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

2 Short title: Individual migration strategy fidelity in guillemots

3 Authors: Benjamin Merkel<sup>1,2,\*</sup>, Sébastien Descamps<sup>1</sup>, Nigel G Yoccoz<sup>2</sup>, David Grémillet<sup>3</sup>, Francis Daunt<sup>4</sup>,  
4 Kjell E Erikstad<sup>5,6</sup>, Aleksey V Ezhov<sup>7,8</sup>, Mike P Harris<sup>4</sup>, Maria Gavrilov<sup>7,9</sup>, Svein-Håkon Lorentsen<sup>10</sup>, Tone K  
5 Reiertsen<sup>5</sup>, Harald Steen<sup>1</sup>, Geir H Systad<sup>11</sup>, Þorkell Lindberg Þórarinnsson<sup>12</sup>, Sarah Wanless<sup>4</sup>, Hallvard  
6 Strøm<sup>1</sup>

7 Affiliations:

8 <sup>1</sup> Norwegian Polar Institute, Fram Centre, P.O. Box 6606 Langnes, 9296 Tromsø, Norway

9 <sup>2</sup> Department of Arctic and Marine Biology, University of Tromsø - The Arctic University of Norway, 9037 Tromsø,  
10 Norway

11 <sup>3</sup> Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry  
12 Montpellier - EPHE, Montpellier, France & FitzPatrick Institute, DST-NRF Centre of Excellence at the University of  
13 Cape Town, Rondebosch 7701, South Africa.

14 <sup>4</sup> Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

15 <sup>5</sup> Norwegian Institute for Nature Research, Fram Centre, P.O. Box 6606 Langnes, 9296 Tromsø, Norway

16 <sup>6</sup> Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, 7491  
17 Trondheim, Norway

18 <sup>7</sup> Association Maritime Heritage, Saint Petersburg, Russia

19 <sup>8</sup> Murmansk Marine Biological Institute, 17 str. Vladimirkaya, 183010 Murmansk, Russia

20 <sup>9</sup> National Park Russian Arctic, 57 Sovetskikh Kosmonavtovo ave., Archangelsk, Russia

21 <sup>10</sup> Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, 7485 Trondheim, Norway

22 <sup>11</sup> Norwegian Institute for Nature Research, Thormøhlensgate 55, 5006 Bergen, Norway

23 <sup>12</sup> Northeast Iceland Nature Research Centre, Hafnarstétt 3, 640 Húsavík, Iceland

24 \*Corresponding author, email: merkel.benjamin@gmail.com/ benjamin.merkel@npolar.no, phone: +47 777 50 573

25

26 Authorship: BM, HStr, NGY and SD designed the study; BM analysed the data with help from NGY; BM  
27 wrote the paper with contributions from SD, HStr, NGY and DG; HStr, SD, FD, KEE, AVE, MPH, MG, DG,  
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38 across the Northeast Atlantic.

## 39 Abstract

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

44 **Location:** North Atlantic

45 **Taxon:** *Uria* spp.

46 **Methods:** We quantified consistent individual differences in inter-annual spatial distribution and  
47 habitat occupied throughout the non-breeding period using a large geolocator tracking dataset of  
48 729 adult seabirds breeding at 13 colonies across the Northeast Atlantic and repeatedly tracked up  
49 to seven years over a nine year period. Additionally, we used a similarity index to calculate relative  
50 fidelity to either geographic sites or habitats and linear mixed effects models to assess persistence of  
51 spatial site fidelity over multiple years.

52 **Results:** Both, guillemot species exhibited IMSF across a large part of the genus' range which  
53 persisted over multiple years. Individuals of both species and almost all colonies showed fidelity to  
54 geographic sites and not to specific habitats.

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

60 Keywords: guillemots, light-level geolocation, murre, *Uria aalge*, *Uria lomvia*

## 61 Introduction

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

72 Consistent differences in individual behaviour are common in free-living populations, and these can have  
73 far-reaching implications on intraspecific competition, population persistence, community dynamics, and  
74 ultimately species diversity (Bolnick et al., 2003; Dall, Bell, Bolnick, Ratnieks, & Sih, 2012; Piper, 2011).

75 Site fidelity - an animal's tendency to repeatedly use the same geographic area - is a common form of  
76 individual behavioural consistency (Switzer, 1993). In migrants, site fidelity during breeding has been  
77 frequently observed (Bradshaw, Hindell, Sumner, & Michael, 2004; Ceia & Ramos, 2015; Phillips, Lewis,  
78 González-Solís, & Daunt, 2017). Though, less evidence exist for site fidelity outside the breeding season  
79 here termed 'Individual migration strategy fidelity' (IMSF) when within-individual variation in the use of  
80 space during the non-breeding period is less than that across the population as a whole (reviewed in Ceia  
81 & Ramos, 2015; Cresswell, 2014; Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016; Newton,  
82 2008; Phillips et al., 2017). IMSF could be the cause or a consequence of other types of specialization,  
83 such as in diet or habitat with contrasting implications in the context of climate change (Patrick &  
84 Weimerskirch, 2017; Piper, 2011; Wakefield et al., 2015; Woo, Elliott, Davidson, Gaston, & Davoren,  
85 2008). Rapid environmental changes have the potential to favour individuals with flexible migration  
86 strategies (Abrahms et al., 2018; Switzer, 1993), while IMSF could constrain the ability of a population to  
87 track habitat changes (Keith & Bull, 2017; Wiens, 1985).

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

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

109 Here, we assessed if two migratory species, over large parts of their range, display IMSF (or alternatively  
110 generalist migratory behaviour) and if this behaviour is better explained by fidelity to specific sites (i.e.  
111 site familiarity) or habitats (i.e. habitat specialization). The temperate common guillemot (hereafter  
112 COGU, *Uria aalge*) and the Arctic Brünnich's guillemot (hereafter BRGU, *Uria lomvia*) are some of the  
113 most common seabirds in the North Atlantic. They are large (~1kg), deep diving, pelagic feeding, long  
114 lived, and colonial seabirds with strong breeding philopatry (Benowitz-Fredericks & Kitaysky, 2005; A J  
115 Gaston & Jones, 1998). Guillemot annual distribution encompasses a large range of space and  
116 environments in the North Atlantic and Arctic seas (Frederiksen et al., 2016; McFarlane Tranquilla et al.,  
117 2015). These oceans are changing rapidly under climate change (Henson et al., 2017; IPCC, 2013; Lind,  
118 Ingvaldsen, & Furevik, 2018) and some species distributions (e.g. capelin, *Mallotus villosus*, Carscadden,  
119 Gjørseter, & Vilhjálmsson, 2013) and ecosystem compositions are shifting (Beaugrand & Kirby, 2018;  
120 Fossheim et al., 2015; Perry, Low, Ellis, & Reynolds, 2005; Pinsky, Worm, Fogarty, Sarmiento, & Levin,  
121 2013; Wassmann, Duarte, Agustí, & Sejr, 2011). In this context, an understanding of IMSF and the  
122 relative fidelity to geographic sites and habitats as well as its persistence across a genus' range is needed

123 to assess the species' potential resilience to ongoing environmental changes. Initial evidence indicates  
124 that individuals of both species display variable site fidelity during the winter months (McFarlane  
125 Tranquilla et al., 2014) and hence might be able to adapt to a shifting habitat (Abrahms et al., 2018;  
126 Switzer, 1993).

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

## 131 Material and Methods

### 132 *Data*

133 Fieldwork was conducted at 13 breeding colonies spanning 56°N to 79°N and 16°W to 55°E in the  
134 Northeast Atlantic (figure 1). Some colonies in close spatial proximity to each other (< 160 km) which  
135 exhibited similar space use patterns were combined resulting in nine breeding populations (table 1).  
136 BRGU and COGU breed sympatrically in four of these populations. We used archival light-level loggers  
137 (also GLS or “geolocators”) to estimate the spatiotemporal locations of individuals throughout the non-  
138 breeding period. These devices record light intensity and time which can be used to estimate  
139 approximate latitude (i.e. day length) and longitude (i.e. time of noon) positioning twice daily. They are  
140 attached to a leg ring with cable ties (logger, ring, and cable ties < 0.5% adult body mass). During the  
141 summers of 2007 to 2017 we captured adult guillemots with noose poles at different sites and equipped  
142 them with light-level loggers which we retrieved in subsequent years (overall retrieval rate > 60%).  
143 Individuals were chosen opportunistically in most cases from birds breeding on cliff ledges on the  
144 landward edge of the colony. This resulted in 1332 annual tracks (641 BRGU, 691 COGU) of 729  
145 individuals (357 BRGU, 372 COGU) of which 376 were tracked for two to seven years over periods of two

146 to nine years (168 BRGU, 208 COGU, table 1). All subsequent analyses were conducted in R 3.4.3 (R  
147 Development Core Team, 2018). All loggers (models: Mk15 (British Antarctic Survey, Cambridge, UK),  
148 Mk3006 (Biotrack, Wareham, UK), F100, C250 & C330 (Migrate Technology, Cambridge, UK) or L250A  
149 (Lotek, St. John's, Newfoundland, Canada)) also recorded temperature and salt water immersion  
150 ("wet/dry") data which were used in combination with recorded light data to increase location accuracy  
151 (estimated median accuracy: 150-180 km, Merkel et al., 2016; see SI 1 for more details). In some  
152 populations, blood or feather samples were collected and used to determine the sex of individual birds  
153 (details in table 1) by DNA extraction using the DNeasy 96 Blood and Tissue Kit (Qiagen, Hilden,  
154 Germany) and afterwards polymerase chain reaction (PCR) using Qiagen's Multiplex PCR Kit. Sex was  
155 then determined using the primers M5 (Bantock, Prys-Jones, & Lee, 2008) and P8 (Griffiths, Double, Orr,  
156 & Dawson, 1998). Gender was included in the analyses to account for the possibility of sex-specific  
157 migratory behaviour and its potential effect on our measure of site fidelity during parts of the non-  
158 breeding period.

### 159 *Data Analysis*

160 Do guillemots display IMSF?

161 To test our hypothesis that guillemots display IMSF as site fidelity throughout the non-breeding period,  
162 we used the concept of nearest neighbour distance (NND, Guilford et al., 2011). Individual annual tracks  
163 were split into ten day bins starting 1 July. A resolution of ten days was chosen to retain a sufficient  
164 number of locations for each bin for further analysis while accounting for possible seasonal differences.  
165 The centre for each individual ten day bin was estimated as the geographic median (initial position with  
166 minimum distance to all other locations). NND in space was calculated as Euclidian distance in polar  
167 stereographic projection between ten day centroids for repeat tracks of the same individual in different  
168 years (intra-individual) as well as different individuals from the same species and breeding population



169 tracked in the same year (inter individual). Next, we averaged NND of all pairwise comparisons at each  
170 time step for each individual with two or more repeat tracks (i.e.  $\geq 2$  years of tracking). Following  
171 Wakefield et al. (2015), we used a randomization procedure to test - for each species and population  
172 considered - if individuals exhibit IMSF at each time step. The null hypothesis (generalist migratory  
173 behaviour, i.e. a lack of IMSF) at each time step was that observed intra-individual NND is greater than or  
174 similar to population-wide NND calculated with randomly assigned bird individuals (1000 permutations  
175 without replacement). If the null hypothesis is correct, then observed intra-individual NND should not be  
176 significantly smaller than the estimated population-wide NND distribution. We tested this at each ten  
177 day time step using a one-tailed t-test (significance at  $p = 0.05$ ) between exhibited intra-individual NND  
178 and population-level NND. To account for the possibility of sex-specific behaviour the same procedure  
179 was also applied to each sex separately for populations where the sexes were known (table 1). To test if  
180 a lack of site fidelity could be explained by variability in timing rather than flexible space use (i.e. IMSF,  
181 but with a time lag), we calculated intra-individual as well as inter-individual NND at each time step for a  
182 wide temporal sliding window (70 days, figure S1). Using this temporally integrated measure of fidelity  
183 we ran the same procedure as described above for both sexes combined as well as each sex separately.

184 Do guillemots display habitat fidelity?

185 To tested if individuals exhibit habitat specialisation throughout the non-breeding period we quantified  
186 the occupied habitat using eight ecologically relevant oceanographic parameters (Fort, Porter, &  
187 Grémillet, 2009; Fort et al., 2013; McFarlane Tranquilla et al., 2015); three sea surface temperature  
188 variables (absolute, distance to fronts, predictability), two sea surface height variables (absolute,  
189 distance to meso-scale eddies), surface air temperature, distance to the marginal sea ice zone and  
190 bathymetry (see SI 1 for more details). The habitat occupied was then assessed using the concept of  
191 environmental space (Broennimann et al., 2012) defined as the first two axes of a Principal Component  
192 Analysis (PCA) of all environmental parameters calibrated on the available environment. To capture the

193 variability of the available environment, 20000 points with equal spatial coverage across the entire study  
194 area (figure S2) were sampled every two weeks for the entire study period (2007-2017). All individual  
195 positions were projected onto the PCs (PC1 = 44% and PC2 = 19%, figure S3). Occupied environmental  
196 space was then calculated using Gaussian kernel utilization distributions (UD, standard bandwidth, 200 x  
197 200 pixel grid, adehabitatHR package, Calenge, 2006) at each ten day step following Broennimann et al.  
198 (2012). These UDs were used to calculate ten day median habitats for each track. Based on these we  
199 calculated intra-individual and inter-individual NND (only for individuals from the same species, breeding  
200 at the same population and tracked during the same year) in environmental space. Using these  
201 computed NNDs and the same randomization procedure as described above for Cartesian space  
202 (Wakefield et al., 2015), we tested if individuals exhibit fidelity to specific habitat at each time step.

203 Is IMSF better explained by site familiarity or habitat specialisation?

204 To discern if IMSF is better explained by site familiarity (fidelity to specific sites) or habitat specialisation  
205 (fidelity to specific habitats) we quantified species- and population-specific relative fidelity to sites and  
206 habitats using the similarity index developed by Patrick and Weimerskirch (2017). This index is a ratio  
207 ranging from 0 (all individuals are generalists within the considered population) to 1 (all individuals are  
208 specialists). At each ten day step for each repeat individual the sum of all instances for which intra-  
209 individual NND was smaller than inter-individual NND was divided by the number of inter-individual  
210 NNDs computed (see Patrick and Weimerskirch (2017) for more details). Next, we averaged similarity for  
211 individuals with more than one pair of repeat tracks. This similarity was calculated in Cartesian as well as  
212 environmental space. Relative fidelity to either space was tested by subtracting individual habitat  
213 similarity from site similarity. Using two-tailed t-tests, we determined if the estimated population-wide  
214 distribution was significantly different from 0 (significance at  $p = 0.05$ ) and hence either site ( $>0$ ) or  
215 habitat specific ( $<0$ ). In addition, environmental similarity was calculated for each abiotic parameter

216 described above and relative fidelity for sites or a given environmental parameter was tested separately  
217 to estimate the robustness of our results.

218 Does site fidelity persist across several years?

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

## 226 Results

227 Do guillemots exhibit IMSF?

228 Overall, both species exhibited individual migration strategy fidelity (IMSF) as indicated by colony-  
229 specific significantly smaller intra-individual NND compared to the Null hypothesis (i.e. generalist  
230 migratory behaviour) across their studied range (figure 2). But, some seasonal and population-specific  
231 variability was apparent. Generalist migratory behaviour was shown during spring (approx. February -  
232 May depending on population) and in part of the autumn (August/September) across species and  
233 populations as a consequence of little population wide variability in migration strategies. Moreover,  
234 there was some variation among populations and populations displaying little population wide NND did  
235 not generally exhibit IMSF given the accuracy of the tracking method used (median error of 150-180 km,  
236 Merkel et al., 2016) (figure 3). But, some populations - with little population wide NND (e.g. COGUs from  
237 Bjørnøya & Hjelmsøya) - displayed IMSF during mid-winter (December/January) when the proportion of  
238 twilight events (north of 66°N) and hence location estimates missing was high (figure S4). IMSF was also

239 visible for each sex separately in both species and all populations tested with some populations  
240 exhibiting sex-specific differences during autumn and in part spring (figure S5 & S6).  
241 Higher variability in intra-individual NND was apparent in some populations (e.g. BRGU Bjørnøya,  
242 particularly in late winter (February/March, figure 4). Integrating NND over a wide temporal window (70  
243 days) demonstrated that some spatial variability could be explained by timing (i.e. similar areas have  
244 been utilised, but not necessarily at the same time), while general results remained unchanged (figure 2).

245 Is IMSF better explained by site familiarity or habitat specialisation?

246 In all populations of both species, little habitat fidelity was apparent (except for BRGU from Hornøya and  
247 COGU from Jan Mayen, figure S7). Further, fidelity to geographic sites rather than abiotic habitat was  
248 predominant for both species and all populations throughout the entire non-breeding period (figure 5).  
249 The same pattern could be observed for each sex (figure S8 & S9) as well as each environmental  
250 parameter (figure S10), separately. The only indication for fidelity to a specific abiotic feature rather than  
251 a specific site could be seen in both species for bathymetry during spring (figure S10).

252 Does site fidelity persist across several years?

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

## 257 Discussion

258 In this study, we identified individual migration strategy fidelity (IMSF) for the genus *Uria*, which was  
259 independent of sex, and occurred throughout the entire Northeast Atlantic during most of the non-  
260 breeding period. This was apparent as fidelity to geographic sites rather than preferences for specific

261 habitats. Importantly, IMSF persisted across multiple years in all considered populations. Suggesting that  
262 in the Northeast Atlantic IMSF is the norm in COGUs and BRGUs - independent of occupied habitat.

### 263 *IMSF in guillemots*

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

284 behaviour. This argument is further strengthened by the observed general persistence of IMSF when  
285 accounting for the temporal flexibility in all studied populations across multiple years.

### 286 *Instances of generalist migratory behaviour*

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

306 *Is IMSF better explained by site familiarity or habitat preference?*

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

325 By contrast, we identified IMSF across our studied range which persisted over multiple years for all  
326 populations with more than 2 years of data as is predicted if IMSF is caused by site familiarity (Piper,  
327 2011; Switzer, 1993). The ontogeny of individual migration strategies and the relative roles of genetic  
328 control (Liedvogel, Åkesson, & Bensch, 2011; Newton, 2008), social learning (Jesmer et al., 2018; Keith &  
329 Bull, 2017) and individual exploration (Guilford et al., 2011) therein is poorly understood. However,

330 subsequent migrations seem to be influenced by learning of navigational map features *en route*  
331 (potentially visual, olfactory or magnetic) which in turn lead to individual site familiarity through  
332 experience and further refinement of individual migration strategies (Guilford et al., 2011; Spiegel &  
333 Crofoot, 2016; Van Bemmelen et al., 2017). Thus, the above discussed temporal flexibility in site fidelity  
334 can also be accounted for by learning as individuals could have the potential to switch between multiple  
335 known sites if conditions at the occupied site becomes unfavourable (the “win-stay, lose-switch” rule;  
336 Switzer, 1993) and the individual is not impeded in its movement (due to moulting, chick presence or  
337 pre-laying attendance). By being faithful to known wintering areas, individuals reduce costs of sampling  
338 other suitable wintering areas, in particular when flight costs are high such as in guillemots (Elliott et al.,  
339 2013), and thus diminish uncertainty from successive migrations (Abrahms et al., 2018; Cresswell, 2014).  
340 This suggests that these species, which exhibit nested area restricted search (Fauchald et al., 2000),  
341 select for sites at the mesoscale and potentially for specific habitats and preys at smaller scales  
342 (Fauchald, 2009). Site familiarity is also important as conditions at different staging sites must be  
343 considered unknown to the individual due to the large distances covered. Consequently, individual  
344 migration routes can generally be assumed to have developed in response to historically expected  
345 conditions (Thorup et al., 2017; Van Moorter et al., 2016).

346 Contrastingly, incidences have been documented of apparent large-scale shifts in winter distributions of  
347 guillemots in accordance with changing climatic conditions, which suggests some flexibility in their  
348 migratory behaviour (Veit & Manne, 2015). All data collection for this study has been conducted within a  
349 relative short period of time (nine years), with the maximum period an individual was tracked extending  
350 over nine years (seven of those with tracking data), which only covers a part of the lifetime of these long-  
351 lived species. Also, data was gathered within the same marine pelagic regime in the North Atlantic  
352 (Beaugrand & Kirby, 2018) and after the unpredicted collapse of sea ice in the Barents Sea in 2006 which  
353 has persisted to the present (Lind et al., 2018). Hence, inferences made on IMSF in these species - even



354 though valid and based on a rather unique dataset - need to be viewed with caution and might not hold  
355 under different oceanic regimes (Veit & Manne, 2015).

### 356 *Conclusion*

357 In this study we found strong support for mesoscale IMSF (individual migration strategy fidelity) for  
358 COGU and BRGU from multiple breeding populations across the Northeast Atlantic regardless of habitat  
359 utilized. Our data suggest that this was best explained by site familiarity (Piper, 2011; Switzer, 1993)  
360 rather than by habitat specialisation. Historically, site familiarity was most likely a sufficient strategy for  
361 these long-lived species (Abrahms et al., 2018; Bradshaw et al., 2004; Switzer, 1993). In the light of a  
362 rapidly changing physical and biological environment, these species might not be able to adjust their  
363 migration strategies fast enough (Abrahms et al., 2018), particularly if migration strategies are  
364 established during the first years of life (Dall et al., 2012) as also suggested for other seabirds (Guilford et  
365 al., 2011; Van Bemmelen et al., 2017) and some ungulate species (Jesmer et al., 2018; Sawyer et al.,  
366 2018). This might also be the case for other long lived migrants, particularly if they exhibit similar high  
367 costs of movement as in guillemots (Elliott et al., 2013) and consequently potential severe constraints  
368 upon large-scale movement capabilities and hence high sensitivity towards habitat loss (Taylor & Norris,  
369 2010).

370

### 371 Data Availability Statement

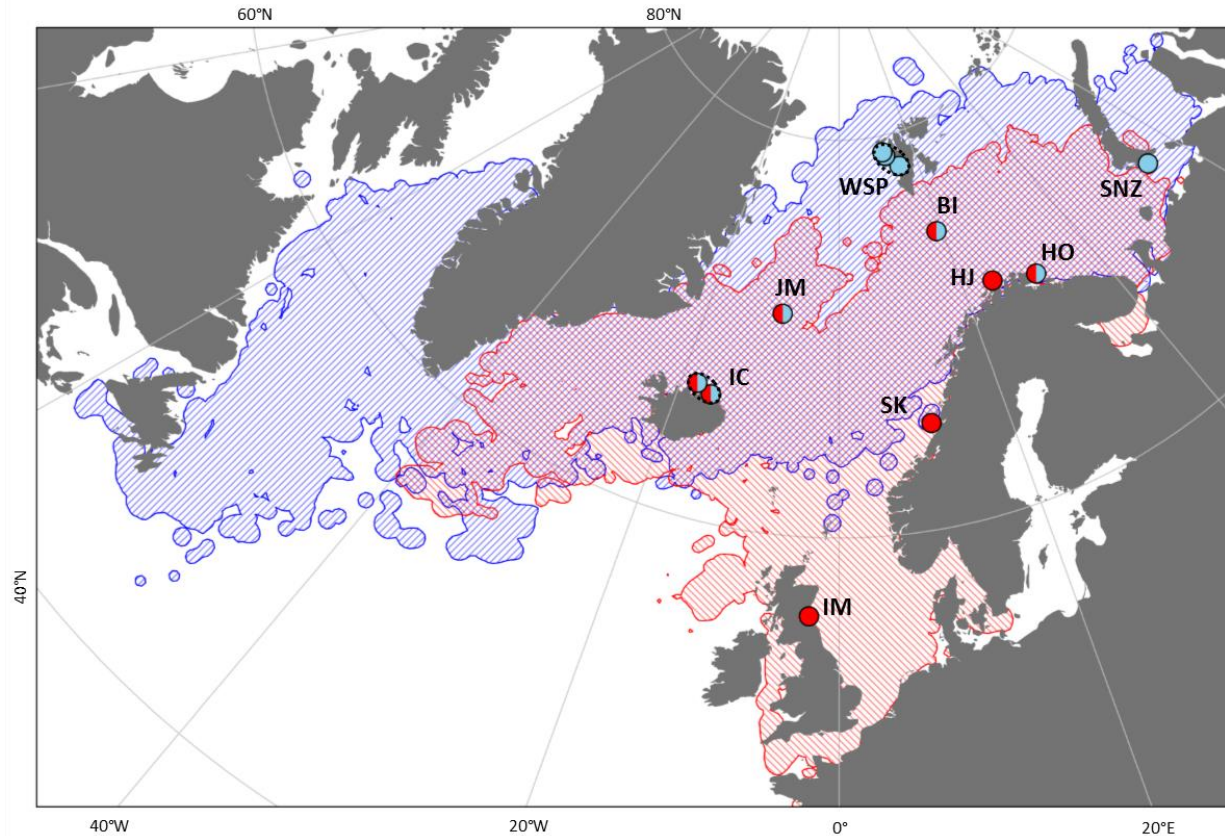
372 Data are available through the Norwegian Polar Data Centre (doi: [10.21334/npolar.2020.9c9deb08](https://doi.org/10.21334/npolar.2020.9c9deb08)).

373 Tables and Figures

374 **Table 1.** Available tracking data. Some colonies (in parentheses when applicable) have been merged into populations for the purpose of this  
 375 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  
 376 added in parentheses.

breeding population (colonies)	acronym	location	Common guillemot (COGU)					Brünnich's guillemot (BRGU)				
			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	2011-17	91	46 (15f, 27m)	28 (12f, 15m)	2-4	-	-	-	-	-
Sklinna	SK	65.22°N 10.97°E	2011-17	83	52	25	2-3	-	-	-	-	-
Hjelmsøya	HJ	71.07°N 24.72°E	2011-17	52	34	14	2-3	-	-	-	-	-
Northeast Iceland (Grimsey, Langanes)	IC	66.44°N 15.80°W	2014-17	37	26	9	2-3	2014-17	42	28	13	2-3
Jan Mayen	JM	71.02°N 8.52°W	2011-17	86	47 (20f, 19m)	23 (14f, 9m)	2-5	2011-17	136	66 (19f, 36m)	39 (13f, 21m)	2-5
Hornøya	HO	69.98°N 32.04°E	2011-17	146	82 (16f, 24m)	53 (7f, 17m)	2-3	2009-17	140	79 (23f, 27m)	35 (12f, 16m)	2-4
Bjørnøya	BI	74.50°N 18.96°E	2007-17	196	85 (42f, 28m)	56 (27f, 21m)	2-6	2007-17	156	65 (25f, 25m)	42 (18f, 21m)	2-7
Western Spitsbergen (Amfifjellet, Ossian Sars fjellet, Diabasodden)	WSP	78.75°N 13.20°E	-	-	-	-	-	2007-17	112	78 (30f, 40m)	25 (12f, 12m)	2-3
Southern Novaya Zemlya (Kara Gate)	SNZ	70.59°N 55.02°E	-	-	-	-	-	2015-17	55	41	14	2

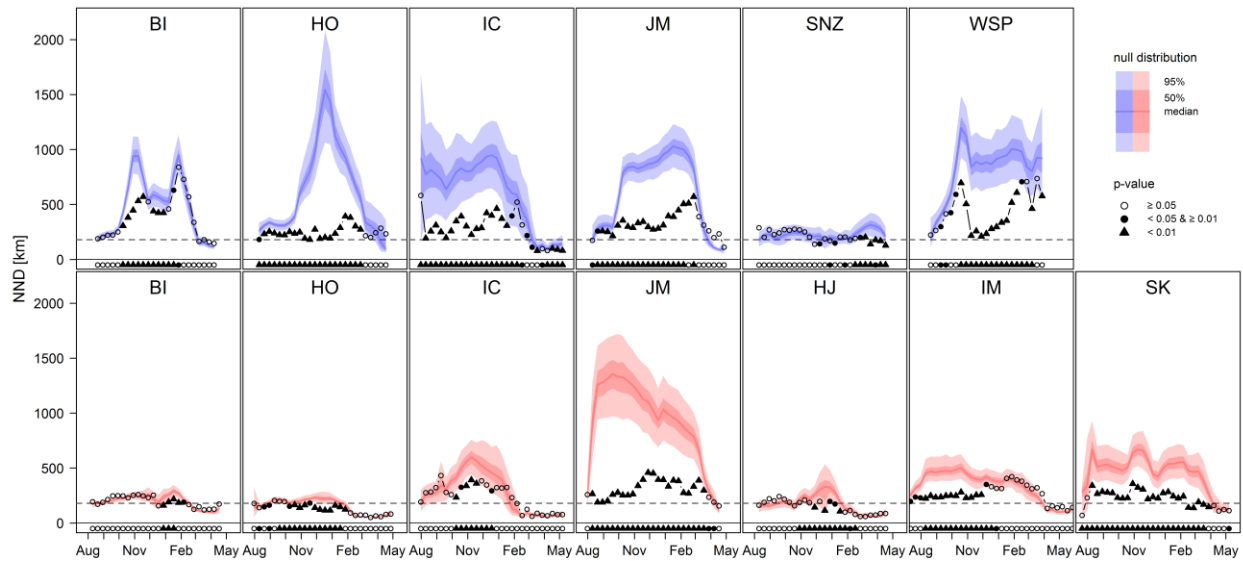
377



378

379 **Figure 1.** Map of the study extent (in polar stereographic projection). Circles denote study colonies with  
 380 different colours indicating the presence of the two species (Brünnich's guillemots in blue & common  
 381 guillemot in red; colony names detailed in table 1). Colonies combined for the purpose of this study are  
 382 encircled with dashed ellipsoids. Shaded blue and red areas illustrate the total annual extent for each  
 383 species breeding at the displayed colonies based on individuals tracked by light-level geolocation.

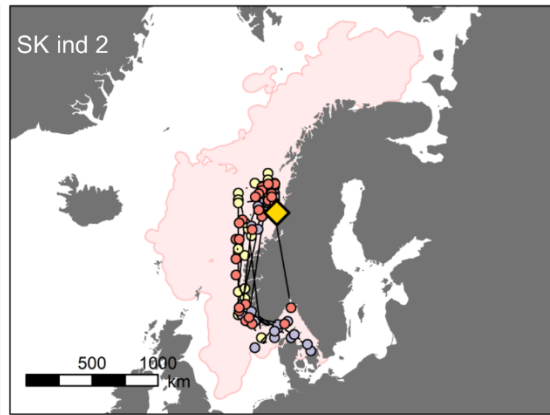
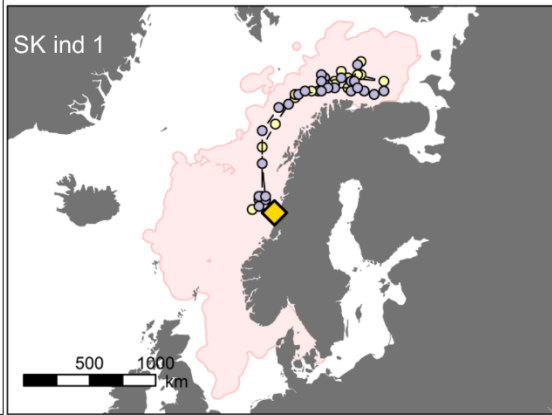
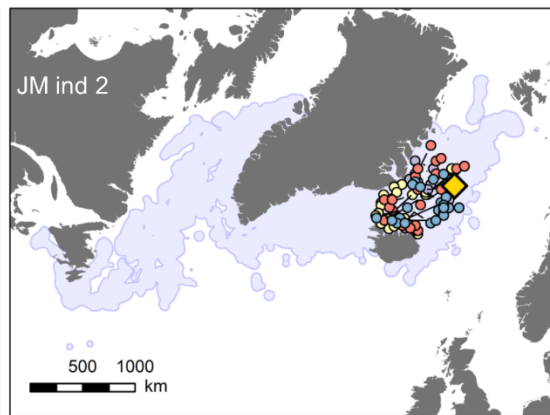
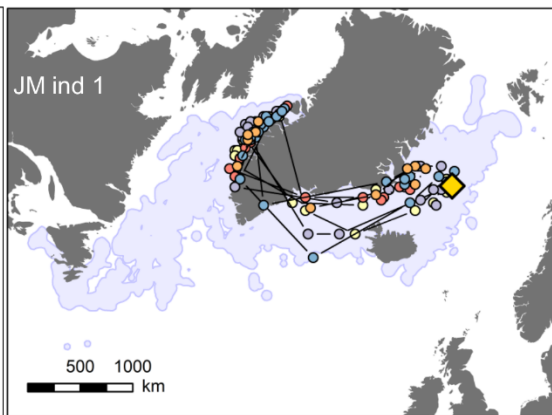
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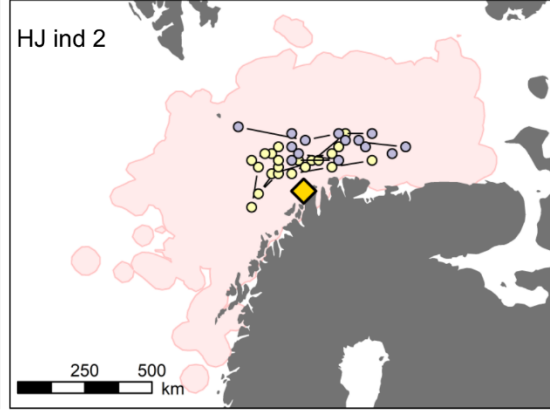
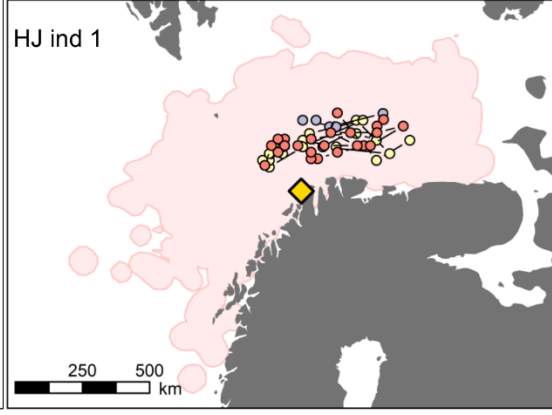
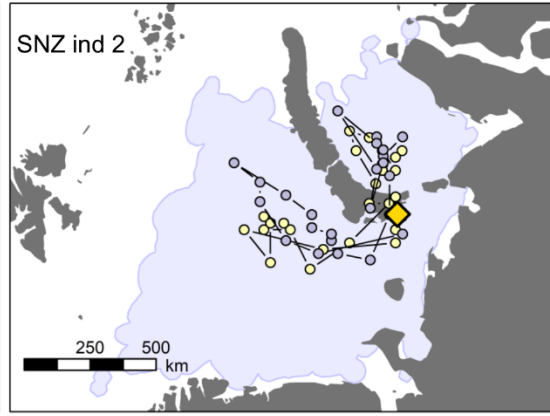
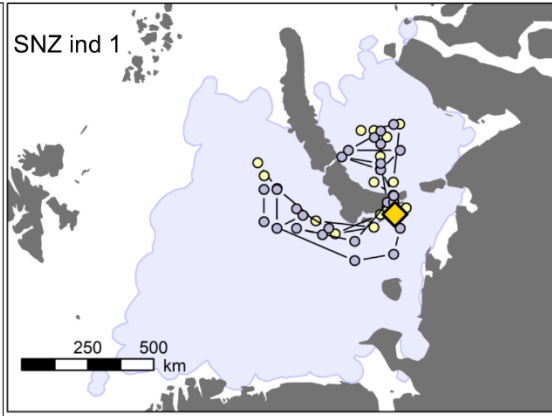
385

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

Large population-wide variation in migration strategies

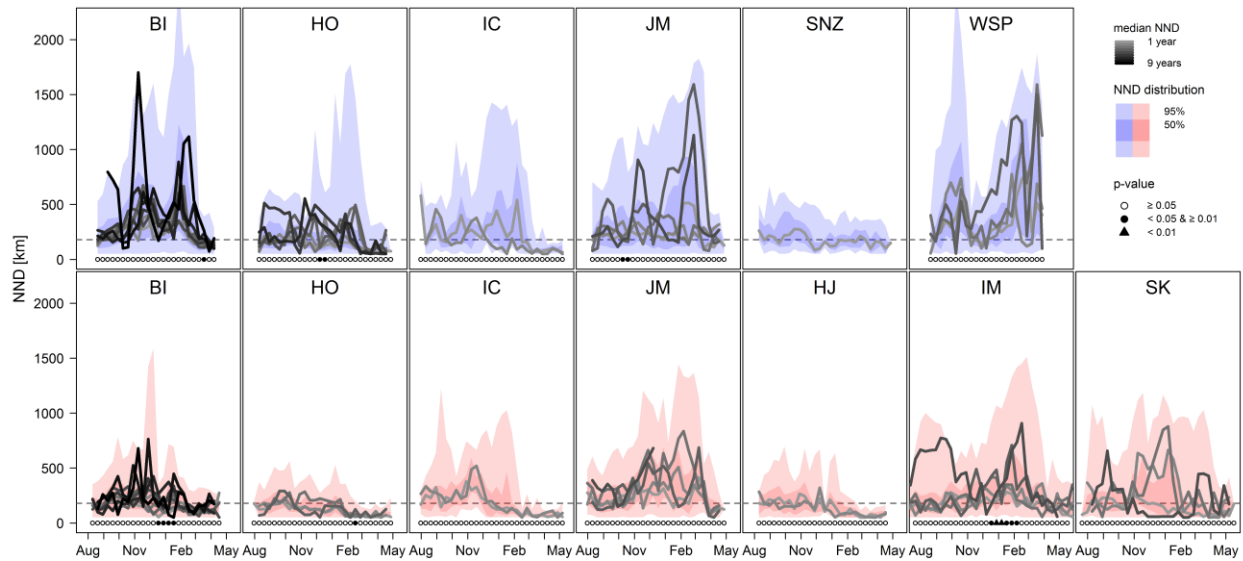


Little population-wide variation in migration strategies



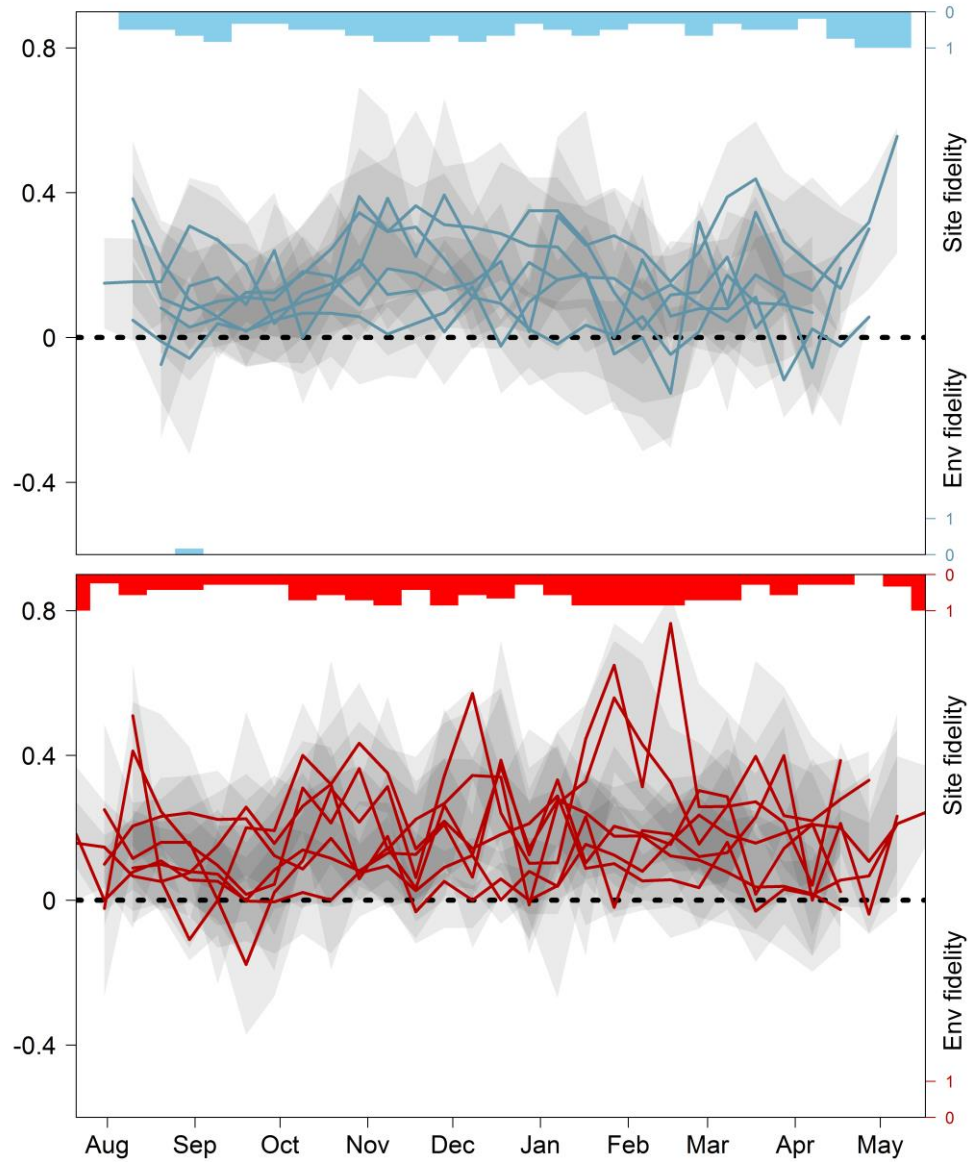
396 **Figure 3.** Example tracks of eight individual guillemots that have been tracked for two to four years. The  
397 top four panels illustrate non-breeding movements of example individuals from the two different species  
398 (Brünnich's and common guillemot with blue and red background, respectively)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

406



407

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



415  
 416 **Figure 5.** Brännich's (blue) and common guillemot (red) species- and breeding population-specific  
 417 similarity (ranging from -1 to 1) throughout the non-breeding period where values above 0 indicate  
 418 relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Each line represents  
 419 the median fidelity for a given population. Semi-transparent grey shaded areas illustrate population-wide  
 420 25% to 75% quartile range in individual fidelity values with darker colours indicating overlapping ranges  
 421 between populations. Bar plots at the top and bottom of each panel illustrate the proportion of  
 422 populations with significant fidelity (i.e. significantly different from 0 at  $p = 0.05$ , scale on the right) to  
 423 either sites (at the top) or habitat (at the bottom) during each ten day step.



425 Supplementary information

426 Additional method information & results

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643 Biosketch

644 Benjamin Merkel is a marine ecologist. His research interests include movement ecology, spatial  
645 analyses, visualization of complex data and computational modelling.

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