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Tracking a northern fulmar from a Scottish nesting site to the Charlie-Gibbs Fracture Zone: Evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites[☆]



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ABSTRACT

The seas above mid-ocean ridges are biodiversity hotspots in an otherwise largely oligotrophic environment, but the nature and extent of linkage between these offshore regimes and coastal ecosystems remains uncertain. Using a combination of GPS and geolocation tracking data, we show that a male fulmar, breeding on the Scottish coast, foraged over areas of persistent thermal fronts along the Charlie-Gibbs Fracture Zone (CGFZ) of the Mid-Atlantic Ridge during the incubation period. The bird travelled over 6200 km in 14.9 days. First-passage time analysis identified seven areas of restricted search, four on the shelf and three in the vicinity of the Mid-Atlantic Ridge. Previous studies of incubation foraging trip durations at this site suggest that a trip of this duration is unusual, and further work is required to assess the extent to which different individuals use these offshore resources. Nevertheless, these data highlight the potential importance of high sea areas beyond the limits of national jurisdiction when considering the management and conservation of seabirds breeding in NW Europe, and raises the potential for even greater linkage between the CGFZ and seabirds breeding colonies in other regions.

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1. Introduction

In recent years, the sea above the Charlie-Gibbs Fracture Zone (CGFZ) has become recognised as a region of rich biodiversity (Letessier et al., 2011, 2012), providing an important foraging area for a broad suite of marine predators, including fishes (Fossen et al., 2008), seabirds (Bogdanova et al., 2011; Egevang et al., 2010; Frederiksen et al., 2012) and mammals (Doksæter et al., 2008; Skov et al., 2008). As a result, the region has been designated as a large High Seas Marine Protected Area by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Commission) and the North-East Atlantic Fisheries Commission (NEAFC) (OSPAR, 2010). However, the nature and extent of linkage between these offshore areas and coastal ecosystems remains uncertain. Some of the animals (e.g. cetaceans, fishes) feeding in these areas remain in the pelagic environment throughout their life. But seabirds must return to land to breed, and an understanding of the relationship between these high seas regions and seabird breeding sites is essential to support

efforts to conserve their populations. For example, European legislation calls for specific action to protect birds and their habitats (European Commission, 2009) with a particular focus on reduction of incidental bycatch of seabirds in fishing gears within European Union waters (FAO, 2008). However, outwith territorial waters the legislation is more difficult to enforce.

Previous surveys of seabirds at sea (e.g. Boertmann, 2011) have been unable to determine the breeding origin, fidelity or frequency of use of individuals observed in high seas areas such as the CGFZ. Furthermore, seabirds do not recruit until they are several years old, and may skip breeding in some years. Consequently, even when seabirds have been observed in the CGFZ during the breeding season, these individuals may represent birds from the non-breeding component of the population that spend extended periods foraging at sea.

Tracking technologies have recently revealed that seabirds from Icelandic, Scottish and Canadian breeding colonies may spend some of their time over the Mid-Atlantic Ridge (MAR) area (Bogdanova et al., 2011; Egevang et al., 2010; Mallory et al., 2008a). Most published studies provide examples of seabirds foraging in this region during the winter, when individuals do not need to return regularly to coastal breeding colonies. To date, the only example of actively breeding adult birds that foraged over the CGFZ has been a study of Cory's shearwaters (*Calonectris diomedea*), which breed approx. 1200 km away on the Azores archipelago (Magalhães et al., 2008).

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In this paper, we present tracking data from an adult male northern fulmar (*Fulmarus glacialis*) breeding on a Scottish island, which demonstrate that seabirds breeding at colonies on the European continental shelf can actively forage in the MAR area during the breeding season. This finding emphasises the trophic importance of high seas beyond the limits of national jurisdiction when considering the management and conservation of seabirds, and highlights the potential for even greater linkage between the CGFZ and seabird breeding colonies in other regions.

2. Study species

Northern fulmars, a circumpolar boreal species, are the most widespread and abundant seabird in the North Atlantic, breeding on coastal cliffs and grassy slopes from Arctic islands to the coast of Brittany, France (Mitchell et al., 2004). As generalist predators and scavengers, they consume a variety of fish, squid, crustaceans and offal (Phillips et al., 1999). Typical of other Procellariids, they are long-lived (Grosbois and Thompson, 2005), with a breeding period that extends, at Scottish colonies, from laying a single egg in mid-May, to fledging in late August (Dunnet, 1991). Foraging trips during the breeding season are considered to be constrained in range and duration because both partners share incubation (Mallory et al., 2008b), and then continue to take turns brooding and feeding the chick until fledging (Hamer and Thompson, 1997; Phillips and Hamer, 2000). Foraging trips during the breeding season have been reported to have a maximum duration of 18 days (Mallory et al., 2008b), and assumed to be limited to a maximum range of 580 km (Thaxter et al., 2012) based upon published information on foraging trip durations during chick rearing (Furness and Todd, 1984).

3. Methods

The study was conducted at a fulmar breeding colony on Eynhallow, an uninhabited island in Orkney, off the north coast of Scotland (59°8'N, 3°7'W). This colony has been the subject of detailed demographic studies since 1950 (Dunnet, 1991). On-going tracking studies at Eynhallow seek to define the range of foraging by adults during the breeding season, and broad-scale winter distribution patterns. This paper presents data from tracking records that shows how far and for how long one fulmar forages.

3.1. Datalogger deployment and recovery

To attach and recover dataloggers, fulmars were caught under licence on the nest using a net or noose. In May 2012, 22 birds were fitted with a GPS logger (attached to mantle feathers using strips of Tesa® waterproof tape; MobileAction® iGot-U GT-120, weight 18 g after modification) and geolocator (using a cable tie around a Darvic leg ring; BAS Mk15, 3.6 g). Together the devices weigh ~3% of the birds' body mass. The GPS was set to record position every hour for the duration of the battery life or foraging trip, whichever came first. Geolocators (GLS) logged light levels (Phillips et al., 2004), and whether the device was wet or dry (see Mackley et al., 2011), every 3 s, and stored summary data (maximum light level and number of wet samples) every 10 min. Although these devices were used on deployments over single foraging trips in May 2012, they had previously been fitted to over 100 birds between 2008 and 2011, allowing daily data collection until recovery in subsequent breeding seasons.

The data presented in this paper were collected from an adult male (sexed using morphometric measurements, Dunnet and Anderson, 1961), fulmar (#1568), which had bred at the same nest

site, with the same partner, since 2001. This bird was captured on the nest at 12:06 BST on May 23, 2012, while its female partner was on a foraging trip. Following capture, we removed a GLS logger that had previously been fitted to this male in July 2010, and a new GLS logger and GPS tag were then applied before he was resettled onto the nest. Both the new GLS logger and GPS tag were then recovered at 10.00 BST on June 10, 2012, after the male bird had completed one foraging trip and returned to relieve the incubating female. Following recovery, the male bird was resettled on the nest.

3.2. Analyses

GPS data were downloaded using the manufacturer's software, and tracks plotted using ESRI Arc GIS 10. Great circle distances between each at-sea location and the nest site were calculated. Flight speeds between successive GPS locations were also calculated using great circle distances. We identified core foraging or resting areas using first-passage time (FPT) analysis (Fauchald and Tveraa, 2003; Pinaud and Weimerskirch, 2007), using the 'adehabitatLT' package (Calenge, 2006) in R 2.12.2 (R Development Core Team, 2008).

Data on light levels and activity were downloaded from the GLS logger, extracted and filtered using the BASTrak software suite (Fox, 2010). Sunsets and sunrises were manually identified using the programme TransEdit; the solar angle of elevation was set as -3.5° . All data from the equinoxes were excluded to avoid periods when latitude estimation was not possible, and noon and midnight positions were then visualised in ArcGIS. Activity data, available as the number of wet samples within each 10-min period through the deployment, were then used to classify the activity within each 10-min sample as completely dry, completely wet or mixed. Subsequently, sequences of these records were analysed to define the duration of extended bouts of each of these activity category.

Remote sensing data from microwave (AMSR-E, TMI, WindSAT) and infrared sea surface temperature (SST; AVHRR, MODIS) sensors were used to locate persistent oceanic fronts. Merging these data, seven-day composite front maps (Miller, 2009) were derived. More detailed descriptions of these methods are presented in Miller et al. (2013).

4. Results

4.1. General foraging trip pattern and areas of restricted search

GPS loggers were recovered from 12 out of 22 tagged birds. In May and June 2012, GPS tracks indicated that 10 male and 2 female birds made foraging trips ranging from 4 to 15 days during incubation. Most trips were within 100 km of the breeding colony, one male travelled to the eastern North Sea (approx. 800 km). Of particular interest was male fulmar, #1568, who flew 2500 km west to the MAR as described in detail below. The foraging characteristics of the remaining 11 birds will be reported elsewhere.

Following tagging on May 23, bird #1568 remained on the egg until the return of his partner. At around 10:30 BST on May 26, 2012, he left the nest site and spent the next 48 h to the northwest of Orkney, before embarking on a sustained flight (11 h) to the middle of the Shetland-Faeroes Channel (Fig. 1A). After spending approximately 18 h around the Wyville Thompson Ridge, he headed WSW into the mid-Atlantic Ocean, remained around the CGFZ region for 2–3 days and then headed due east. After 19 h his route deviated to the ESE towards Ireland, reaching Galway Bay where he spent 8 h before turning north along the Irish coast.

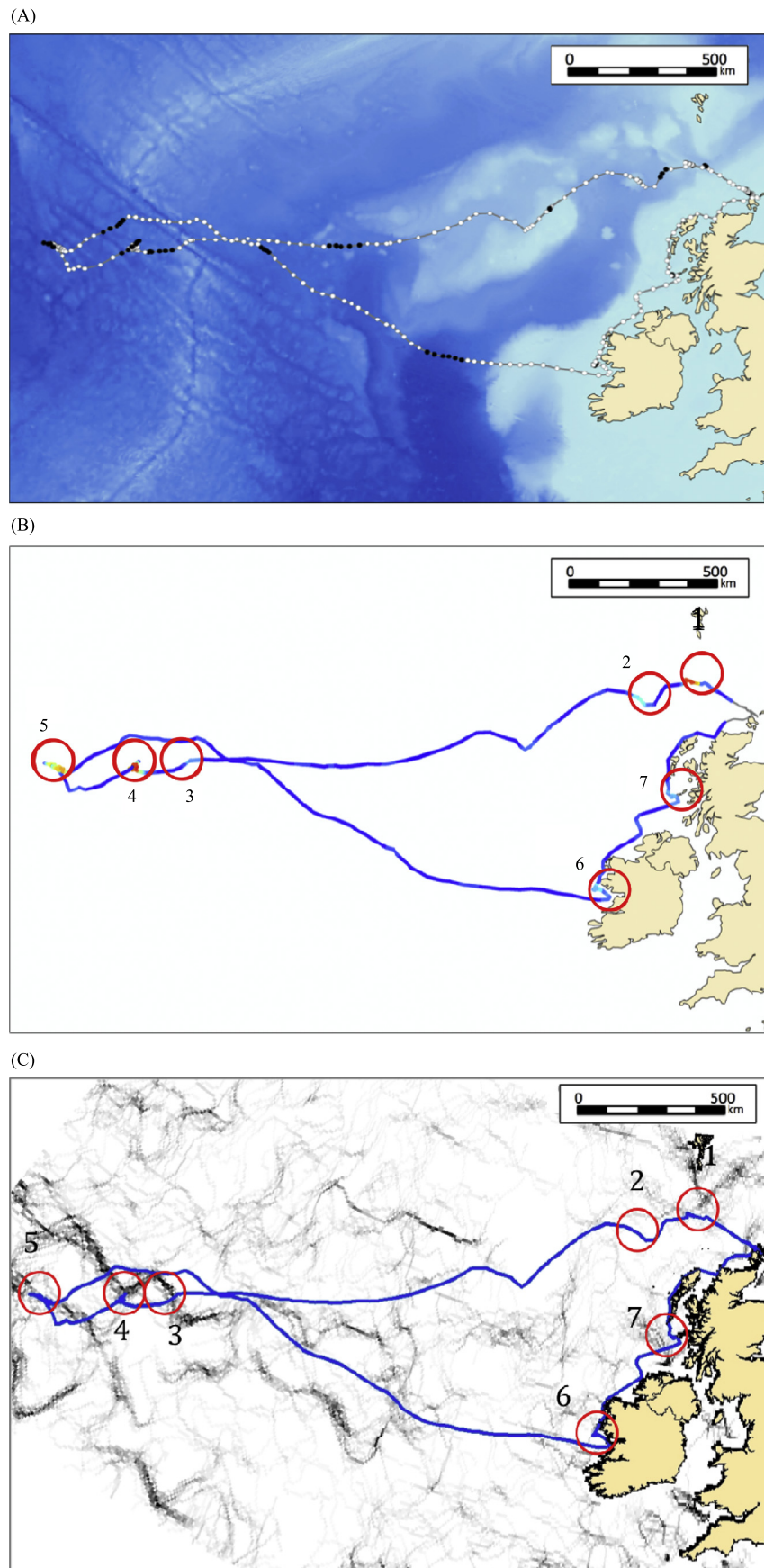


Fig. 1. Maps showing the foraging trip GPS track of bird #1568 from Eynhallow to the Mid-Atlantic Ridge and back. (A) Shows periods of night (dark circles) and light (white circles) on a bathymetric chart (darker colours indicate deeper water). (B) shows the regions of ARS as identified by first-passage time (warmer colours indicate higher FPT). ARS regions are circled and numbered. (C) Shows the GPS track overlaid on a composite front map showing the position and strength of thermal fronts, averaged between 31 May 2012 and 06 June 2012 (darker greys indicate stronger fronts in terms of gradient and persistence). ARS regions are circled and numbered.

After 18 h he flew to the west of Tiree and the Outer Hebrides, headed east at the northern tip of the Isle of Lewis, and followed the coast around the NW tip of Scotland to return to Eynhallow at ~21:00 on June 9, 2012.

Based upon great circle distances between the hourly GPS locations, the total foraging trip length was 6219 km, which the bird completed in 14.9 days. Data from the GLS logger provided information on local dawn and dusk (Fig. 2), and show how the bird's distance from the colony varied through this period during different light and dark periods. FPT analysis identified seven apparent regions of area-restricted search (ARS) during the trip (Fig. 1B): one on the Wyville Thompson Ridge in the Faeroes-Shetland channel (60°N, 7°W); one on the Rosemary Bank, off the NW of Scotland; three within the CGFZ/SPF region; one in outer

Galway Bay, Ireland; and one W of the island of Tiree, Scotland. Comparing these areas of ARS with oceanic fronts present at this time (Fig. 1C) revealed that the bird's activity around the CGFZ was concentrated near the SPF.

4.2. Year-round distribution

The geolocator deployed on this bird in July 2010 indicated that, whilst dispersing widely across the North Atlantic, including time in the Labrador Strait and Norwegian Sea, the bird had clearly visited the CGFZ during the previous 24 months (Fig. 3). Also of note is that relatively few geolocator positions occur between the MAR and the UK, suggesting (as with this study) rapid transits between the MAR and European shelf waters.

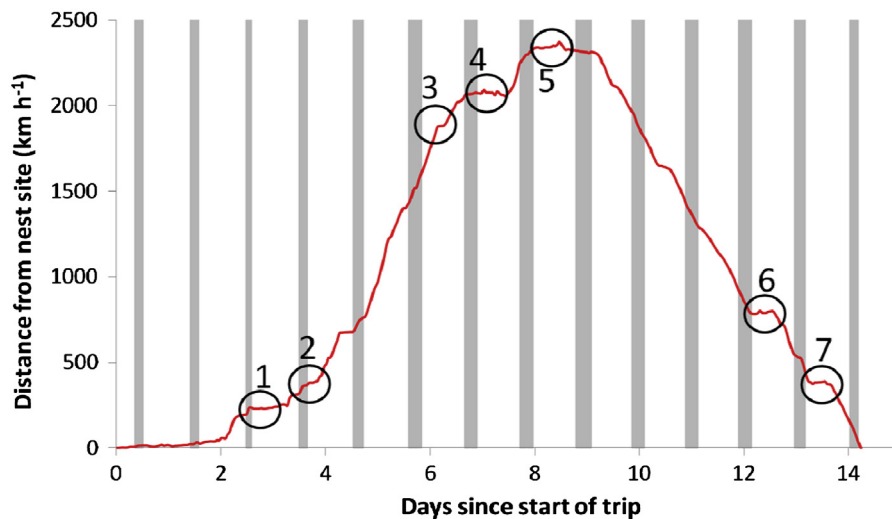


Fig. 2. Graph showing distance from nest site on Eynhallow through time. Black circles indicate the location of ARS regions, as identified by FPT analysis. Numbers correspond to numbers in Fig. 1b and c. Local daylight and darkness indicated by light and dark bars.

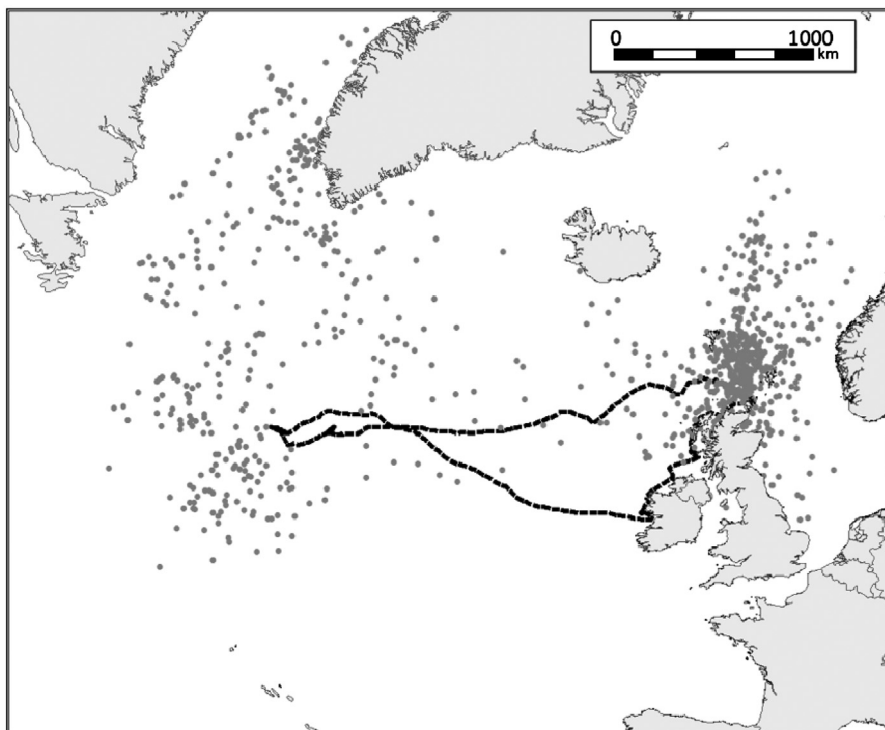


Fig. 3. Map showing North Atlantic region, with foraging trip from this study (dashed line) presented alongside twice-daily locations from preceding 2 years of geolocator tracking (double-smoothed; Phillips et al., 2004).

4.3. Activity and flying speed

There were two periods of ARS at the beginning and end of the trip, and three whilst the bird was around the MAR (Figs. 1b and 2). We explored wet/dry patterns and flight speed within each of these ARS, and during the major transits across the Atlantic. Flying speeds during the transits were similar on both outward and return journeys. The distance between ARS 2 on the Porcupine Bank and ARS 3 at the CGFZ was 1610 km, and was flown in 55 h, giving an overall travel speed of 28.6 km h⁻¹. The maximum hourly speed was 63.3 km h⁻¹. This outward journey was associated with strong E/SE winds associated with a deep depression (971mb at 0000 UTC, 31 May 2012) in the central North Atlantic. On the return trip, the distance between ARS 5 at the CGFZ and ARS 6 in Galway Bay was 2055 km, and was flown in ~73 h, giving an overall travel speed of 27.7 km h⁻¹ and a maximum hourly speed of 48.7 km h⁻¹. This return journey was undertaken in largely headwind conditions, with a deepening low-pressure area to the SW of the UK resulting in a northeasterly airflow.

Flight speeds were faster during these transits (median=30.1, range=0.57–63.3, *n*=134) than during periods of ARS (median=4.43, range=0.42–24.9, *n*=99; Wilcoxon Rank Sum test, *W*=1362, *p*<0.001, *df*=1). During transits, flight speeds were faster during the day (median=33.8, range=3.41–63.3, *n*=105) than at night (median=16.7, range=0.57–34.1, *n*=29; Wilcoxon

Rank Sum test, *W*=522, *p*<0.001, *df*=1), but there was no significant difference between flight speeds by day (median=4.08, range=0.81–24.9, *n*=78) or night (median=7.33, range=0.42–23.5, *n*=21) during periods of ARS (Wilcoxon Rank Sum test, *W*=1008, *p*=0.1067, *df*=1; Fig. 4).

Periods of ARS varied from <3 to >30 h, with three occurring completely in local daylight, two in complete or pre-dominant darkness, and the two longest being primarily in daylight (Table 1). The shortest of these periods was the last ARS, to the west of Tiree (Fig. 1B), when the bird spent almost all of its time on the water in the dark. In all other cases, activity in the ARS regions showed a prevalence of both mixed and wet behaviours (median 94%, range 83–100%), with very little time spent dry (median 5.5%, range 0–17%) (Table 1). Conversely, during the long transits to the east/west, the majority of time was spent dry (median 43%, range 42–44%) or engaged in mixed wet/dry behaviour (median 43%, range 38–47%), with minimal time spent on the water (median 14%, range 8–20%). Within ARS areas, hourly GPS positions indicated that the bird still searched extensively, with average distance covered per h ranging between 3.5 and 9.5 km. The longest periods of mixed activity occurred during the two long ARS over the CGFZ (Table 2). Data from the long transits suggest that sustained periods of flight typically lasted about 30 min, interspersed with periods of mixed activity or total immersion on the water.

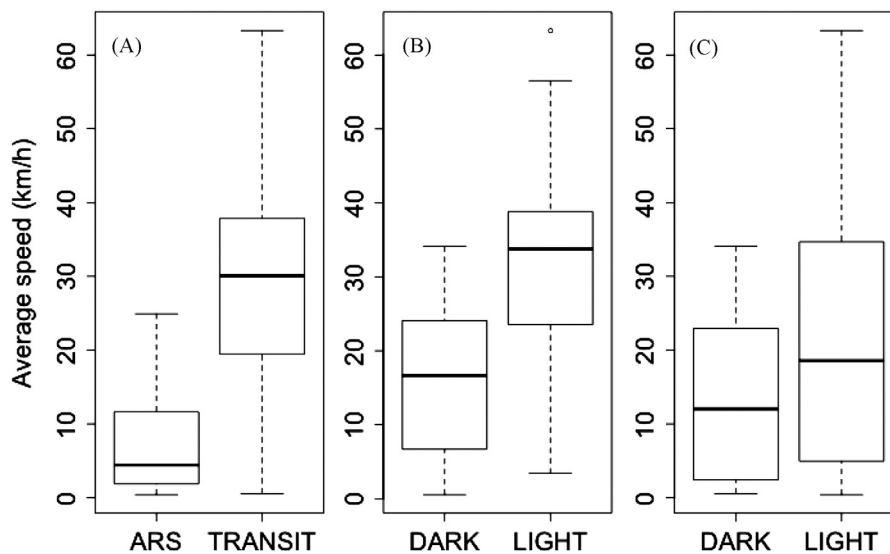


Fig. 4. Boxplots showing (A) the difference in flight speed between transits and regions of ARS; (B) the difference in flight speed between periods of light and dark during transits; and (C) the difference in flight speed between periods of light and dark during ARS.

Table 1

Table showing details of activity in ARS regions and two major transits.

	Start date and time	End date and time	Duration (h)	Duration (days)	% Time in local darkness	Mean speed (km/h)	Max speed (km/h)	% 3-s samples wet	Proportion of 10 min periods		
									Dry	Mixed	Wet
ARS 1	5/29/2012 3:18	5/29/2012 19:55	16.62	0.69	0.0	3.52	–	78.13	0.10	0.33	0.57
ARS 2	5/30/2012 3:54	5/30/2012 10:46	6.87	0.29	0.0	8.26	–	79.15	0.02	0.45	0.52
ARS 3	6/1/2012 17:45	6/1/2012 20:44	2.98	0.12	0.0	7.10	–	87.94	0.00	0.39	0.61
ARS 4	6/2/2012 6:20	6/3/2012 3:32	21.20	0.88	22.7	9.52	–	59.47	0.06	0.53	0.41
ARS 5	6/3/2012 13:14	6/4/2012 19:24	30.16	1.26	22.0	6.93	–	59.17	0.05	0.62	0.33
ARS 6	6/7/2012 20:47	6/8/2012 4:27	7.68	0.32	80.4	9.05	–	59.45	0.17	0.50	0.33
ARS 7	6/8/2012 22:48	6/9/2012 1:46	2.96	0.12	100.0	2.22	–	97.06	0.00	0.08	0.92
Westbound	5/30/2012 10:46	6/1/2012 17:45	54.99	2.29	20.8	28.58	63.30	33.03	0.42	0.38	0.20
Eastbound	6/4/2012 19:24	6/7/2012 20:47	73.38	3.06	25.2	27.66	48.66	21.84	0.44	0.47	0.08

Table 2

Table listing descriptive statistics of activity bouts during ARS and transits.

	Dry bout durations (min)				Mixed bout durations (min)				Wet bout durations (min)			
	Mean	SE	Max	n	Mean	SE	Max	n	Mean	SE	Max	n
ARS 1	37	27	90	3	23	5	70	14	54	22	190	11
ARS 2	10	–	10	1	30	9	70	6	37	10	70	6
ARS 3	–	–	–	0	60	20	80	2	110	–	110	1
ARS 4	27	17	60	3	88	32	300	9	104	30	190	5
ARS 5	18	6	40	5	81	24	290	14	75	25	190	8
ARS 6	62	43	190	4	23	4	40	10	25	6	50	6
ARS 7	–	–	–	0	–	–	–	0	210	–	210	1
Westbound	34	4	130	57	31	4	160	67	34	8	90	11
Eastbound	38	7	240	37	25	3	110	49	54	21	280	12

5. Discussion

Seabirds often forage in high sea regions distant from their breeding colonies during post-breeding dispersal or the winter (Frederiksen et al., 2012; Mallory et al., 2008a). However, our study highlights the potential linkage between coastal and mid-ocean ecosystems within the fulmar breeding season. Information on the duration of foraging trips during incubation is available from only a small number of individual fulmars (Mallory et al., 2008b), suggesting that, whilst such a long trip may be unusual, it was probably not exceptional. For example, incubation trip durations of 16 days and 18 days have been recorded for fulmars breeding at sites in Alaska and arctic Canada (Mallory et al., 2008b).

No previously published tracking data during the incubation period exist to compare foraging ranges of fulmars at this or other sites, but we recorded such an extensive range in only one of the 12 individuals tracked using GPS loggers during our study. Previous satellite tracking studies of fulmars in northern Europe and North America have shown that birds may travel long distances on foraging trips, the furthest recorded being 32,000 km in 239 days over the winter period (Mallory et al., 2008a), however most of these data were collected during the post-breeding period or from failed breeders (Falk and Moeller, 1997; Hatch et al., 2010; Mallory et al., 2008a). Longer-term GLS data collected from bird #1568 indicates that he returned to the CGFZ region in other seasons and in other years (Fig. 3). Whilst these GLS data lack the accuracy of GPS tracks, they do provide excellent opportunities for broader scale and longer term studies that can in future be used to assess the extent to which different individuals use the MAR and similar offshore areas over extended periods of time. Fulmars tracked using satellite tags from the Canadian high Arctic (Devon Island) were found to migrate into the NW Atlantic between Canada and Iceland, and East to the CGFZ during the winter (Mallory et al., 2008a). Together, these studies highlight that fulmars from both North American and European colonies may overlap in their usage of the MAR during the non-breeding season.

First-passage time analysis demonstrated that the bird in this study exhibited area-restricted searching behaviour at seven stages during its trip, both on the shelf and in the mid-Atlantic. The occurrence of oceanic thermal fronts over this period suggested that the bird associated with areas known to be productivity hotspots (Letessier et al., 2012). Furthermore, this bird appeared to concentrate its foraging in the region of the SPF. Little is known of the diet of fulmars outside the chick-rearing period (Owen et al., in press). However, it is clear that fulmars are primarily surface-feeding visual predators or scavengers (Garthe and Furness, 2001). In this study, the small percentage of flight time and the high proportion of mixed activity during the longer periods of ARS suggest that foraging probably involves short searching flights within prey patches,

followed by brief periods on the water to capture and consume prey (Table 2). The majority of these episodes occurred during daylight hours, which is consistent with the visual nature of the fulmars' foraging, but these activity patterns could also be influenced by the diurnal vertical migration of prey in the region (Sutton et al., 2008).

Activity data from the GLS loggers indicate that the bird also engaged in mixed activity during the long transits, where short flights were interspersed with regular contact with sea water. This mixed activity may be indicative of foraging whilst travelling. Flight speed during these phases of the trip was similar during the westbound and eastbound transits, despite different environmental conditions and wind strengths. Given the regular bouts of wet or mixed activity (Table 2), and the assumption that speed is uniform in a straight line between hourly position fixes, these are likely minimum estimates of flying speeds. Furthermore the meandering path of Procellariids engaged in dynamic soaring (Pennycuik, 2002; Tickell, 2000) is likely to result in much faster instantaneous travel speeds than those speeds calculated from distance between hourly positions.

GPS data highlight that the bird did not embark on the westbound transit of this foraging trip immediately after leaving the nest, instead, spending several days to the NW of Orkney (Fig. 1A). Whilst the decision to remain in this area may have been due to favourable local foraging conditions, this period coincided with a large and stable anticyclone in the region. Previous research has highlighted the high energetic cost that this species incurs when flying in low wind speeds, and it is possible that the delayed departure to foraging grounds on the MAR was a response to insufficient winds for energetically efficient flight (Furness and Bryant, 1996). On the return leg, the fastest flight speeds were attained ~100 km to the west of the Irish coast, as the bird flew close to an area of low pressure centred over the British Isles, where wind speeds were probably the highest encountered during the foraging trip. Inspection of the activity patterns and locations within the trip suggest that in the absence of such adverse wind conditions, this bird could have completed the foraging trip in just 11 or 12 days.

The observations detailed within this paper highlight how GPS and GLS tracking can now be used to explore the extent to which other breeders from this colony use distant offshore resources. Previous work at this colony provided evidence that reproductive rates (Thompson and Ollason, 2001) and adult survival (Grosbois and Thompson, 2005) were influenced by the North Atlantic Oscillation (NAO). At the time, it was suggested that effects on reproduction and survival could result from known relationships between the NAO and potential prey stocks. However, the discovery that birds make long foraging trips during the incubation period highlights that changes in wind speed related to the NAO (Pirazzoli et al., 2010) could affect the cost of flying to different foraging grounds (Furness and Bryant, 1996). In the Southern Ocean, wandering albatrosses breeding on Crozet Island have shifted their at-sea distribution southwards and shown higher breeding success, corresponding with an increase in intensity and polewards shift in prevailing winds (Weimerskirch et al., 2012). Future tracking studies should examine how variation in wind fields may influence fulmar foraging trip characteristics in different parts of their foraging range.

In Pacific fulmar colonies (Hatch et al., 2010), one negative consequence of using distant foraging areas during the breeding season is the risk of mortality from being caught on hooks in a wide range of different longline fisheries. In this study, the single fulmar travelled through areas where the Spanish demersal longline fishery catches over 50,000 birds per year, mostly great shearwaters *Puffinus gravis* and fulmars (Anderson et al., 2011). On the same trip, the bird traversed areas where Faroese demersal longliners regularly record fulmars as bycatch. The possibility of

bycatch also exists from pelagic fisheries over the MAR (OSPAR, 2010). This study shows that even birds breeding several thousand kilometres from such areas may be at risk of bycatch. Many breeding colonies are situated outwith regions where longline fishing occurs, but evidence is mounting that these birds are still at risk from fisheries bycatch. Consequently, conservation programs that focus entirely on territorial waters adjacent to breeding sites are likely to underestimate the management practices that are necessary to wide-ranging species such as fulmars.

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Appendix A. Supplementary material

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.dsr2.2013.04.011>.

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