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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.

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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, murre, *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 (Alerstam, 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, & Sih, 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; Ceia & Ramos, 2015; Phillips, Lewis, González-Solís, & 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 Ceia & 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, Gjørseter, & Vilhjálmsson, 2013) and ecosystem compositions are shifting (Beaugrand & Kirby, 2018; Fosshem 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

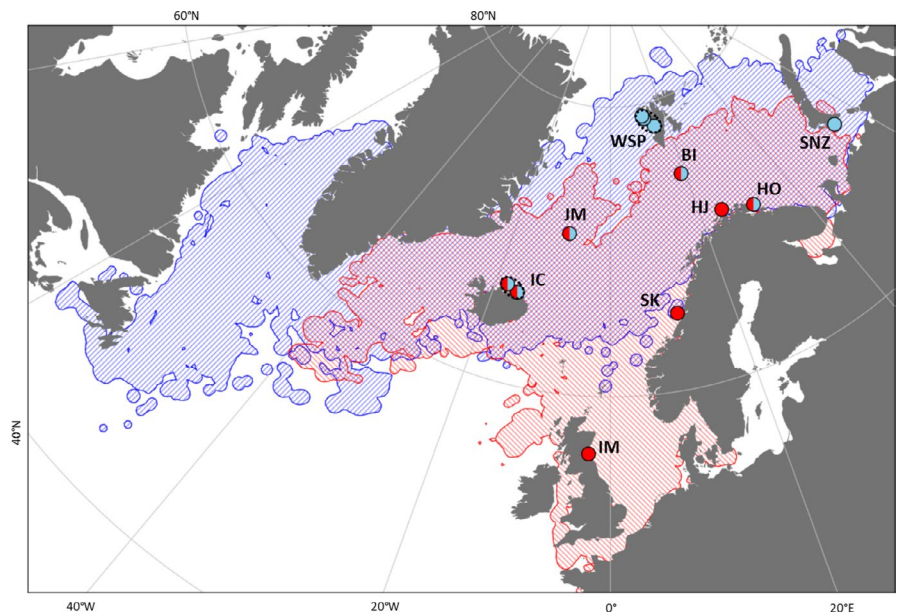




TABLE 1 Available tracking data. Some colonies (in parentheses when applicable) have been merged into populations for the purpose of this study. Tracking years denote first and last year of tracking and include gap years in many cases. Number of known females (f) and males (m) are added in parentheses

Breeding population (colonies)	Common guillemot (COGU)						Brünnich's guillemot (BRGU)					
	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	IM	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	–	–	–	–	–
Hjelmøya	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 (Amfjället, Ossian Sars fjellet, Diabasodden)	WSP	78.75°N 13.20°E	–	–	–	–	–	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 M5 (Bantock, Prys-Jones, & Lee, 2008) and P8 (Griffiths, Double, Orr, & Dawson, 1998). Gender was included 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 nearest 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 stereographic 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 repeat tracks (i.e. ≥ 2 years of tracking). Following Wakefield et al. (2015), we used a randomization procedure to test—for each species and population 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 distribution. We tested this at each 10-day time step using a one-tailed *t* test (significance at $p = .05$) 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 integrated 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 marginal 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 (PC1 = 44% and PC2 = 19%, Figure S3). Occupied environmental space was then calculated using Gaussian kernel utilization distributions (UD, standard bandwidth, 200×200 pixel grid, adehabitatHR package, Calenge, 2006) at each 10-day step following Broennimann et al. (2012). These UDs were used to calculate 10-day median habitats 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 individuals are generalists within the considered population) to 1 (all individuals 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-individual 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 $p = .05$) 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 environmental 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).

Higher variability in intra-individual NND was apparent in some populations (e.g. BRGU Bjørnøya), particularly in late winter (February/March, Figure 4). Integrating NND over a wide temporal window (70 days) demonstrated that some spatial variability could be explained by timing (i.e. similar areas have been utilized, but not necessarily at the same time), while general results remained unchanged (Figure 2).

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

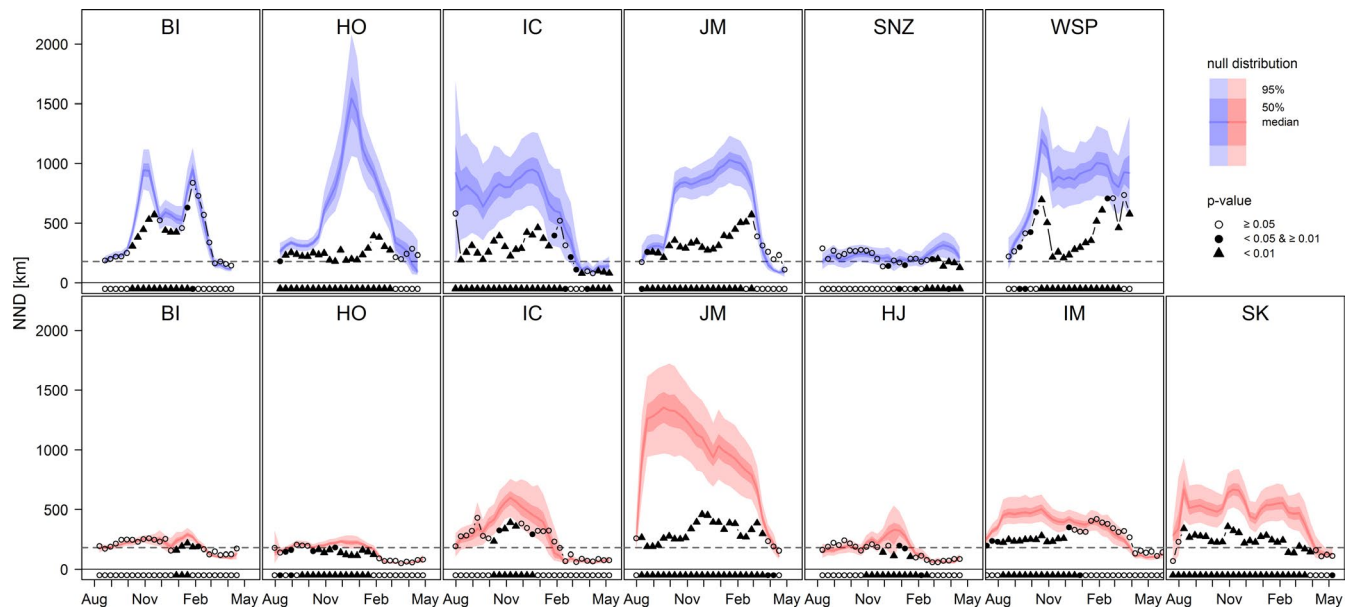
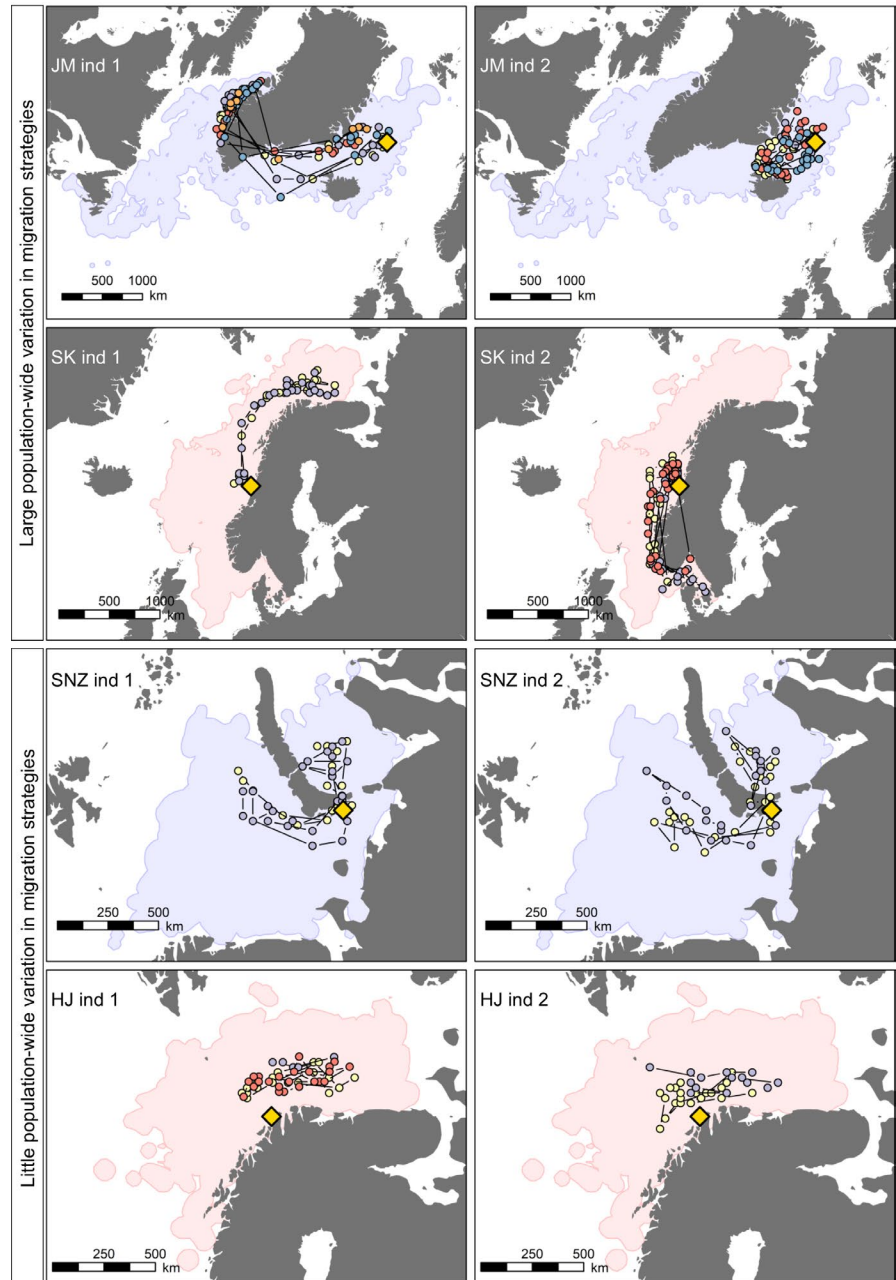


FIGURE 2 Brünnich's (blue) and common guillemot (red) mean species- and breeding population-specific intra-individual nearest neighbour distance (NND, black symbols) compared to the null hypothesis, that is, generalist migratory behaviour (red and blue light and dark shades indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black filled symbols correspond to a mean species- and breeding population-specific intra-individual NND significantly smaller than the null distribution (i.e. IMSF). Grey stippled line in each plot represents the approximate accuracy of light-level geolocation positions. Bottom row in each panel depicts individual spatial consistency over a 70-day sliding window (with black symbols corresponding to a mean intra-individual NND significantly smaller than the null)

FIGURE 3 Example tracks of eight individual guillemots that have been tracked for 2–4 years. The top four panels illustrate non-breeding movements of example individuals from the two different species (Brünnich's and common guillemot with blue and red background, respectively) breeding at two colonies (Jan Mayen, JM and Sklinna, SK) with large population-wide variability in migration strategies (shown as coloured shape depicting approximate annual extent of all tracked individuals from the given colony). The lower four panels illustrate non-breeding movements from individuals breeding at colonies with little population-wide variability in migration strategies (southern Novaya Zemlya, SNZ and Hjelmsøya, HJ). Positions denote annual 10-day median tracks with different years illustrated in different colours. Note the different scales in each panel and that positions often overlap between years and hence might be partly obscured. Yellow diamonds in each panel denote the colony location for that individual



throughout the entire non-breeding period (Figure 5). The same pattern could be observed for each sex (Figures S8 and S9) as well as each environmental parameter (Figure S10), separately. The only indication for fidelity to a specific abiotic feature rather than a specific site could be seen in both species for bathymetry during spring (Figure S10).

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,

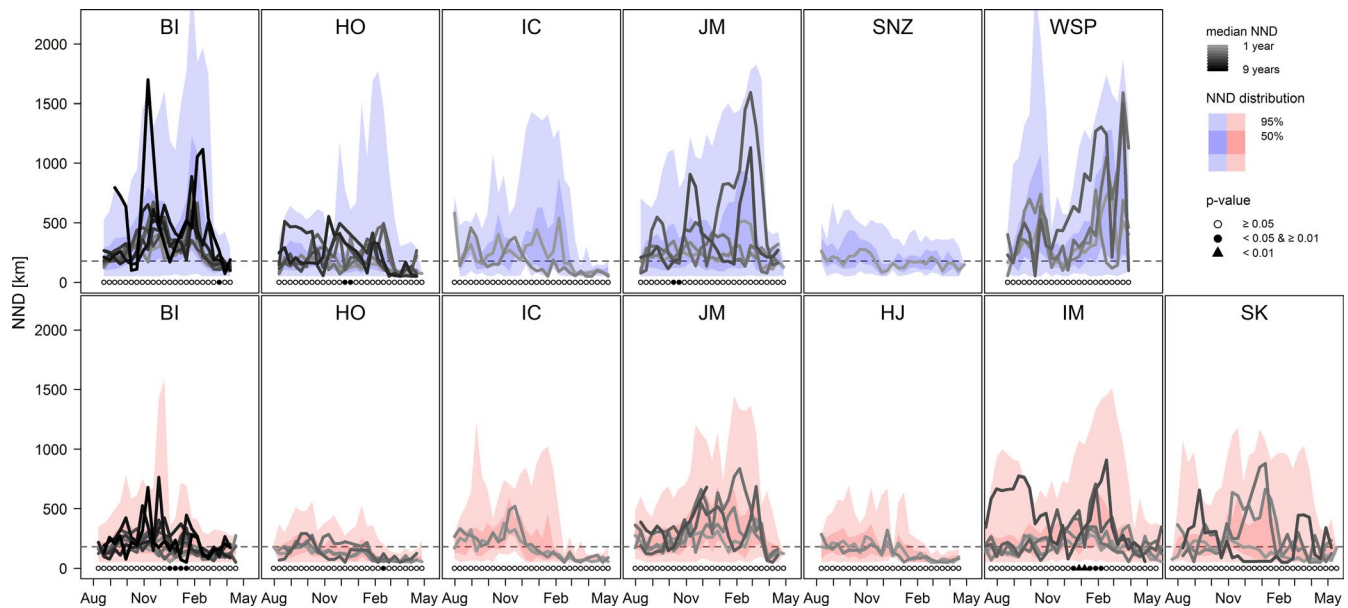


FIGURE 4 Brunnich's (blue) and common guillemot (red) species- and breeding population-specific intra-individual nearest neighbour distance (NND) with varying time lag. Grey shaded lines present median within-individual NND with time lag ranging from 1 year (grey) to 9 years (black). Coloured areas in the background of each panel represent the distribution of all intra-individual NND regardless of time lag. Symbols in bottom of each panel indicate the probability that including time lag explains the data better than the null model for 70-day sliding windows. Grey stippled line in each plot represents the approximate accuracy of light-level geolocation positions

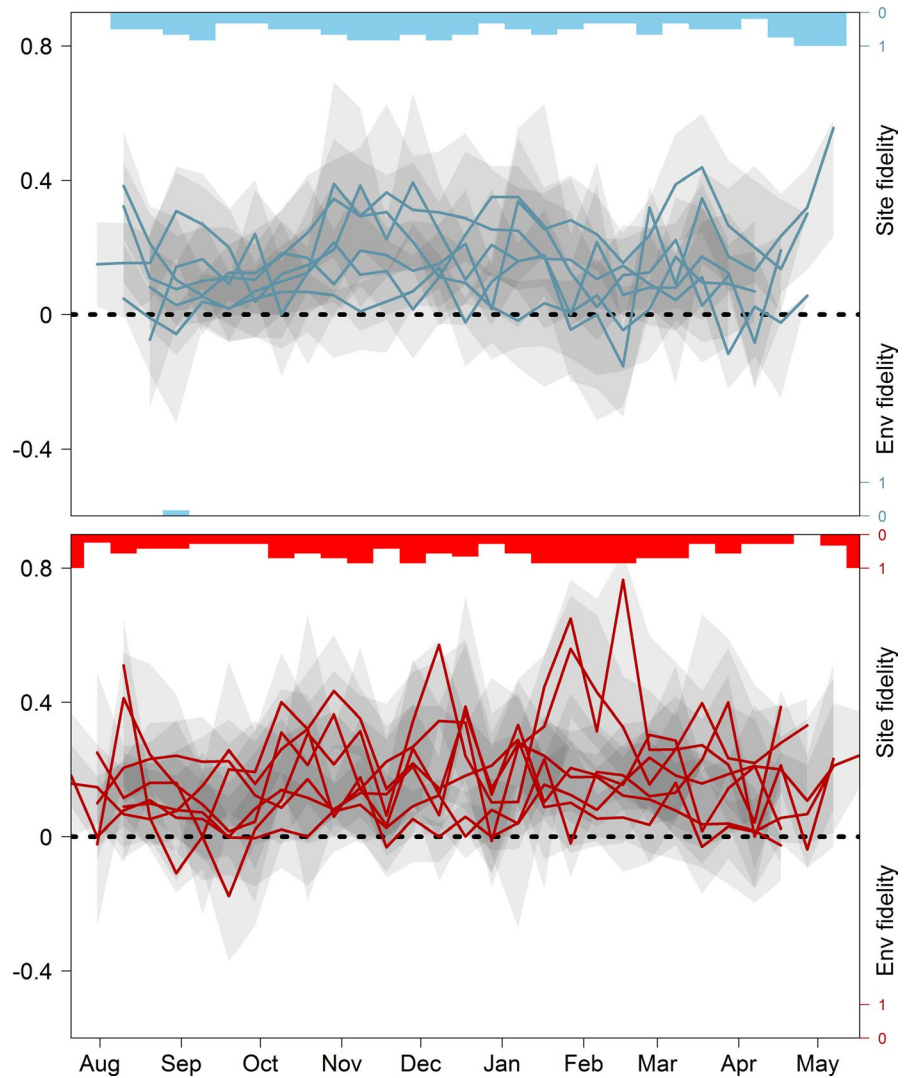
& Monteith, 2018), fishes (Brodersen et al., 2012; Thorsteinsson, Pálsson, Tómasson, Jónsdóttir, & Pampoulie, 2012) as well as in monarch butterflies (*Danaus plexippus*, Yang, Ostrovsky, Rogers, & Welker, 2016). Furthermore, it seems to be common in seabirds at a regional level and more ambiguous at the mesoscale (Phillips et al., 2017). In a previous study, COGU and BRGU breeding in the Northwest Atlantic were considered to exhibit flexibility in their winter space use (McFarlane Tranquilla et al., 2014). By contrast, we found strong support for the hypothesis that individuals of both species in populations in the Northeast Atlantic display IMSF at the mesoscale. However, we also observed temporal variation in space use, particularly during late winter when IMSF for some populations was not exhibited at the 10-day step resolution, but only when NND was integrated over a wider 70-day temporal window. This suggests some temporal flexibility such that individuals utilize the same areas in different years, but not necessarily at the same time during the winter months as has also been shown for long-tailed skuas (*Stercorarius longicaudus*, Van Bemmelen et al., 2017). This temporal flexibility seems to occur only within the range of known sites for a particular individual. McFarlane Tranquilla et al. (2014) also reported behavioural flexibility in the mid-winter spatial distribution (defined in their study as January), particularly BRGUs, breeding in the Northwest Atlantic, tracked over multiple winters. Here we could illustrate that, particularly during late winter (February/March) IMSF was more variable, but could be explained by timing differences. Consequently, the reported flexibility by McFarlane Tranquilla et al. (2014) might also be explained by temporal flexibility during the winter months between individual-specific sites rather than generalist migratory behaviour. This argument is further strengthened by

the observed general persistence of IMSF when accounting for the temporal flexibility in all studied populations across multiple years.

4.2 | 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

FIGURE 5 Brünnich's (blue) and common guillemot (red) species- and breeding population-specific similarity (ranging from -1 to 1) throughout the non-breeding period where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Each line represents the median fidelity for a given population. Semi-transparent grey shaded areas illustrate population-wide quartile range (25%–75%) in individual fidelity values with darker colours indicating overlapping ranges between populations. Bar plots at the top and bottom of each panel illustrate the proportion of populations with significant fidelity (i.e. significantly different from 0 at $p = .05$, scale on the right) to either sites (at the top) or habitat (at the bottom) during each 10-day step



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, Montevecchi, & 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; Fosheim 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

(Piper, 2011; Switzer, 1993). The ontogeny of individual migration strategies and the relative roles of genetic control (Liedvogel, Åkesson, & Bensch, 2011; Newton, 2008), social learning (Jesmer et al., 2018; Keith & Bull, 2017) and individual exploration (Guilford et al., 2011) therein is poorly understood. However, subsequent migrations seem to be influenced by learning of navigational map features en route (potentially visual, olfactory or magnetic) which, in turn, lead to individual site familiarity through experience and further refinement of individual migration strategies (Guilford et al., 2011; Spiegel & Crofoot, 2016; Van Bemmelen et al., 2017). Thus, the above-discussed temporal flexibility in site fidelity can also be accounted for by learning as individuals could have the potential to switch between multiple known sites if conditions at the occupied site become unfavourable (the 'win-stay, lose-switch' rule; Switzer, 1993) and the individual is not impeded in its movement (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, & Skarsfjord, 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 accordance 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 species (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).

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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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SUPPORTING INFORMATION

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

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