

Tagging and Tracking of Seabirds on the West Coast of Scotland

August 2026



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Tracking of Leach's Storm-Petrel from St Kilda and European Storm-Petrel from Treshnish Isles

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Contractor/grant recipient: RSPB



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1. Summary

A rapid expansion of offshore renewable energy infrastructure is underway in the Atlantic waters off the west coast of Scotland. This expansion is driven by Scottish Government and UK Government clean energy targets as part of the transition to Net Zero by 2045 in Scotland (Scottish Government 2020) and 2050 for the whole of the UK (BEIS 2021). To meet these targets while protecting biodiversity, it is vital to gather information on the marine distribution and behaviour of seabirds. Such information will help inform measures to avoid, mitigate and compensate for any negative impacts on seabirds from marine renewables and other human activities.

Little is currently known about the marine distribution and behaviour of two seabird species that occur in Scottish waters, Leach's Storm-petrel *Hydrobates leucorhous* and European Storm-petrel *H. pelagicus*. Their small size, remote breeding locations and nocturnal colony attendance makes them challenging to study. However, recent advances in technology to reduce the size and weight of tracking tags now permit the tracking of even the smallest seabird species, such as Storm-petrels, to provide information on their marine distribution.

This report provides results from fieldwork completed in 2021, 2023 and 2024 by RSPB staff to track, during the breeding and non-breeding seasons, Leach's Storm-petrels from the largest UK colony, St Kilda, and European Storm-petrels from the Treshnish Isles, Inner Hebrides. No tracking was possible during 2022 due to restrictions on the capture and handling of seabirds in Scotland due to the outbreak of Highly Pathogenic Avian Influenza (HPAI). We present GPS tracking data on breeding season foraging trip characteristics, utilisation distributions (UDs), overlap with proposed offshore wind farms (OWFs) and habitat associations. We also report attempts to deploy geolocator tags on both species and present the first information from Leach's Storm-petrels tracked outside the breeding season from a UK colony.

Whilst not an original aim of the project, we report results of blood sampling a small number of birds to assay for antibodies to HPAI.

Leach's Storm-petrel

Data were obtained from a total of 50 birds tracked using GPS tags across the three field seasons, resulting in 78 complete trips by birds actively engaged in breeding attempts. We excluded from all analyses six further short trips undertaken by a bird that was no longer attending an active nest, and five additional, atypical, shorter trips (of five different individuals) that were considered to have resulted from birds prevented from accessing their nests to resume incubation due to researchers' activity at the nest on nights they returned. These birds returned to the sea for a further day, before being recaptured. The sample of 78 trips considered to represent normal foraging behaviour of birds attending active nests averaged 52.2 ± 20.2 hr in duration, 281.2 ± 103.6 km maximum distance from the colony and 848.4 ± 332.7 km total distance. Leach's Storm-petrels were very consistent between years in their direction of travel and foraging distribution, and habitat association modelling showed they selected deep water and areas of higher sea surface temperature. The tracking data indicated no overlap between Leach's Storm-petrel foraging areas and currently proposed offshore wind energy development.

Only three birds of 20 birds fitted with ring-mounted geolocator tags in 2021 were recaptured (in 2023, due to prohibition of fieldwork in 2022). Two birds had lost their tags, associated with leg injuries likely caused by the tagging procedure. The third individual retained its tag and appeared healthy. The tracking data showed that it departed the colony in mid September (indicating successful breeding) and migrated southward off the West coast of Ireland, and wintered in the Benguela current and mid-Atlantic. In light of the low recapture rate of birds tagged with geolocators, no further tagging was carried out.

No antibodies to any form of avian influenza virus were found in blood samples from eight breeding Leach's Storm-petrels sampled in 2023 on St Kilda, indicating lack of recent exposure to HPAI. Samples taken from a further four individuals in 2023 were insufficient for analysis.

European Storm-petrel

A total of 38 birds were successfully GPS tracked across the three field seasons resulting in 48 complete trips averaging 36.9 ± 17.3 hrs in duration, 116.6 ± 53.0 km maximum distance from the colony and 418.6 ± 178.0 km total distance (model estimates accounting for similarities of multiple trips by the same individual). Habitat association modelling showed reduced usage of areas more distant from the colony (reflecting central-place foraging constraints), but increasing usage with increasing seabed slope, which may increase mixing of the water column and accessibility of prey. The tracking data indicated overlap between European Storm-petrel foraging areas and currently proposed offshore wind energy development. Nineteen of 38 tracked individuals spent time in areas leased for windfarm development; across all tracked birds the proportion of distance at sea per trip within these areas averaged $3.5\% \pm 6.8$ (0 – 28.8%).

None of 20 birds fitted with ring-mounted geolocator tags in 2021 were recaptured in 2023, whereas 7 of 22 control birds (that were only ringed) were re-encountered that year. It is likely that the difference on re-capture rates was due to the tagging procedure, and no further tagging was carried out.

No antibodies to any form of avian influenza virus were found in a blood sample from a single breeding European Storm-petrel caught in the Treshnish Isles in 2023, indicating lack of recent exposure to HPAI. Samples taken from a further three individuals in 2023 were insufficient for analysis.

2. Introduction

Scotland's coasts and seas support internationally important marine biodiversity, and the Scottish Government has made strong, high-level commitments to the protection of the nation's rich natural heritage. A key responsibility of Scottish Government's Marine Directorate is to manage Scotland's seas for prosperity and environmental sustainability, and to achieve good environmental status to help ensure a healthy and sustainable environment. The economic pressures on the marine environment have substantially increased in recent years, and are set to increase still further, in the face of the growing concern over climate change. The Scottish Government's Climate Change Plan (2018) has set out the need to achieve a net-zero carbon target for 2045, enshrined in the Climate Change Act (2009, amended 2019), which will require the development of extensive areas for marine renewable energy extraction in the near future (Figure 1). Ensuring that future developments do not adversely impact Scotland's internationally important marine ecosystems, and especially the designated features of protected sites, is of utmost importance.

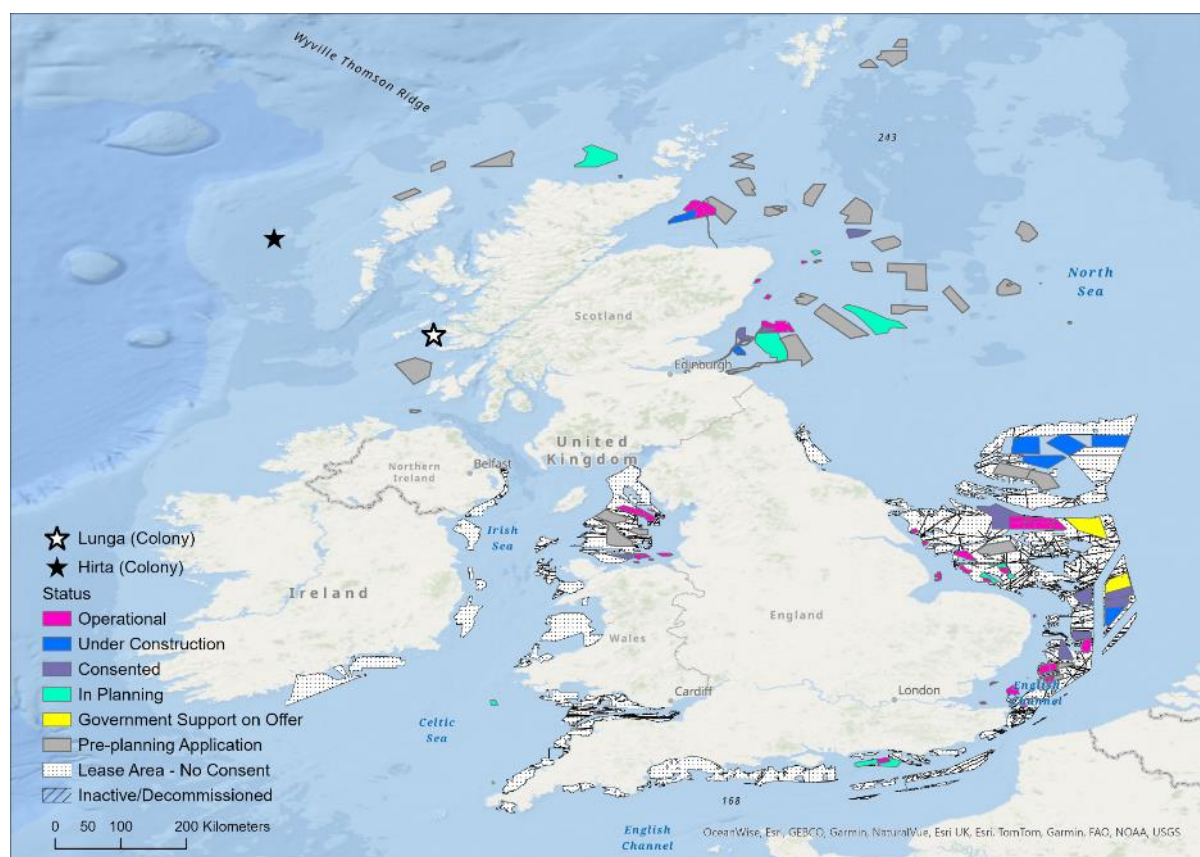


Figure 1. Overview of published offshore wind (OWF) lease areas around Britain and Ireland as of January 2025 symbolised by planning stage and the location of the breeding colonies in this study. Hirta (St Kilda Archipelago, Leach's Storm-petrel) and Lunga (Treshnish Archipelago, European Storm-petrel). Map produced in Arc GIS Pro (ESRI 2021) using data published on the Crown Estate spatial hub hosted on Arc GIS online (Crown Estate 2021) and Marine Renewable Energy Ireland (MaREI) (2021).

Information on the marine distribution and behaviour of seabirds is essential to assess whether, and if so where, seabirds may be exposed to high levels of threat from marine activities, which could jeopardise the conservation status of protected species and sites. Information on seabird marine distribution and behaviour also informs understanding of drivers of population change. The earliest information on the distribution of seabirds at sea around the UK was obtained from boat-based transect surveys (Blake et al. 1984), and more recently from aerial surveys (Buckland et al. 2012), which have been used to determine potential overlap of seabird distributions with those of marine threats to which they may be vulnerable, such as oil pollution (Williams et al. 1994, Webb et al. 2016), fisheries bycatch (Bradbury et al. 2017) and offshore wind farms (Marine Scotland Science 2018). Whilst transect based at-sea surveys provide an effective means of simultaneously surveying multiple species in any given area, such surveys may be economically unfeasible for species that travel very considerable distances from the breeding colony, and disperse over extremely large areas, in search of food during the breeding season. There is also uncertainty about the detectability of smaller species like storm-petrels, especially when close to the sea surface. Furthermore, at-sea surveys rarely provide information on the breeding status, or colony provenance, of the individual seabirds counted and are limited by weather and daylight conditions. Hence, it is difficult to determine which breeding colonies may be impacted, and to what extent, by a particular, localised, marine threat.

Recent advances in GPS tracking technology have resulted in reductions in the size, weight and cost of electronic tracking devices, enabling researchers to track large numbers of seabirds from breeding colonies, and to estimate colony-level (and in some cases regional-scale) marine distribution (e.g., Wakefield et al. 2017). GPS tags and other biologging devices can also provide information on seabird behaviour at sea, such as the location, and depth, of diving behaviour, locations of surface feeding, roosting, flight height and flight speed, and even ship-following behaviour. Such information may be of crucial importance in determining the extent to which seabirds may be vulnerable to threats including fishery bycatch, turbine collision, or surface pollution, when the distributions of seabirds and threats overlap.

Leach's Storm-petrel is classified by IUCN as "Vulnerable" to global extinction (BirdLife International 2018) and was recently red-listed in a recent update to the Birds of Conservation Concern BoCC (Stanbury et al. 2024) following steep population declines at breeding colonies in the northwest Atlantic. The entire UK population breeds within Scotland, with six sites designated as Special Protection Areas (SPAs) for the species. Whilst population trends in the UK are not completely known, a large decline has been recorded within the largest UK colony on St Kilda (Newson et al. 2008, Deakin et al. 2021). The extent to which the marine distribution of birds from protected colonies may overlap with marine pressures is currently unknown. Published information on the species' distribution at sea in UK waters currently derives entirely from at-sea transect surveys, many of which are now somewhat dated (e.g. Bloor et al. 1996, Pollock et al. 2000) resulting in significant knowledge gaps (Deakin et al. 2022). This study represents the first tracking of this species in the UK.

The UK holds internationally important numbers of breeding European Storm-petrels, with more than 88% of the UK population located within Scotland (Burnell et al. 2023), and eight Scottish colonies designated as SPAs for the species. The extent to which the marine distribution of birds from these colonies may overlap with marine pressures is currently poorly known. Since the European Storm-petrel species is Amber listed in the UK due to having a restricted number of breeding sites (Stanbury et al. 2024), understanding its distribution at sea is a priority to underpin sensitive marine planning and to inform the species' conservation. As with Leach's Storm-petrel, published information on the species' distribution at sea currently derives almost entirely from at-sea transect surveys (e.g. Waggitt et al. 2019), although recent work has demonstrated that European Storm-petrels can be successfully tracked using GPS tags during the breeding season (Critchley et al. 2019, Bolton 2021).

This report summarises the results of fieldwork undertaken in 2021, 2023 and 2024 under two related projects to track Leach's Storm-petrels from St Kilda and European Storm-petrels from the Treshnish Isles. The first project, entitled "Tagging and Tracking of Seabirds in West Coast of Scotland" (Lots 2 and 3) was awarded to RSPB in March 2020 as a result of a competitive tender submitted in February 2020 (tender reference CORR/5536). The objectives of that project were:

1. To track a minimum of 10 individuals of each storm-petrel species using GPS tags during the breeding season, to characterise their foraging distribution during the breeding season, annually from 2020 - 2022.
2. To track up to 20 individuals of each species using geolocator (GLS) tags to characterise their migration routes and wintering areas in each of the non-breeding seasons 2020-21 and 2021-22.

This onset of this project was delayed due to restrictions imposed by the UK government in response to the Covid pandemic in March 2020. Fieldwork commenced in 2021 when restrictions were lifted, resulting in GPS tracking of both species, and deployment of 20 GLS tags on each species, for retrieval in 2022. However, fieldwork was again prevented in 2022, when NatureScot imposed a ban on all seabird fieldwork in response to the outbreak of Highly Pathogenic Avian Influenza (HPAI). The Scottish Government Marine Directorate awarded a grant to RSPB ("Petrel tagging project extension") in January 2023 to enable a further two years of data collection, 2023 and 2024, in order to complete the project. The grant for the project extension had the following specific aims:

1. Retrieve previously deployed GLS tags and undertake an additional year of GLS tagging of European Storm-petrel (Treshnish Isles) and Leach's Storm-petrel (St Kilda).
2. Acquire an additional year of GPS tracking data on European Storm-petrel (Treshnish Isles) and Leach's Storm-petrel (St Kilda).
3. Produce colony specific foraging distribution maps (including associated GIS files), including behaviours, habitat associations, temporal variation and uncertainty, to better understand potential for the species to encounter or interact with offshore wind farms during the breeding season

4. Where possible, undertake an assessment of HPAI impacts on population sizes and breeding success, potentially including blood antibody testing, ensuring that data used to inform impact assessments are robust.

Here we report on the work undertaken in 2021 under the original contract, and on the work undertaken in 2023 and 2024 under the grant awarded for project extension.

3. Methods

3.1 Fieldwork timing and objectives

The timing of fieldwork on Hirta, St Kilda and on Lunga, Treshnish Isles varied slightly across the three study years, mainly in response to improved understanding of the timing of breeding of the two species at the study sites, and the most appropriate time to carry out tagging operations. The timing of fieldwork and objectives of each campaign are shown in Table 1. All fieldwork was undertaken under all appropriate licences and permissions from NatureScot, BTO, the landowners and the RSPB HPAI exceptions panel.

Table 1. Timing and objectives of fieldwork conducted on St Kilda and Treshnish Isles 2021-2024.

Leach's Storm-petrel

Hirta, St Kilda 57.81° N -8.60° W

Year	Fieldwork period	Objectives
2021	8 th June – 15 th July	GPS and GLS tagging
2023	16 th June – 31 st July	GLS tag retrieval GPS and GLS tagging, blood sampling for HPAI assay.
2024	12 th June – 27 th July	GPS tagging and GLS tag retrieval.

European Storm-petrel

Lunga, Treshnish Isles 56.49° N, -6.42° W

Year	Fieldwork period	Objectives
2021	19 th July – 8 th August	GPS and GLS tagging
2023	27 th May – 2 nd June	GLS tag retrieval, blood sampling for HPAI assay.
2023	28 th July – 17 th August	GLS tag retrieval, GPS tagging, blood sampling for HPAI assay.
2024	16 th July – 19 th August	GPS tagging and GLS tag retrieval, assessment of HPAI impacts

3.2 GPS tracking

The small size of Leach's Storm-petrels and European Storm-petrels currently precludes the use of tags which allow remote data download. Some manufacturers are in the process of developing miniaturised GPS tags capable of remote download and a small number of prototype tags supplied by TechnoSmart were trialled during the 2023 fieldwork for this project. However, they performed very poorly and were not used further. Only one of four supplied tags collected data during pre-deployment trials and the fourth tag failed to download data to the base station during nine days of deployment. The bird was recaptured and the tag was removed. The tag antenna was found to have broken and the solar panel had suffered corrosion. Therefore, throughout this project we used archival GPS tags supplied by PathTrack (nanoFIX® GEO-Mini) which are the lightest (c. 0.93g) and smallest (18 x 11 x 4mm) commercially available avian GPS tags, and which had been used successfully for tracking European Storm-petrels previously (Bolton 2021). To maximise the chances of recapturing birds for tag retrieval and data download, individuals were tagged at sites where an active breeding attempt was confirmed or considered very likely (see below). Nests were found through playback of recordings of their calls from a handheld loudspeaker (Gilbert et al. 1998). This method was used both during the day and at night. Responses from birds in burrows indicated possible breeding sites, which were then monitored for potential use as study nests. Where possible, the status of the nest (e.g., pre-breeding, incubation) was confirmed through direct visual inspection of the nest chamber, or by use of an endoscope where the nest chamber was not directly visible. If the nest chamber could not be inspected, consistent occupation of a nest site indicated through repeated response to playback over multiple days was taken as an indication of breeding.

Where nest chambers were sufficiently accessible, birds were caught for tag deployment by direct removal from the nest by hand. However, the nest entrances of Leach's Storm-petrels were too narrow and long for removal by hand, so birds were caught by placing a trap at the nest entrance to catch birds as they departed to begin a foraging trip. GPS tags were attached to the central four tail feathers using thin strips of adhesive Tesa® tape (c. 0.1g). The tag attachment method was temporary and if it was not possible to recapture the bird to remove the tag, it would fall off after a period of a few weeks. To retrieve tags deployed on Leach's Storm-petrels, we placed a trap at the nest entrance to catch the tagged bird on its return. Traps were constantly observed using thermal imaging equipment (Helion Pulsar binoculars or monocular, various models) for capture of returning birds. For European Storm-petrels, where nest entrances were generally unsuitable for use of such traps, but nest chambers were accessible by hand, we checked nests daily following tagging and if the tagged bird had returned from a foraging trip and was present in the nest during the day, the tag was retrieved the following evening. During the post-brooding stage, when the tagged birds did not remain in the nest during the day, we watched nests using thermal imaging equipment at night until the tagged bird was observed to return, and the bird was caught by hand in the nest chamber to retrieve the tag.

Assessment of potential impacts of GPS tagging and tracking on (i) foraging behaviour and (ii) nest survival rates was complicated by the lack of accessibility of many nests chambers for marking birds (for individual recognition to assess nest attendance patterns) and assessment of nest contents (to assess egg and chick survival rates). Most Leach's Storm-petrel nests could not be accessed directly to mark birds or view the nest occupants. However, the majority of nesting Leach's Storm-petrels responded consistently to late-evening playback at the burrow entrance of recordings of calls. Since calls differ between the sexes, playback therefore permits identification of the bird present at each nest each day and allows collection of data on nest attendance patterns of untagged birds. In 2021 we compared foraging trip duration of tagged birds during the period of tag deployment with the foraging trips of: (i) the same individuals prior to tagging and (ii) all untagged birds. The first analysis was conducted using Wilcoxon matched-pairs analysis, and the second analysis used a linear mixed effects model. For the mixed model, we included all first trips of tagged birds ($N = 14$) as well as all trip duration data recorded at a further 37 nests ($N = 94$) throughout the study period (18th June – 10th July). As we did not have information on breeding stage for all nests, we could not include this as a random effect in the model, and instead included the date of the start of the trip as a fixed effect (Julian date, centred and rescaled). Nest was included as a random effect to account for multiple measurements from some nests. Trip duration data was square-root transformed to meet the assumption of normality of residuals. For both analyses we inferred foraging trip duration for untagged birds from the duration of periods between successive incubation bouts. Tracking indicated that birds spent the entire period between successive incubation bouts at sea.

For European Storm-petrels, the inaccessibility of many nest sites similarly meant that it was not always possible to individually mark birds or identify which of the breeding pair was present. Nest attendance data were therefore not sufficiently complete to identify differences in nest-attendance patterns between tagged and non-tagged birds before and after tagging. In 2021 daily nest survival was compared for the 23 nests where tagging of birds occurred and 52 control nests to check for an effect of tagging on nest survival. Whilst periods of temporary egg neglect are common in this species (Davis 1957), a period of six consecutive days of an egg being unattended was considered to indicate nest failure. The loss or damage of an egg or chick was also considered to be a nest failure. Nests were monitored for up to 27 days and we compared daily survival rates of nest where tagging occurred and control nests, using a binomial model.

3.3 GLS tracking

In order to track birds throughout the course of the non-breeding season, geolocator (GLS) tags (0.43g W30A9-SEA Migrate Technology) were deployed in July and August 2021 using long-term attachment methods, based on protocols developed by researchers in Spain (European Storm-petrel) and Canada (Leach's Storm-petrel). Each tag was attached using monofilament cord and marine epoxy to an overlapped darvic ring, and fitted to the tibia. To minimise handling of birds and associated disturbance in the colony, most GLS tags were fitted during the same capture event as GPS tag retrieval. Additional birds were tagged with GLS devices after removal from nests by hand, either during the chick-rearing stage or late in the incubation stage, when birds are more robust to disturbance. Where possible, the mates of all tagged birds were ringed and processed as controls.

To retrieve GLS tags deployed in 2021 (and to assess any impacts of GLS tagging) all nests that had been occupied by birds fitted with GLS tags, and their controls, were monitored regularly when fieldwork resumed in 2023 using playback and/or visual inspection of the nest contents. Traps and/or mist nets were deployed at night at the entrances of nests that were found to be occupied, and also (on a less frequent basis) at those nests where no response to playback was ever obtained (in case occupants did not respond to playback). We noted the extent of recapture effort directed at both GPS-tagged birds and their controls, in order to avoid biasing effort towards either group. Any recaptured birds that have been fitted with GLS tags in 2021 (and controls) were inspected for sign of injury and any GLS tags removed. Potential impacts of GLS tagging were assessed by comparing the recapture rates of GLS tagged birds and controls.

3.4 Assessment of HPAI impacts

In 2023 blood samples were taken from the brachial (wing) vein 12 Leach's Storm-petrels on St Kilda (Figure 2) and four European Storm-petrels on Treshnish, under a Home Office Licence issued to Mark Bolton, working in collaboration with Dr Emma Cunningham (Edinburgh University). Additional work was undertaken by RSPB (under separate funding) to resurvey the main breeding colonies of Leach's Storm-petrels on St Kilda (Dun, and Carn Mor, which jointly held nearly 80% of the entire population of St Kilda in the most recent survey in 2018). This work was carried out as part of the RSPB [HPAI seabird survey project](#). Data analysis is scheduled for 2025 and will be reported separately.

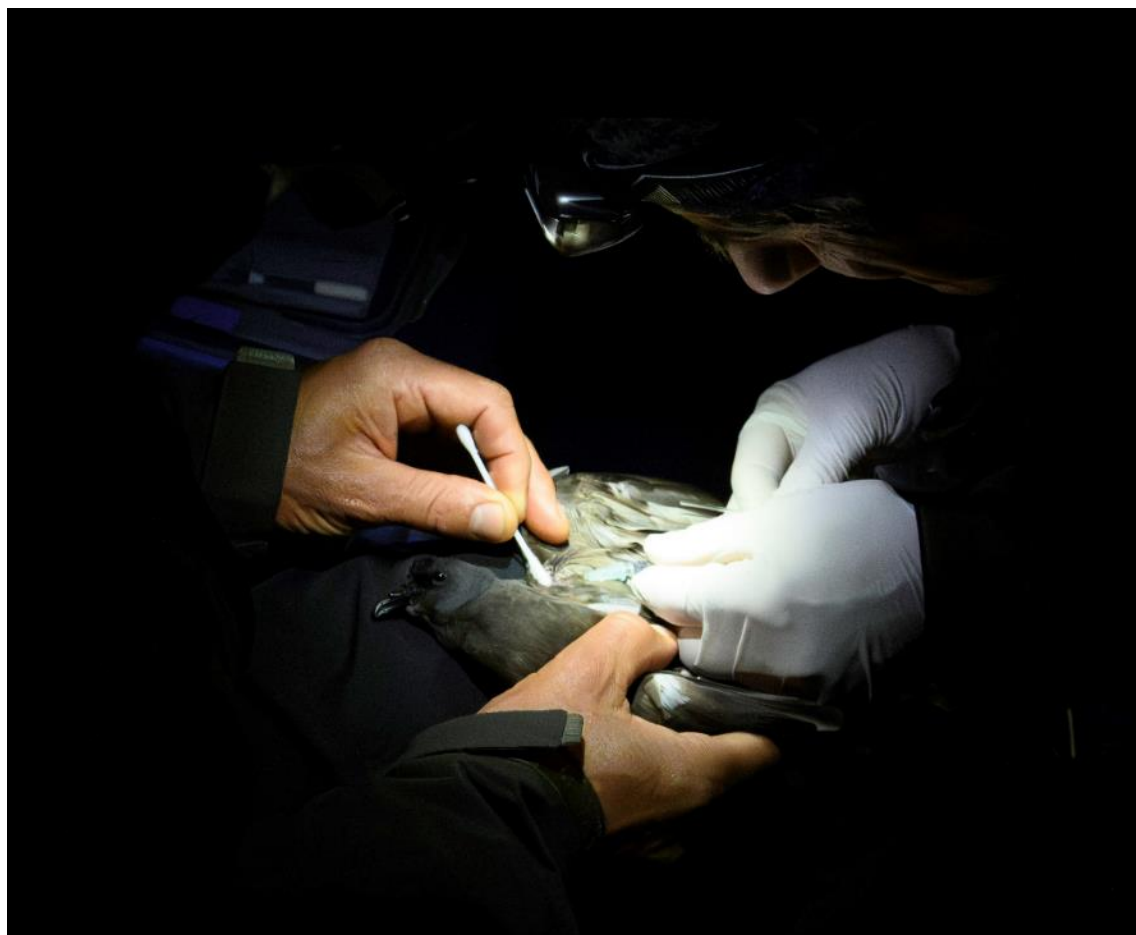


Figure 2. Taking a blood sample from a Leach's Storm-petrel, St Kilda for analysis for antibodies to Highly Pathogenic Avian Influenza virus.

3.5 GPS Data Analysis

I. Data processing and trip metrics

Data were processed in RStudio (R Core Team 2023 & Posit team 2023). To provide information about trip metrics, GPS tracks were split into trips based on departure from and return to the colony using the 'tripSplit' function of the track2KBA R package (Beal et al. 2021). Departure and return buffer thresholds were set on the basis of visual inspection of tracks. For Leach's Storm-petrels, a departure buffer of 5 km and a return buffer of 30 km was used. For European Storm-petrels a departure buffer of 5 km and a return buffer of 10 km was used because the tracks included movements of birds foraging relatively close to the colony. To validate the trips identified by the 'tripSplit' function, trips were also manually labelled in ArcPro. Care was needed to ensure 'tripSplit' correctly identified partial trips. An additional label of 'Almost Complete' was added for trips where, due to tag failure or low battery, the track terminated just short of the colony or there was a longer interval between fixes than the tag was programmed to record. These "Almost Complete" trips were included in summaries of maximum distance from the colony (where maximum distance was known) but not for total distance or trip duration (which were not accurately recorded).

We used the 'tripSummary' function of track2KBA to estimate the total distance travelled, maximum distance from the colony and duration for each trip. The distance between the first and last point of the trip and the colony location was added to distance calculations in instances where trips started or ended at sea. However, when estimating trip duration, the 'tripSummary' function assumes the start and end times of a trip are those recorded at the first and last GPS location for that trip. Where these locations are at sea (i.e. because the bird's presence at the colony before and after the trip was not recorded, due to difficulty for the tag in viewing satellites when the bird is below ground), the trip duration will be underestimated. To account for this, tracks were rooted to the colony by appending the colony location at the start of the trip, one timestep prior to the first recorded location at sea. This ensured that trip duration and total distance travelled were comparable between trips. No additional timestamps were added to the end of trips to avoid overestimating trip durations. For Leach's Storm-petrels, trips were labelled as being from one of two breeding stages: incubation and chick-rearing. Where there was evidence that disturbance during trapping attempts or a failed breeding attempt had altered the birds' behaviour, trips were excluded from the overall summaries and further analyses, as follows. One bird lost its egg whilst at sea on a foraging trip, and thereafter did not remain at the nest by day. Instead it made a series of trips that included several short-range, short-duration trips, unlike other birds with active nests (Table 4). In addition, there were a few occasions when birds returned to the colony during the egg stage, but did not enter the nest to resume incubation – instead they returned to the sea for a further day, before returning to the nest the following night. This resulted in a few short duration (one day) and short range trips being recorded during incubation, (when birds are typically at sea for 2-3 days). These “aborted” nest visits occurred on nights when captures of these birds were attempted, Whilst it is not clear to what extent the observed behaviour was normal, or whether birds were hindered from entering their nests by nocturnal fieldwork activities, as a precaution these short trips following are excluded from analysis. These cases applied to the following trips for Leach's Storm-petrels during the incubation phase: 2021_BT27403_44_02 (Nest Failure), 2021_BT27403_44_03 (Nest Failure), 2021_BT27403_44_04 (Nest Failure), 2021_BT27403_44_05 (Nest Failure), 2021_BT27403_44_06 (Nest Failure), 2021_BT27403_44_07 (Nest Failure), 2021_BT27406_38_02, 2021_BT27420_46_02, 2023_BT27462_45_02, 2024_NT63501_122_02, 2024_NT63501_122_03.

To assess the degree of individual specialisation in space use we used the function 'indEffectTest' from track2KBA (Beal et al. 2021). The function uses a bootstrapping procedure to compare random pairs of trips which comprise either (i) two trips from the same individual, or (ii) two trips from different individuals. An asymptotic two-sample Kolmogorov-Smirnov test compares within-individual and among-individual variance in 50% UD. To allow for the possibility that foraging areas might differ between breeding stages, the test was applied separately to foraging locations during incubation and chick-rearing stages (i.e. pairs of trips from different individuals were drawn from the same breeding stage).

For European Storm-petrels trips from 2021 only were summarised by breeding stage as all birds tracked in 2023 and 2024 was conducted during the chick-rearing period. Where we found evidence of individual specialisation in space use, such that multiple trips performed by the same individual could not be regarded as independent, or broadly representative of a large sample of tracked individuals, summary statistics were derived from the output of linear mixed-effects models with individual ID used as a random term to derive individual-level (not trip-level) estimates. Since model outputs relate to standard error (SE) of the mean rather than sample standard deviation (SD) we estimated sample SD from equation 1 below (DF = Degrees of Freedom).

$$SE \times \sqrt{(DF + 1)} \quad - \text{eqn 1.}$$

Where there was no evidence of individual specialisation, we considered that multiple trips by the same individual were representative of a sample of single trips from multiple individuals, and calculated summary statistics (and conducted statistical hypothesis testing) directly on the raw trip-level data. Where there was evidence of individual specialisation we calculated summary statistics and conducted hypothesis testing using a random effects model to account for non-independence of trips undertaken by the same individual.

The 'lme4' package (Bates et al., 2015) was used to build linear mixed-effects models with individual as a random effect. For each variable (trip distance, maximum distance and duration) four models were produced. The null model contained only individual ID as a random effect, this was compared with a model including both year and breeding stage, just year or just breeding stage. Where multiple models revealed a significant effect, AIC was used to select the best performing model.

Representativeness was assessed using the 'repAssess' function in the track2KBA R package (Beal et al. 2021). This function assesses how representative is the assessment of space use derived from the tracked sample, compared with the estimated extent of colony-level space use. The function implements a bootstrapping procedure to iteratively resample the utilisation distributions of individuals within the sample and then models the relationship between space use of all individuals in the sample and sample size. The output is a score between 0 and 100 reflecting the extent of colony-level space use identified from the tracked sample. Scores above 70% indicate that the dataset is highly representative of the space use at the colony level (Beal et al. 2021).

Maps of bird movements were produced in R using the ggOceanMaps package (Vihtakari 2024). Manual labelling of trips to validate the automated labelling of trips by track2KBA and production of the maps showing overlap between the European Storm-petrels and OWF lease areas was performed in Arc GIS pro 2.8.8 (ESRI 2021). Data on the location of Scottish Offshore Windfarm Areas (OWFs) and those in English, Welsh and Northern Irish waters are freely available via the Crown Estate spatial hub hosted on Arc GIS online (Crown Estate 2021). Data on the location of relevant OWFs in Republic of Ireland waters were sourced from Marine Renewable Energy Ireland (MaREI 2021) via the Irish government's open data portal (Open Data Portal 2024).

II. Home Range Estimation

The observed utilisation distributions (UDs) of both species were estimated using the 'ks' package in R to produce 25%, 50% and 95% kernels (Chacon & Duong (2018)). UD's were produced across all birds, by year, by time of day and by breeding stage. The 'ks' package has the benefit of including a number of 'bandwidth selector' functions for automating the selection of the optimal smoothing factor for building the kernel density surface. For our data, the 'Hpi' function was selected as the bandwidth selector. This was chosen because it can handle the inclusion of negative values associated with co-ordinates in decimal degrees.

Marine Habitat Association

To help inform future spatial planning of marine development such as offshore wind, a key objective of this project was to improve our understanding of marine habitat use by foraging Leach's Storm-petrels and European Storm-petrels. A common approach to understanding habitat use is resource selection modelling whereby, for each observed location, a number of pseudo-absences are generated within a given domain (Johnson 1980, Boyce et al. 1999, Aarts et al. 2012). The domain refers to the area available to the animal, i.e. where the animal could feasibly have been present, and is set by the researcher. Resource selection functions (RSF) then compare the environmental conditions in these available locations with the conditions at the locations where the animal was observed to be present (Paton and Matthiopoulos 2016). In the context of the standard resource selection function there is no single optimal method for determining the area available to an animal (Paton and Matthiopoulos 2016). Moreover, the exact choice of the available domain dictates the scale at which habitat selection is being considered and is therefore key to model interpretation (Johnson 1980, Northrup et al. 2022). For seabirds, common approaches include using the maximum observed distance from the colony (e.g. Wakefield et al. 2017) or the observed home range (Cleasby et al. 2024). These methods have been shown to effectively characterize broad-scale seabird habitat use, providing reasonable predictive performance (Wakefield et al. 2017). However, RSF approaches can introduce issues arising from the non-independence and spatio-temporal autocorrelation of location data obtained by telemetry because they are derived from methods developed for point count data (Alston et al. 2023). To address some of these issues and make use of the fine-scale movement data from telemetry studies, Fortin et al. (2005) suggested resampling step lengths (distances between successive observed locations) and turn angles (deviations from previous bearings) to generate random movements and thus available points, conditional on the previously observed locations. This process creates stratified datasets, with a distinct set of available points associated with each observed location. Such models are commonly termed step selection functions (SSF) and are focussed on fine-scale habitat selection at the scale of GPS sampling intervals (Klappstein et al. 2021, Alston et al. 2023).

Here, we implemented a SSF procedure to investigate fine-scale habitat selection in European and Leach's Storm-petrel (Mercker et al. 2021). Step selection functions are well suited to the analysis of habitat selection in wide ranging species such as petrels. This is because SSFs consider an animal's track as a series of discrete sequential steps separated by constant time intervals, where each step is defined by the distance moved and turning angle (Thurfjell et al. 2014). The habitat characteristics associated with landing point for the next step are compared with those from a set of pseudo-absences generated from the observed range of turning angles and step lengths as illustrated in Figure 3. A key advantage of the SSF approach is that it resolves the challenge associated with defining what is 'available' to an animal by using parameters of animal movement to define availability (Forester et al. 2010). An SSF approach enables effective characterisation both long-range attraction and shorter-range local resource selection.

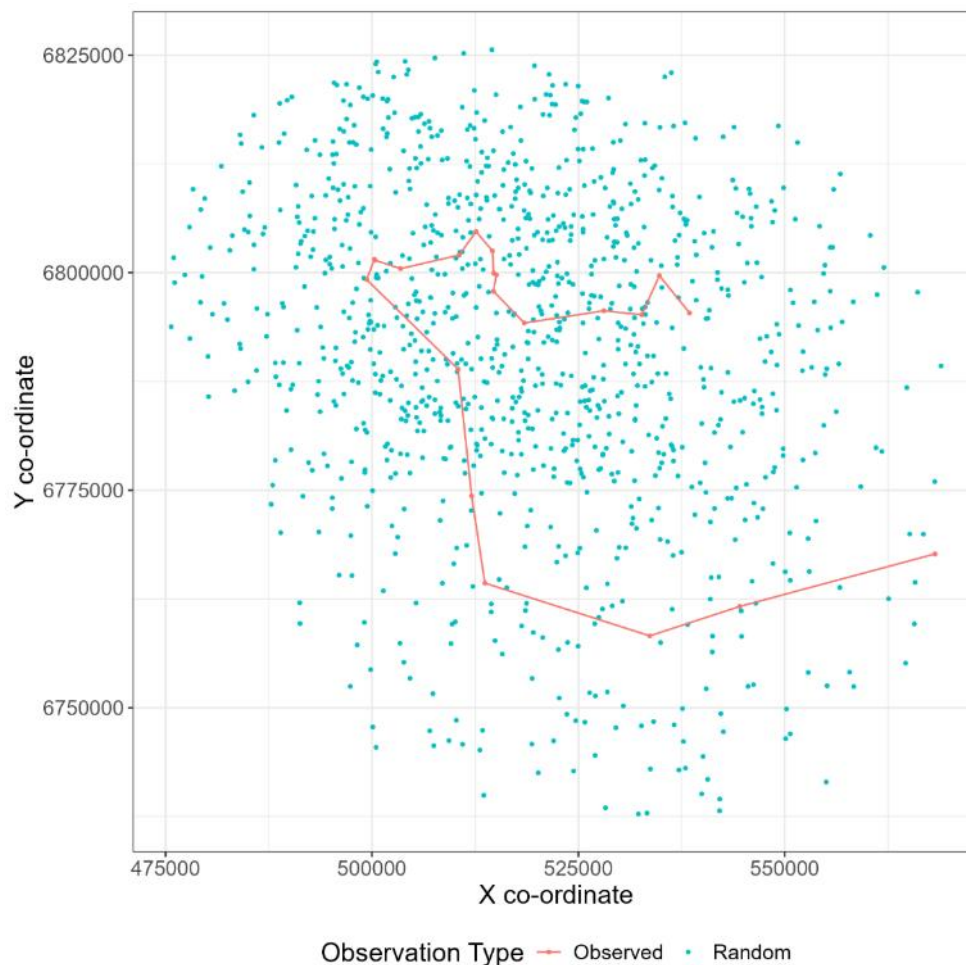


Figure 3. Example step selection function (SSF) showing the observed path (red) vs. the randomly generated available points (blue) associated with each step along the path as the animal moves through space.

Collating Suitable Environmental Covariates for SSF

To examine habitat selection in both storm-petrel species, we chose to incorporate a range of potentially important environmental covariates to which storm-petrels might respond. Given the wide array of covariates that could be considered, we focused on those that have been shown to be important for other UK seabirds (e.g. Wakefield et al. 2017) to generate a suitable yet manageable set of environmental covariates for modelling purposes. Additionally, covariates had to be freely available over the same spatio-temporal extent as the storm-petrel tracking data, which further reduced the number of available covariates.

In total, the static environmental covariates we selected were: (1) Distance by sea from the colony (km), where distance by sea was calculated using the centre point of each cell contained within a regular grid (1 km² resolution) encompassing the area defined as available to each colony. This area was defined as a radius around the colony that extended to 1.1 x the maximum foraging range observed at each colony (Wakefield et al. 2017); (2) water depth (metres, m) which was derived from Global Bathymetry and Topography at 15 Arc Sec: SRTM15+ V2.5.5 bathymetry data (Tozer et al. 2019) with a nominal resolution of 15 arc seconds (approximately 500 x 500 m pixel size at the equator); (3) seabed slope (°) which was generated from the same bathymetry data used to estimate water depth using the terra package; (4) Distance from the coast (km) at 1 km x 1 km resolution; (5) benthic habitat derived from the EUSeaMap 2021 (Vasquez et al. 2021). Data from EUSeaMap was processed in R to simplify the 29 habitat categories into six broad categories: '1:Rock', '2:Coarse Substrate', '3:Sediment', '4:Sand', '5:Mud', '6:Reef or other biogenic habitat' and 'Unlabelled'. The numeric code (1-6) associated with each habitat category was then used to generate a raster surface at a resolution of 0.01° x 0.01° (Approximately 1.11 km x 1.11 km). In addition, the following dynamic variables included were: (6) Sea Surface Temperature (SST, °C) at 1 km² resolution using Multi-Scale Ultra High Resolution (MUR) SST data ([MUR SST](#) was accessed on 15/02/2025). Daily sea surface temperature (SST) data were downloaded for each date on which tracking data were available across the years. For each spatial grid cell, the average SST for each year of the study was calculated using the daily SST data corresponding to the specific tracking period in that year (from the date of the first to the last GPS observation) ; (7) the magnitude of ocean SST front gradients (°C / 1 km) estimated via the grec package (Lau-Medrano 2020) using daily SST data and the front detection algorithms developed in Belkin and O'Reilly (2009). As with SST, yearly averages of thermal front gradient were calculated by averaging across daily values that covered the tracking period in each year; (8) mass concentration of chlorophyll-a in sea water (CHL-a, mg/m³) at ~7 km² resolution monthly from June to August, downloaded from the Copernicus Marine Service (CMS)([CMS](#), date accessed: 22/01/2025). Monthly maps of chlorophyll each year were then averaged to give an estimate of mean chlorophyll per spatial grid cell across the summer (June to August) in that year; (9) the magnitude of ocean chlorophyll gradients (mg/m³ / 7 km) estimated via the grec package (Lau-Medrano 2020) using monthly chlorophyll data and the front detection algorithms developed in Belkin and O'Reilly (2009); (10) Simpson-Hunter stratification parameter (S, Simpson et al. 1974) this index ($S = \log_{10}(hu^{-3})$) combines measurements of u = mean current speeds (ms⁻¹) and h = depth (m) into a single measurement which helps to identify mixed, frontal, and stratified water columns (Bowers & Simpson 1987, Holt & Umlauf 2008). Water depth data was obtained as described above and current speed data was obtained from the Copernicus Marine Service ([CMS](#), date accessed: 07/02/2025). Current speed was downloaded for each date for which tracking data was available at 12:00:00 (midday) at ~ 8 km² resolution and averaged across the observed tracking period each year. To calculate the Simpson-Hunter parameter, the current data were smoothed using bilinear interpolation to ensure its resolution matched that of the depth data; (11) Net primary production of biomass expressed as carbon per unit volume in sea water (NPP, mg/m³/day) at a monthly ~ 7 km² resolution ([CMS](#)). For each year, average NPP per grid cell over the tracking period was then calculated.

Fitting SSFs and Model Selection

For both Leach's and European Storm-petrel, step-selection functions were fitted using the `hmmSSF` R package that allows for the inclusion of non-linear habitat associations (Klappstein et al. 2021). One requirement of SSFs is that movement data are sampled at regular time intervals to ensure step lengths and movement remain consistent throughout a tracking period and across different individuals. Movement trajectories were regularised for each identified foraging trip in turn to ensure periods at the colony in between trips. To regularize movement trajectories, we used the `track_resample` function from the `amt` package to resample tracks at a regular 1 hour interval with a tolerance of 1 minute (min) for both petrel species. We chose a 1-hour interval as this reflected the lowest sampling resolution observed for some individuals in both datasets. Some individuals were tracked at higher resolutions than 1-hour intervals (15 min or 30 min intervals), however resampling at such shorter sampling intervals would lead to loss of information from individuals with coarser sampling regimes or an increasing reliance on interpolated points for such individuals.

For each observed point, we generated a paired sample of 50 potentially available points. These available points were sampled using a non-parametric movement kernel within the `hmmSSF` package. Specifically, available points were selected uniformly from a disc centred on the previous observed location, with the disc radius (R) set close to the maximum observed step length to ensure adequate spatial coverage (Klappstein et al. 2022; Michelot et al. 2024). The advantage of using a non-parametric kernel to generate available points is that we do not need to provide a specific distribution for either step lengths or turning angles. However, the non-parametric approach requires more available points to be sampled for accurate parameter estimation hence our choice to sample $n = 50$ available points per observed point (Klappstein et al. 2024). Once a dataset of observed and available points was constructed, we then used the `terra` package to extract the relevant environmental covariates observed at each point.

SSFs were fitted as conditional logistic regression models implemented as generalised additive models (GAM), which allow covariates to be fitted as non-linear smoothers, using the *mgcv* R package. Following, Klappstein et al. (2024) these GAMs were constructed as Cox Proportional Hazard (CPH) models. Due to the relatively large number of environmental covariates examined we conducted model selection in a forward stepwise fashion. First, we ran models including each candidate environmental covariate in turn as either a standard linear effect or a non-linear smoother and judged how well model fit was improved compared to a null model that contained no environmental covariates. For some variables which took large values on their original scale (distance from colony, depth, NPP, distance from the coast) we also considered models in which model coefficients and non-linear smooths were estimated on the log-scale. Following Klappstein et al. (2024) our null model still included terms for step lengths and turning angles modelled using non-linear splines to describe the distribution of these movement variables. All smoothers were fitted as shrinkage splines (so that smooths can be penalised out of the model if not required), except for those related to turning angles, where cyclical splines were used to account for the circular nature of this parameter. Due to potential collinearity between covariates, we excluded models that included two covariates with a correlation greater than $r = 0.4$. In such cases, the covariates selected first in the stepwise modelling process were preferred. Additionally, we did not include both water depth and the Simpson-Hunter parameter in the same models, as water depth is used as the denominator in the equation to estimate the latter. In the results we report the finally selected model for each species.

Model performance was assessed using model Akaike Information Criterion (AIC) scores, by default the *mgcv* package reports a 'corrected' conditional AIC which accounts for uncertainty in model smoothing parameters which will tend to favour simpler models (Wood et al. 2016, Klappstein et al. 2024). The best performing model in this first step was then selected as the basis for the next step in the model selection process until reaching a model at which including further covariates no longer led to improvements in model AIC. Once the best performing model was selected, we considered the effect of including additional two-way interactions between the environmental covariates included in this model and the following group-level predictors: 1) whether an observation was recorded at day or night (calculated using the *r.suntools* package (Bivand & Luque 2024) to determine the timing of sunrise and sunset at specific locations and timestamps); 2) whether a bird was classified as incubating or chick rearing; and 3) the year of the study. If the inclusion of a two-way interaction improved model fit, it was retained otherwise it was removed.

3.6 Geolocator data processing

Geolocation data processing was carried out using R 4.2.3 (R Core Team 2023). We used the `preprocessLight` function of the 'TwGeos' package (Lisovski et al. 2016) to process log-transformed light data using a light threshold of 1 log lux. This threshold allowed us to define sunrise and sunset (twilight events), which occur when the light values exceed or fall below this threshold, respectively. With this function, we estimated the hour of sunrise and sunset, inspected the integrity of the light curve of each day and manually adjusted the time of sunrise or sunset where the time appeared incorrect in comparison with the observed light profile of preceding and subsequent days. These incorrect times likely occurred due to interference of feathers covering the light sensor. We manually adjusted the incorrect time of twilight to the mean time between the previous and the following days, except in those cases when there was a small peak of light (below the light threshold we defined) before (or after, in the case of sunset) the twilight time assigned automatically; in those cases, we moved the transition to this small peak of light. Subsequently, we used the 'Solar/Satellite Geolocation for Animal Tracking (SGAT)' package (Sumner et al. 2009, Lisovski & Hahn 2012), which applies Markov chain Monte Carlo (MCMC) simulations to estimate and refine the locations of the tracked individual. For this analysis, we first calculated the zenith angle and the error distribution around the twilights based on the calibration period of the geolocator at a known location. We also generated a gamma distribution of flight speeds between 0 and 25 km/h based on the average speed values from the GPS tracking element of this project. We then used the `thresholdPath` function to obtain the initial path of the bird, which is needed to begin the MCMC simulations. Furthermore, we generated a spatial mask to avoid any locations over land. We used these parameters and started by drawing an initial 200 samples for burn-in and tuning of the proposal distribution. A further 300 samples were drawn to evaluate chain convergence before drawing another four MCMC chains of 3,000 samples each to describe the ultimate posterior distribution and the most likely migration path. Despite using a high `tol` (tolerance on the sine of the solar declination) value when running the `thresholdPath` function (which defines how many locations should be linearly interpolated around the equinox), we still had to remove unrealistic values near the equinox periods.

3.7 Overlap with Offshore Wind Areas

For European Storm-petrels, a time in area analysis was performed to estimate the proportion of time spent during each foraging trip in proposed OWF areas (no foraging trips of Leach's Storm-petrels overlapped with OWF lease areas). To prevent underestimation of the number of individuals interacting with OWFs and control for different sampling frequencies, tracking data were linearly interpolated to a 1-minute sampling interval. This was achieved using the `'mt_interpolate'` function from the `move2` package in R (Kranstauber et al. 2024).

Spatial data on the locations of OWFs in British and Irish waters was used to generate a raster surface of unique IDs whereby each ID related to a specific wind farm in the data set. The 'terra' package (Hijmans 2025) was then used to overlay the tracking data (including the points generated from interpolation) onto the raster surface to extract the ID of any OWFs. Points which did not overlap with an OWF were assigned a value of zero. The numeric ID was then used to append the name of each relevant OWF to the data set. The total time spent in each OWF per trip was then used to calculate the percentage of time spent in OWFs during each foraging trip.

4. Results

4.1 GPS tag deployment and retrieval rates

The numbers of GPS tags deployed, retrieved, containing usable data, and trips obtained are shown in Table 2 for both species in each of the three study years.

Table 2. Summary of tags deployed, retrieved and numbers of trips were recorded for each storm-petrel species.

	Leach's Storm-petrel	European Storm-petrel
Year	2021	2021
Number of GPS tags deployed	15	23
Number of GPS retrieved	14 ¹	19
Number of retrieved tags containing usable data	14	17
Total number of trips obtained	26 (21 complete, 2 almost complete)	26 (21 complete, 3 almost complete)
Year	2023	2023
Number of GPS tags deployed	20	14
Number of GPS retrieved	19	12
Number of retrieved tags containing usable data	19	12
Total number of trips obtained	41 (38 Complete)	21 (18 complete, 2 almost complete)
Year	2024	2024
Number of GPS tags deployed	20	8
Number of GPS retrieved	17	7
Number of retrieved tags containing usable data	17	7
Total number of trips obtained	35 (29 complete, 1 almost complete)	10 (9 complete)

¹ The remaining bird was recaptured, but the tag had detached.

4.2 Impacts of GPS tagging

Within the limits of data availability (see methods) there were no signs of adverse impacts of tagging operations on either species. The size and weights of the tags are within the limits of conventional GPS tags used successfully on these species for several years, using identical attachment methods, without signs of adverse impacts. Over the course of the three years of fieldwork, the overall recapture rates were extremely high (93% for Leach's and 84% for European Storm-petrel) and all birds appeared fully healthy and had maintained a good weight when recaptured. The inability to recapture several birds in 2024 resulted from field teams having to evacuate St Kilda and Treshnish prematurely. Comparison of nest attendance patterns and nest survival rates of tagged and control birds also indicated no quantifiable impacts of tagging as follows: we found no difference in the duration of foraging trips of tagged Leach's Storm-petrels compared to the foraging trip directly prior to tagging for the same individual (Wilcoxon signed-rank test $N = 7$, $P = 0.09$), though there was a trend towards shorter trips when tagged. This may be due to trips generally becoming shorter as breeding progresses, and a mixed-effects model found that trip duration decreased with date ($X^2_2 = 22.69$ $P < 0.0001$), but found no additive effect of tagging on trip duration ($X^2_2 = 0.0039$ $P=0.95$), and no interaction effect of date and tagging ($X^2_2 = 2.24$ $P=0.33$). For European Storm-petrels, daily nest survival rates were slightly (but not statistically significantly) higher at 23 nests where tagging occurred, compared with 52 control nests (0.991 ± 0.005 SE and 0.986 ± 0.0038 SE respectively, $X^2 = 0.5296$ $P=0.47$).

On the basis of the data available, we found no evidence to suggest that the birds' foraging behaviour or breeding success was affected by the tagging procedures.

4.3 Individual specialisation

4.3.1 Leach's Storm-petrel

There were similar levels of overlap in locations of core area usage during both incubation and chick-rearing stages among pairs of trips drawn at random from within or between individual Leach's Storm-petrels, indicating an absence of individual specialisation ($D = 0.3741$ $P=0.35$ and $D=0.1702$ $P=0.053$ for incubation and chick-rearing stages respectively, Figures 4 and 5). We therefore considered that trips made by the same individual were independent, and calculated summary statistics directly from the raw trip-level data.

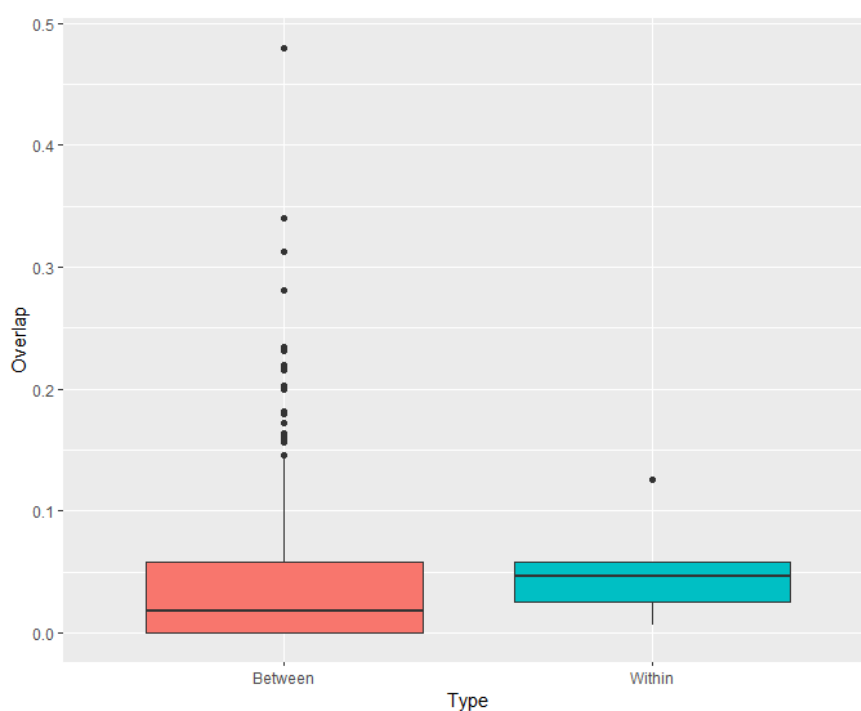


Figure 4. Overlap of core area (50% UD) usage among pairs of foraging trips drawn from within and between individual Leach's Storm-petrels during the incubation stage ($D = 0.37$, $P = 0.35$).

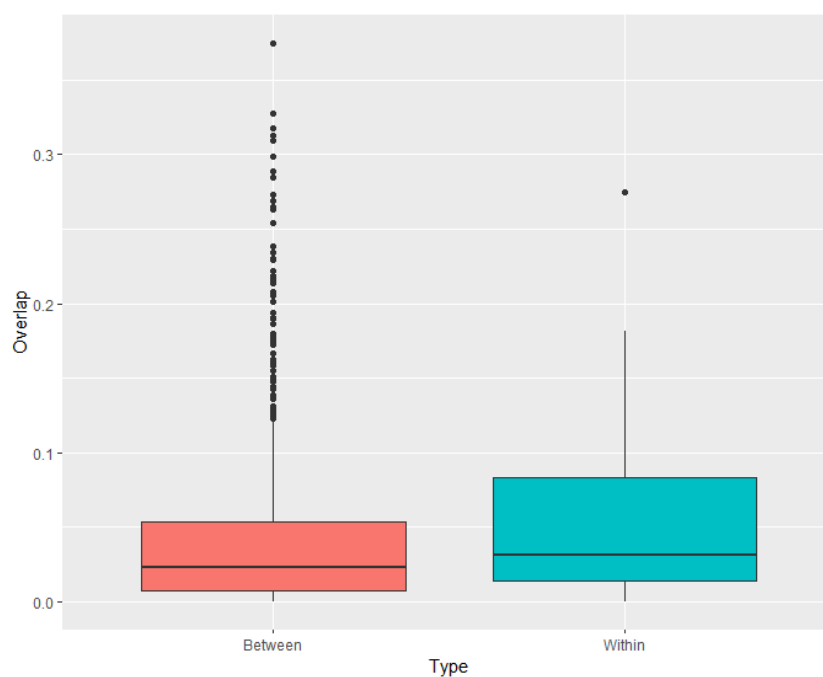


Figure 5. Overlap of core area (50% UD) usage among pairs of foraging trips drawn from within and between individual Leach's Storm-petrels during the chick stage ($D = 0.17$, $P = 0.053$).

4.3.2 European Storm-petrel

For the small number ($n=5$) of European Storm-petrels tracked during the incubation stage (in 2021 only) only a single foraging trip was obtained, so there was no need, or possibility, to compare within- and between-individual space use. Among chick-rearing birds, we found significantly greater overlap in core area usage among trips by the same individual than among individuals (Figure 6, $D = 0.45$, $P < 0.001$). We therefore considered that trips made by the same individual were not independent, and derived summary statistics from mixed effects models that included individual identity as a random term.

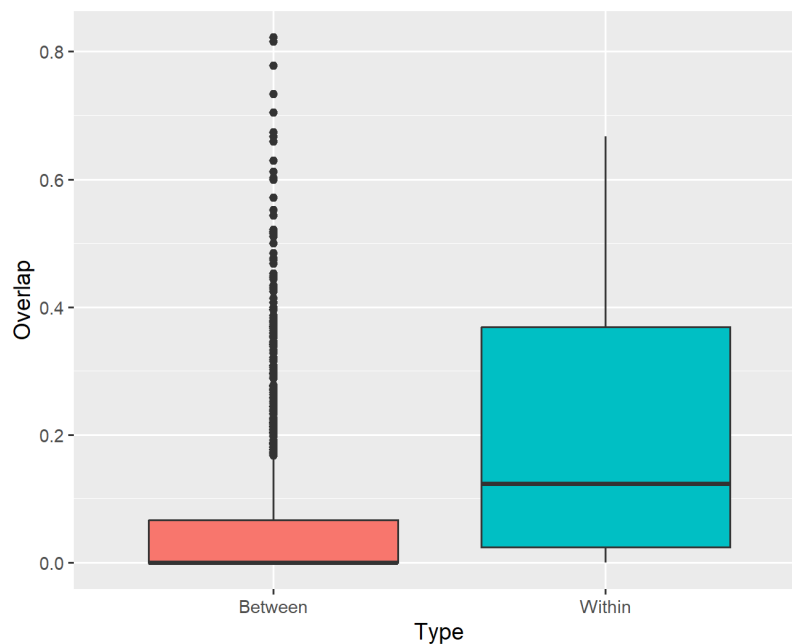


Figure 6. Overlap of core area (50% UD) usage among pairs of foraging trips drawn from within and between individual European Storm-petrels during the chick stage ($D = 0.45$, $P < 0.001$).

4.4 Representativeness of colony-level foraging distributions

Bootstrap resampling of the samples of tracked Leach's and European Storm-petrels indicated that the samples achieved acceptably high representativeness of the wider space use relating to their respective colonies as a whole (representative values of 89.3% and 81.5% respectively, Figures 7 and 8). The sample of tracking data collected by this project can therefore be considered to provide a good representation of space use by Leach's Storm-petrels breeding on Hirta, St Kilda and European Storm-petrels breeding on Lunga, Treshnish Isles.

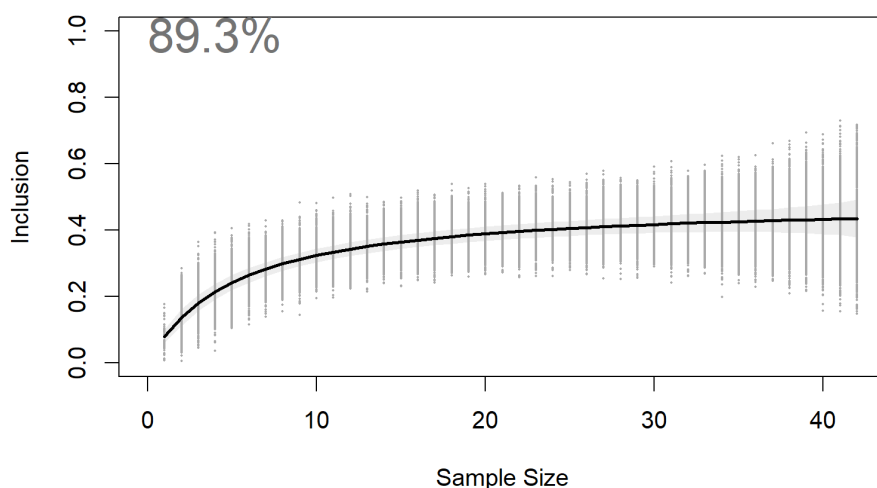


Figure 7. Representativeness of the sample of foraging trips obtained from 50 Leach's Storm-petrels breeding on St Kilda

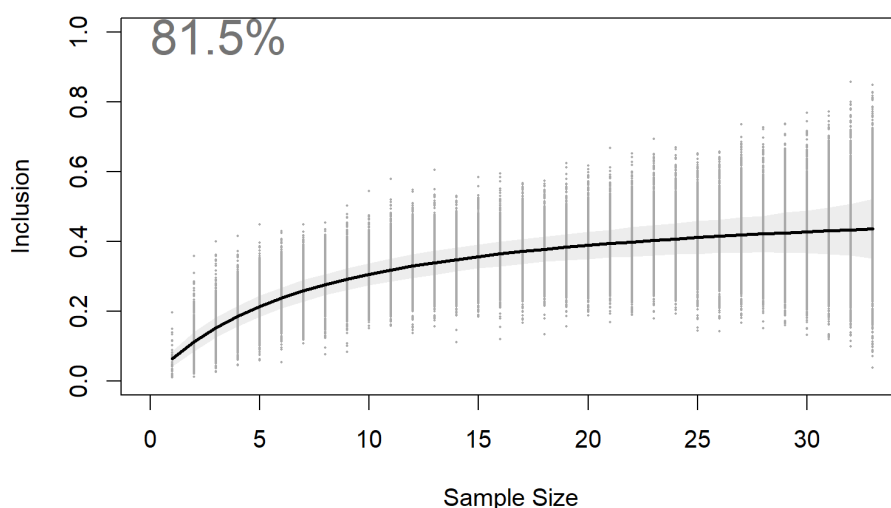


Figure 8. Representativeness of the sample of foraging trips obtained from 38 European Storm-petrels breeding on Lunga, Treshnish Isles.

4.5 Trip metrics and marine distributions

Summary trip statistics for both Leach's and European Storm-petrel are presented in Table 3. For Leach's Storm-petrel only the overall mean and standard deviation figures are derived from model estimates because within each breeding stage category there was no evidence of individual specialisation. As such individual trips can be regarded as independent. For Leach's Storm-petrel it was necessary to exclude trips 02 - 07 for nest 44 because these were associated with a failed breeding attempt and therefore not considered to be representative. Five further trips where incubating birds had departed the colony very soon after arriving were also excluded because these were thought to be linked to failed re-capture attempts and therefore the birds were unlikely to be exhibiting natural behaviour.

For European Storm-petrel the trip analysis suggests potential for foraging specialisation within individuals. As such, to avoid potential bias due to the presence of multiple trips for some individuals at the chick rearing stage, the mean and standard deviation values presented for trip duration, total distance and maximum range are derived from the output of a linear fixed effects model with individual ID used as a random term to account for the variation in numbers of trips between individuals. This was not necessary for trips for incubating European Storm-petrels because we don't have any cases of multiple trips being recorded by the same individual and can therefore be considered independent.

For European Storm-petrel, only 2021 data were used to test of the effect of breeding stage on trip metrics because no incubating birds were tracked in 2023 or 2024. As such it was necessary to produce separate models to understand the effect of year and breeding stage. Summary statistics for individual trips of Leach's Storm-petrels are presented in Table 4 - 9 and mapped in Figures 9 - 17. Summary statistics for individual trips of European Storm-petrels are presented in Tables 11 - 13 and mapped in Figures 24 - 28.

Table 3. Foraging trip metrics of European Storm-petrels breeding on Treshnish Isles and Leach's Storm-petrels breeding on St Kilda (mean $\pm$ SD, min – max (n = number of complete trips)). For European Storm-petrels, the mean and standard deviation for chick rearing birds were derived from model results. Only data from complete trips are included in the summary of total trip distance and trip duration whereas max distance also includes data from “almost complete” trips. For Leach's Storm-petrels it was necessary to exclude data from 11 trips influenced by external factors (nest failure or nest disturbance) from the sample of trips from incubating birds.

	Year	Leach's Storm-petrel, St Kilda	Leach's Storm-petrel, St Kilda	European Storm-petrel, Treshnish	European Storm-petrel, Treshnish
		Incubation	Chick-rearing	Incubation	Chick-rearing
Trip duration (hours)	2021	63.9 $\pm$ 14.6 45.5 – 90.0 (11)	55.2 $\pm$ 14.6 45.5 – 72.0 (3)	62.3 $\pm$ 24.9 46 - 91 (3)	26.1 $\pm$ 20.0 (18.8 – 48.0) (18)
Trip duration (hours)	2023	48.4 $\pm$ 18.1 48.0 – 95.0 (9)	42.8 $\pm$ 12.9 21.0 – 74.0 (28)	N/A	38.8 $\pm$ 20.9 18.5 – 70.5 (18)
Trip duration (hours)	2024	67.8 $\pm$ 27.9 45.5 – 119.0 (9)	43.4 $\pm$ 18.4 21.0 – 71.5 (18)	N/A	40.8 $\pm$ 31.2 18.5 – 70 (9)
Maximum range (km)	2021	300.9 $\pm$ 60.1 186.3 – 412.1 (11)	259.6 $\pm$ 31.6 217.5 – 293.8 (4)	153.9 $\pm$ 25.1 140.1 – 198.6 (5)	89.6 $\pm$ 69.9 51.9 – 140.4 (19)
Maximum range (km)	2023	329.6 $\pm$ 83.2 261.3 – 517.8 (9)	256.8 $\pm$ 69.2 – 506.4 (28)	N/A	149.3 $\pm$ 73.6 57.4 – 483.5 (20)
Maximum range (km)	2024	421.3 $\pm$ 137.6 286.7 – 637.7 (9)	221.0 $\pm$ 73.7 90.4 – 327.9 (19)	N/A	96.5 $\pm$ 141.3 53.4 – 143.3 (9)

	Year	Leach's Storm-petrel, St Kilda	Leach's Storm-petrel, St Kilda	European Storm-petrel, Treshnish	European Storm-petrel, Treshnish
		Incubation	Chick-rearing	Incubation	Chick-rearing
Total distance (km)	2021	962.8 ± 179.9 697.8 – 1322.9 (11)	806.2 ± 74.1 743.6 – 888.0 (3)	602.6 ± 253.1 441.0 – 894.3 (3)	303.3 ± 204.7 53.4 – 920.3 (18)
Total distance (km)	2023	1032.7 ± 196.3 722.4 – 1308.9 (9)	713.6 ± 236.2 209.0 – 1249.3 (28)	N/A	481.5 ± 216.1 201.2 – 1084.7 (18)
Total distance (km)	2024	1286.4 ± 491.9 827.3 – 2269.9 (9)	684.2 ± 273.0 287.3 – 1190.2 (18)	N/A	441.4 ± 420.3 190.4 – 714.4 (9)

4.5.1 Leach's Storm-petrel trip metrics

Mean trip duration across all birds and years was 52.2 ± 20.2 hours. This was found to differ significantly between breeding stages (Kruskal-Wallis $X^2_2 = 26.95$, $df = 1$, $P < 0.001$) with incubating birds spending longer at sea (66.5 ± 19.9 hours) than chick rearing birds (43.8 ± 15.1 hours). A difference between years was also confirmed (Kruskal-Wallis $X^2_2 = 9.16$, $df = 2$, $P = 0.002$) with birds spending more time at sea in 2021 (62.0 ± 14.6 hours) compared to 2023 (49.0 ± 17.9 hours) or 2024 (51.5 ± 24.4 hours). This indicates that foraging behaviour was more similar in 2023 and 2024 than in 2021.

The mean maximum range (distance travelled from the colony) across all birds was 281.2 ± 103.6 km. This varied significantly with breeding stage (Kruskal-Wallis $X^2_2 = 23.03$, $df = 1$, $P < 0.001$). Incubating birds travelled further from the colony (347.2 ± 106.7 km) compared to birds attending chicks (243.7 ± 81.4 km). The effect of year was not significant (Kruskal-Wallis $X^2_2 = 1.42$, $df = 2$, $P = 0.49$).

Total trip distance averaged across all birds tracked from St Kilda was 848.4 ± 332.8 km. As with maximum distance and total distance incubating birds (1084.9 ± 333.9 km) travelled significantly further than those attending chicks (708.5 ± 242.5 km) (Kruskal Wallis $X^2_2 = 27.10$, $df = 1$, $P = 0.002$). No significant difference between years was found (Kruskal Wallis $X^2_2 = 3.62$, $df = 2$, $P = 0.16$).

Table 4. Summary of complete trips of Leach's Storm-petrels tracked during incubation in 2021. N = number of locations.

Ring Number	Nest ID	Trip Start Time	Trip end Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27401	8	27/06/2021 01:00	29/06/2021 23:30	141	833.2	224.8	359.5	70.5
BT27414	9	30/06/2021 02:00	03/07/2021 00:00	70	868.4	278.2	325	70
BT27417	30	01/07/2021 01:00	03/07/2021 00:00	95	799.8	293.2	325	47
BT27417	30	03/07/2021 23:30	05/07/2021 23:30	79	920.8	329.6	327.7	48
BT27424	32	04/07/2021 00:00	05/07/2021 23:00	93	901.3	315.7	335.5	47
BT27406	38	22/06/2021 02:00	25/06/2021 00:00	68	964.7	292	352	70
BT27406	38	25/06/2021 03:00	26/06/2021 00:00	22	NA	136.7	295.6	NA
BT27403	44	20/06/2021 02:00	23/06/2021 01:00	72	1322.9	412.1	266.5	71
BT27403	44	23/06/2021 01:00	24/06/2021 00:00	24	325.8	120.3	261.6	23
BT27403	44	24/06/2021 01:00	25/06/2021 00:00	24	314.2	136	303.5	23
BT27403	44	25/06/2021 01:00	27/06/2021 00:00	47	722.8	260	350.9	47
BT27403	44	27/06/2021 02:00	28/06/2021 00:00	23	303	118.4	292.6	22
BT27403	44	28/06/2021 02:00	30/06/2021 00:00	46	646	175.2	341.8	46
BT27403	44	30/06/2021 01:00	02/07/2021 00:00	48	739.8	273.6	337.3	47
BT27420	46	02/07/2021 00:30	05/07/2021 00:30	139	1133.2	348.4	335.9	72
BT27420	46	05/07/2021 01:30	05/07/2021 23:30	44	437.5	166.8	284.9	22
BT27413	57	27/06/2021 02:30	29/06/2021 00:00	89	697.8	186.3	359.7	45.5
BT27408	58	26/06/2021 00:00	29/06/2021 00:00	71	996.3	299.7	346.7	72
BT27431	62	09/07/2021 01:00	12/07/2021 19:01	73	1151.8	330	329.2	90

Table 5. Summary of complete trips of Leach's Storm-petrels tracked during chick rearing in 2021.

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27425	47	05/07/2021 00:30	08/07/2021 00:30	98	743.6	261.1	313.2	72
BT27425	47	08/07/2021 01:30	09/07/2021 22:30	63	NA	266	324	NA
BT27426	26	08/07/2021 02:30	10/07/2021 00:00	91	888	217.4	4.5	45.5
BT27427	40	09/07/2021	11/07/2021 00:00	96	787.1	293.7	336.5	48

Table 6. Summary of complete trips from Leach's Storm-petrels tracked in 2023 during the incubation phase.

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27408	38	30/06/2023 23:30	03/07/2023 00:30	99	1002	316.2	331.8	49
BT27452	44	08/07/2023 01:00	12/07/2023 00:00	89	1043.4	299.1	346.5	95
BT27462	45	06/07/2023 01:00	09/07/2023 00:00	72	1052.2	287.4	340.7	71
BT27462	45	09/07/2023 01:00	10/07/2023 00:00	24	345.2	110.7	277.5	23
BT27463	48	01/07/2023 01:30	05/07/2023 00:00	190	1242.4	292.1	338.5	94.5
BT27467	35	08/07/2023 02:00	11/07/2023 00:00	71	1308.9	517.8	285.5	70
BT27471	124	11/07/2023 01:00	13/07/2023 23:30	140	898.5	268.5	278.8	70.5
BT27473	103	11/07/2023 02:00	14/07/2023 00:00	140	1201.2	413	310.4	70
BT27477	108	14/07/2023 01:00	16/07/2023 01:00	47	722.4	311.4	328.5	48
BT27477	108	16/07/2023 23:00	18/07/2023 23:00	48	823.2	261.3	350	48

Table 7. Summary of complete trips of Leach's Storm-petrels tracked in 2023 during the chick rearing phase.

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27405	38	15/07/2023 03:00	17/07/2023 00:00	46	757.6	259.2	289.8	45
BT27416	46	20/07/2023 03:00	22/07/2023 00:00	44	590.9	177.2	342.6	45
BT27416	46	22/07/2023 01:00	22/07/2023 23:00	21	209	69.2	222.2	22
BT27416	46	23/07/2023 02:00	23/07/2023 23:00	22	308.8	127.5	297.8	21
BT27416	46	24/07/2023 01:00	25/07/2023 23:00	47	672.7	185.7	340.3	46
BT27465	59	06/07/2023 02:00	08/07/2023 00:00	46	829.9	300.8	349.9	46
BT27465	59	08/07/2023 02:00	10/07/2023 00:00	47	883.1	298.9	344.2	46
BT27465	59	10/07/2023 01:00	11/07/2023 23:00	47	767.5	256.2	350.3	46
BT27472	111	13/07/2023 02:00	14/07/2023 23:00	46	942.1	336.9	307.4	45
BT27472	111	15/07/2023 00:00	17/07/2023 22:00	71	1249.3	427.8	258	70
BT27472	111	18/07/2023 01:00	19/07/2023 23:00	47	701.2	258.1	344.5	46
BT27474	112	19/07/2023 22:00	22/07/2023 00:00	50	773.5	218.2	357.2	50
BT27474	112	22/07/2023 02:00	23/07/2023 00:00	23	546.1	250.2	327.6	22
BT27474	112	23/07/2023 01:00	24/07/2023 02:00	24	535.1	253.2	318.1	25
BT27474	112	24/07/2023 02:00	26/07/2023 00:00	47	722	241.4	306.6	46
BT27474	112	26/07/2023 03:00	27/07/2023 23:00	45	927.6	313.6	352.6	44
BT27476	45	14/07/2023 21:00	17/07/2023 23:00	72	1204.9	506.4	234	74
BT27476	45	18/07/2023 02:00	20/07/2023 00:00	46	834.3	312.3	325.5	46
BT27476	45	20/07/2023 00:00	20/07/2023 23:00	24	294	116.1	225.1	23
BT27479	116	13/07/2023 01:00	14/07/2023 23:00	47	673.4	259.7	338.6	46
BT27479	116	15/07/2023 01:00	16/07/2023 23:00	47	683.6	242.6	291.2	46
BT27479	116	17/07/2023 02:00	18/07/2023 23:00	45	691.9	261.9	346.3	45

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27484	122	18/07/2023 02:00	18/07/2023 23:00	22	453.7	184.9	343.7	21
BT27484	122	19/07/2023 00:00	20/07/2023 23:00	48	748.5	233.5	346.1	47
BT27484	122	21/07/2023 01:00	22/07/2023 23:00	47	766.8	262.1	344.2	46
BT27486	11	23/07/2023 00:00	24/07/2023 22:00	47	660.7	215.2	304.4	46
BT27486	11	21/07/2023 02:00	23/07/2023 00:00	47	607.2	246.4	328.6	46

Table 8. Summary of complete trips of Leach's Storm-petrels tracked in 2024 during the incubation phase.

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27444	48	30/06/2024 02:30	04/07/2024 00:02	181	1603	286.7	NA*	93.5
NT42977	150	08/07/2024 01:30	10/07/2024 00:00	88	867.7	300.9	337.9	46.5
NT42984	58	10/07/2024 01:30	11/07/2024 23:00	91	1099	470.4	260.3	45.5
NT42984	58	13/07/2024 02:00	15/07/2024 00:30	94	1191	500.2	346.7	46.5
NT42989	52	12/07/2024 03:00	14/07/2024 01:00	91	827.3	327.5	296.1	46
NT42989	52	14/07/2024 23:00	17/07/2024 00:00	97	933.8	370.5	318.8	49
NT42991	158	11/07/2024 01:00	13/07/2024 23:00	140	1011.8	289.8	350.6	70
NT42994	119	13/07/2024 01:00	16/07/2024 23:00	187	1774.1	634.7	342.1	94
NT63501	122	17/07/2024 00:29	21/07/2024 23:29	235	2269.9	611.3	329.8	119
NT63501	122	22/07/2024 02:29	22/07/2024 23:59	42	235.7	82	303.1	21.5
NT63501	122	23/07/2024 02:29	23/07/2024 22:59	42	257.8	81.9	236.6	20.5

Table 9. Summary of complete trips of Leach's Storm-petrels tracked in 2024 during the chick rearing phase.

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
BT27472	109	08/07/2024 02:00	11/07/2024 00:00	93	865.2	258.5	341.7	70
BT27472	109	11/07/2024 00:00	12/07/2024 23:30	95	782	246.5	342.7	47.5
BT27472	109	13/07/2024 02:00	13/07/2024 23:00	43	287.3	116.8	290.4	21
BT27472	109	14/07/2024 02:00	15/07/2024 22:00	34	NA	289.4	316.6	NA
NT42955	146	30/06/2024 01:33	30/06/2024 22:33	42	339.4	101.9	236.4	21
NT42962	121	01/07/2024 01:59	03/07/2024 23:27	139	923.4	268.1	352.2	69.5

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
NT42971	137	06/07/2024 01:30	08/07/2024 00:30	95	833.3	250.6	298.6	47
NT42971	137	08/07/2024 02:30	09/07/2024 01:00	46	543	210	313	22.5
NT42971	137	09/07/2024 01:30	10/07/2024 00:00	46	384	141.2	292.1	22.5
NT42971	137	10/07/2024 01:00	11/07/2024 23:30	94	857.5	239.1	353.3	46.5
NT42983	144	10/07/2024 02:30	11/07/2024 23:00	87	737.7	210.8	334.1	44.5
NT42983	144	12/07/2024 01:30	12/07/2024 23:30	45	318.2	90.4	253.4	22
NT42983	144	13/07/2024 01:30	14/07/2024 23:30	92	853.2	278.6	338.7	46
NT42988	152	12/07/2024 02:00	14/07/2024 23:00	138	1190.1	298.3	212.9	69
NT42988	152	15/07/2024 01:00	16/07/2024 23:30	92	770.1	269	321.7	46.5
NT42995	138	15/07/2024 23:30	18/07/2024 23:00	143	1055.6	327.9	307.1	71.5
NT42995	138	19/07/2024 01:00	20/07/2024 23:00	90	761.8	298.9	346.1	46
NT63505	133	21/07/2024 02:30	22/07/2024 00:00	43	378.7	141.8	308	21.5
NT63505	133	22/07/2024 01:00	24/07/2024 00:00	46	434.4	161	328	47

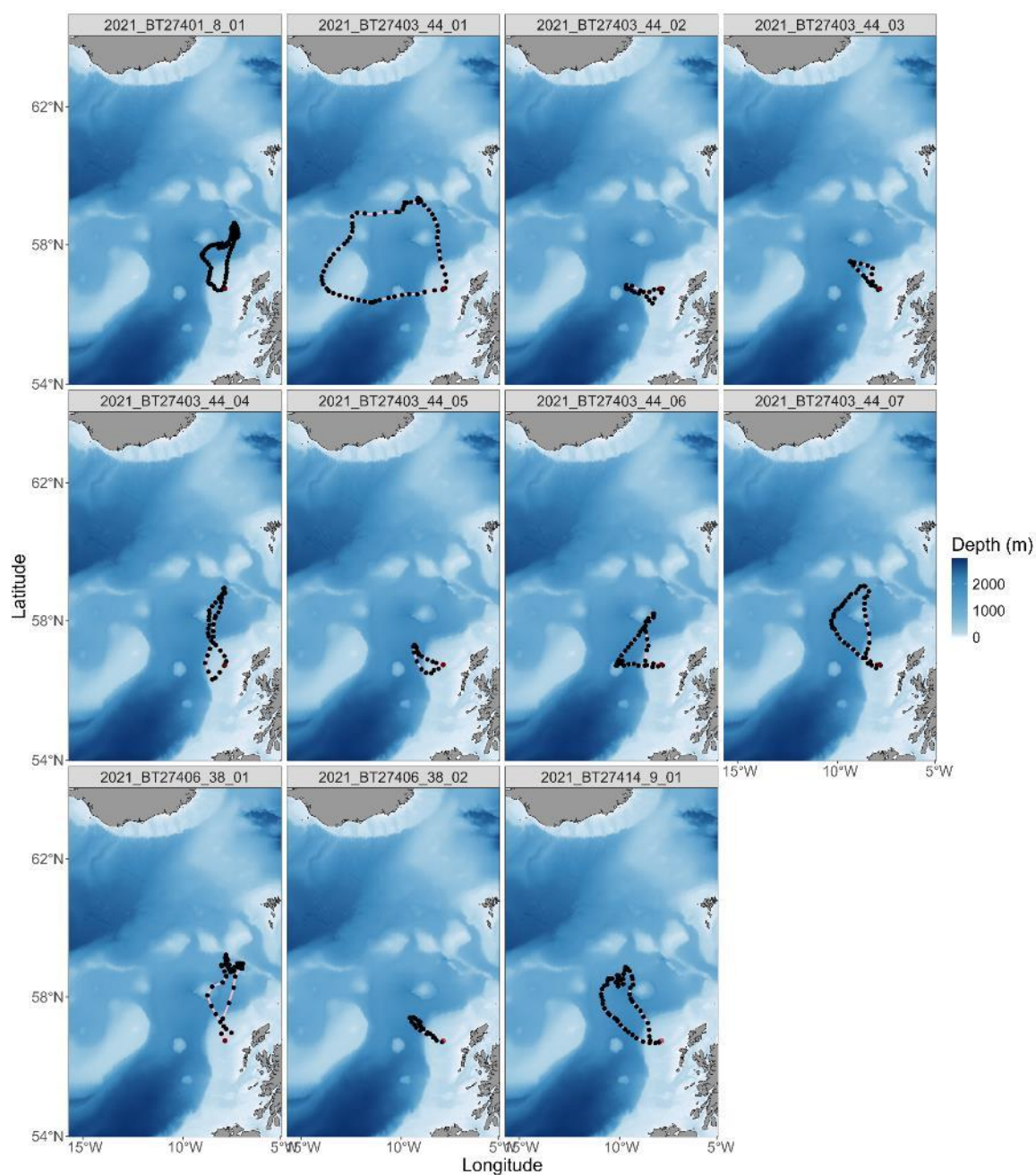


Figure 9. Complete trips of Leach's Storm-petrels during incubation tracked between June and July of 2021. Trip 38_02 is classified as an 'almost complete' trip.

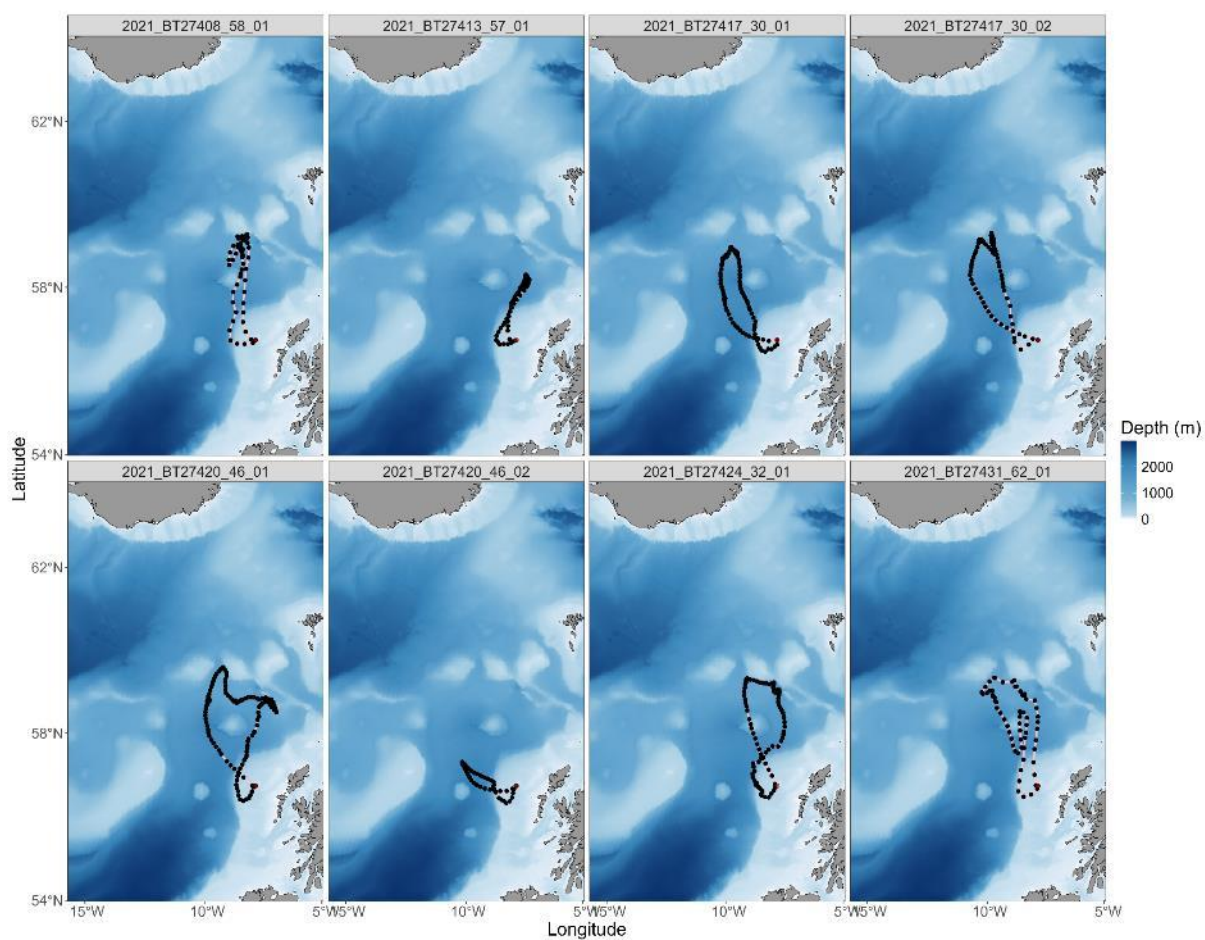


Figure 10. Complete trips of Leach's Storm-petrels during incubation tracked between June and July of 2021.

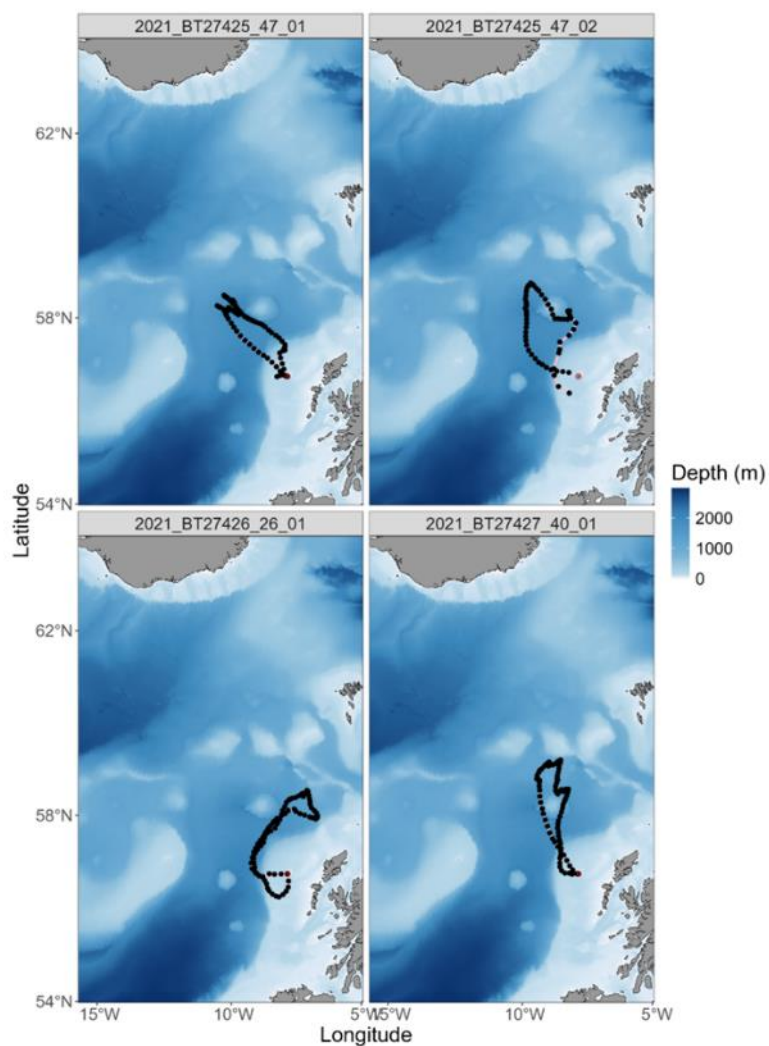


Figure 11. Complete trips of Leach's Storm-petrels during chick provisioning tracked between June and July of 2021. Trip 47_02 is considered to be an 'almost complete' trip.

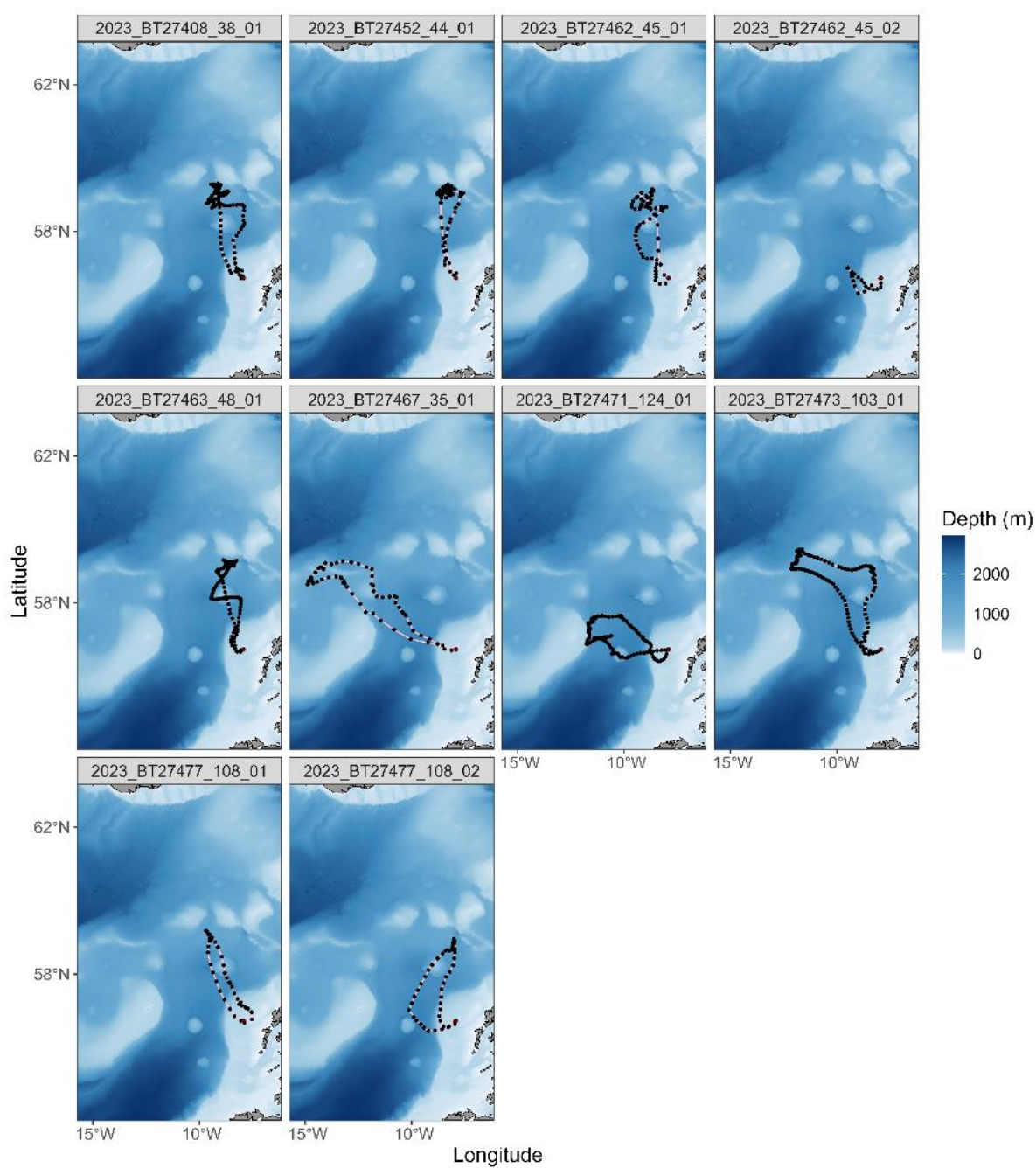


Figure 12. Complete trips of Leach's Storm-petrels during incubation tracked between June and July of 2023.

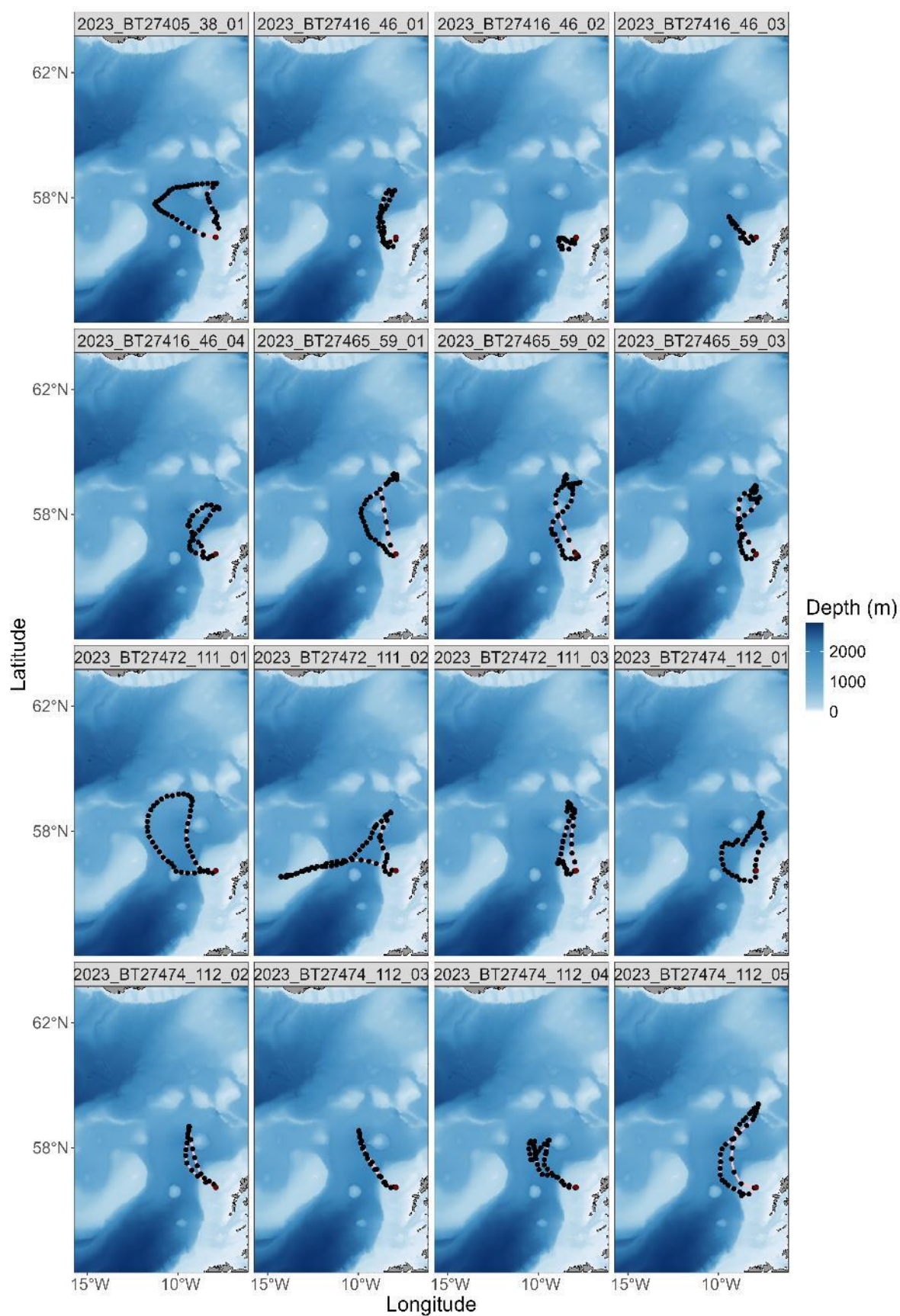


Figure 13. Complete trips (1 – 16) of Leach's Storm-petrels during chick provisioning tracked between June and July of 2023.

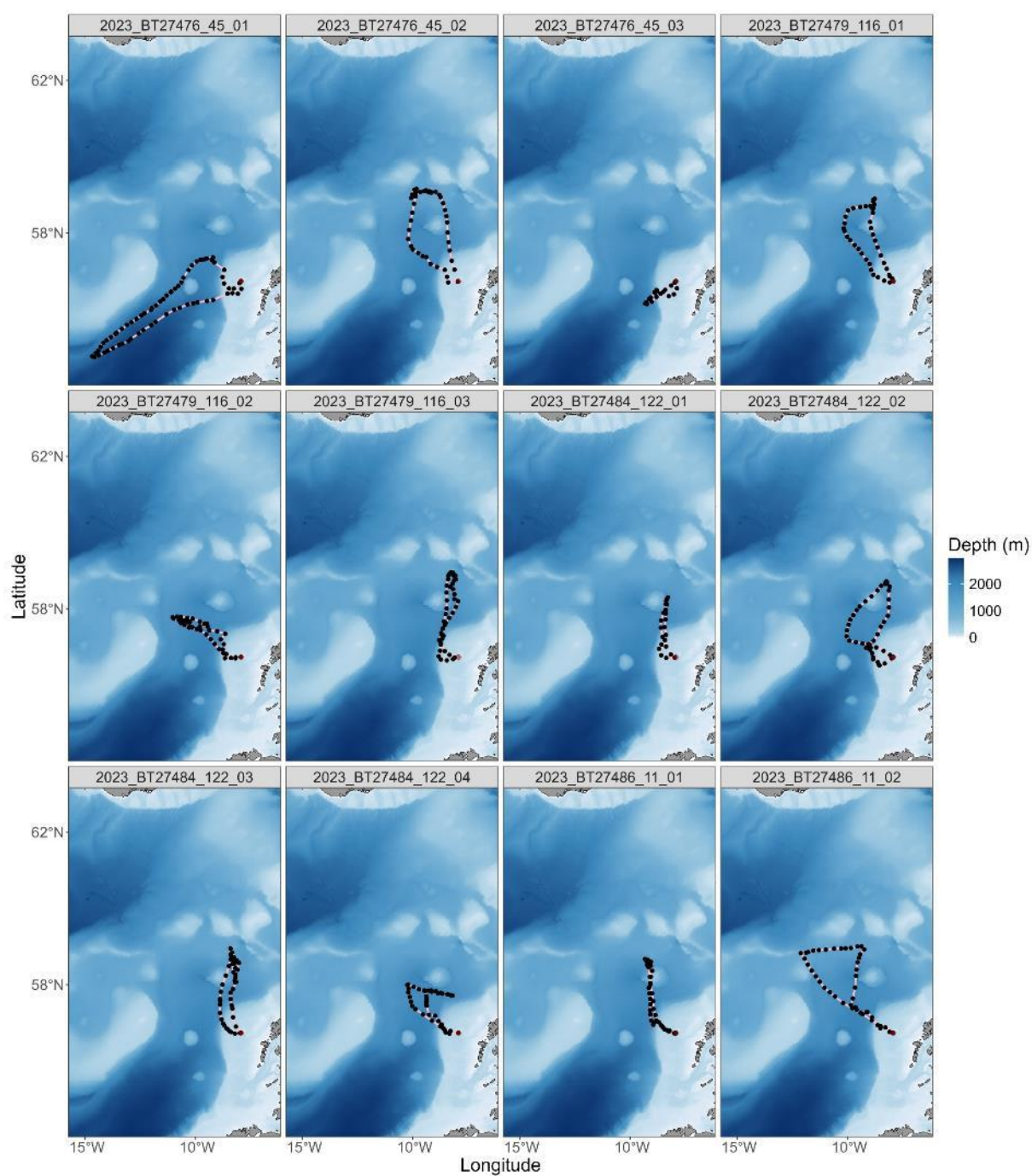


Figure 14. Complete trips of Leach's Storm-petrels (17 – 28) during chick provisioning tracked between June and July of 2023.

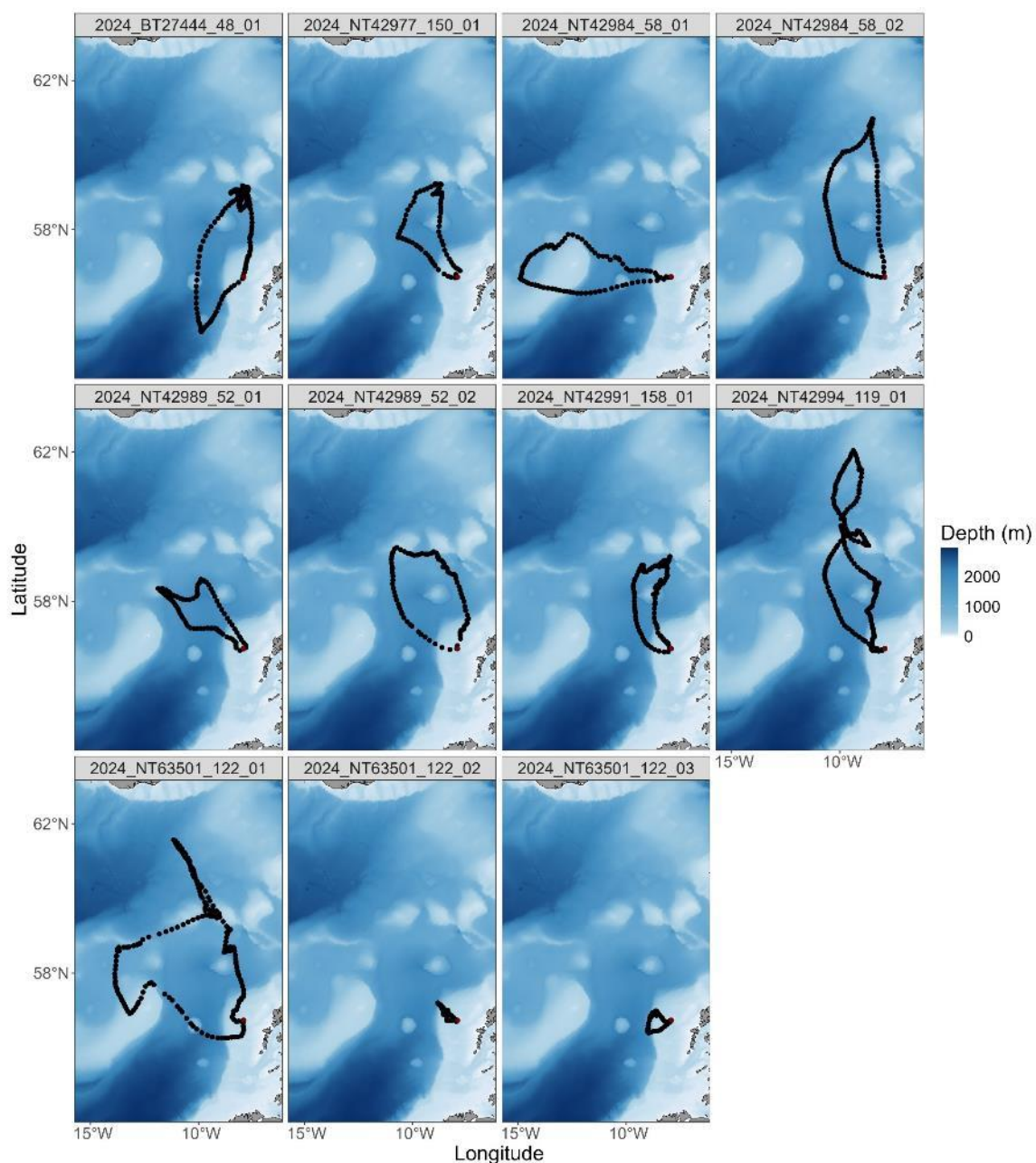


Figure 15. Complete trips of Leach's Storm-petrels during incubation tracked between June and July of 2024.

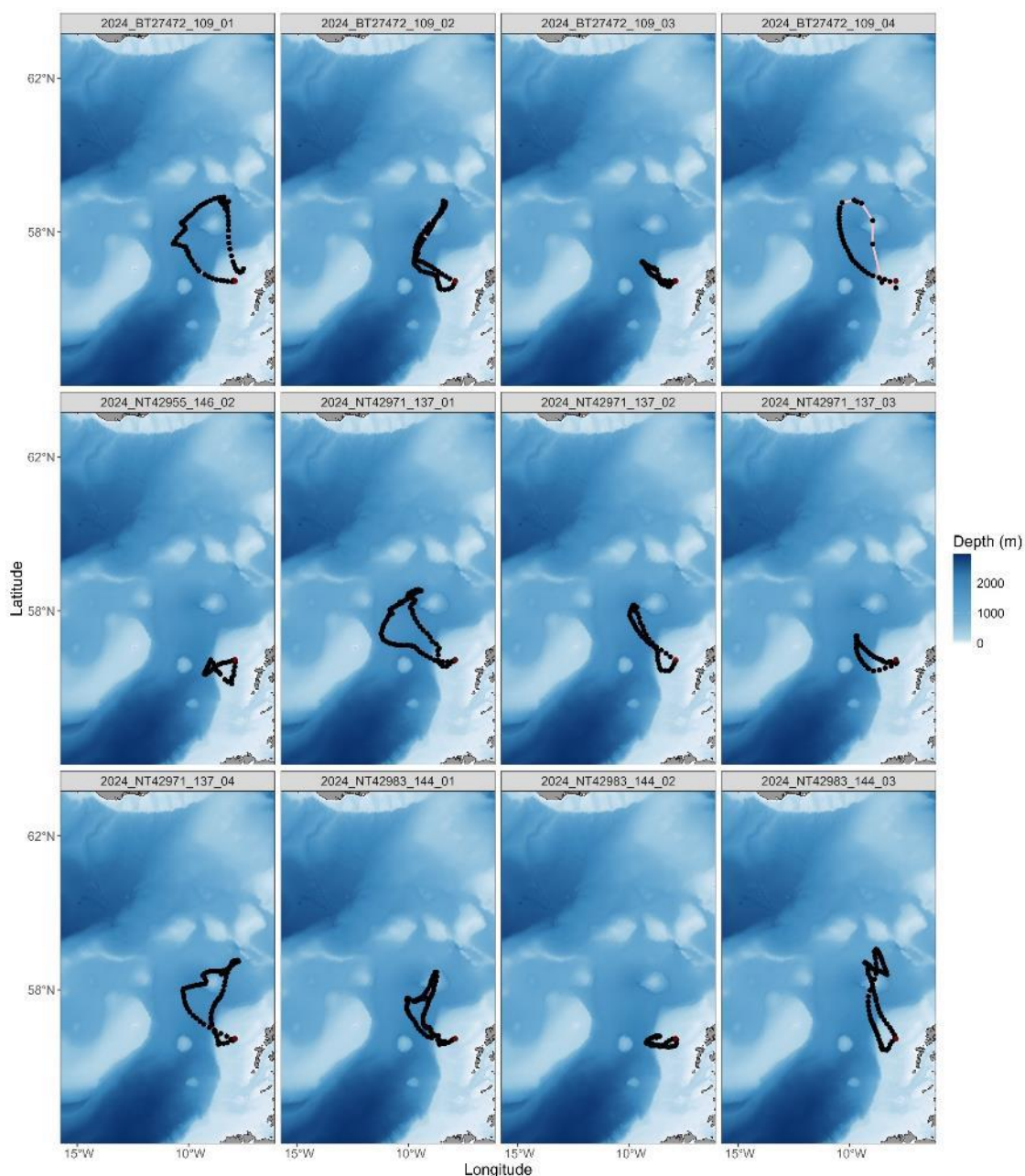


Figure 16. Complete trips (1 – 12) of Leach's Storm-petrels tracked during chick rearing between June and July of 2024. Trip 109_04 is classified as an “almost complete” trip because it returned to the colon but the battery began to fail resulting in a likely underestimate of total trip distance and duration.

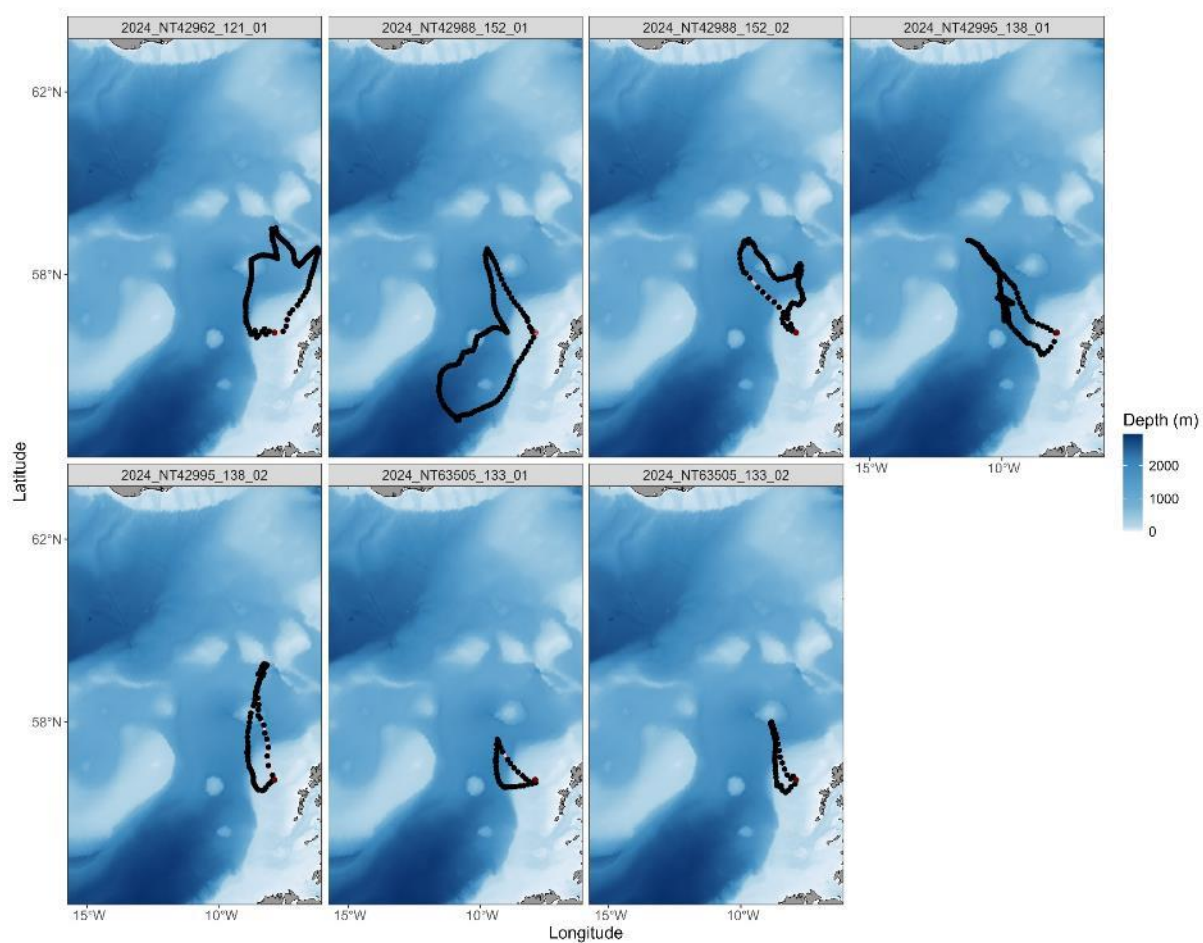


Figure 17. Complete trips of Leach's Storm-petrels (13 - 19) tracked during chick rearing between June and July of 2024

Figures 18 - 20 present the movements of all Leach's Storm-petrels tracked from St Kilda in 2021, 2023 and 2024.

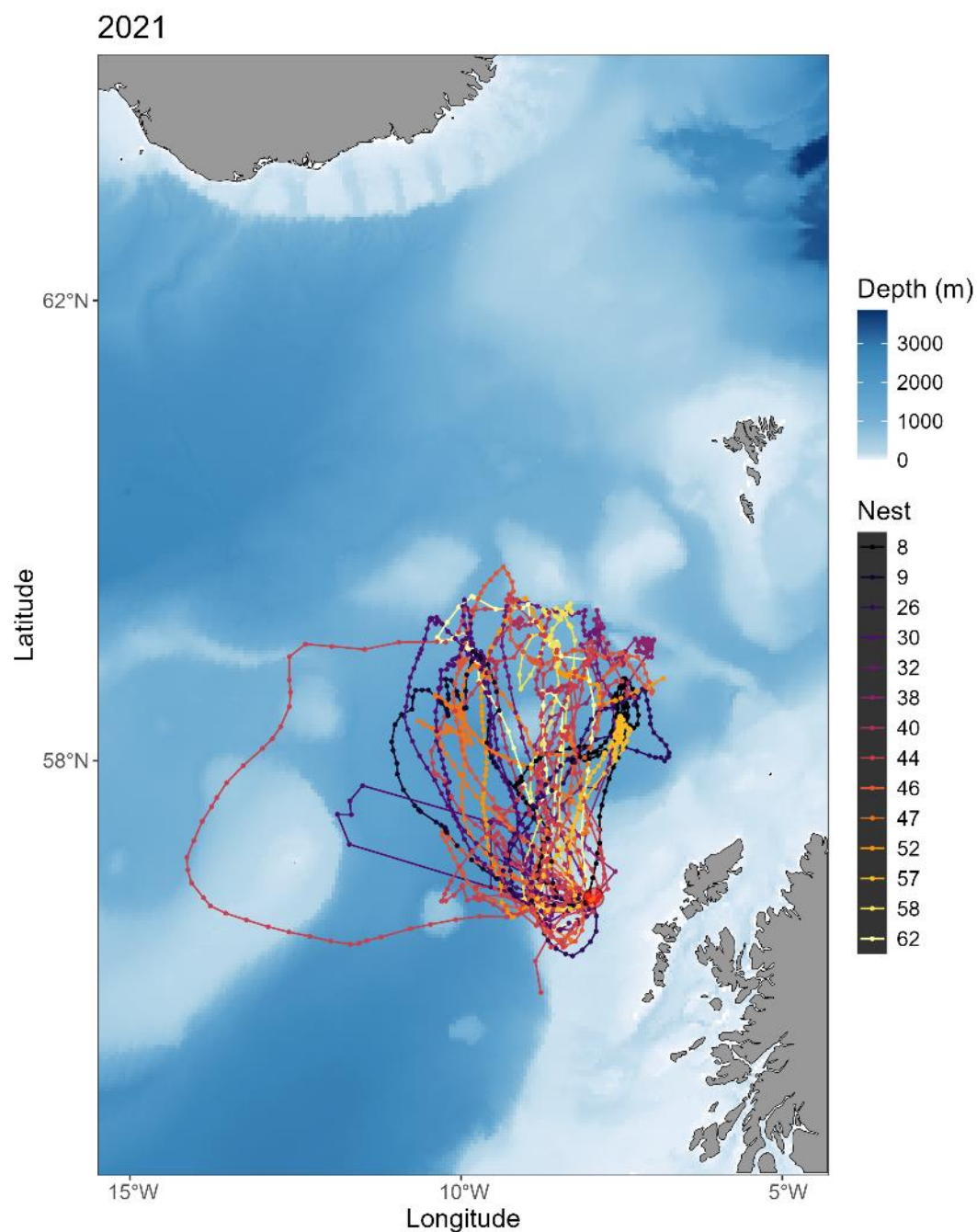


Figure 18. The raw tracks of all Leach's Storm-petrel individuals tracked in 2021 from St Kilda (including partial trips). Note: the period for which each individual was tracked will vary. Colony indicated by a red circle.

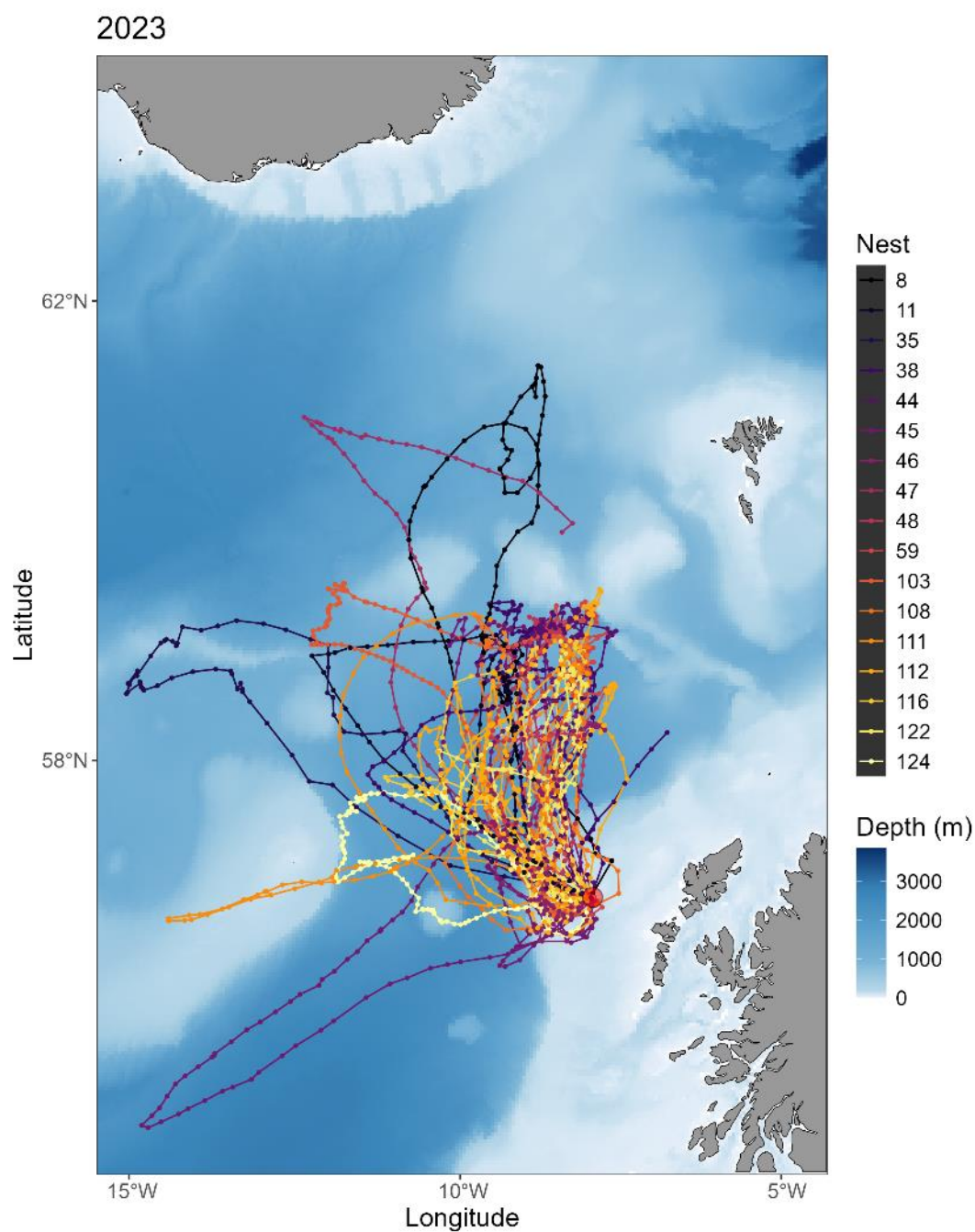


Figure 19. The raw tracks of all Leach's Storm-petrel individuals tracked in 2023 from St Kilda (including partial trips). Note: the period for which each individual was tracked will vary. Colony indicated by a red circle.

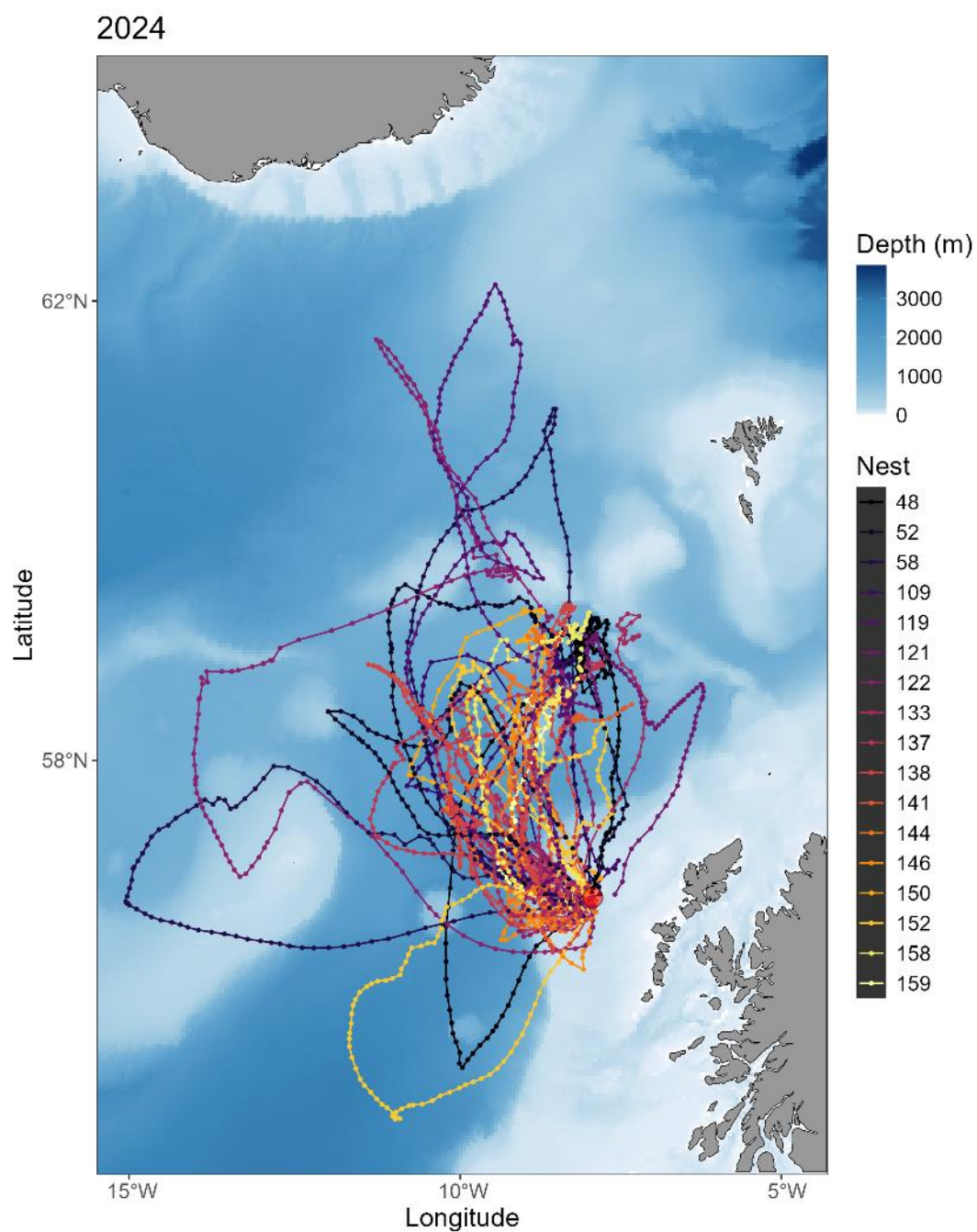


Figure 20. The raw tracks of all Leach's Storm-petrel individuals tracked in 2024 from St Kilda (including partial trips). Note: the period for which each individual was tracked will vary. Colony indicated by a red circle.

4.5.1.1 Leach's Storm-petrel Utilisation Distributions

The utilisation distributions (UDs) of Leach's Storm-petrels tracked from Hirta (Figure 21) highlighted the core foraging and home range of the tracked birds. These UD were calculated for complete and 'almost complete' trips only and exclude any trips associated with possible disturbance at the nest ($n = 5$) or failed breeding attempts ($n = 6$). The core usage range (50% KDE) includes an area to the North of St Kilda (approximately centred on $-59^{\circ}\text{N } 8^{\circ}\text{W}$), and an area to the West of the colony likely reflecting predominant commuting routes to and from the colony (Figure 21A). As expected, birds are more likely to be present close to the colony at night than during the day (Figure 21B and C). The utilisation distributions appear to be broadly consistent between years (Figure 21D - F). This agrees with the analysis of the trip statistics in which no significant effect of year on maximum distance from the colony or total travel distance was found. In contrast to this, incubating birds appeared to target different areas (Figure 21G) compared with those attending chicks (Figure 21H).

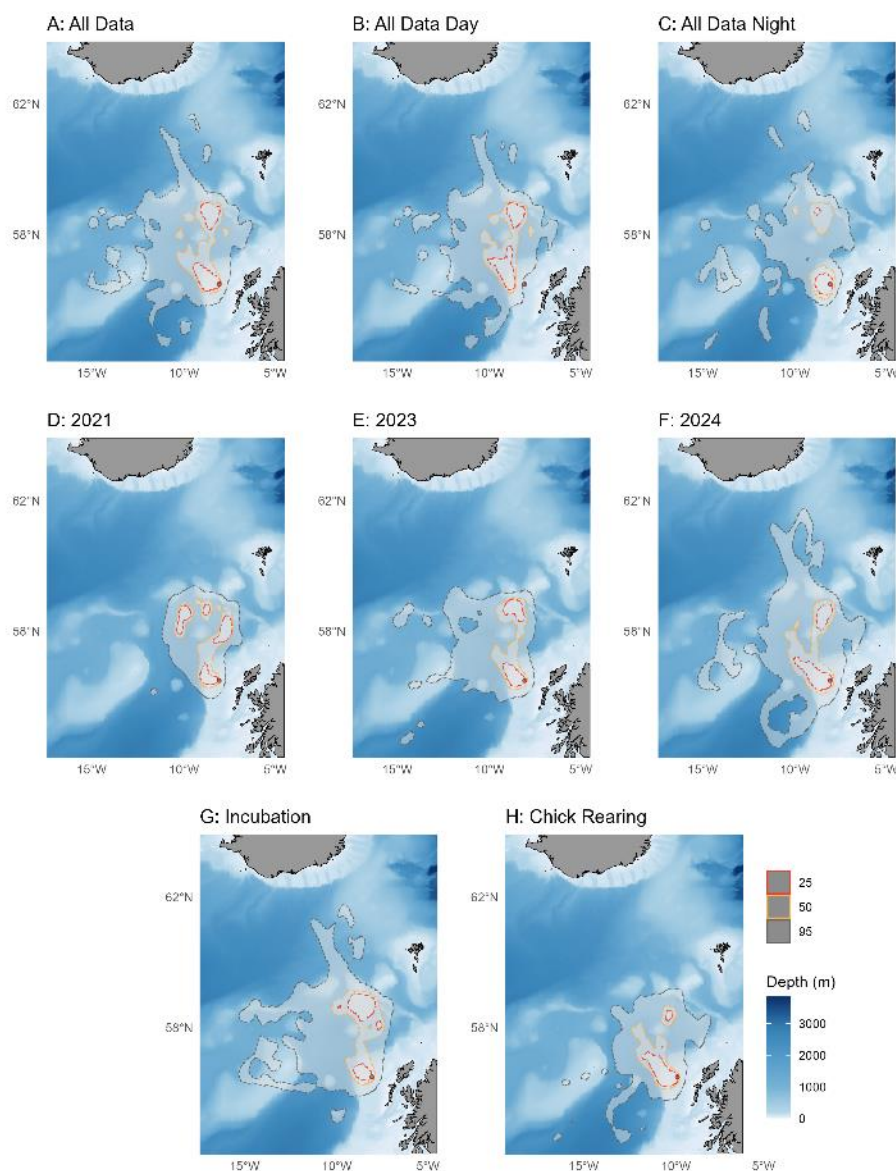


Figure 21. Utilisation distributions (UDs) of foraging Leach's Storm-petrels represented by 25%, 50% and 95% kernels. Panel A shows the overall UD, panels B and C display the UD for different times of day, panels D – F display the UD of birds tracked in each year (2021, 2023 and 2024), panels G and H display the UD for birds by breeding phase.

4.5.1.2 Leach's Storm-petrel foraging habitat selection

The top-selected model for Leach's Storm-petrel breeding on Hirta, St Kilda included non-linear smoothers for log-transformed water depth and SST (Table 10). The non-linear smoother for SST also incorporated a two-way interaction with time of day (day vs. night). Additionally, linear terms for seabed slope and surface chlorophyll concentration were included in the model.

Of these retained covariates, water depth was highly correlated with both distance from the colony and distance from the coast. However, models including either distance from the colony or distance from the coast showed errors related to model convergence, which led to our preference for selecting models that included log-transformed water depth instead. Habitat usage of Leach's Storm-petrels declined as water depth increased from relatively shallow depths of approximately 25 m to 150 m. Beyond this point, habitat usage began to increase from 200 m to 1000 m, with a slight peak in usage around 1000 m (Figure 22).

During the day, we found that habitat usage was positively associated with SST, with a slight peak in usage occurring when SST was in the range of $\sim 12.5^{\circ}\text{C}$ to 13°C (Figure 23). In contrast, at night, there was little evidence that SST influenced habitat usage, though there was slight evidence of reduced usage of areas with higher SSTs ($> 14.75^{\circ}\text{C}$, Figure 23). Additionally, model coefficients suggested that seabed slope was negatively associated with habitat usage, while surface chlorophyll was positively associated with habitat usage (Table 10).

Table 10. Results for gam SSFs for European and Leach's Storm-petrel. Tables shows outputs for best performing model (on the basis of model AIC scores) for each species. Covariates were included as either on-linear smooths (s) or as parametric coefficients (β). When fitted as parametric coefficients covariates were standardized prior to modelling. Parametric coefficients are reported together with associated 95% confidence intervals (CI). For non-linear smooths we report associated χ^2 and p values. N = 4173 observations for European Storm-petrel; N = 6105 observations for Leach's Storm-petrel. Each observation was paired with N = 50 available points.

European Storm-petrel

Model Parameter	Model Output
s(Step)	$\chi^2= 6777$, p = < 0.001
s(Turning Angle)	$\chi^2= 2663$, p = < 0.001
s(log(Distance from Colony, day)	$\chi^2= 100.75$, p = < 0.001
s(log(Distance from Colony, night)	$\chi^2= 76.01$, p = < 0.001
s(log(NPP))	$\chi^2= 25.42$, p = < 0.001
s(Seabed Slope)	$\chi^2= 17.08$, p = 0.005
s(Magnitude of Chlorophyll Gradient)	$\chi^2= 6.98$, p = 0.043

Leach's Storm-petrel

Model Parameter	Model Output
β_{zCHL}	0.126 (95% CI: 0.047 – 0.21)
$\beta_{zSeabed Slope}$	-0.045 (95% CI: -0.0077 - -0.082)
s(Step)	$\chi^2= 6243$, p = < 0.001
s(Turning Angle)	$\chi^2= 7700$, p = < 0.001
s(log(Water Depth))	$\chi^2= 52.20$, p = < 0.001
s(SST, day)	$\chi^2= 23.80$, p = 0.002
s(SST, night)	$\chi^2= 27.75$, p = < 0.001

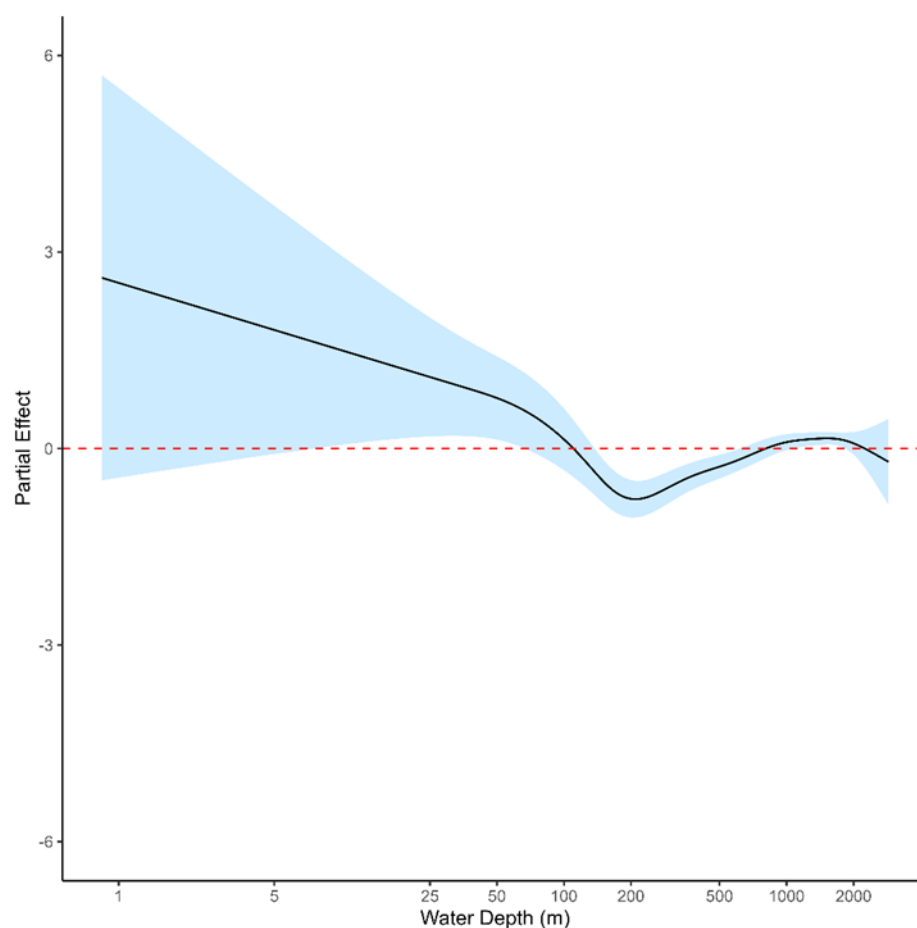


Figure 22. Partial effect plots showing the contribution of water depth on habitat usage from an SSF for Leach's Storm-petrel breeding on Hirta, St Kilda. A 95% CI envelope around model estimates is displayed as a shaded blue polygon. The horizontal dashed line represents where the y-axis is 0. The x-axis displays water depth on the log scale.

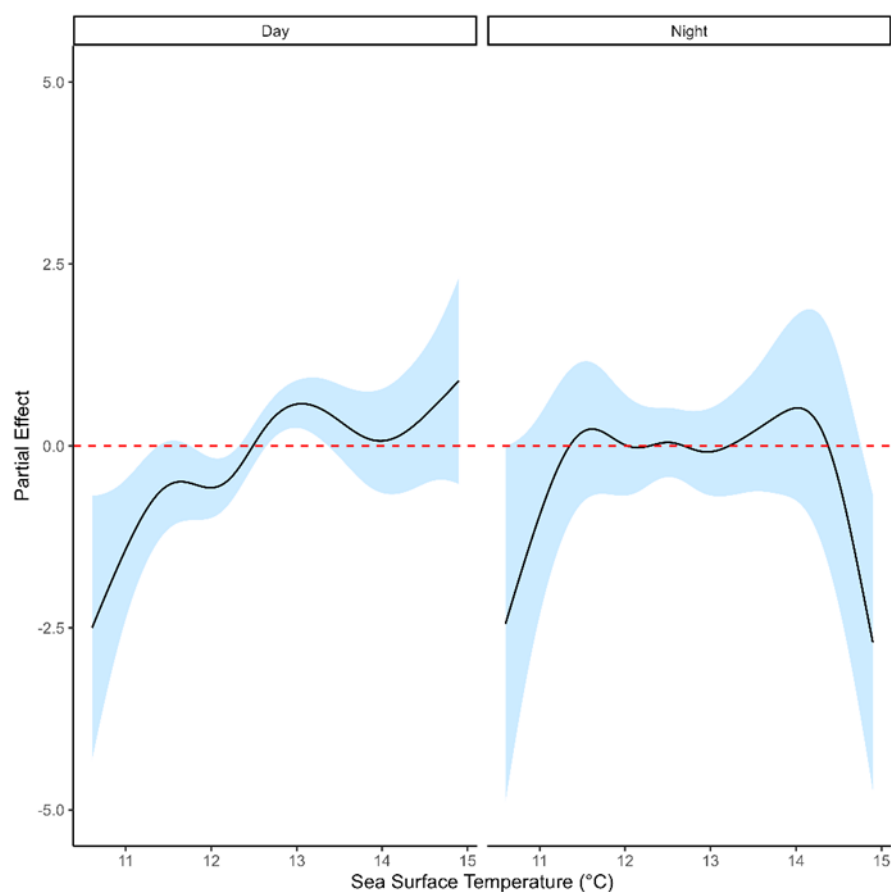


Figure 23. Partial effect plots showing the contribution of SST on habitat usage, during either day or night, from an SSF for Leach's Storm-petrel breeding on Hirta, St Kilda. A 95% CI envelope around model estimates is displayed as a shaded blue polygon. The horizontal dashed line represents where the y-axis is 0.

4.5.2 European Storm-petrel trip metrics

The modelled mean trip duration across all birds and years was 36.9 ± 17.3 hours. As with total trip distance and maximum range, this was found to differ significantly between breeding stages in 2021 (GLMM Estimate = 35.9, SE = 8.0, $P = 0.001$). Incubating birds spent significantly longer at sea (61.3 ± 24.9 hours) than those provisioning for chicks (26.1 ± 19.6 hours). However this result is derived from only 3 complete trips for incubating birds and as such should be taken as indicative only. There were small, but significant differences among years in the duration of trips of chick-rearing birds: trip durations were shorter in 2021 (26.1 ± 20.0 hours) than 2023 (38.8 ± 4.0 hours, GLMM Estimate = 12.7, SE = 5.8, $P = 0.039$) and 2024 (40.8 ± 5.2 hours, Estimate = 14.7, SE = 6.8, $P = 0.038$).

The modelled mean maximum range (accounting for multiple non-independent trips for some individuals) across all trips was 116.6 ± 53.0 km. In 2021, when birds were tracked both during both breeding stages, birds travelled significantly further from the colony during the incubation stage (153.9 ± 25.1 km) compared to birds attending chicks (89.6 ± 69.9 km, GLMM Estimate = 50.1, SE = 15.9, $P = 0.007$). There was a significant difference in the foraging range of chick-rearing birds in 2021 (89.7 ± 69.9 km) compared with 2023 (149.3 ± 73.6 km, GLMM Estimate = 59.6, SE = 25.7 $P = 0.033$).

The modelled mean total trip distance of birds tracked from Treshnish was 418.6 ± 178.0 km. In 2021 birds travelled significantly further during the incubation stage than those attending chicks (602.2 ± 253.1 and 303.3 ± 204.7 km respectively, GLMM Estimate = 291.2, SE = 92.3, $P = 0.007$). However, this should be interpreted with caution as only three complete trips were obtained from incubating birds in 2021 compared to 18 complete trips for birds attending chicks. There were significant differences among years in the total distance travelled on trips by chick-rearing birds: in 2023 (481.5 ± 222.1 km) the total was considerably greater (GLMM Estimate = 178.2, SE = 77.54, $P = 0.035$) than in 2021 (303.3 ± 211.1 km) and 2024 (441.4 ± 426.5 km).

Table 11: Summary of complete trips by individual for European Storm-petrels tracked during the 2021 field season. There were two further partial trips, for which trip metrics could not be reliably estimated.

Incubating Birds

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
2775286	B06	24/07/2021 02:00	26/07/2021 00:00	47	472.54	141.09	270.02	46
2725247	B07	25/07/2021 00:00	27/07/2021 02:00	51	440.99	143.66	238.32	50
2775516	B16	26/07/2021 23:00	29/07/2021 22:00	72	NA	198.61	247.64	NA
2775511	C07	26/07/2021 03:00	29/07/2021 22:00	90	894.3	140.87	256.54	91
2775512	C08	26/07/2021 01:00	30/07/2021 03:00	95	NA	145.18	259	NA

Birds Attending Chicks

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
2775518	B02b	07/08/2021 23:30	08/08/2021 22:30	91	264.64	62.96	288.6	23
2775518	B02b	09/08/2021 03:15	09/08/2021 22:00	76	263.43	69.71	291.86	18.75
2775518	B02b	10/08/2021 02:30	10/08/2021 23:15	84	206.17	51.95	309.44	20.75
2775525	B12	10/08/2021 23:29	12/08/2021 00:29	50	292.76	114.03	260.71	25
2775525	B12	12/08/2021 00:59	12/08/2021 21:59	42	269.5	96.6	261.5	21
2775525	B12	12/08/2021 21:59	13/08/2021 21:29	47	248.86	93.58	268.85	23.5
2775525	B12	13/08/2021 22:59	14/08/2021 21:59	47	220.49	67.32	294.57	23
2679523	B15	31/07/2021 00:59	02/08/2021 15:44	135	NA	135.38	239.83	NA
2775504	C04	23/07/2021	23/07/2021 22:30	46	346.54	97.26	251.21	22.5
2775504	C04	24/07/2021 01:30	24/07/2021 22:30	42	266.53	67.98	272.22	21
2775506	C11	25/07/2021 00:30	25/07/2021 22:45	87	264.84	106.51	239.64	22.25
2775519	E01	06/08/2021 22:59	07/08/2021 22:59	47	204.88	62.23	332.16	24

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
2775518	w01	02/08/2021 22:14	03/08/2021 22:14	92	304.72	125.76	262.22	24
2775523	w04b	10/08/2021 21:59	12/08/2021 00:29	51	296.82	91.16	252.69	26.5
2775502	W10	21/07/2021 22:30	22/07/2021 23:00	50	301.69	114.4	283.13	24.5
2775502	W10	23/07/2021 02:30	24/07/2021 23:00	85	598.98	109.44	269.54	44.5
2775501	W14	22/07/2021	22/07/2021 22:00	43	193.91	67.19	301.86	22
2775522	W19b	08/08/2021 23:15	10/08/2021 23:15	168	572.26	75.21	263.28	48
2775503	W28	22/07/2021 23:30	24/07/2021 00:30	36	342.81	140.43	253.27	25

Table 12. Summary of complete trips by individual for European Storm-petrels tracked during the 2023 field season. There were two further partial trips, for which trip metrics could not be reliably estimated.

Ring Number	Nest ID	Trip Start Time	Trip End Time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
2775598	B05b	07/08/2023 23:30	11/08/2023 03:00	43	241.06	57.41	249.15	25.5
2775598	B05b	09/08/2023 02:30	11/08/2023 22:00	39	188.06	63.91	250.63	19
2775591	B11a	10/08/2023 21:30	05/08/2023 22:15	83	282.93	104.96	217.91	22
2775591	B11a	13/08/2023 03:00	07/08/2023 22:15	164	519.7	114.82	186	44.25
2725877	B16a	12/08/2023 02:30	13/08/2023 23:30	88	520.88	107.74	259.92	45
277596	B22	06/08/2023 03:14	09/08/2023 21:00	137	1072.04	312.14	162.23	70.5
277596	B22	11/08/2023 23:30	13/08/2023 23:00	120	NA	188.79	156.45	NA
2775600	B24a	02/08/2023 22:30	12/08/2023 21:30	40	266.35	100.98	254.91	21
2775600	B24a	05/08/2023 00:15	14/08/2023 21:30	94	565.39	114.88	229.31	46.5
277601	B27	06/08/2023 02:00	14/08/2023 20:30	140	NA	375.94	1.47	NA
2775592	E01a	04/08/2023 23:45	07/08/2023 21:15	259	1021.04	289.12	169.55	69.5
2725894	T2b	10/08/2023 01:30	07/08/2023 02:29	87	446.82	169.03	164.97	23.25
2736815	W11a	11/08/2023 03:00	12/08/2023 22:30	45	264.6	92.4	273.22	23
2775590	W11b	12/08/2023 00:30	04/08/2023 22:30	190	703.04	188.98	164.98	48
2277597	W4	12/08/2023 23:00	09/08/2023 01:30	53	247.68	108.38	237.04	26
2277597	W4	06/08/2023 22:30	10/08/2023	44	272.73	103.61	230.57	21.5
2277597	W4	10/08/2023 02:00	13/08/2023 02:30	107	1063.97	483.51	280.35	53
2277597	W4	11/08/2023 22:30	13/08/2023 23:00	41	233.13	71.38	252.66	20
277602	W8b	12/08/2023 00:00	14/08/2023 01:30	100	513.19	97.45	331.06	49.5
277602	W8b	14/08/2023 01:30	14/08/2023 21:00	40	243.65	105.99	234.41	19.5

Table 13. Summary of complete trips by individual for European Storm-petrels tracked during the 2024 field season. There was one further partial trip, for which trip metrics could not be reliably estimated.

Ring Number	Nest ID	Trip Start Time	Trip End time	N	Complete trip distance (km)	Max range (km)	Direction (Compass Bearing)	Duration (hours)
2775591	B11a	03/08/2024 22:29	17/08/2024 01:59	51	384.67	131.17	168.9	27.5
2725877	B16b	06/08/2024 03:29	17/08/2024 23:59	49	182.33	66.62	188.1	25
2775916	B23	16/08/2024 22:59	18/08/2024 20:59	87	511.11	117.2	288.76	43.5
2775915	B35	15/08/2024 22:29	17/08/2024 21:58	92	411.78	53.37	11.03	47.5
2775914	B46	07/08/2024 01:59	10/08/2024 21:28	40	259.8	86.64	185.99	19.5
2775912	E01c	10/08/2024 00:29	10/08/2024 00:29	127	703.54	143.28	271.72	70.5
2775912	E01c	10/08/2024 01:58	12/08/2024 20:59	133	703.97	75.82	277.73	68.5
2725414	R02	15/08/2024 22:28	05/08/2024 20:59	90	475.81	107.52	294.98	46.5
2725414	R02	17/08/2024 01:29	07/08/2024 20:59	81	339.65	86.86	278.7	41.5

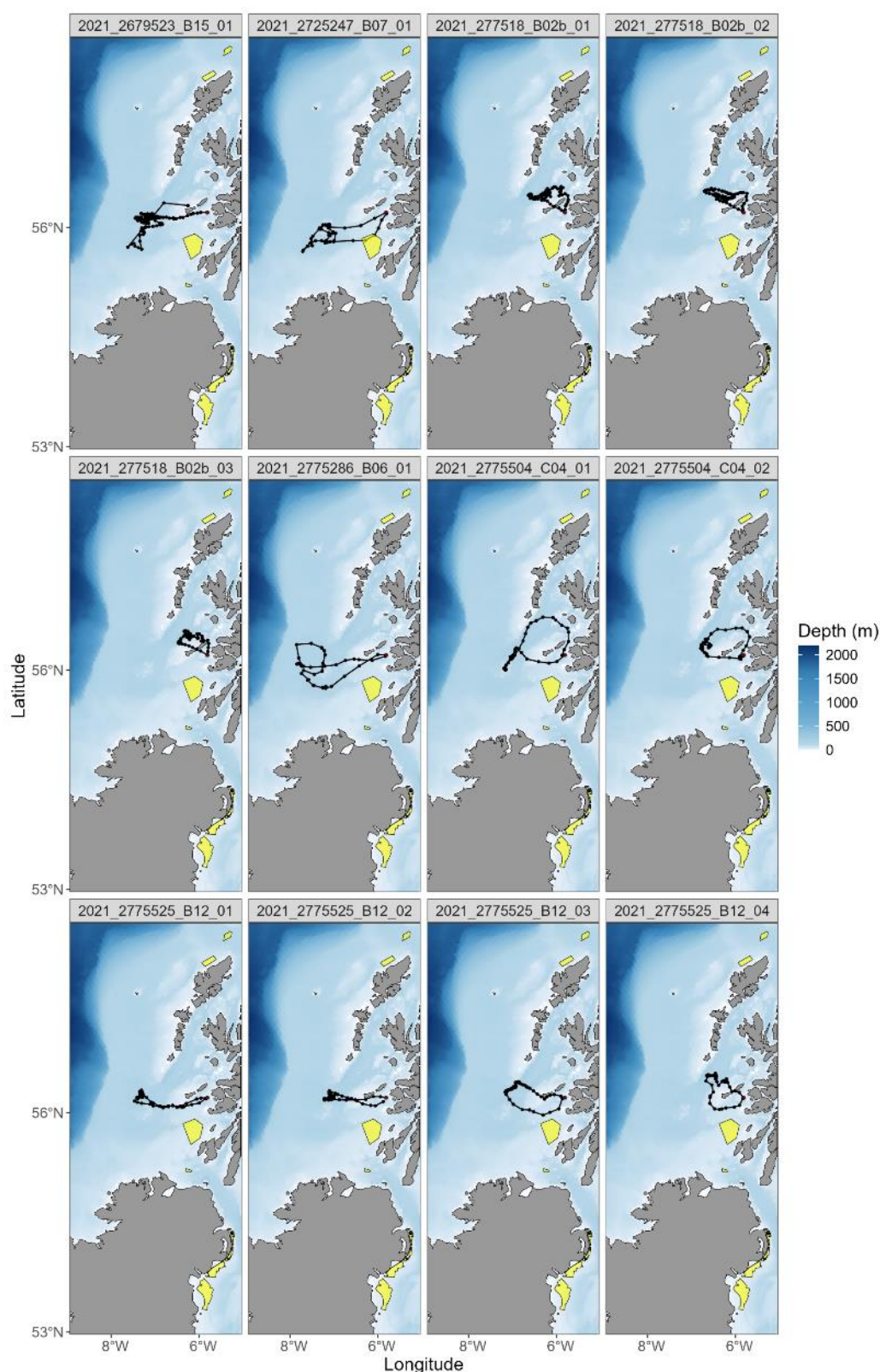


Figure 24. Plots 1 – 12 of 24 complete or almost complete tracks from European Storm-petrels tracked in July and August of 2021. The yellow polygons are proposed OWF areas. Trip B15_01 was “Almost Complete” because the tag failed before the birds had fully returned to the colony but were sufficiently complete to include in summaries of maximum distance and direction.

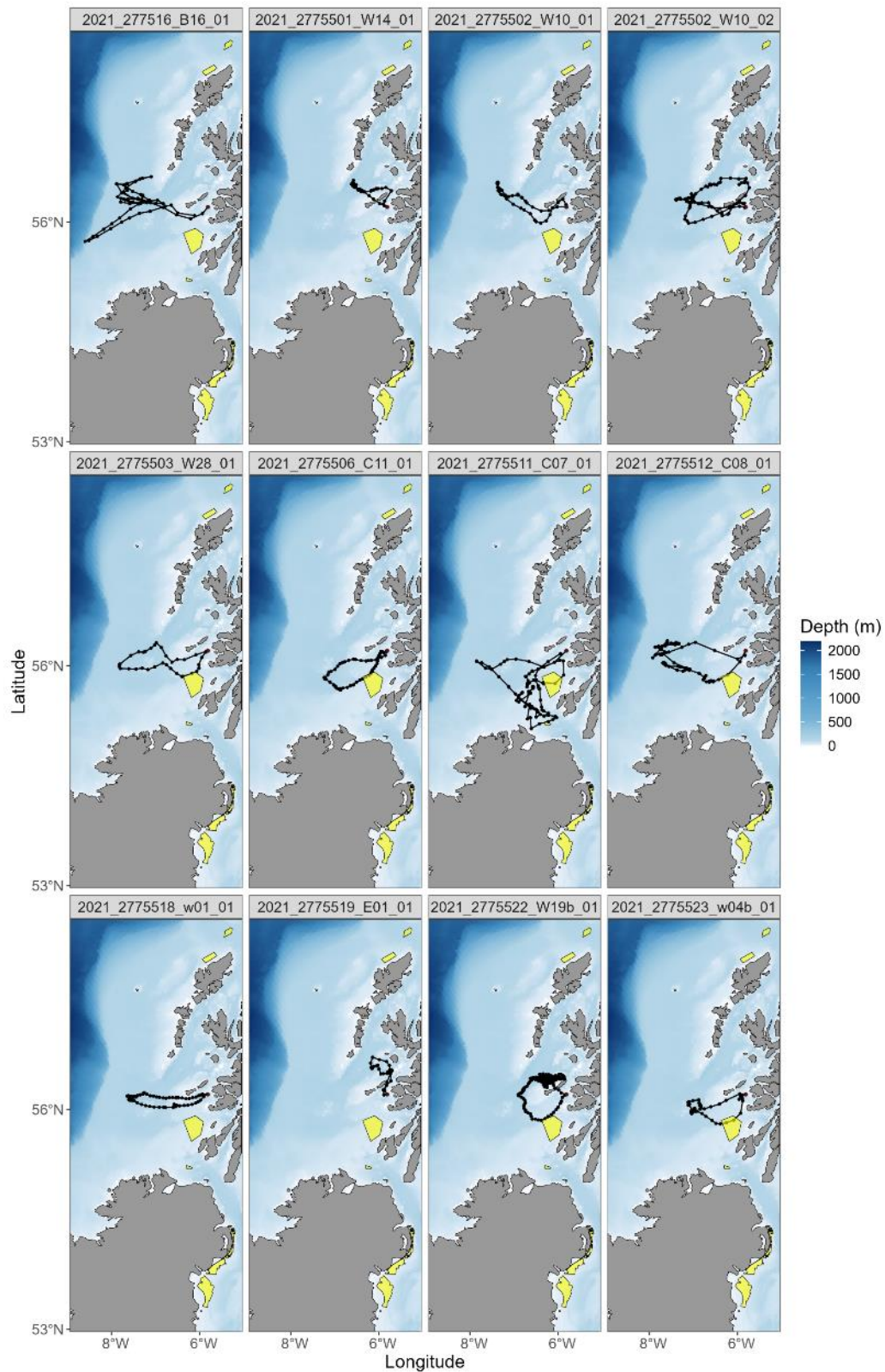


Figure 25. Plots 13 - 24 of 24 complete tracks from European Storm-petrels tracked in July and August of 2021. The yellow polygons are proposed OWF areas. Trips B16_01 and C08_01 were labelled as “Almost Complete” because the tag failed before the birds had fully returned to the colony but were sufficiently complete to include in summaries of maximum distance and direction.

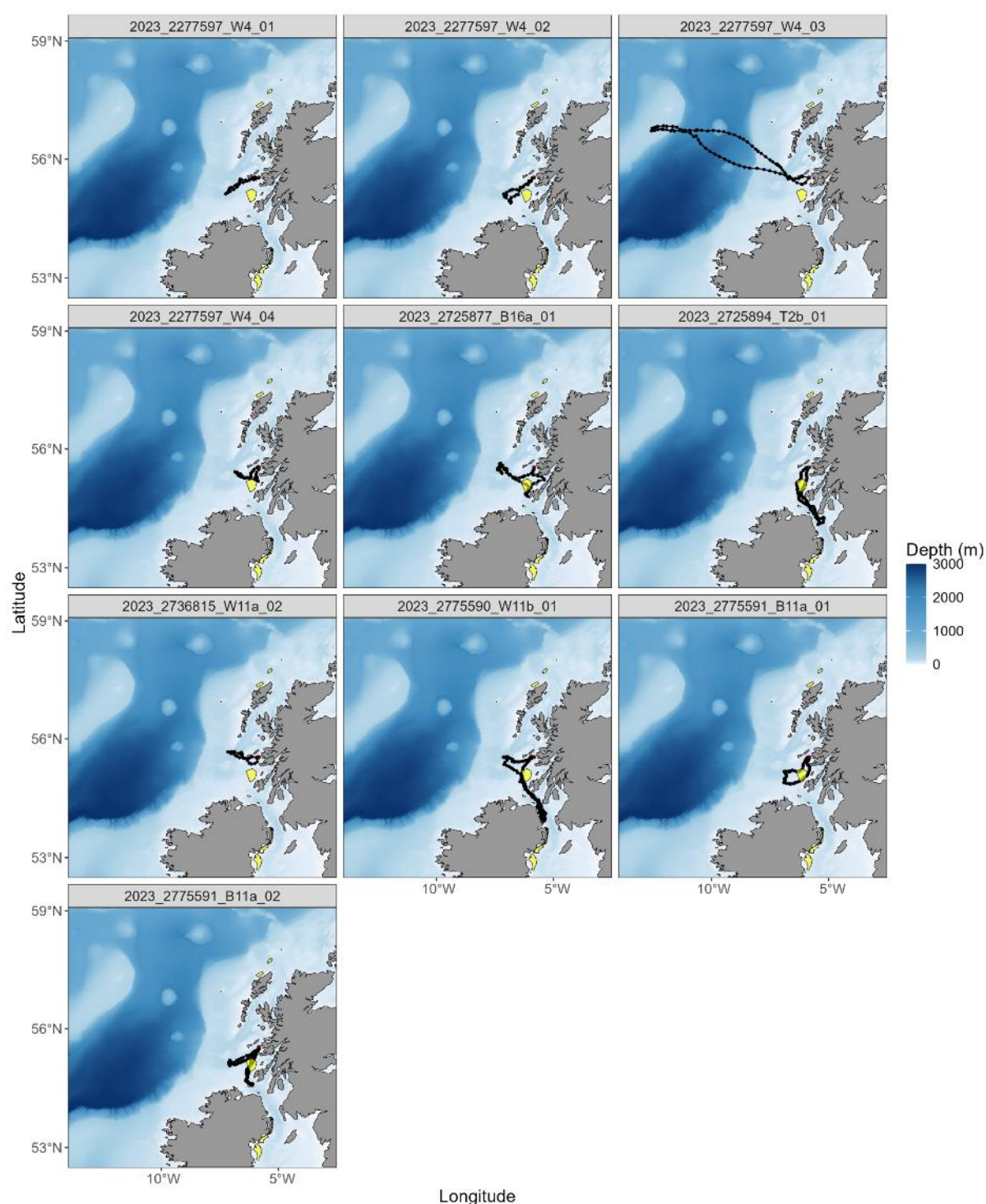


Figure 26. Plot of complete trips (1 – 10) from birds tracked in July and August of 2023. The yellow polygons are proposed OWF areas. The maps are plotted on a wider extent to account for birds in 2023 travelling further than in 2021 and 2024.

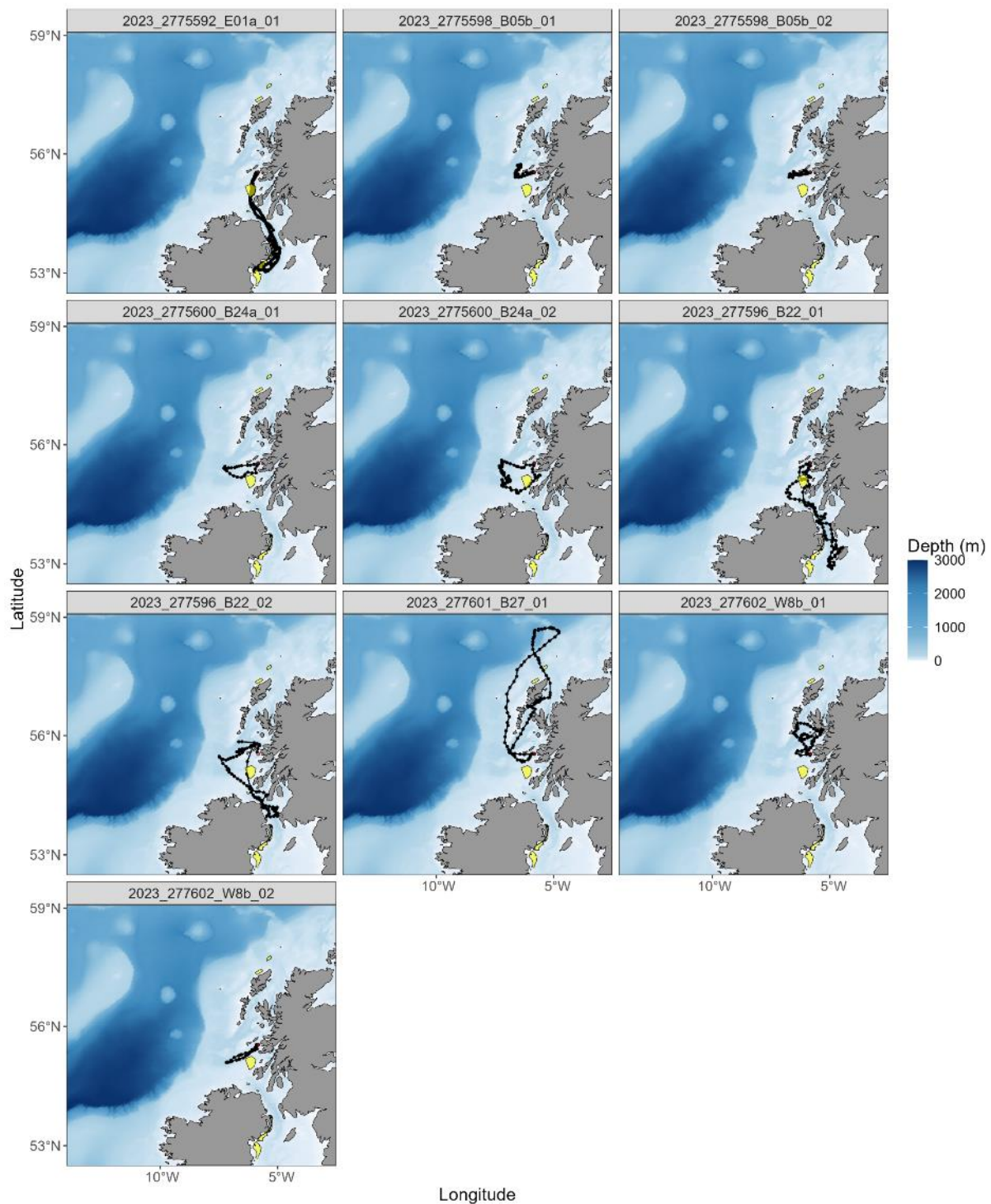


Figure 27. Plot of complete trips from birds tracked in July and August of 2023. The yellow polygons are proposed OWF areas. Trips B22_02 and B27_01 were labelled as “Almost Complete” because the tag failed before the birds had fully returned to the colony but were sufficiently complete to include in summaries of maximum distance and direction. The maps are plotted on a wider extent to account for birds in 2023 travelling further than in 2021 and 2024.

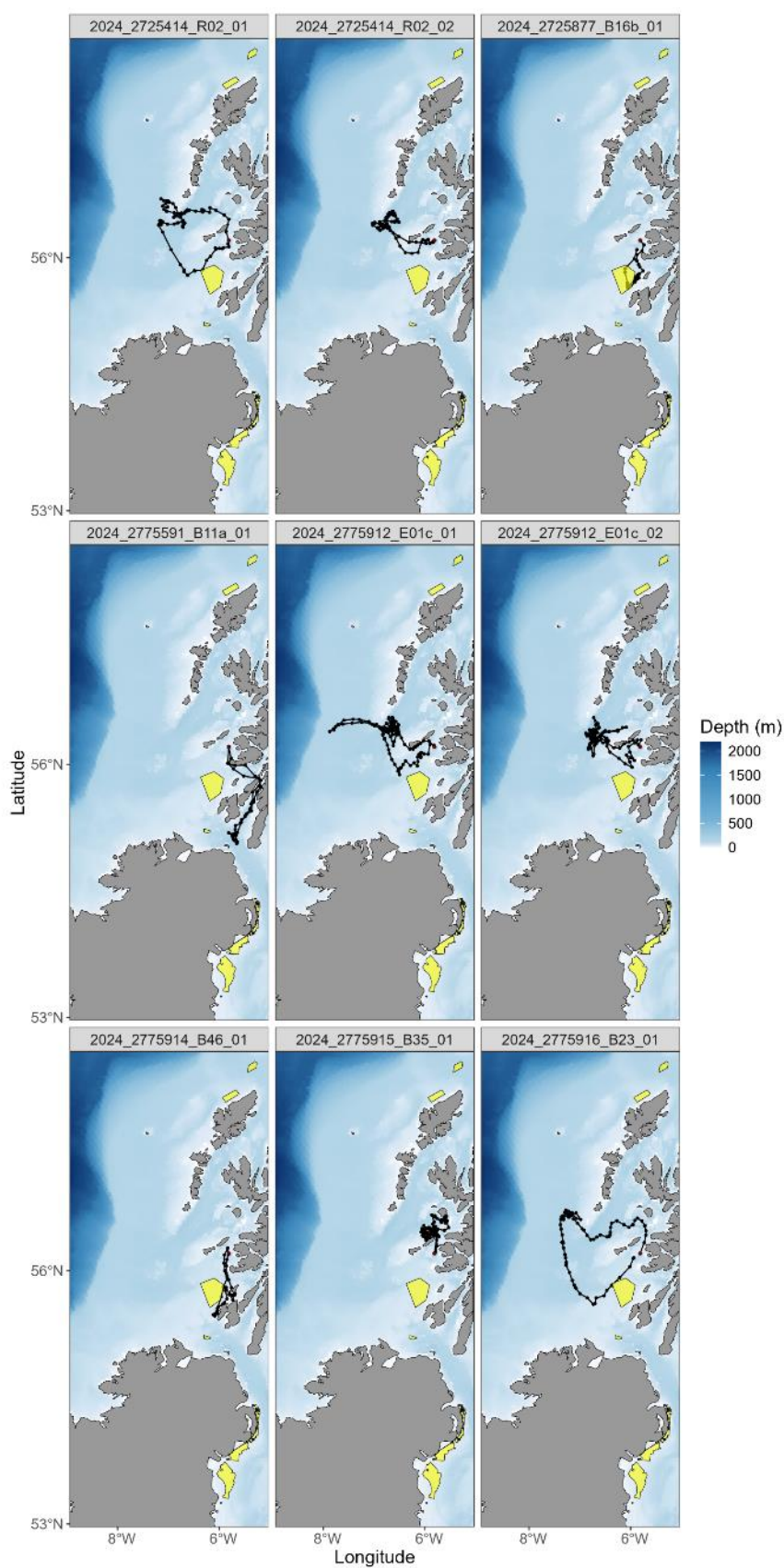


Figure 28. Plot of complete trips from birds tracked in July and August of 2024. The yellow polygons are proposed OWF areas.

Figures 29 - 31 present the movements of all European Storm-petrels tracked from Lunga, Treshnish Isles in 2021, 2023 and 2024

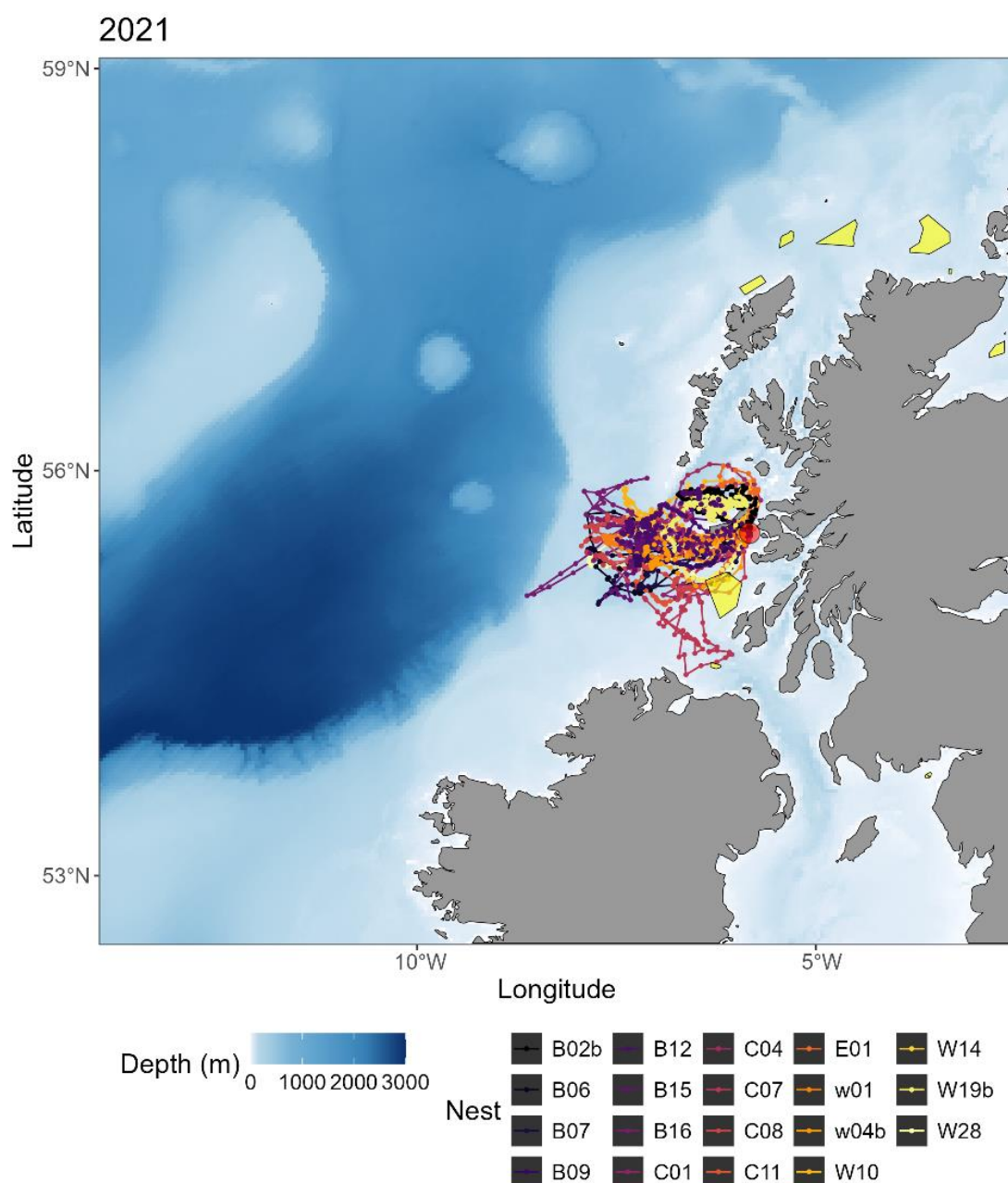


Figure 29. The raw location data from all tracks of European Storm-petrel tracks recorded from the Treshnish colony (indicated by a red circle) in 2021 including partial trips. Scottish OWF lease areas are represented as yellow polygons (Crown Estate 2021).

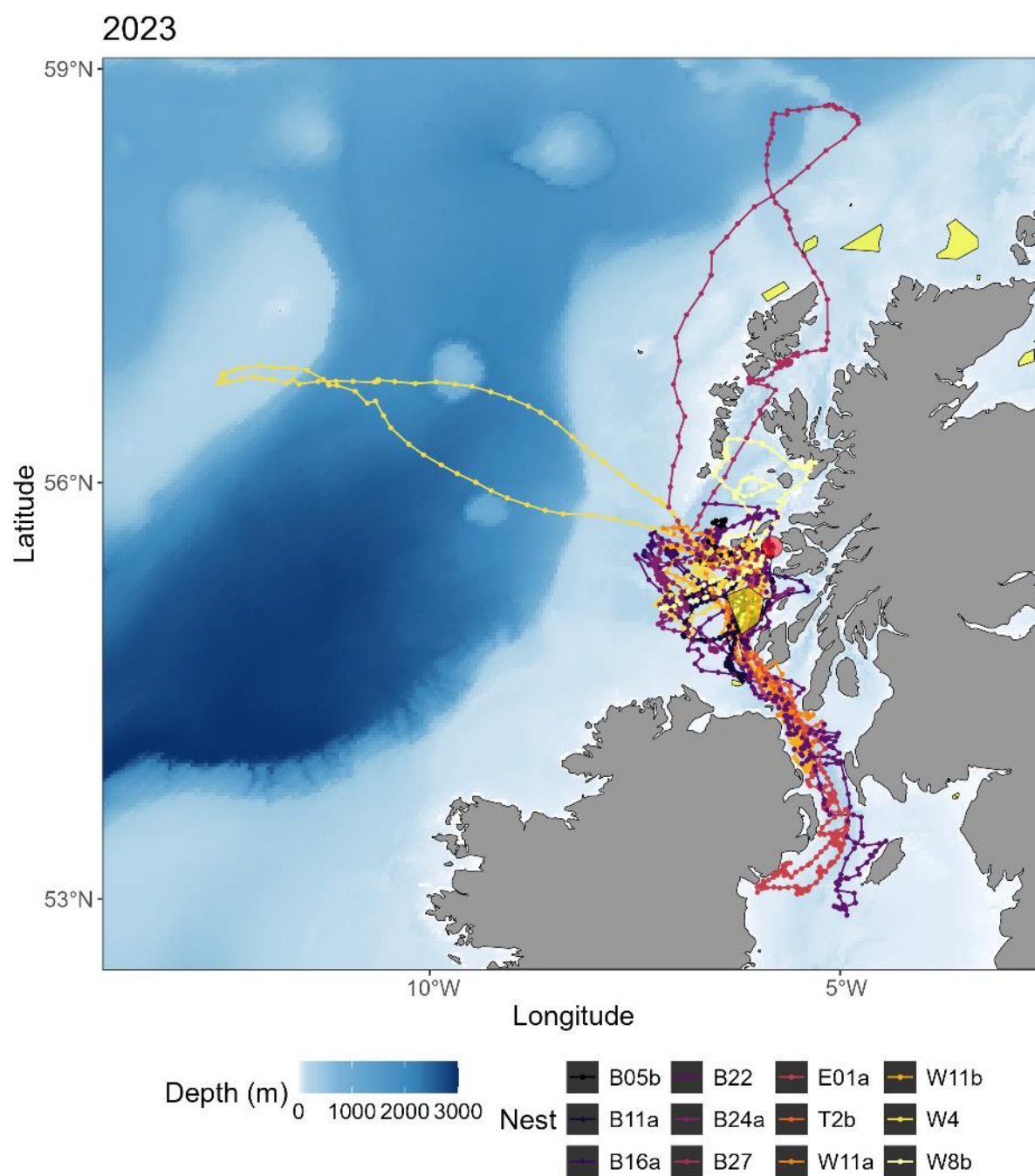


Figure 30. The raw location data from all tracks of European Storm-petrel tracks recorded from the Treshnish colony (indicated by a red circle) in 2023 including partial trips. Scottish OWF lease areas are represented as yellow polygons (Crown Estate 2021).

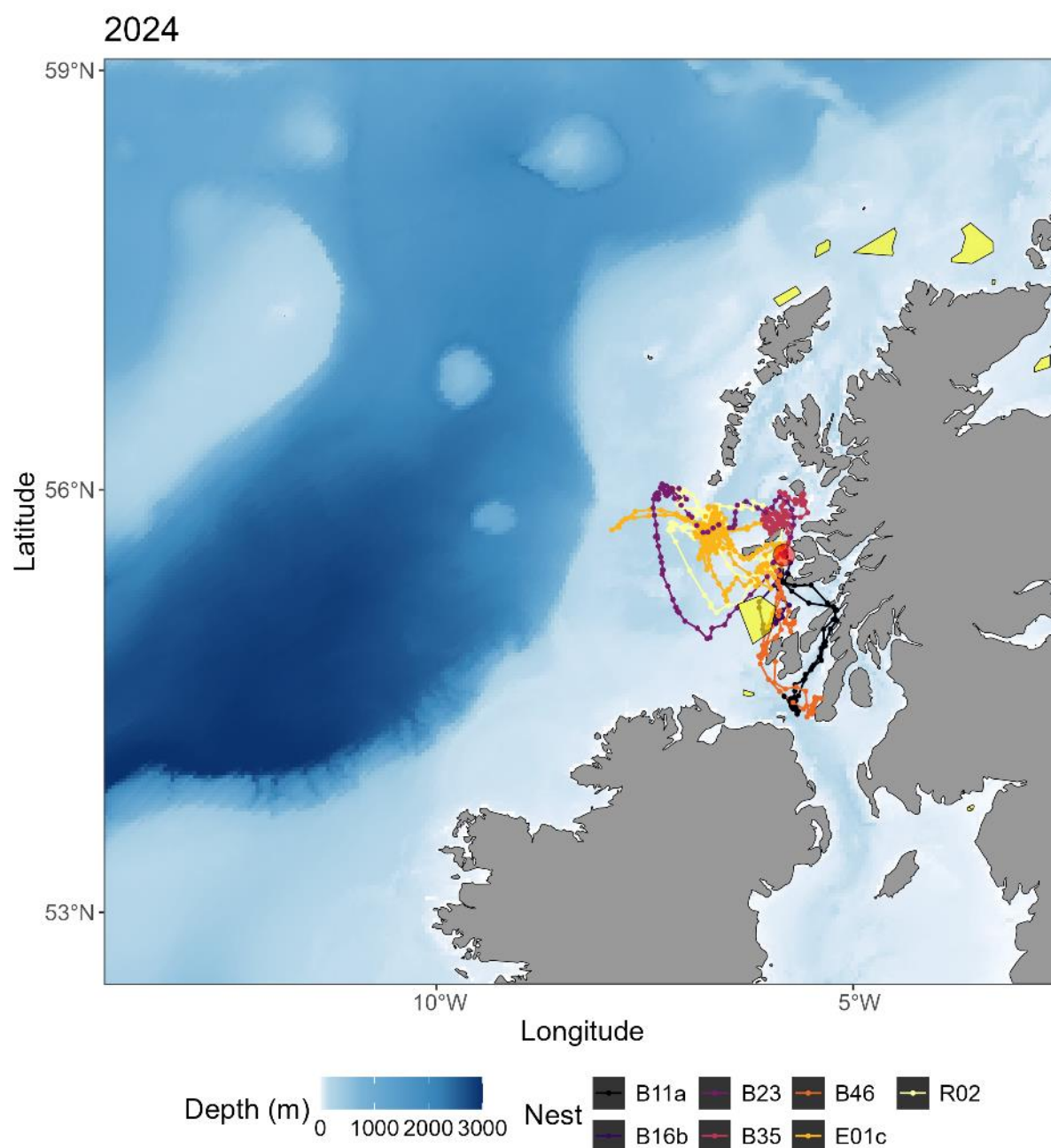


Figure 31. The raw location data from all tracks of European Storm-petrel tracks recorded from the Treshnish colony (indicated by a red circle) in 2024 including partial trips. Scottish OWF lease areas are represented as yellow polygons (Crown Estate 2021).

4.5.2.1 European Storm-Petrel Utilisation Distributions

The utilisation distributions (UDs) of European Storm-petrel in Figure 32 highlight the core foraging and home range of the tracked birds. The 25% UD highlights the importance of an area to the north of Coll and Tiree, particularly during the daytime (Figure 32B). As expected, the night-time UD was concentrated around the colony (Figure 32C). The UD for 2021 (Figure 32D) and 2024 (Figure 32F) were broadly similar with however in 2023 (Figure 32E) the core range (50% UD) was located further to the south and the 2023 home range (95% UD) extended further north and south of the colony than in 2021 and 2024. This reflects the significantly larger variation in maximum distance from the colony observed in 2023 (57.4 km – 483.5 km) compared to the other years (Table 3). In 2021, a small number ($n = 5$) of birds were tracked during the incubation stage of the breeding cycle. The difference in UD supports the results of the trip analysis which indicated a within-year difference between the foraging strategy of incubating birds (Figure 32G) and those who were attending chicks (Figure 32H).

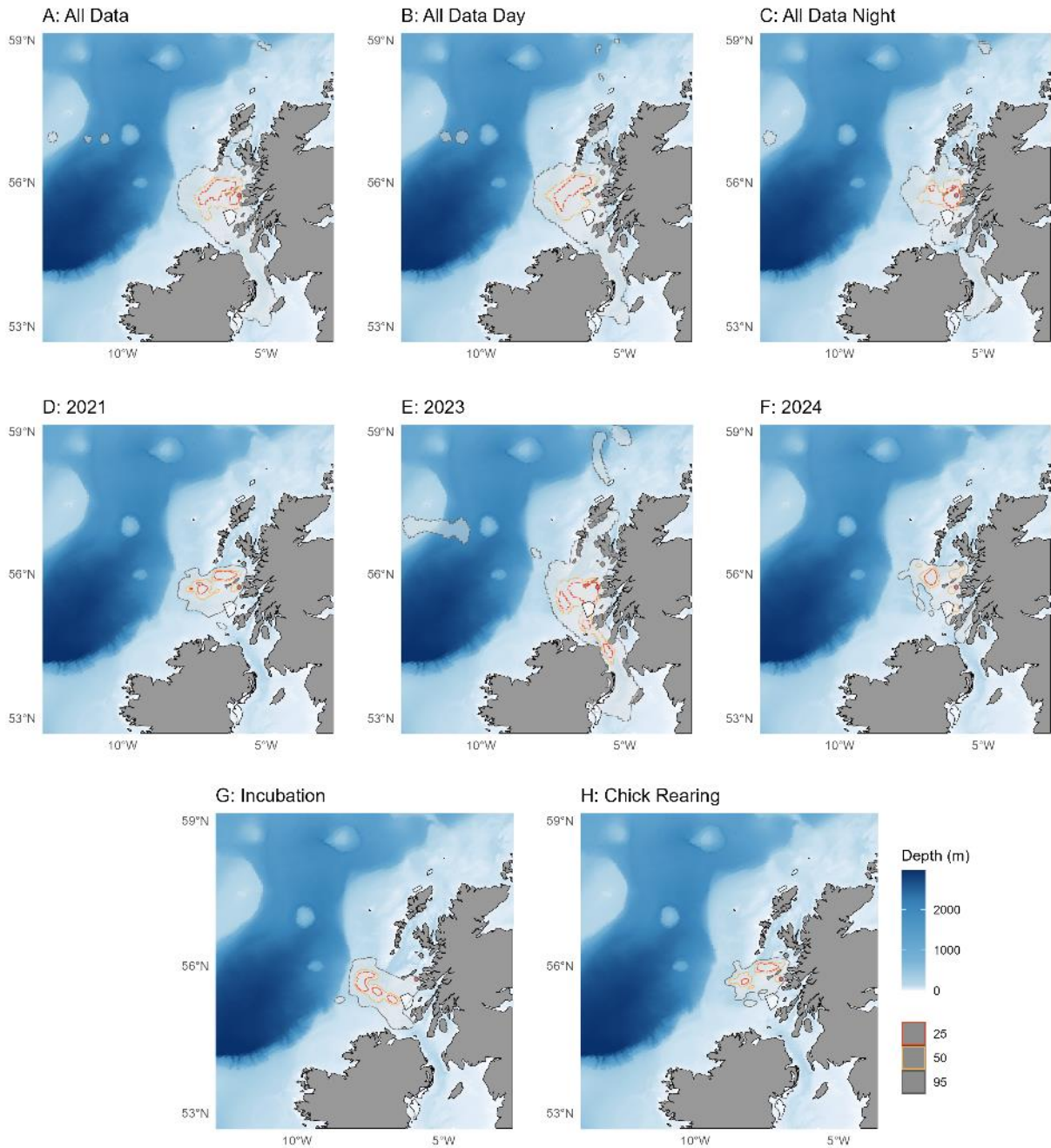


Figure 32. Utilisation distributions (UDs) of Foraging European Storm-petrels represented by 25%, 50% and 95% kernels. Panel A shows the overall UD, panels B and C display the UD for different times of day, panels D – F display the UD of birds tracked in each year (2021, 2023 and 2024), panels G and H display the UD for birds tracked in 2021 only split by breeding phase.

4.5.2.2 European Storm-petrel foraging habitat selection

Based on the forward stepwise model selection approach, the final model for European storm-petrels on Lunga incorporated non-linear smoothers for log-transformed distance from the colony, seabed slope, log-transformed NPP, and the chlorophyll gradient (Table 10). Among these covariates, we also included an interaction between distance from the colony and the time of observation (day vs. night).

We found a clear negative association between European Storm-petrel habitat use and log-transformed distance from the colony during daylight hours, with usage decreasing sharply, particularly after birds were approximately 50 km from the colony (Figure 33). During the night, habitat use also tended to decline with increasing distance from the colony; however, there was evidence of a slight peak in habitat use at approximately 100 km from the colony (Figure 33). It is important to note that the ratio of daytime to night-time observations was 70/30, which introduces a higher level of uncertainty in estimates of behaviour during the night.

We found a positive relationship between seabed slope and habitat usage, with habitat use increasing as seabed slope rose up to a value of approximately 1.5. Beyond this point, the relationship between seabed slope and habitat usage levelled off (Figure 34). For context, the 10%, 50%, and 90% quantiles for seabed slope across the observed and available locations in the European Storm-petrel dataset were 0.12, 0.45, and 1.52, respectively. This suggests that birds tended to use areas with steeper slopes within their observed foraging range.

Habitat usage was highest in areas characterized by low levels of NPP, then levelled off for NPP values between 10 and 25 mg/m³/day (Figure 35). Beyond this point, there was weak evidence suggesting a further decline in habitat usage as NPP increased. However, the estimated 95% confidence intervals were quite wide for higher NPP values which were rarely observed in the dataset. Additionally, habitat usage also declined as the magnitude of chlorophyll gradient increased (Figure 36).

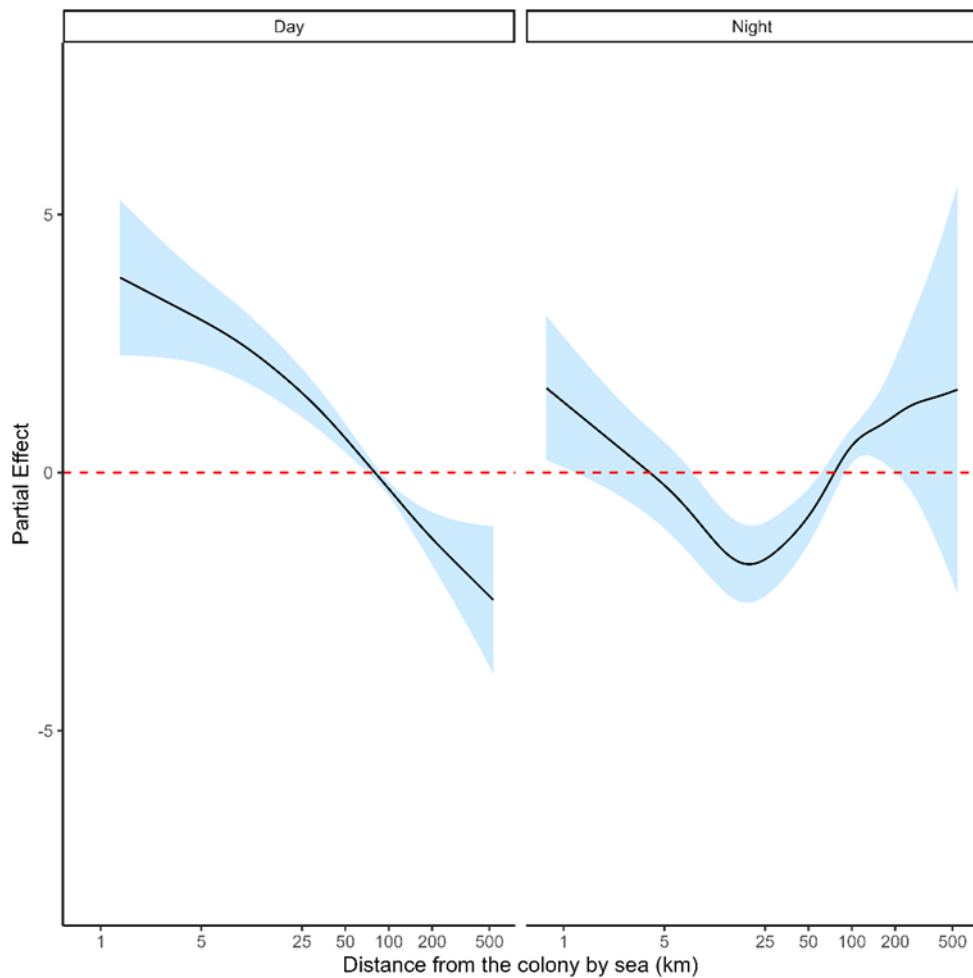


Figure 33. Partial effect plots showing the contribution of log-transformed distance from the colony, during either day or night, on habitat usage from an SSF for European Storm-petrels breeding on Lunga. The plot illustrates the component contribution of each term in the model to the linear predictor. A 95% CI envelope around model estimates is displayed as a shaded blue polygon. The horizontal dashed line represents where the y-axis is 0. Note that the y-axis on these plots is centred around 0 due to the smoothers having a sum-to-zero identifiability constraint, which is required for the model to include multiple smooths and remain identifiable. The x-axis displays distance from the colony on the log scale.

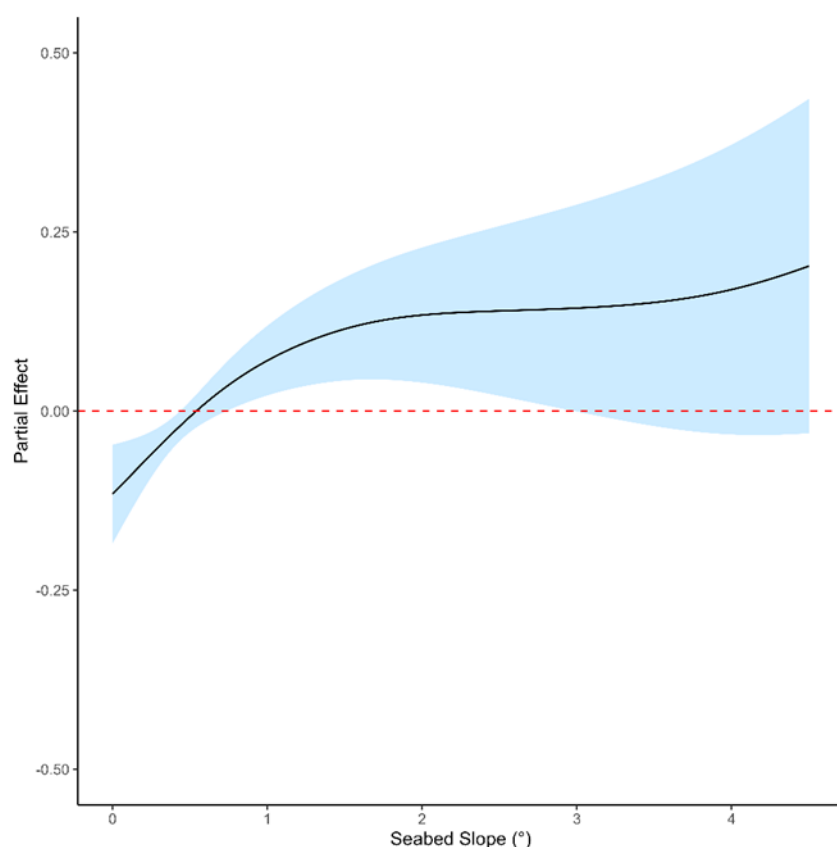


Figure 34. Partial effect plots showing the contribution of seabed slope on habitat usage from an SSF for European Storm-petrels breeding on Lunga. A 95% CI envelope around the model estimates is displayed as a shaded blue polygon. The horizontal dashed line represents where the y-axis is 0. For ease of visualization, the right-hand x-axis is truncated at the 99% quantile of observed and available seabed slope values in the model. Beyond this point, the model-estimated 95% CI envelope becomes extremely wide.

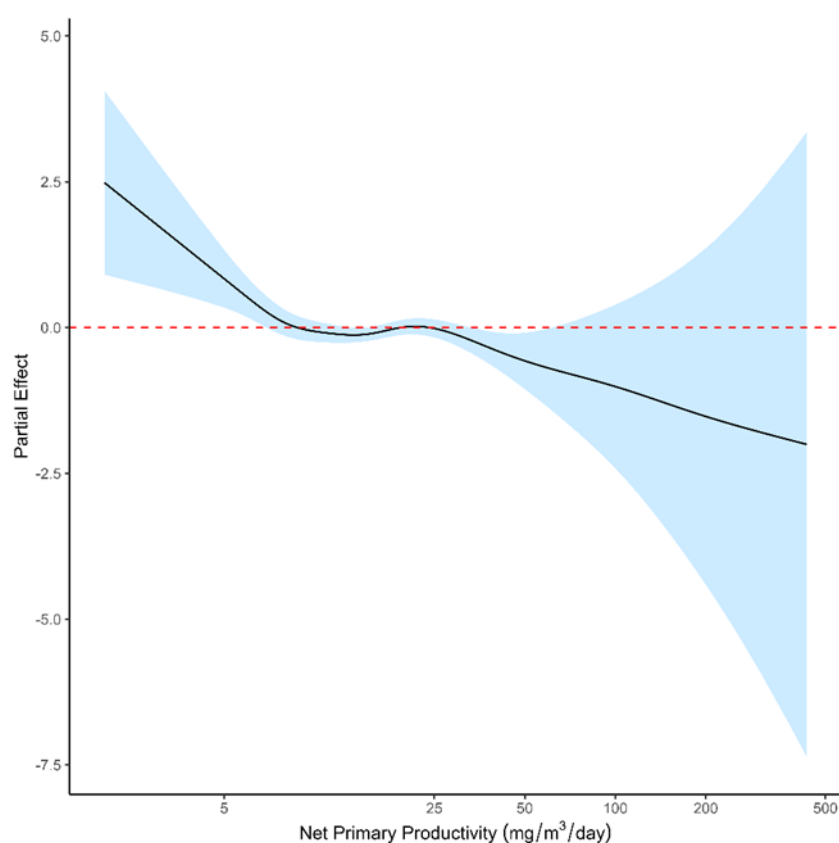


Figure 35. Partial effect plots showing the contribution of log-transformed NPP on habitat usage from an SSF for European Storm-petrels breeding on Lunga. A 95% CI envelope around model estimates is displayed as a shaded blue polygon. The horizontal dashed line represents where the y-axis is 0. The x-axis displays NPP on the log scale.

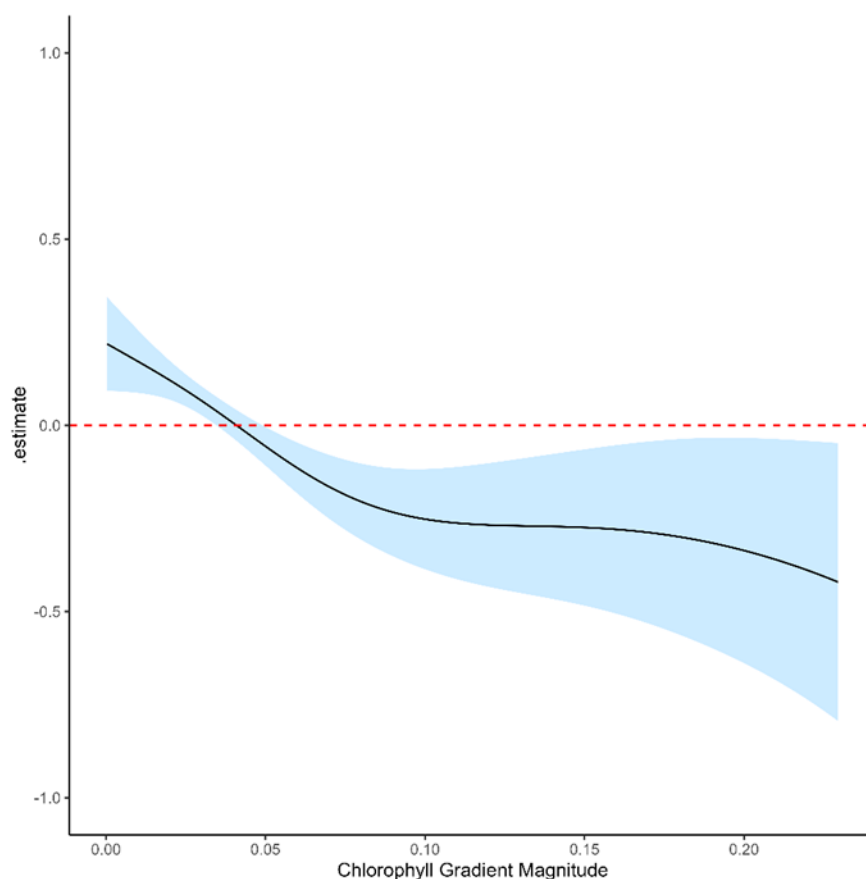


Figure 36. Partial effect plots showing the contribution of the magnitude of chlorophyll gradient on habitat usage from an SSF for European Storm-petrels breeding on Lunga. A 95% CI envelope around model estimates is displayed as a shaded blue polygon. The horizontal dashed line represents where the y-axis is 0.

4.6 Overlap with Offshore Wind Farm lease areas

4.6.1 Leach's Storm-petrel

Leach's Storm-petrels tracked from the breeding colony on St Kilda were observed to consistently use an area to the NNW of St Kilda, remote from current offshore windfarm development areas. Therefore, it is not expected that OWFs included in the current leasing round will impact birds from this colony. The data provide a useful base line for potential future assessments of the impact of marine activities such as shipping and other human activities.

4.6.2 European Storm-petrel

Across all years a total of 19 out of 38 tracked European Storm-petrels accessed leased OWF areas (Figures 37 - 39). The OWF sites accessed were: Machair Wind (Machair Wind Ltd), Talisk Offshore Wind Project (Magnora Offshore Wind N3), Malin (Malin Sea Wind Limited), Lease Area 18 - Northern Ireland (No further Information available) and the Clogherhead OWF lease area off the east coast of the Republic of Ireland. For the 19 birds accessing OWF areas, the proportion of time per trip at sea within OWF sites ranged from 0.03 – 35.2%. Across all tracked birds this equates to a mean of $2.1 \pm 5.7\%$ of time at sea occurring within OWF areas. The OWF area leased to Machair Wind Ltd located to the south-west of Mull falls within the core range (50% KDE) of birds from Lunga (Figure 32). Eighteen of the 19 birds which interacted with OWFs passed through this area (Figures 37 – 39). The other bird which interacted with an OWF area passed through the Talisk Offshore Wind Project area near North Rona. One of the birds tracked in 2023 which travelled south to the Irish Sea passed through an OWF area in Irish waters in addition to the Machair Wind site.

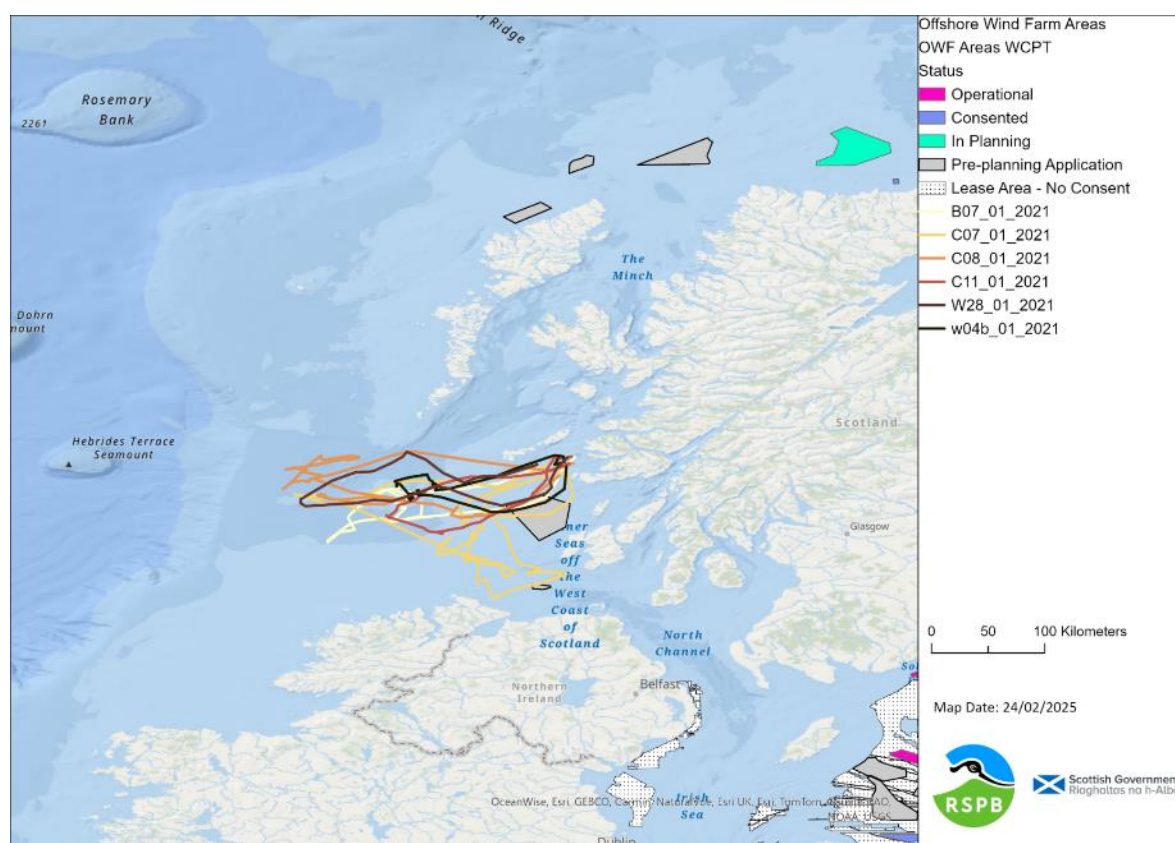


Figure 37. Tracks of European Storm-petrels which appear to have passed through or near to an OWF lease area in 2021. Map produced in Arc GIS Pro (ESRI 2021) using data published on the Crown Estate spatial hub (Crown Estate 2021) and Open Data Ireland (Marine Renewable Energy Ireland (MaREI) 2021).

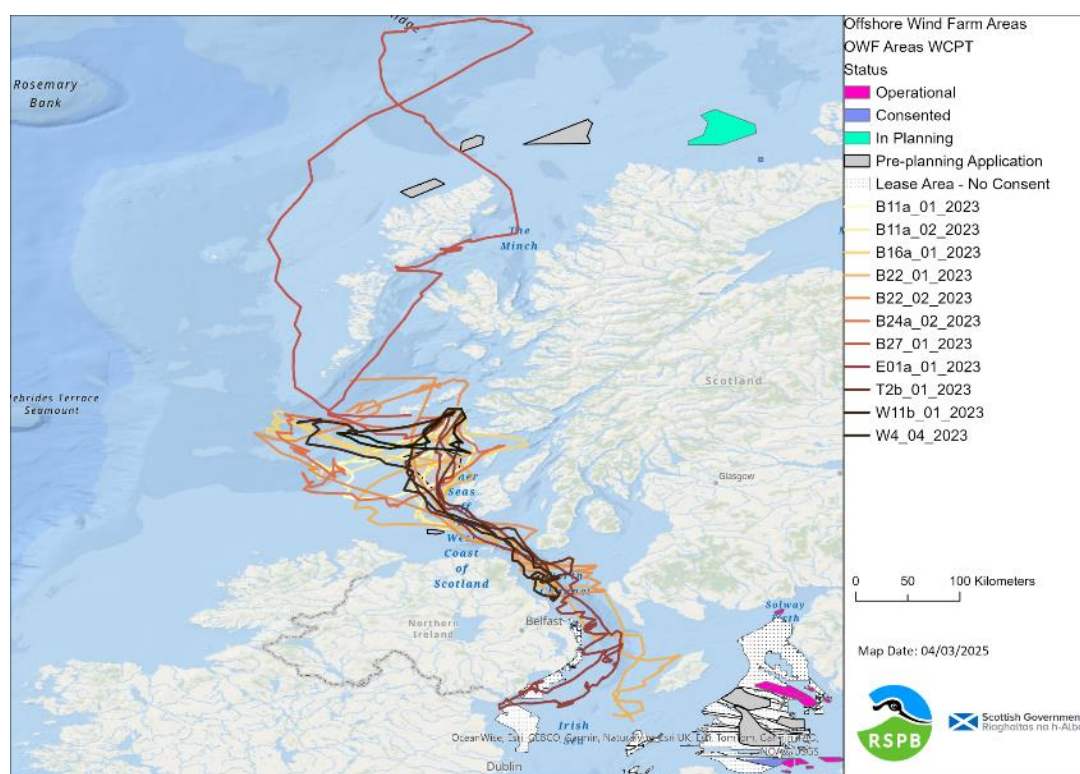


Figure 38. Tracks of European Storm-petrels which appear to have passed through or near to an OWF lease area in 2023. Map produced in Arc GIS Pro (ESRI 2021) using data published on the Crown Estate spatial hub (Crown Estate 2021) and Open Data Ireland (Marine Renewable Energy Ireland (MaREI) 2021).

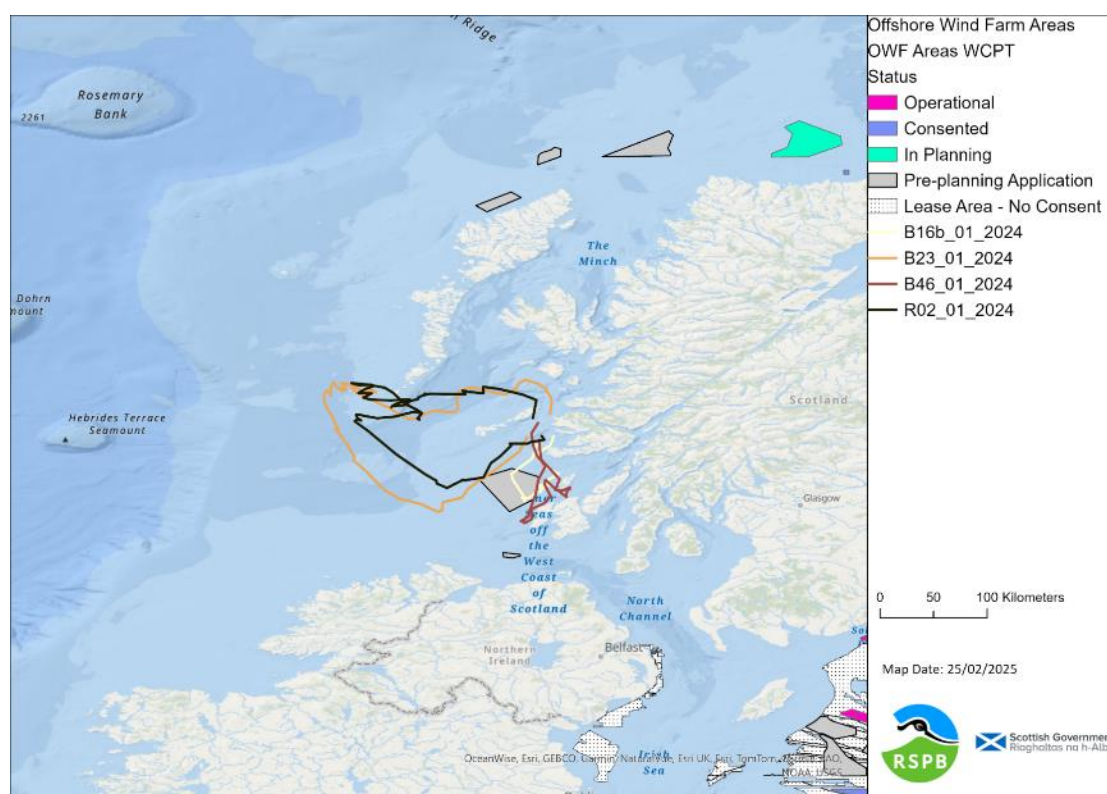


Figure 39. Tracks of European Storm-petrels which appear to have passed through or near to an OWF lease area in 2024. Map produced in Arc GIS Pro (ESRI 2021) using data published on the Crown Estate spatial hub (Crown Estate 2021) and Open Data Ireland (Marine Renewable Energy Ireland (MaREI) 2021).

4.7 GLS tracking

Device effects

Three of 20 Leach's Storm-petrels that had been fitted with GLS tags in 2021 were recaptured in 2023, compared with 11/20 control birds recaptured. Two of the GLS-tagged birds had suffered leg injuries that resulted in the loss of the ring bearing the tag. The other individual retained the GLS tag, which was removed. Close inspection of its leg revealed no sign of injury. One of the control birds recaptured in 2023 had also suffered a similar leg injury, on the unringed leg, which had occurred since it was ringed in 2021.

It is highly likely the injuries observed, and low recapture rates, were caused by the GLS tag deployment, possibly exacerbated by the inability to retrieve tags in 2022. In light of these negative impacts, no further GLS tag deployments were made on Leach's Storm-petrels in 2023.

None of the 20 European Storm-petrels fitted with GLS tags in 2021 were retrapped, in 2023 compared with 7 of 22 controls re-encountered in 2023 (including one bird found freshly depredated by a Short-eared Owl *Asio flammeus*). It is highly likely that the low recapture rates were caused by the tag deployment, possibly exacerbated by the inability to retrieve tags in 2022. No further GLS tag deployments were made on European Storm-petrels in 2023.

In light of these low recapture rates, and likely impacts of ring-mounted GLS tags, Mark Bolton consulted widely with other researchers using the same, or similar, methods to fit GLS tags to a range of Storm-petrel species elsewhere in Europe (Norway, Spain, Iceland, Azores) and Canada. As a result, it became apparent that whilst some studies had been successful, achieving high return rates and no signs of injury, others have encountered similar problems of low (or zero) recapture rates and birds with leg injuries. The group of researchers agreed to supply data on ring size and design, fitting method, and recapture rates of tagged birds and controls. The information was compiled into a database, comprising 57 studies, which indicated that the likely cause of the problems encountered by some workers were due to small differences in ring size, leading to ring fit being slightly too tight on occasion. Agreement has been reached on best-practice ring design, size and fitting method, and the need for adequate controls in future GLS tagging studies, to assess potential impacts. It is expected that as a result of these changes, it will be possible to resume GLS tagging of Storm-petrels in UK.

Movements of Leach's Storm-petrel outside the breeding season

Data obtained from the single GLS tag retrieved from a Leach's Storm-petrel in 2023, tagged during incubation in July 2021, indicate that it continued to undertake several further incubation shifts (shown by whole days of light shading of the tag as the bird remained in its nest burrow, Figure 40) and commenced migration in mid-September (shown by the abrupt divergence of recorded light intensities from the local light cycle), suggesting it bred successfully. The locations show a southward migration to the west of Ireland, rather than an alternative route through the Irish Sea. Thereafter it travelled to waters off Mauritania (October) and Benguela (December) followed by a trans-Atlantic westward movement to waters of the central Atlantic between January and March (Figure 41). The tag battery unfortunately did not last for the whole deployment, meaning that no data was collected on the bird's return migration.

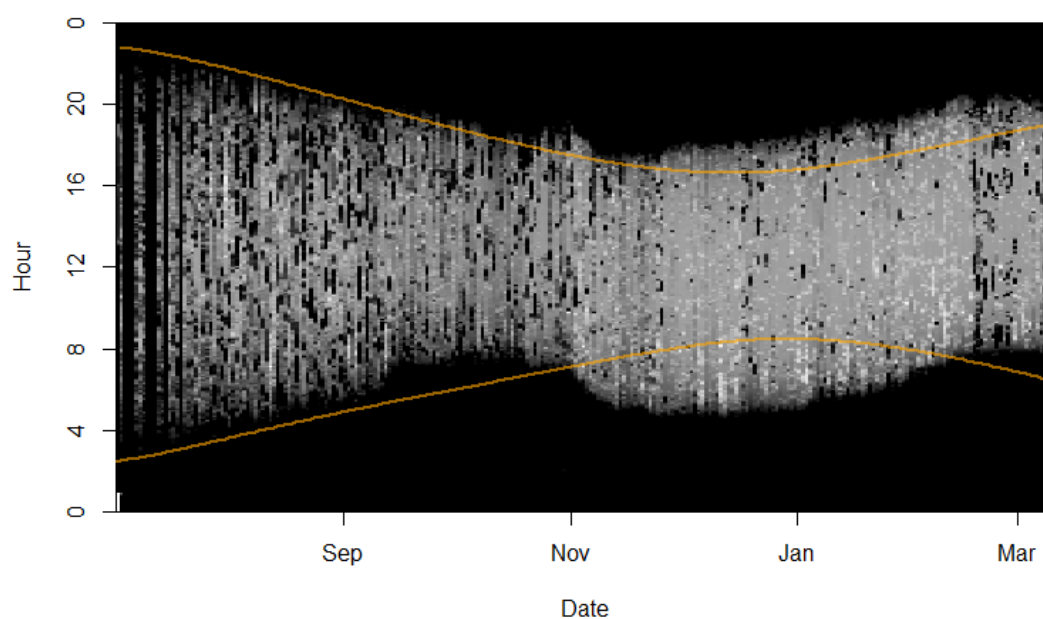


Figure 40. Light-intensity data from the single recovered geolocator deployed in July 2021 on a breeding Leach's Storm-petrel. Each day is represented by a thin vertical line with the light values plotted over time (in order from bottom to top) as greyscale pixels (dark = low light, white = maximum light). The orange curves show the timing of dawn and dusk at the nest location.

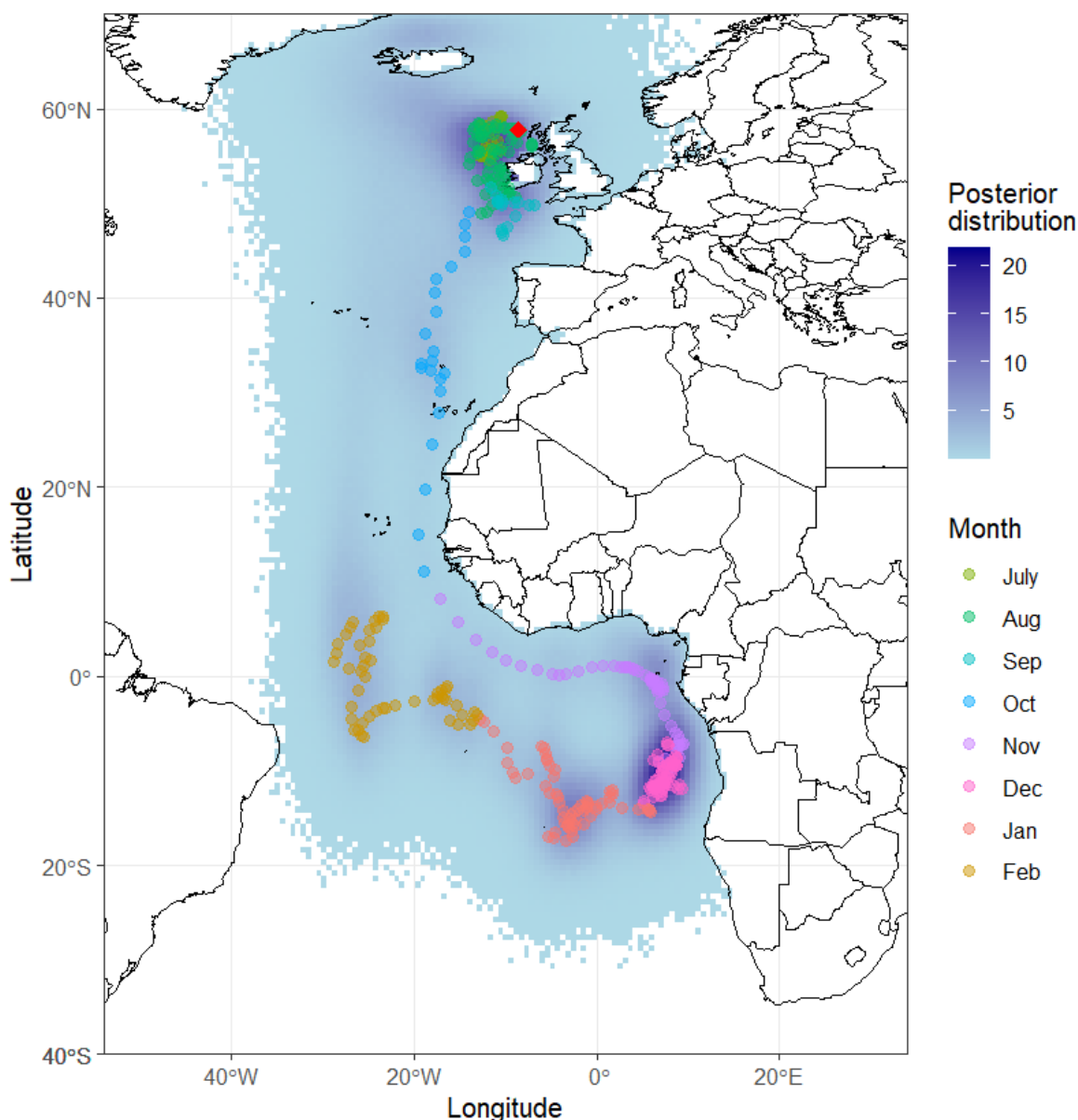


Figure 41. Geolocator data processed using SGAT for a Leach's Storm-petrel breeding on St Kilda (colony indicated by the red diamond). Twice-daily means for the posterior probability are shown as points (coloured by month), and kernel densities associated with the posterior probabilities (representing the uncertainty in geolocator location estimates) are shown from light blue (low probability) to dark blue (high probability). Note, unreliable data around the spring and autumn equinoxes has been removed.

4.8 HPAI impact assessment

Eight blood samples from Leach's Storm-petrels and one from European Storm-petrels were adequate for analysis (by the Animal and Plant Health Agency), and all tested negative for antibodies to Avian Influenza virus.

5. Discussion

5.1. Numbers of Storm-petrels tracked and evidence of impacts on welfare and foraging behaviour

Despite restrictions on fieldwork imposed by the Covid pandemic in 2020 and the outbreak of HPAI in 2022, the extended project achieved the stated objectives of tracking a minimum of 10 individuals of breeding Leach's and European Storm-petrels annually with GPS tags (except for European Storm-petrels in 2024), and the total numbers of individuals tracked across the three years of fieldwork (50 Leach's and 38 European Storm-petrels) considerably exceeded the initial objectives to track a total of 20 individuals of each species during the course of the initial project (10 birds a year for two years). There was no evidence of any impacts of GPS tagging on either species. There were a few occasions when birds returned to the colony during the egg stage but did not enter the nest to resume incubation which may have resulted from nocturnal fieldwork activity in the colony.

In contrast to GPS tracking, the use of ring-mounted GLS tags to obtain information on migration and wintering areas was not successful. The extremely low tag retrieval rates (1/20 and 0/20 for Leach's and European Storm-petrels respectively) may have been exacerbated by the inability to attempt recaptures in the year following deployment. Due to fieldwork restrictions on all seabird research imposed by NatureScot as a result of HPAI in 2022, we were unable to attempt retrieval of tags deployed in July 2021 until July 2023. However, the recapture of appreciable numbers of control birds (11/20 Leach's Storm-petrels and 7/22 European Storm-petrels) and the recapture of two Leach's Storm-petrels that had suffered leg injuries and lost their GLS tags provides strong evidence that GLS tagging was the principal cause of the low recapture rates. Other researchers have encountered similar problems with the use of ring-mounted GLS rings, which are likely to be due to the use of rings that are slightly too close-fitting. As a result of work conducted during the course of this project, recommendations have been made to all those working on Storm-petrel species globally concerning the size, design and methods of fitting ring-mounted GLS tags. As a result of the development of best-practice procedures, it is likely that GLS tracking of Storm-petrel species in UK will be permitted to resume in future projects.

5.2. GPS tracking of Leach's Storm-petrels breeding on St Kilda

A total of 78 complete foraging trips were obtained from tracking 50 individual Leach's Storm-petrels across three breeding seasons (2021, 2023 and 2024). The GPS data revealed a highly consistent pattern of space use across breeding stages (incubation and chick-rearing) and years (Figs 18 – 20). Comparison of within-individual and among-individual space use provided no evidence of individual specialisation of foraging areas: the overlap in core space use among trips by the same individual was similar to the extent of overlap across individuals. The raw tracks and resulting utilisation distributions revealed extensive and consistent use of deep water to the North and northwest of St Kilda, with birds travelling an average of 220 - 360 km from the colony (dependent on year and breeding stage, maximum range recorded = 635km), on trips that lasted 1 - 5 days, and covered a total of 209 – 2,270 km. There was an indication that chick rearing Leach's Storm-petrels exhibited a dual foraging strategy, as observed in other procellariiform species (Phillips et al. 2023). Some birds (such as BT27476 from nest 45 in 2023, Figure 14 and NT42983 from nest 144 in 2024, Figure 16) alternated shorter duration, short-range trips (presumably to less productive areas closer to the colony), to provision the chick more frequently but at the expense of their own body condition, with longer-duration longer range trips (presumably to more productive foraging grounds), to replenish their own body condition.

Modelling of marine distribution using a step-selection function confirmed the selection of deep water (peaking at around 1,500m) and higher sea surface temperatures during daylight. In this case, lower SST values were more common in the northern part of the species foraging range for example the lowest SST values we observed < 12°C occurred exclusively above 58.75 decimal degrees north. The daytime marine distribution of Leach's Storm-petrels breeding on St Kilda matches closely the distribution reported from extensive boat-based surveys conducted between 1979 and 1999 in the seas to the northwest of Scotland (Bloor et al. 1996, Pollock et al. 2000). Those studies reported highest abundances over the Wyville-Thompson Ridge and the Faroe-Bank Channel where they may feed largely on plankton, particularly the euphausiid shrimp *Meganctiphanes norvegica* and the copepod *Temora longicornus* (Cramp and Simmons 1977). Given the regional dominance of the breeding colony on St Kilda (both in the 1990s and currently) the vast majority of Leach's Storm-petrels recorded on boat-based surveys in the seas to the northwest of Scotland are likely to originate from St Kilda. The Faroes Islands are believed to host around 1,000 pairs (Frederiksen 2010) and The Flannans and North Rona hold a total of around 1,000 – 3,000 pairs (Mitchell et al. 2004, Burnell et al. 2023). Bloor et al. (1996) and Pollock et al. (2000) both observed that Leach's Storm-petrels commute between the feeding areas and the breeding colonies during the hours of darkness, which accounts for the absence of daylight records from the vicinity of St Kilda. Here we are able to report for the first time the marine distribution of Leach's Storm-petrels during the hours of darkness, demonstrating high densities of birds in the shelf seas surrounding, and especially to the NW of, St Kilda (Figure 21C). It is notable that we also found high densities of birds during darkness around the Ymir Ridge, to the South of the Faroes Bank, reflecting birds undertaking multi-day foraging trips remaining in the feeding areas at night. Despite travelling very large distances, and roaming over a vast area (c. 164,000 km², more than twice the land area of Scotland), we found no overlap with any areas leased for windfarm

development, due to the highly directional, and entirely pelagic distribution of Leach's Storm-petrels. The contrast in the extent of terrestrial habitat required for nesting, and marine habitat accessed for foraging is striking. The study plot within which the 50 tracked birds nested was approximately 330 m² in extent. This is an area 500 million times smaller than the extent of marine habitat accessed for foraging.

5.3. GPS tracking of European Storm-petrels breeding on the Treshnish Isles

A total of 48 complete foraging trips were obtained from tracking 38 individual European Storm-petrels across three breeding seasons (2021, 2023 and 2024). The GPS data revealed a variable pattern of space use across the three years (Figures 29 - 31). In contrast to Leach's Storm-petrel, comparison of within-individual and among-individual space use indicated a high degree of individual specialisation: the overlap in space use among trips by the same individual was considerably greater than the overlap across individuals. As a consequence, multiple trips by the same individual cannot be regarded as independent.

Whilst there were considerable differences in foraging areas among the three study years, the raw tracks and resulting utilisation distributions revealed a usage pattern that was generally restricted to shelf (neritic) seas within 140 km, and to the West, of the colony. However, in 2023 some birds roamed considerably further (up to 480 km distant from the colony), and in a wider range of directions, extending well beyond the continental shelf to the West of the Hebrides, to the North of North Rona, and into the Irish Sea South of the Isle of Man. In 2023, birds were very light, and chicks poorly fed, indicating that food availability was low. In 2024, when only seven birds were tracked, most birds remained fairly local to the colony, and used the same area to the West of Treshnish (used extensively in 2021) but a few individuals roamed more widely, towards the shelf edge and into the Irish Sea. Had a larger sample of individuals been tracked, it is possible that more extreme movements may have been recorded. It is notable that in 2023 and 2024 extensive usage of inshore waters occurred, with birds visiting coastal areas (of Lewis, Skye, Rum, Coll, Tiree, Jura, Islay, N. Ireland and The Republic of Ireland) at night. The significance of this behaviour is unclear, but European Storm-petrels are known to feed on intertidal isopods at night (D'Elbée & Hémery 1998). It is possible that inshore feeding on isopods reflects a scarcity of high-value prey in offshore areas.

Modelling of marine distribution using a step-selection function demonstrated a clear negative association between habitat use and distance from the colony during daylight hours, reflecting lower usage relative to habitat availability at greater distance from the colony. In contrast, during the night, although the association between habitat use and distance from the colony was negative for distances up to 25km (Fig. 33), beyond this range the relationship was less well defined, with increasing confidence limits at greater distances from the colony.. Within our dataset, negative associations between habitat usage and distance from the colony may be easier to detect during daylight due to the greater number of observations obtained during daylight hours. In contrast, during the night, when birds may travel back toward the colony, we recorded fewer observations at greater distances, making it more difficult to precisely estimate habitat usage in those areas. This challenge is further compounded by the short nights in summer, which resulted in fewer night-time observations overall. The reduced precision in estimating nocturnal habitat usage is reflected in the relatively wide 95% confidence intervals observed at

distances greater than ~200 km from the colony seen in Figure 33. We also found evidence of a slight peak in usage of areas approximately 100 km from the colony. The reason for this peak is unclear, though it may represent birds utilising an important area for nocturnal foraging. Supporting this, UD based exclusively on night-time GPS observations highlight an area of relatively intense space use (based on the 25% UD contours) to the south of the Outer Hebrides (Figure 32), which falls within the relevant distance from the colony. This area is also located near the boundaries of the [Stanton Banks MPA](#) which encompasses a series of granitic ridges rising from 190 m to within only 30 m of the sea surface and is a hotspot for other marine predators as well as European Storm-petrels (Sheehan & Power 2022, Pommier et al. 2023).

We also found a positive relationship between habitat usage and seabed slope. However, as birds were largely restricted to neritic waters a preference for greater seabed slopes largely refers to the environment experienced within the continental shelf rather than birds targeting the continental shelf break itself. For example, only a few birds were seen foraging beyond the shelf break and therefore we had relatively few observations where birds would experience the higher slope gradients associated with this habitat feature.

Habitat usage was negatively associated with both chlorophyll gradient and NPP. Regarding chlorophyll gradient the negative association suggests that European Storm-petrels were not selectively using areas closest to chlorophyll fronts (which are often co-located with thermal front gradients, Belkin and O'Reilly 2007, Xia et al. 2021). Negative associations between habitat usage and NPP may arise in part because higher NPP concentrations tend to occur close to the coast, which is avoided during daylight. Moreover, closer examination of the data revealed that the majority of observed tracking locations characterised by lower NPP values < 8.1 mg/m³/day were observed in 2021 (624 / 675 filtered locations) with most of those clustered in or around the Stanton Banks MPA where NPP values were relatively low in 2021.

More broadly, it should be borne in mind that currently our assessment of habitat selection represents a population-average response and assumes individuals respond in the same way to the environment. However, it is clear from studies on other seabirds that averaging across individuals can mask important levels of individual variation particularly if some individuals show divergent responses to the same covariate (Trevail et al. 2021, Cleasby et al. 2024). Therefore, a potential expansion of the current modelling work may be a greater consideration of such individual variation, especially considering the degree of individual specialisation we observed for European Storm-petrels.

Previous studies to map the distributions of European Storm-petrels in the waters of the West of Scotland (e.g. Pollock et al. 2000, Waggitt et al. 2020) have not shown clearly demarcated concentrations that might correspond to foraging aggregations of birds from specific colonies. Rather they have tended to find a changeable distribution during the course of the breeding season from May to September, which may reflect the influx of very large numbers of wandering immature birds from July. For example, Pollock et al. 2000 found highest densities of European Storm-petrels in June - August around the Wyville-Thompson Ridge, which is probably too remote from colonies in the Hebrides to be an area used extensively by breeding birds. Similarly, Waggitt et al. 2020 present modelled distributions derived from a large

number of at-sea surveys, and show highest densities close to the edge of the continental shelf.

Despite their small size, European Storm-petrels breeding on the Treshnish Isles travelled huge distances and roamed over a vast area (c. 40,000 km², more than half the land area of Scotland). There was considerable overlap with areas leased for windfarm development. Despite the very short duration of tracking of each individual (range 1 – 6 days), 19 of the 38 tracked birds (50%) used at least one of the areas leased for windfarm development. Across all tracked individuals, 3.5% of the distance travelled occurred within lease areas (range 0 – 28.8%). The vast majority (18/19) of individuals that accessed a lease area occurred within the Machair Wind Area, with another bird occurring within the Talisk Area to the North of Lewis. One of the individuals that occurred within the Machair Wind Area also visited the Malin Sea Wind Area.

5.4. GLS tracking of a single Leach's Storm-petrel breeding on St Kilda

The single Leach's Storm-petrel tracked from July 2021 to March 2022 using a GLS tag indicated that it departed the colony in mid September, suggesting it bred successfully. It migrated southward following a route to the West of Ireland, rather than through the Irish and Celtic Seas, and then migrated fairly rapidly southward, pausing for a few days to the North of the Canaries, and then heading rapidly past the coast of Mauritania, following the West African coast to the Benguela current, where it spent a month (December) before heading West to waters around St Helena and Ascension. The tag battery failed in March as the bird was returning northward in the mid-Atlantic. This represents the first information on the migration of Leach's Storm-petrels breeding in UK – there have been no overseas recoveries of any ringed birds from UK colonies. Tracking of 13 individuals from colonies in Canada (Pollet et al. 2019) revealed a trans-Atlantic migration route, to the coast of West Africa, with similar stop-over areas in the Benguela current and the mid-Atlantic around the equator, and additional stop-overs off Mauritania. It seems likely that there is mixing of breeding populations from both sides of the North Atlantic in the migration staging and wintering areas.

5.5. Assessment of HPAI impacts

There was no evidence of any occurrence of HPAI in populations of Leach's Storm-petrels breeding on Hirta, St Kilda, or European Storm-petrels on Lunga, Treshnish Isles. The very limited number of blood samples taken in 2023 for HPAI antibody assay (n=8 Leach's and n=1 European Storm-petrels) tested negative for antibodies to any avian influenza virus. We encountered no dead Storm-petrels of either species during the course of fieldwork in 2023 or 2024. One dead Leach's Storm-petrel was encountered in 2021 (before any outbreak of HPAI among seabirds on St Kilda) at the entrance of a very wide burrow, which was likely shared with, and possibly killed by, a puffin. Whilst we did not undertake any systematic population counts during the course of this project, there was no indication that breeding densities of either Storm-petrel species in our study plots were lower in 2023 or 2024, compared with 2021. Burrow densities of Leach's petrels in the study area on Hirta appeared higher in 2024 than in 2021.

6. Conclusions

- This study represents the first GPS tracking of Leach's Storm-petrels in UK, and only the second study to track European Storm-petrels – and first from the West coast of Scotland. The techniques for capture, handling and tag attachment proved successful. No injuries occurred and the evidence available suggests that (with a few possible exceptions) pattern of nest attendance was similar to that of untagged birds. There was some evidence that a few individuals may have been deterred from returning the nest by nocturnal fieldwork activity and it is suggested that future tracking of these species employs co-deployment of micro VHF tags (0.16g) with GPS tags, that will alert fieldworkers when tagged birds arrive back at the colony, to ensure that disturbance is kept to an absolute minimum.
- In contrast to the GPS tagging, the use of ring-mounted GLS tags in this study was not successful for either species and is likely to have caused welfare impacts. As a result, all GLS tagging of both storm-petrel species ceased. However, as a result of subsequent discussions with storm-petrel researchers elsewhere in Europe and Canada, (some of whom found similar issues and others who have been successful) modified procedures have been recommended, and may now be implemented in future studies in UK.
- The tracking data provide the first information on marine space use of Leach's and European Storm-petrels known to be breeding at protected colonies on the West Coast of Scotland, unbiased by time of day, the birds' activity or observation conditions.
- There was little inter-individual and inter-annual variation in marine space use among the three years of tracking for Leach's Storm-petrel, whereas for European Storm-petrel we found greater variation in space use among both individuals and years. For both species, the sample of foraging trips obtained represented the expected colony-level distribution well (representativeness scores of 89.3% and 81.5% for Leach's and European Storm petrels respectively).
- In broad terms, pattern of marine distribution align with boat-based survey data collected several decades ago (Webb et al. 1990, Bloor et al. 1996, Pollock et al. 2000), showing the use by Leach's Storm-petrels of deep water offshore areas associated with underwater bathymetric features, and use by European Storm-petrels of neritic waters closer to the colony. Modelling of habitat use showed Leach's Storm-petrel densities increased as water depths increased from 200m to 1000m and an association with higher Chl and higher sea surface temperatures. European Storm-petrel distribution was positively associated with seabed slope, and negatively associated with Net Primary Production and chlorophyll gradient.

- The night-time core usage areas of both species were centred closer to the breeding colonies compared with the respective daytime distributions, reflecting the restriction of colony attendance to the hours of darkness. In addition, European Storm-petrels were highly coastal at night, visiting many inshore areas in the Minches, Hebridean and Irish Seas, possibly associated with nocturnal intertidal foraging.
- Both species used extremely large marine areas. The 95% UD of Leach's Storm-petrels covered an area of c. 164,000 km (twice the land area of Scotland) and that of European Storm-petrels extended c. 40,000 km. Despite usage of extremely large marine areas, we found no overlap in space use by Leach's Storm-petrels breeding on St Kilda with areas leased for offshore windfarm development, due to the remote location of the colony, and highly directional foraging movements towards the northeast, to deep water areas. In contrast, we found considerable overlap between area use by European Storm-petrels and offshore windfarm lease areas, reflecting the less remote location of the breeding colony and expansive use of shallow shelf seas, including inshore areas at night. Nineteen of 38 tracked European Storm-petrels passed through at least one offshore windfarm area, and 18 of these birds accessed the Machair Wind site, which lies within the colony-level core foraging area (50% UD). A further four offshore windfarm areas were accessed, including the Talisk area to the North of the North Rona and sites off Northern Ireland and the Republic of Ireland.
- Having demonstrated considerable spatial overlap between areas used by European Storm-petrels and offshore windfarm development areas, and extensive nocturnal movements of storm-petrels, future research should focus on accurately determining flight height and speed, under a range of environmental conditions and across the diurnal cycle, as well as the extent of attraction to navigation lights required for the illumination of offshore structures and vessels associated with offshore windfarms.
- Several extensive offshore windfarm lease areas lie close to the SPA breeding colonies of Leach's and European Storm-petrels of North Rona and the Flannan Islands, and European Storm-petrel colonies of Aukerry, Sule Skerry and Priest Island. Further work is required to track these protected species from these colonies. Tracking of Leach's Storm-petrels will be greatly facilitated by the recent development of 1.5g GPS tags, with capability to remotely download data to a base station. It is anticipated that 1.0g remote download tags, (small enough for deployment on European Storm-petrels) will also become available.
- Further work is also required to characterise the marine distribution of these two storm-petrel species at earlier, and later, breeding stages i.e. pre-laying and early incubation, when birds are more sensitive to disturbance and in late chick-rearing, and outside the breeding season. The use of GLS tags to provide data on movements and marine distribution over longer time periods (many months, or years) could provide such information, and (due to the light-logging capability of such tags) could also reveal the extent to which storm-petrels are exposed to artificial light at night.

- Tracking and assessment of demographic rates (breeding success, survival etc) is greatly facilitated where storm petrels use nest boxes, which allows access to nesting birds with a minimum of disturbance. Better understanding of demographic parameters is important for Collision Risk Models in wind farm assessments. In the longer term it would be highly beneficial to instigate a programme of nest-box installation at key SPA colonies, to facilitate such data collection.

7. Acknowledgements

Claudia Tapia Harris, Nina DaRocha, Brenning Hughes, Alex Starace and Zoe Deakin assisted with fieldwork. Turus Mara transported staff and delivered fresh food and water to Lunga during the field season and thanks to GoToStKilda, for their assistance transporting staff, food and equipment to St Kilda. Many thanks to PathTrack for their technical support to the project, including retrieval of data from tags that showed no signs of life!

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The Scottish Government
St Andrew's House
Edinburgh
EH1 3DG

ISBN: 978-1-80775-398-6 (web only)

Published by The Scottish Government, August 2026

Produced for The Scottish Government by APS Group Scotland, 21 Tennant Street, Edinburgh EH6 5NA
PPDAS1745246 (08/26)

W W W . g o v . s c o t