State-space modelling of geolocation data reveals sex differences in the use of management areas by breeding northern fulmars

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Summary

1. Effective management and conservation of terrestrially breeding marine predators requires information on connectivity between specific breeding sites and at-sea foraging areas. In the north-east Atlantic, efforts to monitor and manage the impacts of bycatch or pollution events within different Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) management regions are currently constrained by uncertainty over the origins of seabirds occurring in each area.

2. Whilst Global Positioning System (GPS) loggers can now provide high resolution data on seabird foraging characteristics, their use is largely restricted to the chick-rearing period. Smaller light-based Global Location Sensors (geolocators) could provide valuable data during earlier phases of the breeding season, but additional information on their accuracy is required to assess this potential.

3. We used incubation trip tracking data from 11 double-tagged (GPS/geolocator) northern fulmars *Fulmarus glacialis* L. within a state-space modelling (SSM) framework to estimate errors around geolocator locations. The SSM was then fitted to a larger sample of geolocator data from the pre-laying exodus using the mean of these error estimates. Geolocator data were first used to compare the trip durations of males and females during this critical pre-laying period. Outputs from the SSM were then used to characterize their spatial distribution and assess the extent of within-colony variation in the use of different OSPAR management regions.

4. During the pre-laying exodus, fulmars from a single colony in the north-east of the United Kingdom foraged widely across several biogeographical regions, up to 2900 km from the colony. Most (60%) males remained within the North Sea region, whereas most (68%) females flew north, foraging within the Norwegian and Barents Sea. A small subset of birds (15%) travelled to the central North Atlantic. Foraging trips by males appeared to be shorter (x = 18 days, n = 20) than by females (x = 25 days, n = 19).

5. *Policy implications.* Our results of state-space modelling of geolocation data collected from northern fulmars show that within-colony variation in ranging behaviour during the breeding season results in sex differences in exposure to threats such as fisheries bycatch and marine plastics. Birds from a single colony dispersed over several north-east Atlantic management areas. These patterns have implications for interpreting trends in colony-based monitoring schemes, and European Union Marine Strategy Framework programmes using these seabirds as an indicator species for monitoring trends in marine litter and prioritizing efforts to mitigate its impact.

Key-words: double-tagging, fisheries bycatch, geolocator validation, GLS, Marine Strategy Framework Directive, north-east Atlantic, northern fulmar, OSPAR, spatial modelling, tracking

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Introduction

Studies of spatial ecology remain a high priority for sea-bird conservation (Wakefield, Phillips & Matthiopoulos 2009; Lewison *et al.* 2012). In European waters, the European Commission Birds Directive obliges member states to maintain populations of wild birds by designating and managing networks of Special Protection Areas (SPA) for rare, vulnerable and migratory species (EU 2009). Alongside these measures, the General Obligations of the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention) require member states to conserve marine ecosystems by protecting their maritime areas against deleterious impacts of human activity such as pollution (van Franeker *et al.* 2011). Such measures are managed by OSPAR across five broad biogeographical regions, from the Barents Sea to the Bay of Biscay and west to the Mid-Atlantic Ridge. However, as a result of their highly mobile nature, most seabird species are unlikely to remain in the maritime area of individual OSPAR nations (e.g. Bogdanova *et al.* 2011). Consequently, conservation efforts are often constrained by uncertainty over the extent to which birds from specific colonies, or individuals of differing sex and age, use particular offshore areas in different phases of the annual cycle (Camphuysen *et al.* 2012; Lascelles *et al.* 2012).

Developments in bird borne transmitters and loggers have demonstrated that seabird foraging may occur many hundreds of km from the colony, even during the breeding season (Phillips *et al.* 2007; Guilford *et al.* 2008; Edwards *et al.* 2013; Thiers *et al.* 2014). These telemetry devices now provide opportunities to evaluate how different age or sex classes from particular colonies interact with specific threats such as renewable developments (Wade *et al.* 2014), oil and gas infrastructure (Ronconi, Allard & Taylor 2015), fisheries bycatch (Anderson *et al.* 2011; Lewison *et al.* 2014) and pollution events (Montevecchi *et al.* 2012). One growing area of concern with respect to chronic pollution is the impact of macro- and microplastics in marine systems (Vegter *et al.* 2014; Wilcox, van Sebille & Hardesty 2015). The distribution of marine plastics can be highly patchy as a result of spatial variation in inputs and ocean currents, leading to accumulation in pelagic systems and ingestion by seabirds (Barnes *et al.* 2009; Gall & Thompson 2015). As a result, seabirds are commonly used to monitor spatial and temporal variation in marine plastic contamination (Wilcox, van Sebille & Hardesty 2015). In the North Atlantic, for example, the high abundance and widespread distribution of Northern fulmars *Fulmarus glacialis* L. (hereafter fulmar) has resulted in their use as the primary indicator species for plastic contamination under the EU Marine Strategy Framework Directive (EU 2008; van Franeker *et al.* 2011). Understanding of spatial and temporal trends in plastic contamination, and the potential impacts of exposure, now requires better information on connectivity between different breeding colonies and pelagic foraging areas. Similarly, efforts to mitigate impacts of plastics upon seabird populations require an understanding of how birds from particular colonies distribute themselves across different marine management areas, such as the OSPAR regions, within different phases of their annual cycle.

Whilst developments in tracking technology (e.g. Global Positioning System; GPS) provide opportunities to obtain satellite-derived locations of individual birds at sea, most studies involve short-term deployments during the chick-rearing period. At this time, birds are easier to capture and re-capture, but foraging ranges are potentially constrained whilst provisioning chicks (Guilford *et al.* 2008; Votier *et al.* 2010). Earlier in the breeding season these central-place constraints are weaker. Consequently, GPS tracking data from a restricted time period are likely to under-represent the full extent of many seabirds' spatial distribution, even within the breeding season. In particular, many *Procellariiformes* (petrels) such as northern fulmars are absent from colonies for long periods between courtship and egg laying (Macdonald 1977). Despite the likely importance of this pre-laying exodus for successful reproduction (Hatch 1990a; Mallory & Forbes 2008), knowledge of their distribution at this time is sparse. Tracking studies during this period are constrained because seabirds are prone to flushing earlier in the breeding season (Safina & Burger 1983; Rojek *et al.* 2007). This makes capturing or recapturing birds to deploy and recover devices difficult or impossible until breeders sit more tightly on eggs or young chicks. Light-based Global Location Sensing (also known as geolocator) loggers (Phillips *et al.* 2004), deployed in preceding seasons, provide the potential to better understand distribution and foraging trip characteristics during periods when short-term deployments are not possible. These geolocator loggers can be ring-mounted and recovered after one or more years. Geolocator loggers have the additional advantage that their small size (<5 g) means that they can be deployed on smaller seabird species (e.g. Egevang *et al.* 2010; Quillfeldt *et al.* 2012).

The primary disadvantage of geolocator devices is that accuracy is low, with errors in the region of 200 km (Phillips *et al.* 2004). Consequently, geolocator data have generally been used to describe broad-scale patterns of year-round distribution (Phillips *et al.* 2006). It remains unclear to what extent more complex modelling of these data (e.g. Jonsen, Flemming & Myers 2005; Thiebot & Pinaud 2010; Lisovski, Hahn & Hodgson 2012; Cleeland, Lea & Hindell 2014; Rakhimberdiev *et al.* 2015) can be used to characterize finer scale movements within individual foraging trips. Previously, only three studies have directly assessed the accuracy of geolocator devices on seabirds, using a combination of light-level geolocator and satellite-derived location estimates. The first of these revealed that a two-stage iterative smoothing algorithm could reduce mean errors of location estimates (Phillips *et al.* 2004). The

mean distance between contemporary geolocator and ARGOS PTT locations from black-browed albatrosses was 186 km, and errors were reduced to 169 km after smoothing. Subsequently, a study of Laysan and black-footed albatrosses compared both light-level and SST-derived geolocations with ARGOS telemetry locations (Shaffer *et al.* 2005). Here, the mean distance between light-derived geolocations and satellite-derived locations was 400 ± 298 km, or 202 ± 171 km when positions were based on light-based longitude and sea-surface temperature (SST)-derived latitude. Finally, a suite of data from double-tagged pinnipeds, birds and fish were used within a two-stage Bayesian state-space model (SSM) to estimate geolocation error and improve location estimates (Winship *et al.* 2012). The SSM (see Jonsen, Flemming & Myers 2005) was fitted to high-precision satellite-derived locations (GPS and ARGOS) and low-precision geolocator data from each double-tagged individual. The primary output from stage one of the model was a mean error, in both latitude and longitude, between raw geolocation data and locations estimated by the state-space model. This resulted in mean errors for two species of albatross of 1·9–3·9° longitude and 1·2–1·9° in latitude (whilst longitude cannot be simply converted to distances, this equates to latitudinal error of 133–211 km).

In this study, we used data from simultaneously deployed geolocator and GPS loggers within Winship *et al.*'s (2012) SSM to estimate the error around geolocator tracking locations from fulmars undertaking long incubation trips. We then use the mean of these error estimates within the same SSM framework, fitted to a larger sample of geolocator-only data, to assess fulmar distribution and trip characteristics during the pre-laying exodus. Finally, we use modelled tracks to compare the spatial distribution of male and female breeders from a single UK colony to assess whether there are sex differences in the extent to which these birds use different OSPAR regions during this early phase of the breeding season.

Materials and methods

Fieldwork was conducted on Eynhallow, Scotland (59·12° N, 3·1° W), where annual visits were made to conduct individual-based demographic studies of fulmars (Dunnet 1991; Thompson & Ollason 2001; Grosbois & Thompson 2005).

Double-tagging experiments were carried out during 2011 and 2012. Fulmars were caught on the nest using a net or noose in late May. A GPS logger (iGot-U GT-120, MobileAction®, Taipei, Taiwan) was attached to mantle feathers using tape (Tesa® 4651, Hamburg, Germany), and a geolocator (Mk 15; British Antarctic Survey, Cambridge, UK) was cable tied to a Darvic leg ring. Total weight of devices was <3% of body mass. GPS devices recorded one position every hour. Geolocator devices recorded light levels (Phillips *et al.* 2004) and whether the device was wet or dry every 3 s, and stored the maximum light level and number of wet samples in each 10 min bin (Mackley *et al.* 2011). In 2011, attempts were made to re-capture birds around hatching in July. In 2012, recapture attempts were made

after their first foraging trip post-egg laying. Detailed investigations of pre-laying exodus trips were made using data from geolocator loggers deployed at this colony between 2006 and 2012, using similar attachment methods, to study winter distribution (Quinn 2014).

GPS data were downloaded using the manufacturer's software. Geolocator data were downloaded, extracted and location estimates generated using the BASTrak software package (British Antarctic Survey). Data were processed within Microsoft Excel, and statistical analyses were carried out using R (R Core Team 2014) and WINBUGS (Lunn *et al.* 2000) using methods described in Winship *et al.* (2012). Data visualization and mapping were conducted in Arc GIS 10.0 (ESRI, Redlands, CA, USA).

ANALYSIS OF DOUBLE-TAGGING DATA

GPS data were first filtered to include only those periods when birds were away from the nest on foraging trips. Times of departure or return to the nest were based upon times of the first and last locations >500 m from the nest.

Geolocator data on light levels were analysed to produce twice-daily location estimates (Fox 2010), based upon day length and the times of noon and midnight, in turn derived from sunrise and sunset transitions (see Supporting Information). The light sensor was sometimes shaded by body feathers, especially when on the nest, resulting in uncertainty around some sunrise and sunset estimates. Light traces were therefore examined to identify likely periods on the nest. There were also periods of uninterrupted 24-h daylight. Whilst positions could not be estimated for these days, this confirmed that birds were in northern latitudes.

Geolocator files were also filtered to include only those periods when GPS data confirmed that birds were off the nest. GPS-derived times for the start and end of foraging trips were then included in the geolocator location data file.

For each double-tagged individual in turn, a Bayesian SSM (Winship *et al.* 2012) was fitted simultaneously to geolocator and GPS data sets. The high-precision GPS data were used in the SSM to estimate probability distributions for true positions (states), using the first difference correlated random walk process model described by Jonsen, Flemming & Myers (2005). Location states at each regularized time step (1 day) were estimated from GPS data, using movement parameters based upon mean direction of movement and mean turning angle. Speed within time steps was derived as a vector, based on movement in latitude and longitude between time t and $t + 1$, as a function of speed during the previous time step and movement parameters. The model assumes linear movement between two time points.

The observation model related the two data sources to the true animal locations:

$$y_i = \mu_i + \varepsilon_i$$

where y_i *is the i*th pair of GPS/geolocator latitude/longitude data, μ_i is the corresponding true latitude and longitude, and ε_i is the random, normally distributed, serially independent observation error. True locations were calculated from estimated states that were regular in time. The process is described in detail by Winship *et al.* (2012).

The model generated one location per bird per day, and means of estimated longitude and latitude geolocation errors were calculated for each double-tagged individual. Overall mean errors from

the sample of double-tagged individuals were applied to data sets for birds which had only been tracked using geolocator loggers.

DEFINING THE PRE-LAYING EXODUS

Individual pre-laying exodus trips were defined by investigating the light and activity traces from geolocator loggers recovered from 67 adults studied by Quinn (2014). We focused our investigations on the subset of birds that had light data from the early breeding season (15 April–30 June) and which were members of pairs where observations of an egg confirmed they had bred in that season. In some cases, activity data were incomplete due to limited memory capacity.

Initial exploratory analyses considered those cases where both members of the pair were carrying geolocators. Light and, where available, activity traces were examined simultaneously for each pair member to determine when both birds were at the colony. Where transition from an irregular to a clean light trace occurred concurrently with the transition from dry to wet/mixed activity (Fig. S1), it was assumed that the bird had departed to sea after a period on land.

Return time was estimated from the first long dry period (>6 h) after an extended period where the logger was periodically wet. Typically, this corresponded with transitions from well-defined days and nights to an irregular light trace, as the logger became hidden under body feathers whilst on the nest. This supported the assumption that the bird was at the colony. Trip durations were estimated from these departure and return times.

Analyses of data from tracked pairs indicated that estimates of the duration of the pre-laying exodus could be derived from the geolocator light traces alone. Light traces from all other birds in the data set were then analysed to estimate the dates and times of departure from, and return to, the nest using the same rules. Available geolocator light files were subsequently analysed as outlined earlier to estimate locations for each day and night through individual pre-laying exodus trips. If data were available for multiple years, only 1 year was selected. To maximize sample size within a single year, 2011 data were preferentially retained. If 2011 data were not available, data from one other year were selected at random. Where no sunsets or sunrises occurred on days with constant daylight, no daily location estimates could be made. All such instances of constant daylight were recorded separately as this indicated that these birds were in high latitudes at this time (Table S1).

STATE-SPACE MODELLING OF PRE-LAYING EXODUS TRIPS

For each individual pre-laying exodus trip, the SSM was fitted to geolocator positions using the mean geolocation error estimate from the double-tagging experiment (Table 1). Start and end times for each pre-laying exodus trip were included in the data file, and fixed to the latitude and longitude of the colony.

Modelled daily locations from the SSM were then explored in ArcGIS. The maximum distance from the colony during each trip was characterized by identifying the furthest modelled location from the colony and both the preceding and subsequent locations. The mean of these three most distant locations was then used to estimate foraging range from the colony and categorize each pre-laying exodus trip to an OSPAR biogeographical region (OSPAR 1992). Generalized linear mixed-effects models were

used to investigate the effect of sex on the maximum distance from colony, departure date and pre-laying exodus duration for these birds. In all three models, year was included as a random effect to account for interannual variability. Linear mixed-effects models were conducted using 'lme4' (Bates *et al.* 2014) and with 'lmerTest' (Kuznetsova, Brockhoff & Christensen 2013) to estimate degrees of freedom and calculate *P*-values (all tracking data are available online in the Dryad Digital Repository; Edwards, Quinn & Thompson 2016).

Results

In 2011, data loggers were deployed with the intention of recovery in July and only one of nine birds tagged was recovered with both loggers attached. Five birds failed in their breeding attempt and were not seen again that year, and three birds had lost their GPS logger. In 2012, recovery attempts were made in June after just a single trip and both loggers were recovered from 10 of 22 birds tagged. Of the remaining birds, two lost their geolocator logger and four birds lost their GPS logger. Fourteen birds (2011, *n* = 8; 2012, *n* = 6) were not recaptured within the year of study.

Double-tagged birds varied considerably in their foraging trip duration, range and distribution during the incubation period, with individuals using an area spanning 50° of longitude and 8° of latitude (Fig. 1). Fitting the SSM to these data (e.g. Fig. 2) produced a mean geolocation error (in degrees) for each trip (Table 1). The overall mean error was $\pm 0.212°$ longitude and $\pm 0.391°$ latitude.

Additional geolocator data were available from the pre-laying exodus period for 39 actively breeding fulmars (20 males; 19 females). Sex affected pre-laying exodus

Table 1. Summary data for each trip in double-tagging study. Standard Deviations (SD) of errors in longitude and latitude, in degrees, estimated from the state-space model (Winship *et al.* 2012) that was fitted to both geolocator (GLS) and GPS data collected from double-tagged individuals during the incubation period. Also included are the trip durations (d) and numbers of locations used to fit the model. Averages are means in the case of error values, and medians for trip duration and numbers of location

Year_BirdID	$\widehat{SD}_{lon}$ error (± °)	$\widehat{SD}_{lat}$ error (± °)	Duration (days)	No. GPS locations	No. GLS locations
2011_1890	0·024	0·310	8·69	213	18
2012_1568	0·114	0·399	14·06	348	30
2012_1153	0·074	0·193	11·90	290	25
2012_1854	0·059	0·173	9·88	176	14
2012_1915	0·315	0·496	2·61	64	7
2012_1911	0·056	0·302	14·20	157	29
2012_1355	0·116	1·212	5·08	126	11
2012_1631	0·735	0·057	3·92	97	8
2012_1641	0·090	0·086	2·91	72	7
2012_1893	0·184	0·260	1·80	45	5
2012_1580	0·572	0·808	3·69	64	8
Average	0·212	0·391	7·16	150	14·7

Fig. 1. GPS tracks showing the distribution of 11 double-tagged fulmars, tracked during incubation. The inset map focuses on the eight birds that remained closer to the colony.

Fig. 2. An example illustrating the state-space modelled track in relation to the raw GPS data and independent daily locations determined from the geolocation logger. Black dots indicate daily geolocator locations. The red line shows the estimated track from the SSM fitted to both GPS and geolocator data, whereas the blue line shows the estimated track from the SSM fitted to the geolocator data only. The GLS data and model estimates correspond to the GPS track displayed in black in Fig. 1. (See Fig. S3 for additional examples).
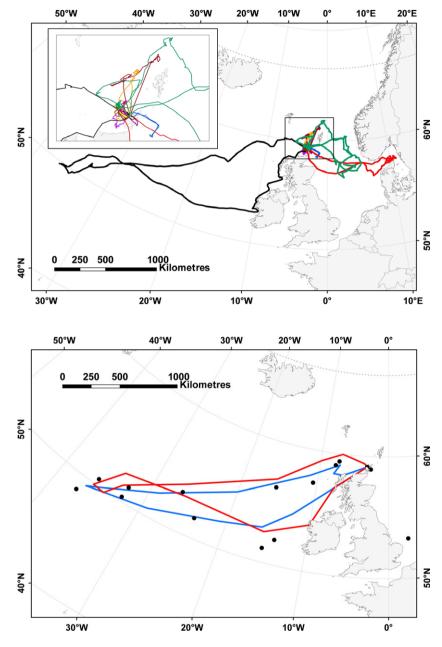
duration, with trips by males being 7·08 days ± 1·69 (SD) shorter than those of females ($t_{36.53} = -4.2$, $P < 0.001$; Fig. 3). There was a sex difference in departure date, with females departing about 6·13 days ± 1·5 (SD) earlier than males ($t_{36.5} = 4.1$, $P < 0.001$). Sex also affected the maximum distance from the colony, with males staying 496·6 km ± 243·1 (SD) closer to the colony, although this effect was weaker due to higher variability within sexes ($t_{37} = -2.04$, $P = 0.049$) (Table 2).

The extent to which birds were found in different OSPAR regions (Table 3) differed between sexes (Fig. 4; $\chi^2 = 8.16$, df = 2, $n = 39$, $P < 0.05$). Most females (68%) foraged over the Norwegian Shelf in OSPAR region I, and most males (60%) remained within the greater North Sea area (regions II/III). Numbers of birds using the mid-Atlantic were small (Table 3), but one did forage west of the OSPAR region within the Northwest Atlantic Fisheries Organisation's (NAFO) management area. Overall, 14 birds (36%) foraged to the north of the Arctic Circle (latitude 66·23° N). Six individuals (three male, three female) lost an average of 10 geolocator locations (range 1–22) due to 24-h daylight (see Fig. S5 for examples).

Birds that foraged in OSPAR Region I carried out significantly longer trips than birds using Region II (*t*-test, $t = 2.62$, df = 26·2, $P = 0.014$). Birds that foraged in Region V appeared to carry out longer trips than birds that foraged in Region II, but sample size ($n = 5$) was too small for statistical comparison. Overall, pre-laying exodus duration varied linearly with maximum distance from the colony (linear model; $n = 39$, $r^2 = 0.89$, $P < 0.001$; Fig. 5).

Fig. 3. Sex differences in (a) pre-laying exodus trip durations and (b) pre-laying exodus trip departure dates (in Julian days) of adult fulmars breeding at the Eynhallow colony. Box plots show medians with interquartile ranges. Data are from all years (2008–2012). For sample sizes, see Table 2.
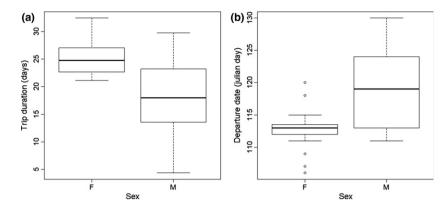
Table 2. Characteristics of the pre-laying exodus trips of breeding male and female fulmars, as determined from data on variation in light levels collected from geolocator loggers. Trip durations for male birds may be inaccurate due to their behaviour (see Discussion)

	Male	Female
Sample size	20	19
Departure date		
Median	29 April	23 April
Range	21 April to 10 May	16 April to 30 April
Return date		
Median	17 May	18 May
Range	8 May to 23 May	14 May to 28 May
Trip duration (days)		
Median	18·0	24·8
Range	4·4–29·8	21·1–32·5

Table 3. Sex differences in the occurrence of geolocator tagged fulmars in each of the OSPAR management regions. Each individual was classified to a foraging region based on the mean of the three locations that were most distant from the breeding colony during the pre-laying exodus (see Fig. 4)

	Male	Female
Sample size	20	19
Birds in OSPAR region I		
Number	6	13
%	30	68
Birds in OSPAR region II/III		
Number	12	3
%	60	16
Birds in OSPAR region V/NAFO		
Number	2	3
%	10	16
Maximum distance from colony (km)		
Mean	942 ± 773	1438 ± 743
Range	24–2792	385–2887

Discussion

Earlier studies indicated that fulmars undertake a 3- to 4-week pre-laying exodus (Macdonald 1977; Hatch 1990b; Danielsen & Bengtson 2009), but no data previously existed on where birds foraged at this time. Our studies
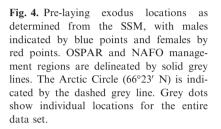
revealed that fulmars from a single Scottish colony may forage across three very different biogeographical regions, over 25° of latitude, and 78° of longitude, during this early part of the breeding season. These data suggest a maximum range of 2890 km from the colony, far surpassing the previous assumed 580 km foraging range for breeding fulmars used to identify critical areas for UK seabirds (Thaxter *et al.* 2012).

CHARACTERIZING GEOLOCATION ERRORS

These inferences were made possible by using a SSM approach to model tracks based upon lower resolution geolocation data from archival loggers deployed over multiple seasons. In turn, this approach depended upon estimates of location error that were obtained through concurrent deployment of high-precision GPS data loggers and geolocators. Estimated geolocation errors for these double-tagged fulmars were comparable to those found in Winship *et al.*'s (2012) multispecies study, although our estimates were smaller, for both longitude and latitude, than the 2–4° errors they found for the two seabirds in their study. Our data provide the first estimates of geolocation error for non-*Diomedeidae* species of seabirds, and the first for tracks within the North Atlantic, increasing confidence in the usefulness of geolocator location data for studying of spatial ecology of wide-ranging seabirds across this region. Although smaller than the errors reported in previous studies, it is possible that the birds' behaviour and plumage differences contribute to the lower errors found in this study, and these errors may not be applicable to other species, to other locations, or other times of year.

DURATION OF THE PRE-LAYING EXODUS

Estimates of the duration of the pre-laying exodus (Table 2) were longer than previously reported at Scottish colonies, although not unprecedented at other North Atlantic sites (Danielsen & Bengtson 2009). The tendency for shorter male trips was consistent in all studies. Another Scottish study reported durations of 21 days for females and 12 days for males (Macdonald 1977), whilst
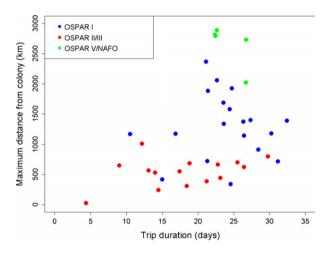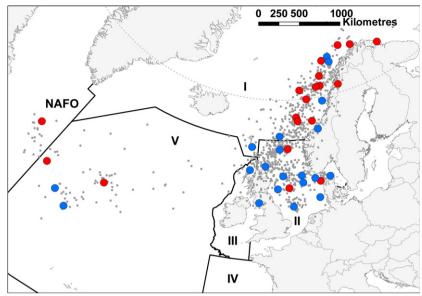
Fig. 4. Pre-laying exodus locations as determined from the SSM, with males indicated by blue points and females by red points. OSPAR and NAFO management regions are delineated by solid grey lines. The Arctic Circle (66°23′ N) is indicated by the dashed grey line. Grey dots show individual locations for the entire data set.

Fig. 5. Scatterplot showing relationship between pre-laying exodus duration and maximum distance from the colony. Blue squares represent birds that foraged in OSPAR Region I (Arctic Waters). Red circles represent birds that foraged in OSPAR Region II (Greater North Sea). Green diamonds represent birds that foraged in the Region V (Wider Atlantic).

Hatch (1990b) recorded pre-laying exoduses of 18 days for females and 12 days for males in the Pacific. Whilst some of these differences may be due to intercolony variability, previous work at the same colony on Eynhallow in the early 1960s also estimated shorter mean durations of 16 days for females and 14 days for males (Dunnet, Anderson & Cormack 1963). The abundance of fulmars at north-east Atlantic colonies has increased dramatically over this period (Mitchell *et al.* 2004). Thus, longer trip duration could be a response to increased intraspecific competition (Lewis *et al.* 2001) or changes in foraging conditions (see also Mallory *et al.* 2008). Observed trip durations for birds foraging within the OSPAR Region II were also more comparable to those seen in the earlier Eynhallow study (Dunnet, Anderson & Cormack 1963),

highlighting the possibility that temporal variation in average trip durations could also reflect changes in the proportion of birds foraging in different biogeographical regions.

Comparison of these studies is potentially constrained by differences in methodology. Here, we used light traces to define the pre-laying exodus, whereas earlier studies directly observed recognizable individuals. Amongst males, activity data highlighted that intermittent dry periods were sometimes longer than expected for birds on long foraging trips (see Edwards *et al.* 2013). A study using cameras in the Faroe Islands found that males often intermittently visit the colony throughout the pre-laying exodus period (Danielsen & Bengtson 2009). Thus, male trip duration may be overestimated if this is indicative of time on land. Pre-laying exodus departure and return times based on geolocator data from females may therefore be more reliable than those from males. In future, a combination of geolocator and time-lapse photography (Gaston *et al.* 2014), or passive integrated transponder (PIT) tagging of individuals (Mallory *et al.* 2008), could be used to define departure and return times more precisely.

ECOLOGICAL AND MANAGEMENT IMPLICATIONS

Previous geolocation studies at this colony demonstrated that adult fulmars were distributed widely across the North Atlantic during the winter (Quinn 2014). This study highlights that fulmars also range widely during the early breeding season when they are expected to be more closely tied to colonies (Thaxter *et al.* 2012). One caveat of geolocator data at this time of year is that birds may encounter constant daylight at high latitudes. As a result, some locations were lost for six birds in our sample (15%), with one individual remaining in constant daylight for 11 days (Table S1). Where no geolocator position is

available, the SSM assumes linear movement between the previous and subsequent true locations. This suggests that the northern extent of some ranges is underestimated, and other approaches are required to understand the extent to which these birds use Arctic waters. Sea-surface temperature recorded by some geolocators could potentially be used to refine latitude estimates (Tremblay, Robinson & Costa 2009).

As seen in other seabird species (Catry *et al.* 2006), there were also sex differences in the extent to which birds from this colony foraged across different north-east Atlantic regions (Fig. 3; Table 3) with males tending to remain in more local waters. This highlights how spatio-temporal variation in food resources and anthropogenic threats may differentially impact male and female fulmars from a single colony. Females may be especially vulnerable to the annual bycatch of many thousands of fulmars in Scandinavian longline fisheries (Anderson *et al.* 2011; Fangel *et al.* 2015) as seen in some Southern Ocean species (Bartle 1990; Croxall & Prince 1990). Similarly, females may be more exposed to threats from the oil and gas developments on the Norwegian Shelf (Wiese *et al.* 2001; Ronconi, Allard & Taylor 2015), particularly if new prospects are developed in these areas (Sällh *et al.* 2014). Previous work has shown that survival in this species at both this (Grosbois & Thompson 2005) and other colonies (Cordes *et al.* 2015) has declined, with sex-specific differences in finer scale patterns of survival (Grosbois & Thompson 2005). Our findings illustrate how sex differences in foraging areas could influence survival, and highlight that demographic models assessing risks from bycatch and oil spills should take sex into account. In contrast, females may be less vulnerable to other environmental stressors. Stomach contents from fulmars collected in Icelandic waters showed lower plastic loading than birds found in the North Sea (Kühn & van Franeker 2012), with evidence that levels of plastics decline with increasing latitude within the North Atlantic. Thus, the tendency for females to make greater use of northern waters within OSPAR Region I may result in fewer females being exposed to marine litter and the effects of vertical transfer of contaminants associated with microplastics (Cole *et al.* 2011). New methods for non-invasively assessing individual exposure to plastics (Hardesty *et al.* 2015) now provide opportunities both to test this hypothesis using instrumented individuals and to explore the reproductive and survival consequences of observed variation in exposure.

In conclusion, this study has demonstrated how a greater understanding of geolocation errors within a SSM framework can increase opportunities to investigate the distribution of wide-ranging seabirds using geolocator loggers. Fulmars from this single Scottish colony foraged within three distinct biogeographical regions, but distributions differed between the sexes. Studies that integrate geolocation data with individual-based studies are now required to explore the demographic consequences of

these patterns. Improved understanding of the consequences of this spatial variation in exposure to different anthropogenic impacts such as bycatch (Lewison *et al.* 2014) and plastic contamination (Wilcox, van Sebille & Hardesty 2015) can then be used to prioritize regional and international efforts to mitigate those impacts.

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Data accessibility

Our tracking data are available online in Dryad Digital Repository http://dx.doi.org/10.5061/dryad.vb322 (Edwards, Quinn & Thompson 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Example of a light and activity trace at start of a foraging trip from a fulmar.

Fig. S2. Example of light, activity and distance from the nest from one double-tagged fulmar.

Fig. S3. Examples of incubation trips made by four double-tagged birds during incubation.

Fig. S4. Examples of modelled tracks fitted to geolocator data from pre-laying exodus.

Fig. S5. Maps showing SSM based tracks of the pre-laying exodus for three individuals.

Table S1. Table of summary data for birds which appeared to forage north of the Arctic Circle.