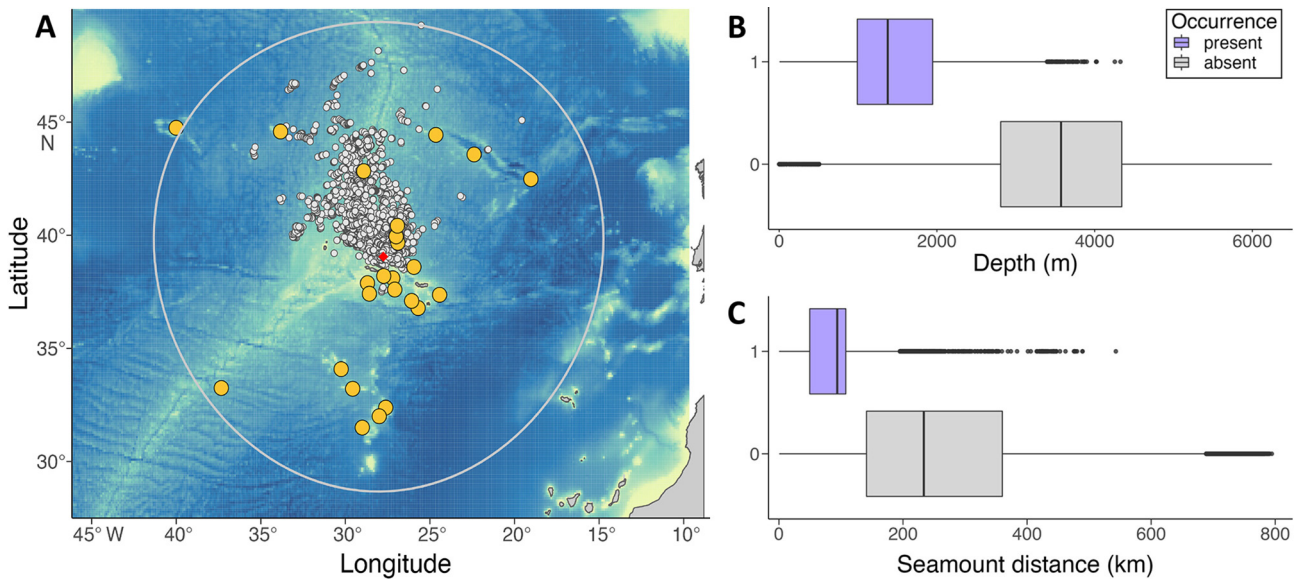
Fig. 4. (A) Foraging locations of Monteiro's storm-petrels (grey) and the location of seamounts (orange) shown with seafloor depth. Red diamond indicates study colony. Grey circle represents potential foraging range and has a radius of 1154 km (max. foraging range) from the center of the colony. (B) Distribution of seafloor depths associated with foraging locations (purple) and random pseudo-absence locations (grey). (C) Distribution of distances to the nearest seamount associated with foraging locations (purple) and random pseudo-absence locations (grey)

Table 1. Candidate generalised additive mixed model (GAMM) configurations in R *mgcv* explaining the occurrence (binomial presence/absence) of Monteiro's storm-petrels. All models contain fixed effects for breeding stage and distance from colony, and random effects (bs = 're') for year and bird ID. The best performing model according to adjusted R^2, deviance explained (dev. expl.), and Akaike's information criterion (AIC) was the full model containing both static (seafloor depth + seamount distance) and dynamic (chlorophyll *a* and sea surface temperature [SST]) environmental covariates. edf: estimated degrees of freedom

Model name	GAMM formula	edf	R^2 adj.	Dev. expl. (%)	AIC	ΔAIC
Null model	gam(occurrence ~ breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	3.0	0.01	0.1	47 704.1	26 465.1
Chl *a*	gam(occurrence ~ *s*(chl *a*, *k* = 5) + breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	35.8	0.04	6.7	44 559.2	23 320.2
SST	gam(occurrence ~ *s*(SST, *k* = 5) + breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	26.9	0.03	6.8	44 488.9	23 249.9
Seamount distance	gam(occurrence ~ *s*(distance from seamount, *k* = 5) + breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	52.4	0.15	22.7	36 993.9	15 754.9
Seafloor depth	gam(occurrence ~ *s*(depth, *k* = 5) + breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	70.8	0.38	46.6	24 943.0	3704.0
Static features only	gam(occurrence ~ *s*(depth, *k* = 5) + *s*(seamount distance, *k* = 5) + breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	74.4	0.44	51.3	22 754.8	1515.8
Static + dynamic features	gam(occurrence ~ *s*(depth, *k* = 5) + *s*(seamount distance, *k* = 5) + *s*(SST, *k* = 5) + *s*(chl *a*, *k* = 5) + breeding stage + *s*(distance from colony, *k* = 5) + *s*(year, bs = 're') + *s*(ID, bs = 're'), family = 'binomial')	84.2	0.48	54.6	21 239.1	0

and modelled response curves showed that the highest probability of foraging occurred at the shallowest depths (Fig. 5A). Adding distance from the nearest seamount, SST and chl *a* improved this model modestly, with the full model performing best (ΔAIC from null model = 24338.44; Table 1) and explaining 61% of the variation in foraging location (Table 1). Response curves showed that the probability of foraging was highest closest to seamounts, at relatively low chl *a* concentration, and at SST between 17 and 23°C (Fig. 5B,C,D).

3.4. Predictions of suitable foraging habitat

Final model predictions of the location of suitable foraging habitat for Monteiro's storm-petrels around the Azores highlighted areas that were relatively shallow and close to seamounts (Fig. 6). The model aligned well with observed foraging locations but also predicted foraging areas south of the Azores Archipelago where the storm-petrels were not observed to forage during the 4 yr study period. Existing MPAs each encompassed some suitable foraging

habitat (Fig. 6). However, many foraging areas remain unprotected by the Azores MPA network, with only 11.4% of observed foraging locations (16% during incubation; 5% during chick-rearing) falling within the boundaries of an existing protected area (Fig. 6).

4. DISCUSSION

4.1. Overview

This is the first study to describe the fine-scale foraging movements and habitat preferences of the Monteiro's storm-petrel. Over 4 consecutive summer breeding seasons, birds from Praia Islet foraged almost exclusively in regions north of the Azores Archipelago and strongly preferred foraging in relatively shallow waters along the mid-Atlantic ridge and near oceanic features like seamounts. Dynamic oceanographic features including SST and chl *a* concentration were secondarily important predictors of foraging in the best model, but observed interannual variation in these parameters did not drive large dif-
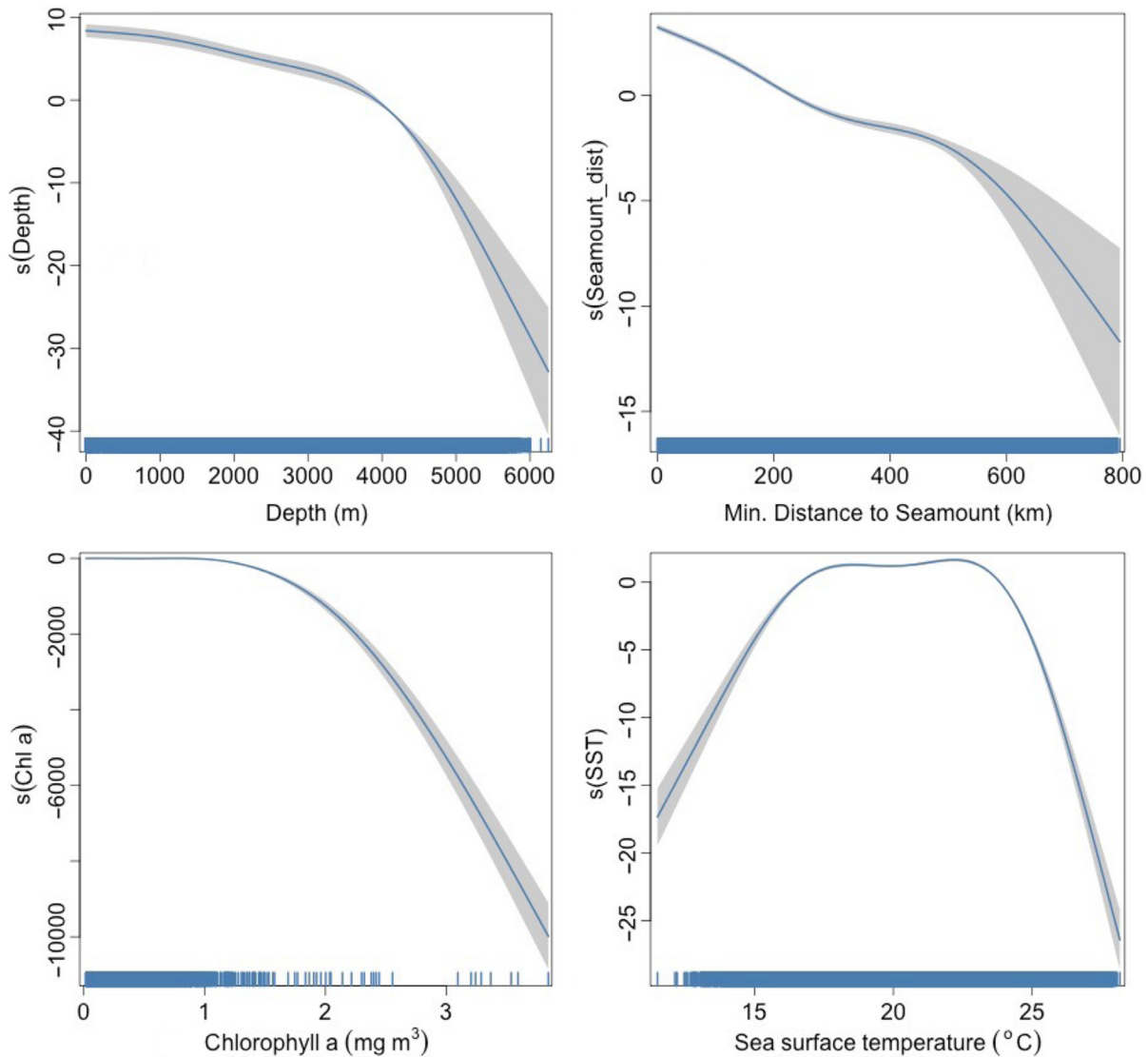
Fig. 5. Generalised additive mixed model (GAMM) partial response curves (±SE; rug plots indicate observational data) depicting relationship between Monteiro's storm-petrel foraging location and (A) depth, (B) distance to the nearest seamount, (C) chl *a* concentration, (D) sea surface temperature (SST)

ferences in foraging location between years. Contrary to a study on Monteiro's storm-petrel using coarse scale data from light-level geolocators (Paiva et al. 2018), male and female birds did not show any distinct differences in the duration or maximum distance of their foraging trips, but similarly to previous studies on other storm-petrel species (e.g. Alho et al. 2022, Collins et al. 2022) the birds flew longer distances and spent longer at sea during incubation than during chick-rearing in all years. The information gathered in this study gives new insight into the ecology of this vulnerable and cryptic seabird that may be useful for understanding at-sea behaviour and aid in strategically increasing overlap between key foraging habitat and MPAs.

4.2. Spatial distribution and habitat selection

The Azores Archipelago is located in the mid-Atlantic Ocean, where most available foraging habitat is over the deep abyssal plain (>4000 m depth). In this environment, Monteiro's storm-petrels preferentially foraged in the shallowest available habitat, with most foraging occurring in waters <2500 m depth (mean = 1500 m). Foraging was associated with the higher density of seamounts to the north of the archipelago (Morato et al. 2008a) and over shelf-breaks along the mid-Atlantic ridge. Topographic features such as seamounts and ridges interact with ocean currents to produce nutrient upwelling and enhance local productivity (Lewison et al. 2012, No-
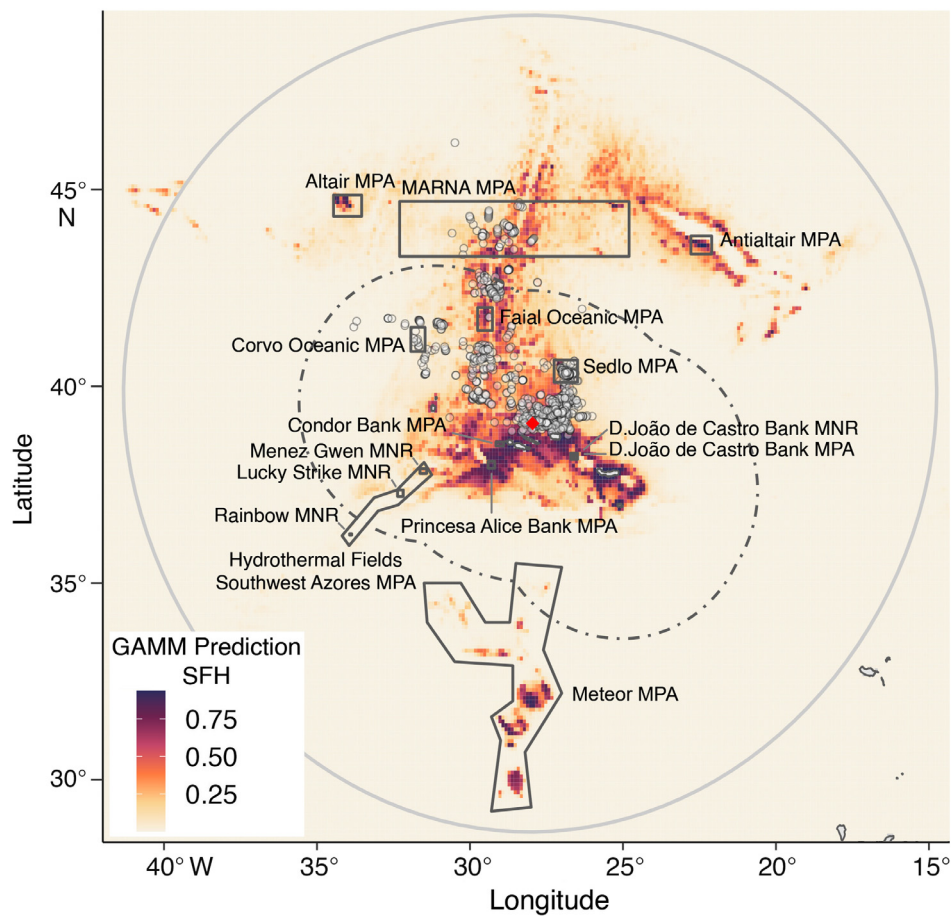
Fig. 6. Predictions for an example year (2018) from the best performing generalised additive mixed model (GAMM) describing suitable foraging habitat (SFH) for Monteiro's storm-petrels using seafloor depth, distance to the nearest seamount, sea surface temperature (SST), chl *a*, and bird ID as a random effect. Locations of observed Monteiro's storm-petrel foraging locations are overlaid with grey points, the Azores 200 nmile exclusive economic zone (EEZ) is shown by a dashed line and marine protected areas (MPAs) and marine natural reserves (MNRs) are outlined by dark grey polygons. Light grey circle represents the potential foraging range and has a radius of 1154 km (max. foraging range) around the center of the colony. Red diamond represents Praia Islet

gueira et al. 2012). Seamounts are known to aggregate both prey and predators (Morato et al. 2008b, Amorim et al. 2009, Paiva et al. 2010), creating biological hotspots and enhanced feeding opportunities for predators in the otherwise featureless open ocean (Cascão et al. 2020).

Monteiro's storm-petrels feed primarily on small myctophid fish and squid (Carreiro et al. 2022) and perform shallow dives to exploit their prey at the near-surface (<5 m). Other studies have shown that prey from the deep scattering layer including myctophids can be enhanced at the near-surface (~10 m depth) in proximity to seamounts, matching an observed increase in seabird density (Haney et al. 1995). This suggests that these features may increase either the total abundance or the accessibility of vertically migrating prey species to surface-feeding and shallow-diving predators including seabirds. Similar

foraging locations and behaviour to those observed in Monteiro's storm-petrels have been described for Cory's shearwaters (Magalhães et al. 2008, Paiva et al. 2010) suggesting that subsurface features such as seamounts and shelf breaks in the northern mid-Atlantic may provide relatively predictable foraging habitat for other near-surface feeding seabirds breeding at the Azores Archipelago.

Monteiro's storm-petrels preferred foraging north of the Azores Archipelago despite the availability of some shallow foraging habitat and seamounts to the south of the breeding colony. Their habitat selection appeared in part related to the presence of cooler, more productive waters available near the northern edge of the petrels' foraging range. This represents a dynamic area dominated by eddies and meanders originating from the Gulf Stream, which forms a transition zone as it passes through the region as the

North Atlantic drift. Despite some variation in SST and chl a concentration between years, there was no dramatic difference in core foraging location or habitat preference resulting from oceanographic changes at the interannual scale. This mirrors findings in a smaller congener, the European storm-petrel *Hydrobates pelagicus*, which also showed highly consistent usage of foraging areas across both years and breeding stages (Bolton 2021).

There was greater variability in the distance travelled from the colony and total distance covered by birds across years than in the duration of foraging trips. This suggests that despite having relatively tight constraints on the amount of time birds can leave their partners (incubation) or offspring (chick-provisioning), petrels have greater flexibility in the locations that they can visit by increasing the amount of ocean covered on a foraging trip. Inter-annual oceanographic variability has been shown to influence nest fidelity (Robert et al. 2014), reproductive performance, and survival of the Monteiro storm-petrel (Robert et al. 2012, 2015), and the links between these parameters and foraging effort and prey availability both within and outside of the breeding season deserve further investigation.

4.3. Differences between sexes and breeding stages

We found no significant inter-sexual segregation within foraging trip characteristics of Monteiro's storm-petrels including trip duration, or maximum distance. A slight sexual size dimorphism in Monteiro's storm-petrels, with females having longer wings than males has been described (Nava et al. 2017, Schäfer 2019). A previous study on Monteiro's storm-petrel at-sea distribution using global location sensors (GLSs) found inter-sexual habitat segregation (Paiva et al. 2018), but our data does not support this hypothesis. The lack of differences in foraging trip characteristics between males and females might be a result of equal investment in parental care (Warham 1990).

Monteiro's storm-petrels made longer foraging trips and covered larger foraging distances during incubation than during chick-rearing. That the birds travelled to more remote foraging areas during the incubation period may be because adults only have to provide for themselves. In contrast, during the chick-rearing period, foraging effort must meet the energy requirements of both parent and offspring. Then, the birds have to come more frequently to the colony to feed their chick and are therefore limited in the distance they can travel to reach more desirable foraging areas.

A bimodal provisioning strategy of alternating long and short foraging trips is known in many procellariiform species, e.g. sooty shearwaters *Ardenna grisea*, wandering albatrosses *Diomedea exulans* or Cory's shearwaters *Calonectris diomedea* (Baduini & Hyrenbach 2003, Magalhães et al. 2008). In Leach's storm-petrels *H. leucorhous* and European storm-petrels *H. pelagicus* unimodal foraging strategies have been described (Baduini & Hyrenbach 2003, Mauck et al. 2023). In some cases, Leach's storm-petrels may show some degree of bimodality, as found by Collins et al. (2022), but with no obvious pattern, with short trips being equally likely in incubation and chick-rearing.

The Monteiro's storm-petrels seem to pursue a unimodal strategy like their close relatives; although chick-rearing birds occasionally conducted longer trips, the majority were close to the colony, and the core foraging range was much more constrained relative to incubating. However, there was some inter-individual variation in the foraging trip duration during incubation with 2 adjoining core ranges, one with a slightly closer maximum extent to the northeast of the colony, and one that extended slightly further to the northwest. Additionally, birds seemed to decrease the foraging trip duration towards the end of the incubation period, similar to what was found for Leach's storm-petrels (Mauck et al. 2023), probably to ensure that they can be at the nest to feed their chick soon after hatching (Weimerskirch 1998, González-Solís 2004).

4.4. Overlap with MPAs

Tracking can provide a useful tool to inform marine conservation planning by enabling the spatial overlap of species and their threats (Lascelles et al. 2016). Amongst seabirds, storm-petrels seem to be the least impacted by bycatch, being more vulnerable to terrestrial threats, especially invasive alien species and problematic native species (Dias et al. 2019). However, they are amongst the most impacted by artificial lights at coastal and offshore industrial sites (Gjerdrum et al. 2021). In addition, a recent review of at-sea threats to these groups (Hydrobatidae and Oceanidae) identified pollution, energy production and mining and climate change as other potential threats (Dias et al. 2019).

The high mobility of megafauna reduces the effectiveness of static area-based management (Hilborn et

al. 2022), but in this study we found a high consistency in the foraging areas used across 4 consecutive breeding seasons, driven by a preference for environmental features including seafloor depth and distance to seamounts that did not change through time. In addition, the Monteiro's storm-petrel is a vulnerable species, and its annual breeding success can, in some years, be very low (Neves et al. 2017). Therefore, protecting the main foraging areas, by restricting the activities with a potential impact on storm-petrels, could contribute to ensuring the viability of the species.

Currently, the foraging locations of this vulnerable species are poorly covered by MPAs, especially during chick-rearing. Recently, the European Commission has committed to designating 30% of EU waters as protected areas by 2030 (30 × 30 target), with at least one-third of these MPAs classified as 'strictly protected' (EU Biodiversity Strategy for 2030). Although it is reported that more than 50% of the cumulative breeding range of procellariiform seabirds are covered by IBAs and SPAs within the EU (Ramirez et al. 2017), only 11.4% of Monteiro's storm-petrel foraging locations overlapped with the sites of existing MPAs. Two current MPAs are important for the birds tracked in this study, namely the 'Nature Reserve of *Monte Submarino* Sedlo' northeast of the colony and the 'mid-Atlantic ridge north of the Azores' (MARNA).

During incubation, 16% of the foraging locations were within MPA zones and during chick-rearing that value was only 5%. This is particularly concerning, as foraging during the chick-rearing stage is crucial for breeding success, when the Monteiro's storm-petrels must provide for both themselves and their chicks (Orians & Pearson 1979). Therefore, it seems important to characterise threats facing Monteiro's storm-petrels at sea and to use this information combined with information on distribution and habitat selection to designate further MPAs for the conservation of this vulnerable species.

Based on the analyses performed in this paper, a strong candidate area for enhanced protection could be the area around and to the south of the Sedlo Seamount. This area was an important core foraging habitat in both breeding stages. Additionally, the birds foraged extensively along the mid-Atlantic ridge, but mainly south of the MARNA MPA closer to the archipelago, another important candidate area to be considered for protection. A total of 95% of the unprotected foraging locations (91% during incubation, 98% during chick-rearing) of the Monteiro's storm-petrels were located inside the boundaries of the EEZ of the Azores, and therefore, it is the responsibility of the Portuguese government to designate new MPAs. Although Portugal was a pioneer in establishing MPAs (Ramirez et al. 2017), the waters covered by IBAs and SPAs currently represent less than 3% of the Portuguese EEZ. The designation of new MPAs protecting the core foraging areas of the Monteiro's storm-petrel and other breeding seabirds may be a good opportunity to increase the proportion of protected Portuguese waters and fulfil the 30 × 30 target.

Ideally, a larger analysis should combine tracking and modelling data for other species of the Azores-breeding seabird community using a multi-model predictive approach to identify biological hotspots for enhanced protection. Of particular importance would be the inclusion of data on foraging areas and habitat suitability of the Monteiro's storm-petrel's sibling species, the more abundant winter breeding band-rumped storm-petrel *H. castro*. By combining habitat modelling with studies on the diet of Azores storm-petrels, it would be possible to assess their vulnerability to changes in prey resources caused by fishing and environmental change.

LITERATURE CITED

Alho M, Catry P, Silva MC, Nunes VL, Granadeiro JP (2022) Revealing the foraging movements and diet of the white-faced storm petrel *Pelagodroma marina* in the NE Atlantic. Mar Biol 169:1–14

Amorim P, Figueiredo M, Machete M, Morato T, Martins A, Santos RS (2009) Spatial variability of seabird distribution associated with environmental factors: a case study of marine important bird areas in the Azores. ICES J Mar Sci 66:29–40

Baduini CL, Hyrenbach KD (2003) Biogeography of procellariiform foraging strategies: Does ocean productivity influence provisioning? Mar Ornithol 31:101–112

Bernard A, Rodrigues ASL, Cazalis V, Grémillet D (2021) Towards a global strategy for seabird tracking. Conserv Lett 14:e12804

BirdLife International (2021) *Hydrobates monteiroi* (Europe assessment). The IUCN Red List of Threatened Species 2021:e.T22735624A166446696. https://dx.doi.org/10.2305/IUCN.UK.2021-3.RLTS.T22735624A166446696.en. (accessed 20 December 2022)

Bolton M (2021) GPS tracking reveals highly consistent use of restricted areas by European storm-petrels *Hydribates pelagicus* breeding at the largest UK colony: implications for conservation management. Bird Conserv Int 31:35–52

Bolton M, Medeiros R, Hothersall B, Campos A (2004) The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: a case study of the Madeiran storm petrel (*Oceanodroma castro*). Biol Conserv 116:73–80

Bolton M, Smith AL, Gómez-Díaz E, Friesen VL and others (2008) Monteiro's storm petrel *Oceanodroma monteiroi*: a new species from the Azores. Ibis 150:717–727

Borges PAV, Costa A, Cunha R, Gabriel R and others (2010) A list of the terrestrial and marine biota from the Azores. Principia, Cascais

Boyd C, Grünbaum D, Hunt GL, Punt AE, Weimerskirch H, Bertrand S (2017) Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. J Appl Ecol 54:1362–1372

Cabral MJ, Almeida J, Almeida PR, Delliger T and others (eds) (2005) Livro vermelho dos vertebrados de Portugal. Instituto da Conservação da Natureza, Lisbon

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Carreiro AR, Bried J, Deakin Z, Jones KB and others (2022) First insights into the diet composition of Madeiran and Monteiro's storm petrels (*Hydrobates castro* and *H. monteiroi*) breeding in the Azores. Waterbirds 44:300–307

Carroll G, Everett J, Harcourt R, Slip D, Jonsen I (2016) High sea surface temperatures driven by a strengthening current reduce foraging success by penguins. Sci Rep 6:22236

Cascão I, Lameiras MO, Prieto R, Santos RS, Silva MA (2020) Temporal patterns in acoustic presence and foraging activity of oceanic dolphins at seamounts in the Azores. Sci Rep 10:3610

Collins SM, Hedd A, Fifield DA, Wilson DR, Montevecchi WA (2022) Foraging paths of breeding Leach's storm-petrels in relation to offshore oil platforms, breeding stage, and year. Front Mar Sci 9:816659

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22:1–34

Davies TE, Carneiro APB, Tarzia M, Wakefield E and others (2021) Multispecies tracking reveals a major seabird hotspot in the North Atlantic. Conserv Lett 14:e12824

De Pascalis F, Pala D, Pisu D, Morinay J and others (2021) Searching on the edge: dynamic oceanographic features increase foraging opportunities in a small pelagic seabird. Mar Ecol Prog Ser 668:121–132

De Pascalis F, Pisu D, Pala D, Benvenuti A and others (2022) Identification of marine important conservation areas for Mediterranean storm petrels *Hydrobates pelagicus melitensis* breeding in Sardinia, Italy. Mar Ornithol 50:205–210

Dias MP, Martin R, Pearmain EJ, Burfield IJ and others (2019) Threats to seabirds: a global assessment. Biol Conserv 237:525–537

Fridolfsson A, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121

Gjerdrum C, Ronconi RA, Turner KL, Hamer TE (2021) Bird strandings and bright lights at coastal and offshore industrial sites in Atlantic Canada. Avian Conserv Ecol 16:22

González-Solís J (2004) Regulation of incubation shifts near hatching by giant petrels: a timed mechanism, embryonic signalling or food availability? Anim Behav 67:663–671

Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. Mar Ecol Prog Ser 391:121–137

Haney JC, Haury LR, Mullineaux LS, Fey CL (1995) Seabird aggregation at a deep North Pacific seamount. Mar Biol 123:1–9

Hazen EL, Abrahms B, Brodie S, Carroll G, Welch H, Bograd SJ (2021) Where did they not go? Considerations for generating pseudo-absences for telemetry-based habitat models. Mov Ecol 9:5

Hilborn R, Agostini VN, Chaloupka M, Garcia SM and others (2022) Area-based management of blue water fisheries: current knowledge and research needs. Fish Fish 23:492–518

Juliano MF, Alves ML (2007) The Atlantic Subtropical Front/current systems of Azores and St. Helena. J Phys Oceanogr 37:2573–2598

Kenward R (2001) A manual for wildlife radio tagging, 2nd edn. Academic Press, New York, NY

Lascelles BG, Taylor PR, Miller MGR, Dias MP and others (2016) Applying global criteria to tracking data to define important areas for marine conservation. Divers Distrib 22:422–431

Lewison R, Oro D, Godley BJ, Underhill L and others (2012) Research priorities for seabirds: improving conservation and management in the 21st century. Endang Species Res 17:93–121

Liang KY, Zeger SL (1986) Longitudinal data analysis using generalized linear models. Biometrika 73:13–22

Magalhães MC, Santos RS, Hamer KC (2008) Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. Mar Ecol Prog Ser 359:283–293

Mauck RA, Pratte I, Hedd A, Pollet IL and others (2023) Female and male Leach's storm petrels (*Hydrobates leucorhous*) pursue different foraging strategies during the incubation period. Ibis 165:161–178

Medrano F, Saldanha S, Hernandez-Montoya J, Bedolla-Guzman Y, Gonzalez-Solis J (2022) Foraging areas of nesting Ainley's storm petrel *Hydrobates cheimomnestes*. Mar Ornithol 50:125–127

Michelot T, Langrock R, Patterson TA (2016) moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. Methods Ecol Evol 7:1308–1315

Monteiro LR, Furness RW (1998) Speciation through temporal segregation of Madeiran storm-petrel (*Oceanodroma castro*) populations in Azores? Philos Trans R Soc Lond B Biol Sci 353:945–953

Monteiro LR, Ramos JA, Furness RW, del Nevo AJ (1996) Movements, morphology, breeding, moult, diet and feeding of seabirds in the Azores. Colon Waterbirds 19:82–97

Morato T, Machete M, Kitchingman A, Tempera F and others (2008a) Abundance and distribution of seamounts in the Azores. Mar Ecol Prog Ser 357:17–21

Morato T, Varkey DA, Damask C, Machete M and others (2008b) Evidence of a seamount effect on aggregating visitors. Mar Ecol Prog Ser 357:23–32

Nava C, Neves VC, Andris M, Dubois MP, Jarne P, Bolton M, Bried J (2017) Reduced population size does not affect the mating strategy of a vulnerable and endemic seabird. Sci Nat 104:103

Neves VC, Nava C, Monteiro EV, Monteiro PR, Bried J (2017) Depredation of Monteiro's storm-petrel (*Hydrobates monteiroi*) chicks by Madeiran wall lizards (*Lacerta dugesii*). Waterbirds 40:82–86

Neves VC, Rund D, Pinho CJ, Vasconcelos R, Bustamante P, Quillfeldt P (2022) Diet of the exotic Madeiran wall lizard: first insights into trophic interactions in an Atlantic seabird sanctuary. Herpetozoa (Wien) 35:107–113

Nogueira E, González-Nuevo G, Valdés L (2012) The influence of phytoplankton productivity, temperature and environmental stability on the control of copepod diversity in the north east Atlantic. Prog Oceanogr 97–100:92–107

Oliveira N, Pipa T, Silva C, Teodósio J, Andrade J (2016) Final Report of the Monteiro's Storm-petrel Project (phase 1). Sociedade Portuguesa para o Estudo das Aves, Lisboa. https://spea.pt/

Oppel S, Bolton M, Carneiro APB, Dias MP and others (2018) Spatial scales of marine conservation management for breeding seabirds. Mar Policy 98:37–46

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Stairs GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, p 155–177

Paiva VH, Geraldes P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010) Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. Mar Biol 157:1385–1399

Paiva VH, Ramos JA, Nava C, Neves V, Bried J, Magalhães M (2018) Inter-sexual habitat and isotopic niche segregation of the endangered Monteiro's storm-petrel during breeding. Zoology 126:29–35

Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population trend of the world's monitored seabirds, 1950–2010. PLOS ONE 10:e0129342

Phillips LR, Carroll G, Jonsen I, Harcourt R, Brierley AS, Wilkins A, Cox M (2022) Variability in prey field structure drives inter-annual differences in prey encounter by a marine predator, the little penguin. R Soc Open Sci 9:220028

Pollet IL, Ronconi RA, Jonsen ID, Leonard ML, Taylor PD, Shutler D (2014) Foraging movements of Leach's storm-petrels *Oceanodroma leucorhoa* during incubation. J Avian Biol 45:305–314

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org

Ramirez I, Tarzia M, Dias MP, Burfield IJ, Ramos JA, Garth S, Paiva VH (2017) How well is the EU protecting its seabirds? Progress in implementing the Birds Directive at sea. Mar Policy 81:179–184

Robert A, Paiva VH, Bolton M, Jiguet F, Bried J (2012) The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. Ecology 93:1944–1952

Robert A, Paiva VH, Bolton M, Jiguet F, Bried J (2014) Nest fidelity is driven by multi-scale information in a long-lived seabird. Proc Biol Sci 281:20141692

Robert A, Bolton M, Jiguet F, Bried J (2015) The survival–reproduction association becomes stronger when conditions are good. Proc Biol Sci 282:20151529

Rodríguez A, Holmes ND, Ryan PG, Wilson KJ and others (2017) Seabird mortality induced by land-based artificial lights. Conserv Biol 31:986–1001

Ronconi RA, Allard KA, Taylor PD (2015) Bird interactions with offshore oil and gas platforms: review of impacts and monitoring techniques. J Environ Manage 147:34–45

Rossby T (1996) The North Atlantic Current and surrounding waters: at the crossroads. Rev Geophys 34:463–481

Rotger A, Sola A, Tavecchia G, Sanz-Aguilar A (2020) Foraging far from home: Gps-tracking of Mediterranean storm-petrels *Hydrobates pelagicus melitensis* reveals long-distance foraging movements. Ardeola 68:3–16

Sansom A, Wilson LJ, Caldow RWG, Bolton M (2018) Comparing marine distribution maps for seabirds during the breeding season derived from different survey and analysis methods. PLOS ONE 13:e0201797

Schäfer W (2019) Spatial distribution of the endemic Monteiro's storm-petrel (*Hydrobates monteiroi*) during breeding season in the Azores Archipelago, northeast Atlantic. MSc thesis, University of Giessen

Warham J (1990) The petrels. Their ecology and breeding systems. Academic Press, London

Weimerskirch H (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. J Anim Ecol 67:99–109

Whittaker RH, Likens GE (1973) Carbon in the biota. Brookhaven Symp Biol 30:281–302

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc B 73:3–36