Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds

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Abstract

Aim: In migratory species, individuals often use fixed and individual-specific migration strategies, which we term individual migration strategy fidelity (IMSF). Our goal was to test if guillemots have flexible or fixed individual migration strategies (i.e. IMSF), if this behaviour is consistent across large parts of the genus’ range and if they were philopatric to geographical sites or a habitat feature.

Location: North Atlantic.

Taxon: Uria spp.

Methods: We quantified consistent individual differences in inter-annual spatial distribution and habitat occupied throughout the non-breeding period using a large geolocator tracking dataset of 729 adult seabirds breeding at 13 colonies across the Northeast Atlantic and repeatedly tracked up to 7 years over a 9-year period. Additionally, we used a similarity index to calculate relative fidelity to either geographical sites or habitats and linear mixed-effects models to assess persistence of spatial site fidelity over multiple years.
Results: Both guillemot species exhibited IMSF across a large part of the genus' range which persisted over multiple years. Individuals of both species and almost all colonies showed fidelity to geographical sites and not to specific habitats.

Main conclusions: Guillemots show IMSF that is best explained by site familiarity (fidelity to specific sites) rather than habitat specialization (fidelity to specific habitats). In the context of rapidly changing environments, favourable habitats may permanently shift locations and hence species displaying IMSF driven by site familiarity—such as the genus *Uria*—may not be able to adjust their migration strategies sufficiently fast to sustain individual fitness and ensure population persistence.

**KEYWORDS**
guillemots, light-level geolocation, murres, *Uria aalge*, *Uria lomvia*

1 | INTRODUCTION

Migratory animals face many challenges in a rapidly changing world (Robinson et al., 2009; Wilcove & Wikelski, 2008) as individuals need to structure their annual schedule to maximize availability of spatially and seasonally fluctuating resources (Aléristam, Hedenström, & Åkesson, 2003; Bridge, Ross, Contina, & Kelly, 2015). Many migrants, such as seabirds, are long-lived species (Schreiber & Burger, 2001). Hence, their overall population growth rate is sensitive to changes in adult survival (Lebreton & Clobert, 1991; Sæther & Bakke, 2000), which depends on their migration behaviour and ability to respond to changes during periods outside the breeding season (Abrahms et al., 2018; Alves et al., 2013; Desprez, Jenouvrier, Barbraud, Delord, & Weimerskirch, 2018). Additionally, reproductive success can also be affected by conditions experienced during the non-breeding season (Alves et al., 2013; Bogdanova et al., 2017; Catry, Dias, Phillips, & Granadeiro, 2013).

Consistent differences in individual behaviour are common in free-living populations, and these can have far-reaching implications on intraspecific competition, population persistence, community dynamics and ultimately species diversity (Bolnick et al., 2003; Dall, Bell, Bolnick, Ratnieks, & Si, 2012; Piper, 2011). Site fidelity—an animal’s tendency to repeatedly use the same geographical area—is a common form of individual behavioural consistency (Switzer, 1993). In migrants, site fidelity during breeding has been frequently observed (Bradshaw, Hindell, Sumner, & Michael, 2004; Celia & Ramos, 2015; Phillips, Lewis, González-Solis, & Daunt, 2017). Less evidence exist for site fidelity outside the breeding season here termed ‘Individual migration strategy fidelity’ (IMSF) when within-individual variation in the use of space during the non-breeding period is less than that across the population as a whole (reviewed in Celia & Ramos, 2015; Cresswell, 2014; Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016; Newton, 2008; Phillips et al., 2017). IMSF could be the cause or a consequence of other types of specialization, such as in diet or habitat with contrasting implications in the context of climate change (Patrick & Weimerskirch, 2017; Piper, 2011; Wakefield et al., 2015; Woo, Elliott, Davidson, Gaston, & Davoren, 2008). Rapid environmental changes have the potential to favour individuals with flexible migration strategies (Abrahms et al., 2018; Switzer, 1993), while IMSF could constrain the ability of a population to track habitat changes (Keith & Bull, 2017; Wiens, 1985).

Individual migration strategy fidelity may be driven by site familiarity, defined as information accumulated about a specific area by an individual (Jesmer et al., 2018; Keith & Bull, 2017; Piper, 2011). That is, by being faithful to wintering areas, individuals reduce the costs of sampling other suitable wintering areas (“always stay” strategy in Cresswell, 2014; Switzer, 1993), which may be particularly important for long-distance migrants (Thorup et al., 2017; Van Moorter, Rolandsen, Basille, & Gaillard, 2016). Long-term IMSF might be advantageous for long-lived species when considered over a long time period or across an entire life span even if it might not be the most favourable strategy every year (Abrahms et al., 2018; Bradshaw et al., 2004; Switzer, 1993). If a species’ migration behaviour is affected by site familiarity (i.e. site fidelity drives IMSF), then IMSF may persist across its entire range and several years as specific sites rather than habitats are selected (Switzer, 1993). Hence, site familiarity may play an important role in habitat selection (Cresswell, 2014; Keith & Bull, 2017; Piper, 2011).

Alternatively, exhibited IMSF could be a consequence of individual specialization in diet and habitat choice in a patchy environment (Abrahms et al., 2018; Patrick & Weimerskirch, 2017). An individual’s resource or habitat choice in heterogeneous environments such as the open ocean can be associated with spatial fidelity (Switzer, 1993). However, selection of sites and habitats are often decoupled from each other as similar habitats can co-occur at different sites (Gómez, Tenorio, Montoya, & Cadena, 2016; Peters et al., 2017). Therefore, IMSF as a consequence of habitat specialization is unlikely to be exhibited in all habitats occupied by a species across its geographical range. Additionally, resource patches can shift in space and time between years. Hence, IMSF may not persist across multiple years throughout a species’
range if it is a consequence of habitat specialization (Patrick & Weimerskirch, 2017; Wakefield et al., 2015).

Here, we assessed if two migratory species, over large parts of their range, display IMSF (or alternatively generalist migratory behaviour) and if this behaviour is better explained by fidelity to specific sites (i.e. site familiarity) or habitats (i.e. habitat specialization). The temperate common guillemot (hereafter COGU, Uria aalge) and the Arctic Brünnich’s guillemot (hereafter BRGU, Uria lomvia) are some of the most common seabirds in the North Atlantic. They are large (~1 kg), deep diving, pelagic feeding, long-lived and colonial seabirds with strong breeding philopatry (Benowitz-Fredericks & Kitaysky, 2005; Gaston & Jones, 1998). Guillemot annual distribution encompasses a large range of space and environments in the North Atlantic and Arctic seas (Frederiksen et al., 2016; McFarlane Tranquilla et al., 2015). These oceans are changing rapidly under climate change (Henson et al., 2017; IPCC, 2013; Lind, Ingvaldsen, & Furevik, 2018) and some species distributions (e.g. capelin, Mallotus villosus, Carscadden, Gjøsæter, & Vilhjálmsson, 2013) and ecosystem compositions are shifting (Beaugrand & Kirby, 2018; Fossheim et al., 2015; Perry, Low, Ellis, & Reynolds, 2005; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Wassmann, Duarte, AgustÍ, & Sejr, 2011).

In this context, an understanding of IMSF and the relative fidelity to geographical sites and habitats as well as its persistence across a genus’ range is needed to assess the species’ potential resilience to ongoing environmental changes. Initial evidence indicates that individuals of both species display variable site fidelity during the winter months (McFarlane Tranquilla et al., 2014) and hence might be able to adapt to a shifting habitat (Abrahms et al., 2018; Switzer, 1993).

Using tracking data from COGUs and BRGUs from 13 colonies across the Northeast Atlantic, we tested the hypothesis that individuals of both species display IMSF across large parts of their range throughout their non-breeding period. Furthermore, we assessed if their migratory behaviour is potentially a consequence of site familiarity or habitat specialization.

### 2 | MATERIALS AND METHODS

#### 2.1 | Data

Fieldwork was conducted at 13 breeding colonies spanning 56°N to 79°N and 16°W to 55°E in the Northeast Atlantic (Figure 1). Some colonies in close spatial proximity to each other (<160 km) which exhibited similar space use patterns were combined resulting in nine breeding populations (Table 1). BRGU and COGU breed sympatrically in four of these populations. We used archival light-level loggers (also GLS or ‘geolocators’) to estimate the spatiotemporal locations of individuals throughout the non-breeding period. These devices record light intensity and time which can be used to estimate approximate latitude (i.e. day length) and longitude (i.e. time of noon) positioning twice daily. They are attached to a leg ring with cable ties (logger, ring and cable ties <0.5% adult body mass). During the summers of 2007–2017, we captured adult guillemots with noose poles at different sites and equipped them with light-level loggers which we retrieved in subsequent years (overall retrieval rate >60%). Individuals were chosen opportunistically in most cases from birds breeding on cliff ledges on the landward edge of the colony. This resulted in 1,332 annual tracks (641 BRGU, 691 COGU) of 729 individuals (357 BRGU, 372 COGU) of which 376 were tracked for 2–7 years over periods of 2–9 years (168 BRGU, 208 COGU, Table 1). All subsequent analyses were conducted in R 3.4.3 (R Development Core Team, 2018). All loggers (models: Mk15 (British Antarctic Survey), Mk3006 (Biotrack), F100, C250 & C330 (Migrate Technology) or L250A (Lotek) also recorded temperature and salt water immersion (‘wet/dry’) data which were used in combination with recorded light data to increase location accuracy (estimated median accuracy: 150–180 km; Merkel et al., 2016; see Supporting Information S1 for more details). In some populations, blood or feather samples were collected and used to determine the sex of individual birds (details in Table 1) by DNA extraction using the DNeasy 96 Blood and Tissue Kit (Qiagen) and afterwards polymerase

![FIGURE 1 Map of the study extent (in polar stereographic projection). Circles denote study colonies with different colours indicating the presence of the two species (Brünnich’s guillemots in blue and common guillemot in red; colony names detailed in Table 1). Colonies combined for the purpose of this study are encircled with dashed ellipsoids. Shaded blue and red areas illustrate the total annual extent for each species breeding at the displayed colonies based on individuals tracked by light-level geolocation [Colour figure can be viewed at wileyonlinelibrary.com](http://example.com)](http://example.com)
TABLE 1  Available tracking data. Some colonies (in parentheses when applicable) have been merged into populations for the purpose of this study. Tracking years denote first and last year of tracking and include gap years in many cases. Number of known females (f) and males (m) are added in parentheses.

| Breeding population (colonies) | Acronym | Location | Tracking years | Annual tracks | Individuals | Individuals with repeat tracks | Years individuals have been tracked repeatedly | Tracking years | Annual tracks | Individuals | Individuals with repeat tracks | Years individuals have been tracked repeatedly |
|-------------------------------|---------|----------|----------------|---------------|-------------|-------------------------------|---------------------------------------------|---------------|---------------|-------------|-------------------------------|---------------------------------------------|
| Isle of May                   | BM      | 56.18°N 2.58°W | 2011–2017     | 91            | 46 (15f, 27m) | 28 (12f, 15m)                | 2–4                                 |               |               |             |                                |                                             |
| Sklinna                       | SK      | 65.22°N 10.97°E | 2011–2017     | 83            | 52           | 25                           | 2–3                                 |               |               |             |                                |                                             |
| Hjelmsøya                     | HJ      | 71.07°N 24.72°E | 2011–2017     | 52            | 34           | 14                           | 2–3                                 |               |               |             |                                |                                             |
| Northeast Iceland (Grimsey, Langanes) | IC | 66.44°N 15.80°W | 2014–2017     | 37            | 26           | 9                            | 2–3                                 | 2014–2017     | 42            | 28           | 13                            | 2–3                                 |
| Jan Mayen                     | JM      | 71.02°N 8.52°W  | 2011–2017     | 86            | 47 (20f, 19m) | 23 (14f, 9m)                | 2–5                                 | 2011–2017     | 136           | 66 (19f, 36m) | 39 (13f, 21m)                | 2–5                                 |
| Hornøya                       | HO      | 69.98°N 32.04°E | 2011–2017     | 146           | 82 (16f, 24m) | 53 (7f, 17m)                | 2–3                                 | 2009–2017     | 140           | 79 (23f, 27m) | 35 (12f, 16m)                | 2–4                                 |
| Bjørnøya                      | BI      | 74.50°N 18.96°E | 2007–2017     | 196           | 85 (42f, 28m) | 56 (27f, 21m)               | 2–6                                 | 2007–2017     | 156           | 65 (25f, 25m) | 42 (18f, 21m)                | 2–7                                 |
| Western Spitsbergen (Amfifjellet, Ossian Sars fjelet, Diabasodden) | WSP | 78.75°N 13.20°E | —             | —             | —                        | —                            | 2–3                                 | 2007–2017     | 112           | 78 (30f, 40m) | 25 (12f, 12m)                | 2–3                                 |
| Southern Novaya Zemlya (Kara Gate) | SNZ | 70.59°N 55.02°E | —             | —             | —                        | —                            | 2015–2017     | 55            | 41           | 14                            | 2                                  |
chain reaction (PCR) using Qiagen’s Multiplex PCR Kit. Sex was then
determined using the primers MS (Bantock, Pry-Jones, & Lee, 2008)
and P8 (Griffiths, Double, Orr, & Dawson, 1998). Gender was in-
cluded in the analyses to account for the possibility of sex-specific
migratory behaviour and its potential effect on our measure of site
fidelity during parts of the non-breeding period.

2.2 | Data analysis

2.2.1 | Do guillemots display IMSF?

To test our hypothesis that guillemots display IMSF as site fidelity
throughout the non-breeding period, we used the concept of near-
est neighbour distance (NND, Guilford et al., 2011). Individual annual
tracks were split into 10-day bins starting 1 July. A resolution of 10 days
was chosen to retain a sufficient number of locations for each bin for
further analysis while accounting for possible seasonal differences. The
centre for each individual 10-day bin was estimated as the geographical
median (initial position with minimum distance to all other locations).
NND in space was calculated as Euclidian distance in polar stereo-
graphic projection between 10-day centroids for repeat tracks of the
same individual in different years (intra-individual) as well as different
individuals from the same species and breeding population tracked in
the same year (inter individual). Next, we averaged NND of all pairwise
comparisons at each time step for each individual with two or more re-
peat tracks (i.e. ≥2 years of tracking). Following Wakefield et al. (2015),
we used a randomization procedure to test—for each species and pop-
ulation considered—if individuals exhibit IMSF at each time step. The
null hypothesis (generalist migratory behaviour, i.e. a lack of IMSF) at
each time step was that observed intra-individual NND is greater than
or similar to population-wide NND calculated with randomly assigned
bird individuals (1,000 permutations without replacement). If the null
hypothesis is correct, then observed intra-individual NND should not
be significantly smaller than the estimated population-wide NND dis-
tribution. We tested this at each 10-day time step using a one-tailed t
test (significance at \( \rho = .05 \)) between exhibited intra-individual NND
and population-level NND. To account for the possibility of sex-specific
behaviour, the same procedure was also applied to each sex separately
for populations where the sexes were known (Table 1). To test if a lack
of site fidelity could be explained by variability in timing rather than
flexible space use (i.e. IMSF, but with a time lag), we calculated intra-
individual as well as inter-individual NND at each time step for a wide
temporal sliding window (70 days, Figure S1). Using this temporally in-
tegrated measure of fidelity, we ran the same procedure as described
above for both sexes combined and each sex separately.

2.2.2 | Do guillemots display habitat fidelity?

To test if individuals exhibit habitat specialization throughout
the non-breeding period, we quantified the occupied habitat using
eight ecologically relevant oceanographic parameters (Fort, Porter, &
Grémillet, 2009; Fort et al., 2013; McFarlane Tranquilla et al., 2015);
three sea surface temperature variables (absolute, distance to fronts,
predictability), two sea surface height variables (absolute, distance
to mesoscale eddies), surface air temperature, distance to the mar-
ginal sea ice zone and bathymetry (see Supporting Information S1
for more details). The habitat occupied was then assessed using the
concept of environmental space (Broennimann et al., 2012) defined
as the first two axes of a principal component analysis (PCA) of all
environmental parameters calibrated on the available environment.
To capture the variability of the available environment, 20,000
points with equal spatial coverage across the entire study area
(Figure S2) were sampled every 2 weeks for the entire study period
(2007–2017). All individual positions were projected onto the PCs
(\(PC_1 = 44\% \) and \(PC_2 = 19\%\), Figure S3). Occupied environmental
space was then calculated using Gaussian kernel utilization distribu-
tions (UD, standard bandwidth, 200 × 200 pixel grid, adehabitatHR
package, Calenge, 2006) at each 10-day step following Broennimann
et al. (2012). These UD were used to calculate 10-day median habi-
tats for each track. Based on these, we calculated intra-individual
and inter-individual NND (only for individuals from the same species,
breeding at the same population and tracked during the same year)
in environmental space. Using these computed NNDs and the same
randomization procedure as described above for Cartesian space
(Wakefield et al., 2015), we tested if individuals exhibit fidelity to
specific habitat at each time step.

2.2.3 | Is IMSF better explained by site familiarity or
habitat specialization?

To discern if IMSF is better explained by site familiarity (fidelity to
specific sites) or habitat specialization (fidelity to specific habitats),
we quantified species- and population-specific relative fidelity to
sites and habitats using the similarity index developed by Patrick and
Weimerskirch (2017). This index is a ratio ranging from 0 (all individu-
als are generalists within the considered population) to 1 (all individu-
als are specialists). At each 10-day step for each repeat individual,
the sum of all instances for which intra-individual NND was smaller
than inter-individual NND was divided by the number of inter-indi-
vidual NNDs computed (see Patrick & Weimerskirch, 2017 for more
details). Next, we averaged similarity for individuals with more than
one pair of repeat tracks. This similarity was calculated in Cartesian
as well as environmental space. Relative fidelity to either space was
tested by subtracting individual habitat similarity from site similarity.
Using two-tailed \( t \) tests, we determined if the estimated population-
wide distribution was significantly different from 0 (significance at
\( \rho = .05 \)) and hence either site (>0) or habitat specific (<0). In addition,
environmental similarity was calculated for each abiotic parameter
described above and relative fidelity for sites or a given environmen-
tal parameter was tested separately to estimate the robustness of
our results.
2.2.4 | Does site fidelity persist across several years?

To test whether site fidelity persists across years (an indication for site familiarity) or weakens linearly over time (an indication for habitat specialization assuming habitat is not connected to space), we modelled species- and population-specific intra-individual NND as a function of time lag (years between repeat tracks) with random slope and intercept for each individual. Next, we used likelihood ratio tests to determine whether these models explain the data better than the intercept-only models (i.e. without accounting for time lag; Wakefield et al., 2015). This procedure was run for 70-day sliding windows throughout the non-breeding period to account for potential timing effects.

3 | RESULTS

3.1 | Do guillemots exhibit IMSF?

Overall, both species exhibited IMSF as indicated by colony-specific significantly smaller intra-individual NND compared to the Null hypothesis (i.e. generalist migratory behaviour) across their studied range (Figure 2). But, some seasonal and population-specific variability was apparent. Generalist migratory behaviour was shown during spring (approx. February–May depending on population) and in part of the autumn (August/September) across species and populations as a consequence of little population-wide variability in migration strategies. Moreover, there was some variation among populations and populations displaying little population-wide NND did not generally exhibit IMSF given the accuracy of the tracking method used (median error of 150–180 km; Merkel et al., 2016; Figure 3). But, some populations—with little population-wide NND (e.g. COGUs from Bjørnøya & Hjelmsøya)—displayed IMSF during mid-winter (December/January) when the proportion of twilight events (north of 66°N) and hence location estimates missing was high (Figure S4). IMSF was also visible for each sex separately in both species and all populations tested with some populations exhibiting sex-specific differences during autumn and in part spring (Figures S5 and S6).

3.2 | Is IMSF better explained by site familiarity or habitat specialization?

In all populations of both species, little habitat fidelity was apparent (except for BRGU from Hornøya and COGU from Jan Mayen, Figure S7). Furthermore, fidelity to geographical sites rather than abiotic habitat was predominant for both species and all populations
3.3 | Does site fidelity persist across several years?

Overall, IMSF persisted across multiple years (up to 9 years, seven of those with tracking data) in all tested populations, when accounting for the timing difference (i.e. using a 70-day sliding window), illustrating that individual site fidelity was not altered by the number of years between repeat tracks (Figure 4).

4 | DISCUSSION

In this study, we identified IMSF for the genus *Uria*, which was independent of sex, and occurred throughout the entire Northeast Atlantic during most of the non-breeding period. This was apparent as fidelity to geographical sites rather than preferences for specific habitats. Importantly, IMSF persisted across multiple years in all considered populations. Suggesting that in the Northeast Atlantic IMSF is the norm in COGUs and BRGUs—-independent of occupied habitat.

4.1 | IMSF in guillemots

Evidence for IMSF has been found in various taxa such as in ungulates (Jesmer et al., 2018; Sawyer, Merkle, Middleton, Dwinnell,
instances of generalist migratory behaviour

Generalist migratory behaviour, that is, an absence of IMSF, was identified to a varying degree in all populations of COGU and BRGU. This can potentially be attributed to several season-specific circumstances originating in different life-history stages during their annual cycle. First, a lack of post-breeding IMSF during autumn could be caused by guillemots undergoing moult of their flight feathers, which renders them flightless (Birkhead & Taylor, 1977; Elliott & Gaston, 2014; Thompson, Wilson, Melvin, & Pierce, 1998). This constrains their movements and hence their capacity to demonstrate IMSF. Additionally, reproductively successful males are accompanying a flightless chick as it departs the colony, which further limits their movement (Elliott et al., 2017; Harris & Wanless, 1990). Thus, it is not surprising that some populations exhibit IMSF only for females during autumn as these are not constrained by a dependent and flightless chick and have the possibility to move large distances after breeding and prior to moulting. Second, various populations of both species displayed a lack of IMSF during spring, which corresponds to the pre-laying period when individuals periodically attend their colony (Gaston & Nettleship, 1981) and are thus constrained in their movement to de-facto central place foraging. However, pre-laying commences at different times across the range of this genus and can begin as early as February on Iceland or as late as April on Spitsbergen (Merkel et al., 2019), while at least some part
of the population on the Isle of May continues colony attendance after the autumn moult throughout the non-breeding period (Harris & Wanless, 2016). This variability in colony arrival timing could explain the variability in time at which generalist migratory behaviour is observed during the end of the non-breeding period for the different populations.

4.3 | Is IMSF better explained by site familiarity or habitat preference?

Persistent IMSF over multiple years was apparent in spatial consistency rather than preferences for specific habitats across the entire study region and throughout the non-breeding period. This suggests that mesoscale IMSF in guillemots is better explained by site familiarity potentially through experience and the use of memory (Davoren, Montecucchi, & Anderson, 2003) rather than being a consequence of habitat specialization. Memory has also been suggested to drive COGU foraging behaviour during breeding (Regular, Hedd, & Montevecchi, 2013). We could not identify any fidelity to habitat rather than sites for any population of either species throughout the entire non-breeding period on the scale investigated. Furthermore, individuals from most populations did not display any habitat fidelity at all. And, for habitat specialization to drive site fidelity, we would have expected that IMSF, if displayed at all, would not persist over multiple years across the genus’ range, particularly in light of the drastic changes in the physical environment of the study region (Henson et al., 2017; IPCC, 2013; Lind et al., 2018; Sgubin, Swingedouw, Drijfhout, Mary, & Bennabi, 2017) and the shifting species distributions and ecosystem compositions (Beaugrand & Kirby, 2018; Carscadden et al., 2013; Fossheim et al., 2015; Perry et al., 2005; Pinsky et al., 2013; Wassmann et al., 2011). However, we cannot rule out the possibility that the abiotic variables selected to describe the available habitat, although ecologically relevant for the study species’, might not be able to reflect guillemot foraging habitat. This is especially true for all satellite-derived parameters used (such as sea surface temperature) as these only reflect surface water conditions, while guillemots are deep-diving foragers.

By contrast, we identified IMSF across our studied range which persisted over multiple years for all populations with more than 2 years of data as is predicted if IMSF is caused by site familiarity
and after the unpredicted collapse of sea ice in the Barents Sea in long-lived species. Also, data were gathered within the same ma-
tracking data), which only covers a part of the lifetime of these short period of time (9 years), with the maximum period an indi-
data collection for this study has been conducted within a relative flexibility in their migratory behaviour (Veit & Manne, 2015). All
dance with changing climatic conditions, which suggests some large-scale shifts in winter distributions of guillemots in accor-
ment (due to moulting, chick presence or pre-laying attendance). By being faithful to known wintering areas, individuals reduce the costs of sampling other suitable wintering areas, in particular when flight costs are high such as in guillemots (Elliott et al., 2013), and thus diminish uncertainty from successive migrations (Abrahms et al., 2018; Cresswell, 2014). This suggests that these species, which exhibit nested area restricted search (Fauchald, Erikstad, & Skarsjford, 2000), select for sites at the mesoscale and potentially for specific habitats and preys at smaller scales (Fauchald, 2009). Site familiarity is also important as conditions at different staging sites must be considered unknown to the individual due to the large distances covered. Consequently, individual migration routes can generally be assumed to have developed in response to historically expected conditions (Thorup et al., 2017; Van Moorter et al., 2016).

Contrastingly, incidences have been documented of apparent large-scale shifts in winter distributions of guillemots in accord-
dance with changing climatic conditions, which suggests some flexibility in their migratory behaviour (Veit & Manne, 2015). All data collection for this study has been conducted within a relative short period of time (9 years), with the maximum period an individual was tracked extending over 9 years (seven of those with tracking data), which only covers a part of the lifetime of these long-lived species. Also, data were gathered within the same marine pelagic regime in the North Atlantic (Beaugrand & Kirby, 2018) and after the unpredicted collapse of sea ice in the Barents Sea in 2006 which has persisted to the present (Lind et al., 2018). Hence, inferences made on IMSF in these species—even though valid and based on a rather unique dataset—need to be viewed with caution and might not hold under different oceanic regimes (Veit & Manne, 2015).

5 | CONCLUSION

In this study, we found strong support for mesoscale IMSF for COGU and BRGU from multiple breeding populations across the Northeast Atlantic regardless of habitat utilized. Our data suggest that this was best explained by site familiarity (Piper, 2011; Switzer, 1993) rather than by habitat specialization. Historically, site familiarity was most likely a sufficient strategy for these long-lived species (Abrahms et al., 2018; Bradshaw et al., 2004; Switzer, 1993). In the light of a rapidly changing physical and biological environment, these species might not be able to adjust their migration strategies fast enough (Abrahms et al., 2018), particularly if migration strategies are established during the first years of life (Dall et al., 2012) as also suggested for other seabirds (Guilford et al., 2011; Van Bemmelen et al., 2017) and some ungulate spe-
cies (Jesmer et al., 2018; Sawyer et al., 2018). This might also be the case for other long-lived migrants, particularly if they exhibit similar high costs of movement as in guillemots (Elliott et al., 2013) and consequently potential severe constraints upon large-scale movement capabilities and hence high sensitivity towards habitat loss (Taylor & Norris, 2010).

ACKNOWLEDGEMENTS

Funding for this study was provided by the Norwegian Ministry for Climate and the Environment, the Norwegian Ministry of Foreign Affairs and the Norwegian Oil and Gas Association through the SEATRACK project (www.seapop.no/en/seatrack) as well as from the Research Council of Norway (project 216547), TOTAL E&P Norway and the TOTAL Foundation and the UK Natural Environment Research Council’s National Capability. We would like to thank Børge Moe, Hålfdan Helgi Helgason and Vegard Sandøy Bråthen for the logistical support within SEATRACK. This work would not have been possible without SEAPOP (www.seapop.no) and the combined effort and long-term engagement of many researchers as well as numerous field assistants all across the Northeast Atlantic.

DATA AVAILABILITY STATEMENT

Data are available through the Norwegian Polar Data Centre (10.21334/npolar.2020.9c9deb08).

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**BIOSKETCH**

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Authors contributions: BM, HStr, NGY and SD designed the study; BM analysed the data with the help from NGY; BM wrote the paper with contributions from SD, HStr, NGY and DG; HStr, SD, FD, KEE, AVE, MPG, MG, SHL, TKR, GHS, HSte, ÞLÞ and SW provided data; FD, KEE, HSte and SW commented on later drafts of the manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Merkel B, Descamps S, Yoccoz NG, et al. Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds. *J Biogeogr*. 2021;48:263–275. [https://doi.org/10.1111/jbi.13883](https://doi.org/10.1111/jbi.13883)