Individual migration strategy fidelity

but no habitat specialization

in two congeneric seabirds

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35 Abstract

36 **Aim:** Consistent differences in individual behaviour are widespread and may affect the average

37 population response to environmental change. In migratory species, individual migration strategy

38 fidelity (IMSF, when individuals use fixed and individual-specific migration strategies) occurs

39 often. It may be driven by either site familiarity (i.e. fidelity to specific sites) or habitat

40 specialization (i.e. fidelity to specific habitats). Under climate change favourable habitats may

41 permanently shift locations and hence IMSF may reduce individual fitness with adverse

42 consequences for populations. Our goal was to test if individuals from the genus *Uria* have

43 flexible or fixed individual migration strategies (i.e. IMSF), if this behaviour is consistent across

44 large parts of the genus' range and if they were philopatric to geographical sites or a habitat

45 feature.

46 **Location:** North Atlantic

47 **Methods:** We quantified consistent individual differences in spatial distribution and habitat

48 occupied throughout the non-breeding period using a large geolocator tracking dataset of 376

49 repeatedly tracked individual adult seabirds tracked up to seven years breeding at nine different

50 sites across the Northeast Atlantic. Additionally, we calculated relative fidelity to either

51 geographic sites or habitats as well as persistence of 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 did not show

54 fidelity to specific habitats while relative fidelity to geographic sites predominated over relative

55 fidelity to habitats. Overall, this indicates that individuals employ IMSF which is best explained by

56 site familiarity rather than habitat specialisation.

57 **Main conclusions:** In the context of rapidly changing environments, vulnerable migratory 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 adult survival rates and ensure population

60 persistence.

61

62 Keywords: guillemots, habitat specialization, individual migration strategy fidelity, light-level

63 geolocation, murres, North Atlantic, site familiarity, *Uria aalge*, *Uria lomvia*

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 maximise availability of spatially and seasonally fluctuating resources (Alerstam, Hedenström, & Åkesson, 2003; Bridge, Ross, Contina, & Kelly, 2015). Many migrants, such as seabirds (Schreiber & Burger, 2001), are long-lived species. 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 geographic 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). Though, less evidence exist for '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). However, site fidelity 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).

IMSF during the non-breeding period 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 costs of sampling other suitable wintering areas and diminish uncertainty from successive migrations (''always stay'' strategy in Cresswell, 2014; Switzer, 1993). This is particularly important for long distance migrants as their migration routes are generally conserved from year to year (Thorup et al., 2017; Van Moorter,

97 Rolandsen, Basille, & Gaillard, 2016). Long term site fidelity might be advantageous for long-lived

98 species when considered over a long time period or across an entire life span even if it might not be

99 the most favourable strategy every year (Abrahms et al., 2018; Bradshaw et al., 2004; Switzer, 1993).

100 If a species' migration behaviour is affected by site familiarity, then site fidelity may persist across its

101 entire range and several years as specific sites rather than habitats are selected (Switzer, 1993). Until

102 recently, site familiarity has received little attention, yet it may play an important role in habitat

103 selection (Cresswell, 2014; Keith & Bull, 2017; Piper, 2011).

104 Alternatively, exhibited IMSF could be a consequence of individual specialisation in diet and habitat

105 choice in a patchy environment (Abrahms et al., 2018; Patrick & Weimerskirch, 2017). An individual's

106 resource or habitat choice in heterogeneous environments such as the open ocean will be associated

107 with spatial fidelity (Switzer, 1993). However, selection of sites and habitats are often decoupled

108 from each other as similar habitats can co-occur at different sites (Gómez, Tenorio, Montoya, &

109 Cadena, 2016; Peters et al., 2017). Therefore, IMSF is unlikely to be exhibited in all habitats occupied

110 by a species across its geographic range. Additionally, resource patches can shift in space and time

111 between years. Hence, IMSF is not expected to persist across multiple years throughout a species'

112 range if it is a consequence of habitat specialisation (Patrick & Weimerskirch, 2017; Wakefield et al.,

113 2015).

114 Here, we assessed if two migratory species, over large parts of their range, display IMSF (or

115 alternatively generalist migratory behaviour) and if this behaviour is better explained by fidelity to

116 specific sites or habitats. The temperate common guillemot (hereafter COGU, *Uria aalge*) and the

117 Arctic Brünnich's guillemot (hereafter BRGU, *Uria lomvia*) are large (~1kg), numerous, deep diving,

118 pelagic feeding, long lived, congeneric colonial seabirds (A J Gaston & Jones, 1998). They show strong

119 breeding philopatry (Benowitz-Fredericks & Kitaysky, 2005; A J Gaston & Jones, 1998), and exhibit

120 strong migratory connectivity throughout their non-breeding period in space as well as in

121 environmental niches (PAPER II). Hence, different breeding populations use distinct areas and

122 environments outside their breeding season. Their annual distribution encompasses a large range of

123 space and environments in the North Atlantic and Arctic seas (Frederiksen et al., 2016; McFarlane

124 Tranquilla et al., 2015). These oceans are changing rapidly under climate change (Henson et al., 2017;

125 IPCC, 2013; Lind, Ingvaldsen, & Furevik, 2018) and species distributions (e.g. capelin, *Mallotus*

126 *villosus*, Carscadden, Gjøsæter, & Vilhjálmsson, 2013) and ecosystem compositions are shifting

127 (Beaugrand & Kirby, 2018; Fossheim et al., 2015; Perry, Low, Ellis, & Reynolds, 2005; Pinsky, Worm,

128 Fogarty, Sarmiento, & Levin, 2013; Wassmann, Duarte, AgustÍ, & Sejr, 2011). In this context, an

129 understanding of IMSF and the relative fidelity to geographic sites and habitats as well as its

130 persistence across a genus' range is needed to assess the species' potential resilience to ongoing

131 climatic changes. Initial evidence indicates that individuals of both species display variable site

132 fidelity during the winter months (McFarlane Tranquilla et al., 2014) and hence might be able to

133 adapt quickly to their changing environment (Abrahms et al., 2018; Switzer, 1993).

134 Using tracking data from 372 COGUs and 357 BRGUs from nine different breeding sites across the

135 Northeast Atlantic, where 208 COGU and 168 BRGU individuals were tracked for at least two winters

136 (maximum of seven winters), we tested the hypothesis that individuals of both species display IMSF

137 across large parts of their range throughout their non-breeding period. Further, we assessed if their

138 migratory behaviour is potentially a consequence of site familiarity or habitat specialisation.

139

Material and Methods

Data

142 Fieldwork was conducted at 13 breeding colonies spanning 56°N to 79°N and 16°W to 55°E in the

143 Northeast Atlantic (figure 1). Some colonies in close spatial proximity to each other (< 160 km) which

144 exhibited similar space use patterns were combined resulting in nine breeding populations (table 1).

145 BRGU and COGU breed sympatrically in four of these populations. We used archival light-level

146 loggers (also GLS or "geolocators") to estimate the spatiotemporal locations of individuals

147 throughout the non-breeding period. These devices record light intensity and time which can be used

148 to estimate approximate latitude (i.e. day length) and longitude (i.e. time of noon) positioning twice

149 daily. They are attached to a leg ring with cable ties (logger, ring, and cable ties < 0.5% adult body

150 mass). During the summers of 2007 to 2017 we captured adult guillemots with noose poles at

151 different sites and equipped them with light-level loggers which we retrieved in subsequent years

152 (overall retrieval rate > 60%). Individuals were chosen opportunistically in most cases from birds

153 breeding on cliff ledges on the landward edge of the colony. This resulted in 1332 annual tracks (641

154 BRGU, 691 COGU) of 729 individuals (357 BRGU, 372 COGU) of which 376 were tracked for at least

155 two years (168 BRGU, 208 COGU, table 1). All subsequent analyses were conducted in R 3.4.3 (R

156 Development Core Team, 2018). All loggers (models: Mk15 (British Antarctic Survey, Cambridge, UK),

157 Mk3006 (Biotrack, Wareham, UK), F100, C250 & C330 (Migrate Technology, Cambridge, UK) or L250A

158 (Lotek, St. John's, Newfoundland, Canada)) also recorded temperature and salt water immersion

159 ("wet/dry") data which were used in combination with recorded light data to increase location

160 accuracy (estimated median accuracy: 150-180 km, Merkel et al., 2016; see SI 1 for more details). In

161 some populations, blood or feather samples were collected and used to determine the sex of

162 individual birds (details in table 1) by DNA extraction using the DNeasy 96 Blood and Tissue Kit

163 (Qiagen, Hilden, Germany) and afterwards polymerase chain reaction (PCR) using Qiagen's Multiplex

164 PCR Kit. Sex was then determined using the primers M5 (Bantock, Prys-Jones, & Lee, 2008) and P8

165 (Griffiths, Double, Orr, & Dawson, 1998). Gender was included in the analyses to account for the

166 possibility of sex-specific migratory behaviour and its potential effect on our measure of site fidelity

167 during parts of the non-breeding period.

168 *Data Analysis*

169 To test our hypothesis that guillemots, across a large part of their range, display IMSF throughout the

170 non-breeding period, we used the concept of nearest neighbour distance (NND, Guilford et al., 2011).

171 Individual annual tracks were split into ten day bins starting 1 July. A resolution of ten days was

172 chosen to retain a sufficient number of locations for each bin for further analysis while accounting for

173 possible seasonal differences. The centre for each individual ten day bin was estimated as the

174 geographic median (position with minimum distance to all other locations). NND in space was

175 calculated as Euclidian distance in polar stereographic projection between ten day centre locations

176 for repeat tracks of the same individual in different years as well as different individuals from the

177 same species and breeding population tracked in the same year. Next, we averaged NND of all

178 pairwise comparisons at each time step for each individual with more than one repeat track.

179 Following Wakefield et al. (2015), we used a randomization procedure to test for each species and

180 population considered if intra-individual NND is smaller than population-level NND at each time step.

181 The null hypothesis (i.e. generalist migratory behaviour) was that observed intra-individual NND is

182 not significantly smaller than population-wide NND calculated with randomly assigned bird

183 individuals (1000 permutations without replacement). Significance was assessed using a one-tailed t-

184 test (significance at p = 0.05) at each time step. To account for the possibility of sex-specific

185 behaviour the same procedure was also applied to each sex separately for populations where the

186 sexes were known (table 1). To test if a lack of site fidelity could be explained by variability in timing

187 rather than flexible space use, we calculated intra-individual as well as inter-individual NND at each

188 time step for a very wide temporal sliding window (70 days, figure S1). Using this temporally

189 integrated measure of fidelity we ran the same procedure as described above for both sexes

190 combined as well as each sex separately.

191 To tested if individuals exhibit habitat specialisation throughout the non-breeding period we

192 quantified the occupied habitat using eight ecologically relevant oceanographic parameters (Fort,

193 Porter, & Grémillet, 2009; Fort et al., 2013; McFarlane Tranquilla et al., 2015); three sea surface

194 temperature variables (absolute, distance to fronts, predictability), two sea surface height variables

195 (absolute, distance to meso-scale eddies), surface air temperature, distance to the marginal sea ice

196 zone and bathymetry (see SI 1 for more details). The habitat occupied was then assessed using the

197 concept of environmental space (Broennimann et al., 2012) defined as the first two axes of a

198 Principal Component Analysis (PCA) of all environmental parameters calibrated on the available

199 environment. To capture the variability of the available environment, 20000 points with equal spatial

200 coverage across the entire study area (figure S2) were sampled every two weeks for the entire study

201 period (2007-2017). All individual positions were projected onto the PCs (PC1 = 44% and PC2 = 19%,

202 figure S4). Occupied environmental space was then calculated using Gaussian kernel utilization

203 distributions (UD, standard bandwidth, 200 x 200 pixel grid, adehabitatHR package, Calenge, 2006) at

204 each ten day step following Broennimann et al. (2012). These UDs were used to calculate ten day

205 median positions for each track. Based on these we calculated intra-individual and inter-individual

206 NND (only for individuals from the same species, breeding at the same population and tracked during

207 the same year) in environmental space. Using these computed NNDs and the same randomization

208 procedure as described above for Cartesian space (Wakefield et al., 2015), we tested if individuals

209 exhibit fidelity to specific habitat at each time step.

210 To discern if IMSF is better explained by site familiarity or habitat specialisation we quantified

211 species- and population-specific relative fidelity to sites and habitats using the similarity index

212 developed by Patrick and Weimerskirch (2017). This index is a ratio ranging from 0 (all individuals are

213 generalists within the considered population) to 1 (all individuals are specialists). At each ten day

214 step for each repeat individual the sum of all instances for which intra-individual NND was smaller

215 than inter-individual NND was divided by the number of inter-individual NNDs computed (see Patrick

216 and Weimerskirch (2017) for more details). Next, we averaged similarity for individuals with more

217 than one repeat track. This similarity was calculated in Cartesian as well as environmental space.

218 Relative fidelity to either space was tested by subtracting individual habitat similarity from site

219 similarity. Using two-tailed t-tests, we determined if the estimated population-wide distribution was

220 significantly different from 0 (significance at p = 0.05) and hence either site (>0) or habitat specific

221 (<0). In addition, environmental similarity was calculated for each abiotic parameter described above

222 and relative fidelity for sites or a given environmental parameter was tested separately to estimate

223 the robustness of our results.

224 To test whether IMSF persists across years (an indication for site familiarity) or weakens linearly over

225 time (an indication for habitat faithfulness assuming habitat is not connected to space), we modelled

226 species- and population-specific intra-individual NND as a function of time lag (years between repeat

227 tracks) with random slope and intercept for each individual. Next, we used likelihood ratio tests to

228 determine whether these models explain the data better than the intercept-only models (i.e. without

229 accounting for time lag, Wakefield et al., 2015). This procedure was run for 70 day sliding windows

230 throughout the non-breeding period to account for potential timing effects.

231

Results

233 *Do guillemots exhibit IMSF?*

234 Overall, both species exhibited individual migration strategy fidelity (IMSF) as indicated by

235 significantly smaller intra-individual NND compared to the Null distribution across their studied range

236 (figure 2). However, some seasonal and population-specific variability was apparent. Generalist

237 migratory behaviour was shown during spring (approx. February - May depending on population) and

238 in part of the autumn (August/September) across species and populations as a consequence of little

239 population wide variability in migration strategies. Moreover, there was some variation among

240 populations and populations displaying little population wide NND did not generally exhibit IMSF

241 given the accuracy of the tracking method used (median error of 150-180 km, Merkel et al., 2016).

242 But, some populations - with little population wide NND (e.g. COGUs from Bjørnøya & Hjelmsøya) -

243 displayed IMSF during mid-winter (December/January) when the proportion of twilight events (north

244 of 66°N) and hence location estimates missing was high (figure S5). IMSF was also visible for each sex

245 separately in both species and all populations tested with some populations exhibiting sex-specific

246 differences during autumn and in part spring (figure S6 & S7).

247 Higher variability in intra-individual NND was apparent in some populations (e.g. BRGU Bjørnøya,

248 particularly in late winter (February/March, figure 3). Integrating NND over a wide temporal window

249 (70 days) demonstrated that some spatial variability could be explained by timing (i.e. similar areas

250 have been utilised, but not necessarily at the same time), while general results remained unchanged

251 (figure 2). Overall, IMSF persisted across multiple years (up to 9 years) in all tested populations, when

252 accounting for the timing difference (i.e. using a 70 day sliding window), illustrating that individual

253 site fidelity was not altered by the number of years between repeat tracks (figure 3).

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

255 In all populations of both species, little individual consistency in occupied habitats was apparent

256 (except for BRGU from Hornøya and COGU from Jan Mayen, figure S8). Further, fidelity to geographic

257 sites rather than abiotic habitat was predominant for both species and all populations throughout

258 the entire non-breeding period (figure 4). The same pattern could be observed for each sex (figure S9

259 & S10) as well as each environmental parameter (figure S11), separately. The only indication for

8

260 fidelity to a specific abiotic feature rather than a specific site could be seen in both species for

261 bathymetry during spring (figure S11).

262

Discussion

264 In this study, we identified individual migration strategy fidelity (IMSF) for the genus *Uria*, which was

265 independent of sex, and occurred throughout the entire Northeast Atlantic during most of the non-

266 breeding period. This was apparent as fidelity to geographic sites rather than preferences for specific

267 habitats. Importantly, IMSF persisted across multiple years in all considered populations. Suggesting

268 that in the Northeast Atlantic IMSF is the norm in COGUs and BRGUs - independent of occupied

269 habitat.

IMSF in guillemots

271 Evidence for IMSF has been found in various taxa such as in ungulates (Jesmer et al., 2018; Sawyer,

272 Merkle, Middleton, Dwinnell, & Monteith, 2018), fishes (Brodersen et al., 2012; Thorsteinsson,

273 Pálsson, Tómasson, Jónsdóttir, & Pampoulie, 2012) as well as in monarch butterflies (*Danaus*

274 *plexippus*, Yang, Ostrovsky, Rogers, & Welker, 2016). Further, it seems to be common in seabirds at a

275 regional level and more ambiguous at the mesoscale (Phillips et al., 2017). In a previous study, COGU

276 and BRGU breeding in the Northwest Atlantic were considered to exhibit flexibility in their winter

277 space use (McFarlane Tranquilla et al., 2014). By contrast, we found strong support for the

278 hypothesis that individuals of both species in populations in the Northeast Atlantic display IMSF at

279 the mesoscale. However, we also observed temporal variation in space use, particularly during late

280 winter when IMSF for some populations was not exhibited at the ten day step resolution, but only

281 when NND was integrated over a wider 70 day temporal window. This suggests some temporal

282 flexibility such that individuals utilize the same areas in different years, but not necessarily at the

283 same time during the winter months as has also been shown for long tailed skuas (*Stercorarius*

284 *longicaudus*, Van Bemmelen et al., 2017). However, this temporal flexibility seems to occur only

285 within the range of known sites for a particular individual. McFarlane Tranquilla et al. (2014) also

286 reported behavioural flexibility in the mid-winter spatial distribution (defined in their study as

287 January), particularly BRGUs, breeding in the Northwest Atlantic, tracked over multiple winters.

288 However, here we could illustrate that, particularly during late winter (February/March) IMSF was

289 more variable, but could be explained by timing differences. Consequently, the reported flexibility by

290 McFarlane Tranquilla et al. (2014) might also be explained by temporal flexibility during the winter

291 months between individual-specific sites rather than generalist behaviour. This argument is further

292   strengthened by the observed general persistence of IMSF when accounting for the temporal

293   flexibility in all studied populations across multiple years.

294   *Instances of generalist migratory behaviour*

295   Generalist migratory behaviour, i.e. an absence of IMSF, was identified to a varying degree in all

296   populations of COGU and BRGU. This can potentially be attributed to several season-specific

297   circumstances originating in different life history stages during their annual cycle. First, a lack of post-

298   breeding IMSF during autumn, could be caused by guillemots undergoing moult of their flight

299   feathers, which renders them flightless (Birkhead & Taylor, 1977; Elliott & Gaston, 2014; Thompson,

300   Wilson, Melvin, & Pierce, 1998). This constrains their movements and hence their capacity to

301   demonstrate IMSF. Additionally, reproductively successful males are accompanying a flightless chick

302   as it departs the colony, which further limits their movement (Elliott et al., 2017; Harris & Wanless,

303   1990). Thus, it is not surprising that some populations exhibit IMSF only for females during autumn

304   as these are not constrained by a dependent and flightless chick and have the possibility to move

305   large distances after breeding and prior to moulting. Second, various populations of both species

306   displayed a lack of IMSF during spring, which corresponds to the period of pre-breeding when

307   individuals periodically attend their colony (A. J. Gaston & Nettleship, 1981) and are thus constrained

308   in their movement to de-facto central place foraging. However, pre-breeding commences at different

309   times across the range of this genus and can begin as early as February on Iceland (PAPER IV) or as

310   late as April on Spitsbergen (PAPER IV), while at least some part of the population on the Isle of May

311   continues colony attendance after the autumn moult throughout the non-breeding period (Harris &

312   Wanless, 2016). This variability in pre-breeding timing could explain the variability in time at which

313   generalist migratory behaviour is observed during the end of the non-breeding period for the

314   different populations.

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

316   Persistent IMSF over multiple years was apparent in spatial consistency rather than preferences for

317   specific habitats across the entire study region and throughout the non-breeding period. This

318   suggests that IMSF in guillemots is better explained by site familiarity potentially through experience

319   and the use of memory (Davoren, Montevecchi, & Anderson, 2003) rather than being a consequence

320   of habitat specialisation. Memory has also been suggested to drive COGU foraging behaviour during

321   breeding (Regular, Hedd, & Montevecchi, 2013). We could not identify any fidelity to habitat rather

322   than sites for any population of either species throughout the entire non-breeding period. Further,

323   individuals from most populations did not display any habitat fidelity at all. And, for habitat

324   specialisation to drive site fidelity we would have expected that IMSF, if displayed at all, would not

325 persist over multiple years across the genus' range, particularly in light of the drastic changes in the

326 physical environment of the study region (Henson et al., 2017; IPCC, 2013; Lind et al., 2018; Sgubin,

327 Swingedouw, Drijfhout, Mary, & Bennabi, 2017) and the shifting species distributions and ecosystem

328 compositions (Beaugrand & Kirby, 2018; Carscadden et al., 2013; Fossheim et al., 2015; Perry et al.,

329 2005; Pinsky et al., 2013; Wassmann et al., 2011). However, we cannot rule out the possibility that

330 the abiotic variables selected to describe the available habitat, although ecologically relevant for the

331 study species', might not be able to reflect guillemot foraging habitat. This is especially true for all

332 satellite derived parameters used (such as sea surface temperature) as these only reflect surface

333 water conditions, while guillemots are deep diving foragers.

334 By contrast, we identified IMSF across our studied range which persisted over multiple years for all

335 populations with more than 2 years of data as is predicted if IMSF is caused by site familiarity (Piper,

336 2011; Switzer, 1993). The ontogeny of individual migration strategies and the relative roles of genetic

337 control (Liedvogel, Åkesson, & Bensch, 2011; Newton, 2008), social learning (Jesmer et al., 2018;

338 Keith & Bull, 2017) and individual exploration (Guilford et al., 2011) therein is poorly understood.

339 However, subsequent migrations seem to be influenced by learning of navigational map features *en*

340 *route* (potentially visual, olfactory or magnetic) which in turn lead to individual site familiarity

341 through experience and further refinement of individual migration strategies (Guilford et al., 2011;

342 Spiegel & Crofoot, 2016; Van Bemmelen et al., 2017). Thus, the above discussed temporal flexibility

343 in site fidelity can also be accounted for by learning as individuals could have the potential to switch

344 between multiple known sites if conditions at the occupied site becomes unfavourable (the "win-

345 stay, lose-switch" rule; Switzer, 1993) and the individual is not impeded in its movement (due to

346 moulting, chick presence or pre-breeding attendance). By being faithful to known wintering areas,

347 individuals reduce costs of sampling other suitable wintering areas, in particular when flight costs are

348 high such as in guillemots (Elliott et al., 2013), and thus diminish uncertainty from successive

349 migrations (Abrahms et al., 2018; Cresswell, 2014). Site familiarity is also important as conditions at

350 different staging sites must be considered unknown to the individual due to the large distances

351 covered. Consequently, individual migration routes can generally be assumed to have developed in

352 response to historically expected conditions (Thorup et al., 2017; Van Moorter et al., 2016).

Conclusion

354 In this study we found strong support for IMSF (individual migration strategy fidelity) for COGU and

355 BRGU from multiple breeding populations across the Northeast Atlantic regardless of habitat utilized.

356 Our data suggest that this was most likely driven by site familiarity (Piper, 2011; Switzer, 1993) rather

357 than by habitat specialisation. Historically, site familiarity was most likely a sufficient strategy for

11

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, especially 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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Supplementary information

Additional method information & results

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572

573 Tables and Figures

574 **Table 1.** Available tracking data. Some colonies (in parentheses when applicable) have been merged into populations for the purpose of this study. Tracking

575 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	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 (Cape Sakhanin)	SNZ	70.59°N 55.02°E	-	-	-	-	-	2015-17	55	41	14	2

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577
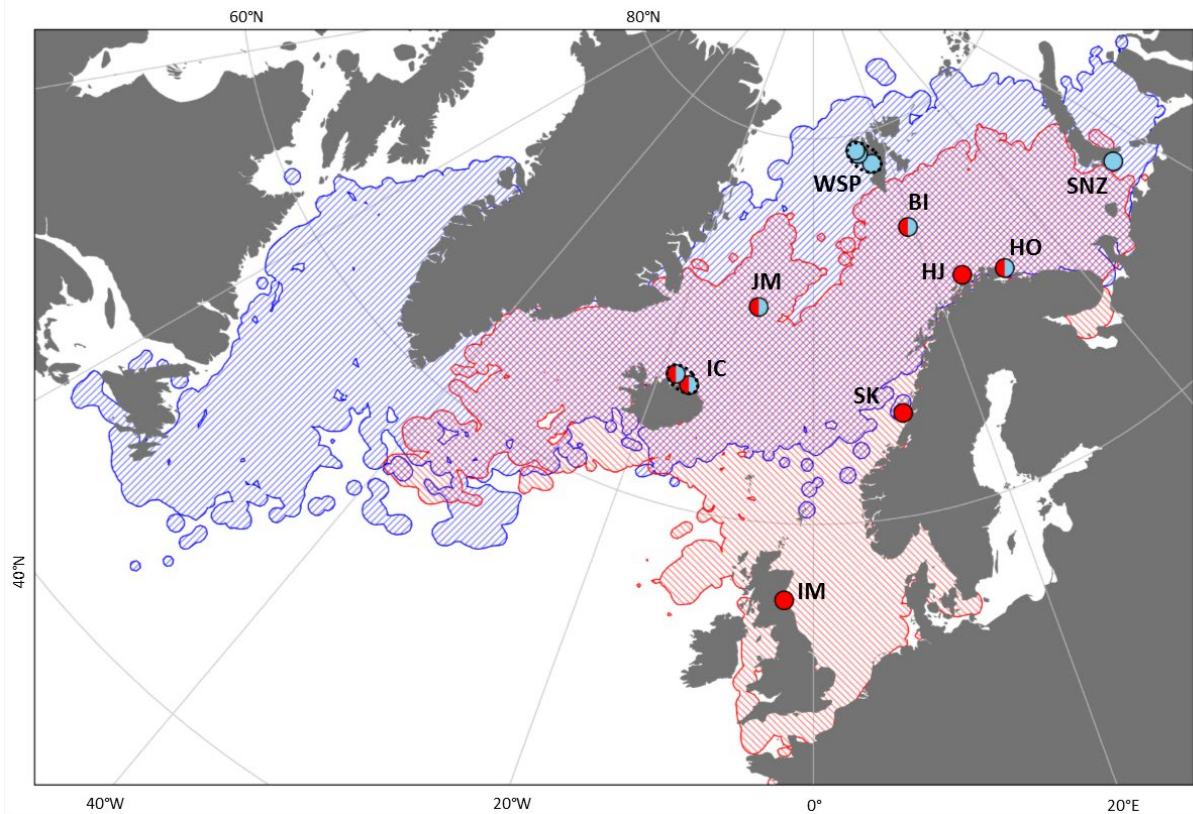
Figure 1. Map of the study extent (in polar stereographic projection). Circles denote study colonies with different colours indicating the presence of the two species (BRGU in blue & COGU in red; colony names detailed in table 1). Colonies combined for the purpose of this study are encircled with dashed 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.

Figure 2. Mean species- and breeding population-specific intra-individual nearest neighbour distance (NND, black symbols) compared to the null distribution (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. Colours correspond to species: BRGU in blue & COGU in red. 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).
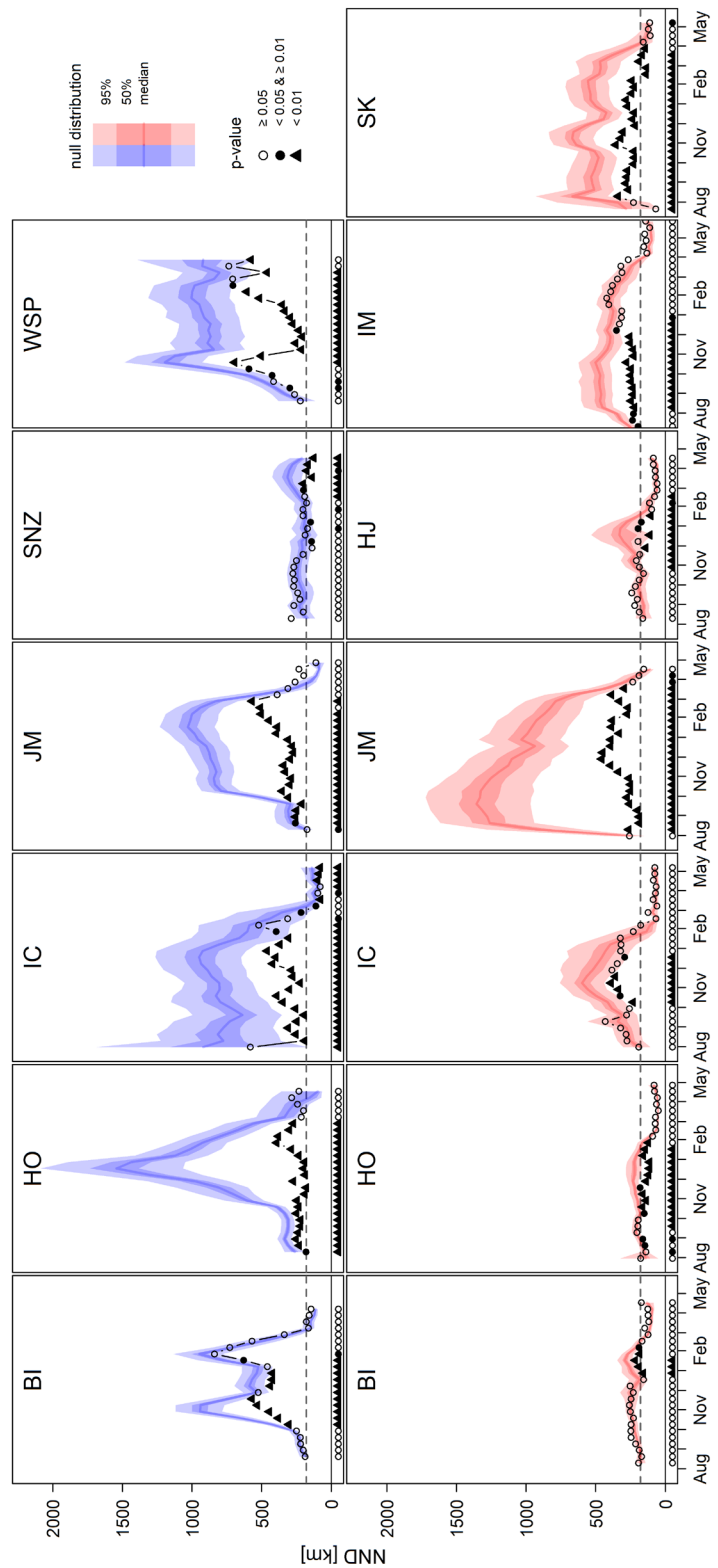
Figure 3. Species- and breeding population-specific intra-individual nearest neighbour distance (NND) with varying time lag (BRGU in blue & COGU in red). Grey shaded lines present median within-individual NND with time lag ranging from one year (grey) to nine years (black). Coloured areas in the background 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.
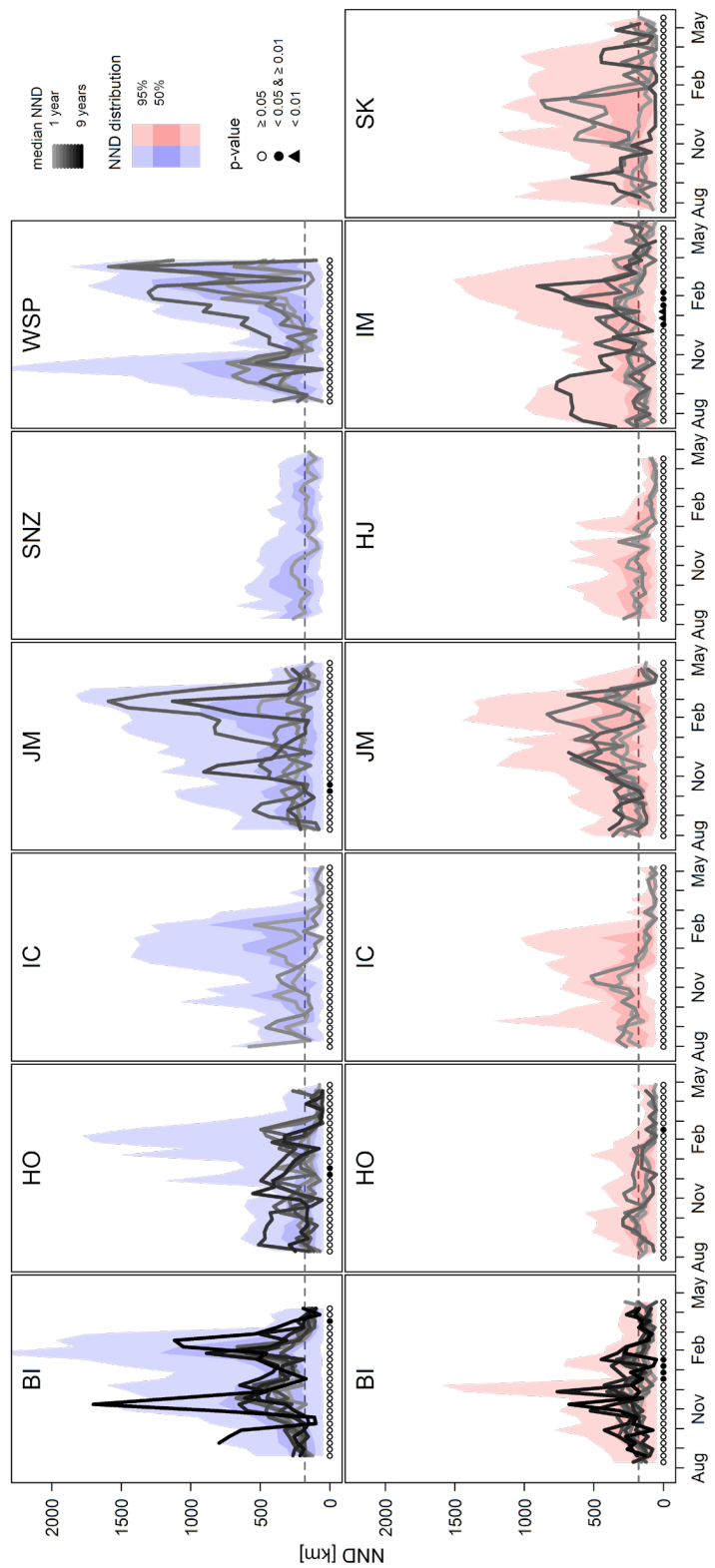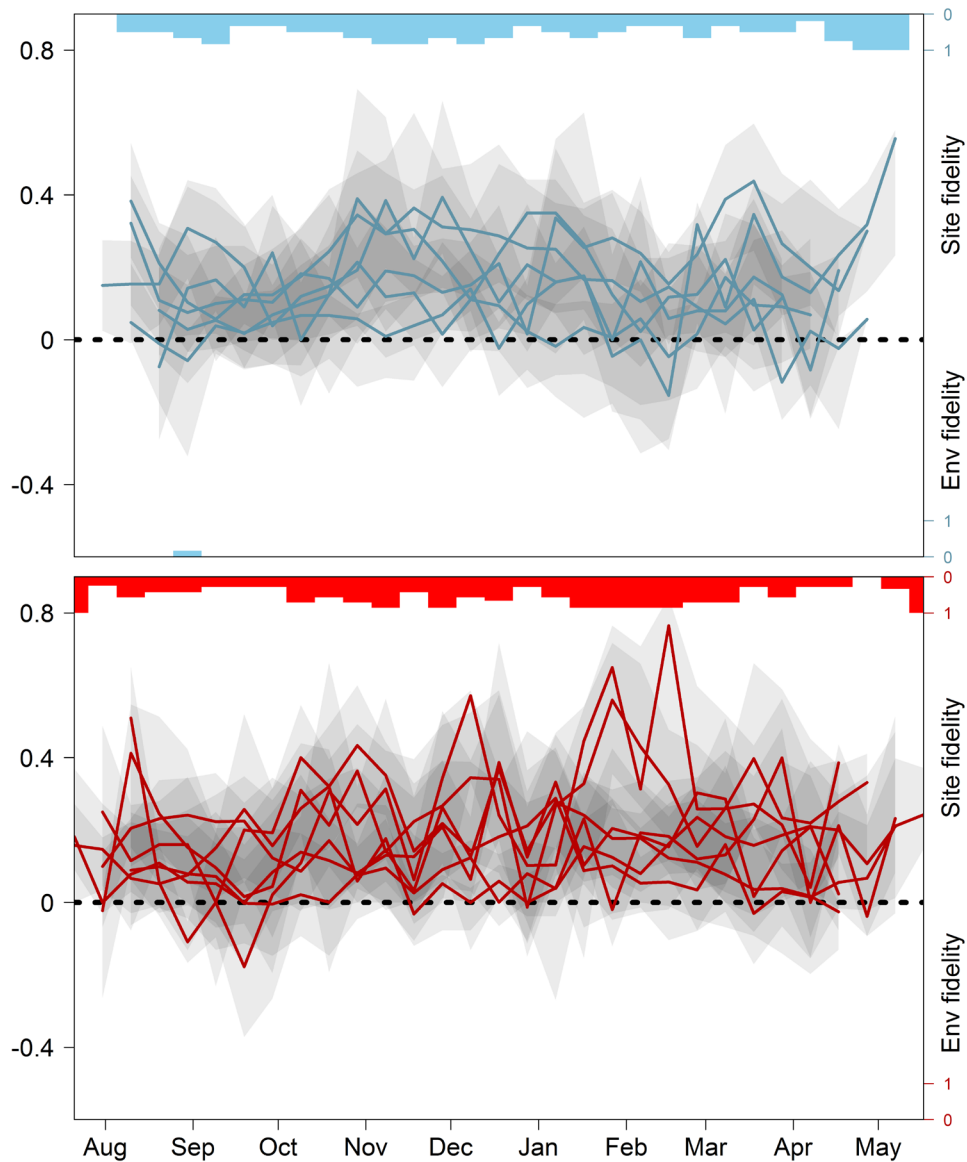
Figure 4. Species- and breeding population-specific similarity (ranging from -1 to 1) throughout the non-breeding period (BRGU in blue & COGU in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Each line represents the median fidelity for a given population. Semi-transparent grey shaded areas illustrate population-wide 25% to 75% quartile range 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 = 0.05, scale on the right) to either sites (at the top) or habitat (at the bottom) during each ten day step.

1 Supplementary Methods

2 *Location estimation from geolocators*

3 Estimated timings of sunrise and sunset (transition times) were computed from light data using

4 TransEdit2 (British Antarctic Survey/BAS, Cambridge, UK), and the `twilightCalc` function

5 (`GeoLight` package; Lisovski & Hahn, 2012) in R 3.4.3 (R Development Core Team, 2018) for BAS,

6 Migrate Technology and Biotrack loggers. Transition times were visually inspected for loggers

7 retrieved during 2014-2017 by the same person. Lotek loggers did not retain raw light intensity data,

8 but rather calculated and recorded latitudes and longitudes based on an onboard algorithm which

9 have been shown to be biased (Frederiksen et al., 2016). Therefore we used these threshold method

10 derived positions to back calculate transition times using the `lotek_to_dataframe` function

11 (`probGLS` package; Merkel et al., 2016). Daily experienced sea surface temperature (SST) was

12 estimated from raw logged temperature data using the `sst_deduction` function (`probGLS`

13 package) with a possible range of -2 to 20°C for Lotek loggers and -2 to 40°C for all other brands.

14 A most probable track for each individual and tracking year was calculated using a method detailed in

15 (Merkel et al., 2016) and implemented in the `prob_algorithm` function (`probGLS` package).

16 Input data were logger recorded transition times, salt water immersion data as well as calculated

17 daily recorded SST data. Daily optimal interpolated high resolution satellite derived SST, SST

18 uncertainty and sea ice concentration data for the algorithm with a 0.25° resolution was provided by

19 NOAA (Boulder, Colorado, US; Reynolds et al., 2007). To improve precision we included land

20 avoidance, an inability to enter the Baltic Sea (except for Common guillemots from the Isle of May)

21 and an evasion of heavy pack ice (>90% sea ice concentration). Each movement path incorporated

22 parameter values based on the ecology of the species and the oceanographic conditions in the North

23 Atlantic (table S1). Usually, it is not possible to estimate the latitude during times of equinox as day

24 length (the proxy for latitude) is very similar everywhere on earth. However, this methodology is able

25 to calculate locations also during times of equinox by among other things utilizing the recorded

26 temperature data and comparing them to satellite derived sea surface temperature (SST) fields. Due

27 to small north-south gradients in SST in certain areas of the North Atlantic (e.g. the Gulf Stream along

28 the Norwegian coast) we limited the boundary box parameter in `prob_algorithm` for certain

29 individuals and colonies after initial assessment of their movement tracks (table S1).Each computed

30 track was afterwards visually inspected and erroneous locations particularly around polar night and

31 midnight sun periods were removed (<1 % of all locations).

Environmental parameters

33 All chosen environmental parameters used to calculate environmental space and their rational are

34 listed in table S2. Fronts in sea surface temperature (SST) and sea surface height anomaly fields were

35 calculated using a canny edge detector (package `imager`, low & high threshold at 90% & 98%,

36 respectively). Bathymetry was log-transformed and all distance measurements were capped at 500

37 km as well as square root-transformed. Predictability in SST was calculated as the sum of constancy

38 and contingency following (Colwell, 1974) over a ten year time period (2007-2016) with 10 equal bins

39 using the `hydrostats` package (figure S3). All variables have been standardized.

40

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83

Supplementary Tables and Figures

Table S1. `probGLS` algorithm input parameters used to compute locations. standard deviation = sd

algorithm parameter	description	value used
`particle.number`	number of particles computed for each point cloud	2 000
`iteration.number`	number of track iterations	100
`loess.quartile`	remove outliers in transition times based on local polynomial regression fitting processes (Lisovski & Hahn, 2012)	used with k = 10
`sunrise.sd & sunset.sd`	shape, scale and delay values describing the assumed uncertainty structure for each twilight event following a log normal distribution	2.49/ 0.94/ 0[1]
`range.solar`	range of solar angles used	-7° to -1° (except for C250 logger from SK: -4° to -2°)
`boundary.box`	the range of longitudes and latitudes likely to be used by tracked individuals	90°W to 120°E & 40°N to 81°N; except for 91% COGU tracks from IM with 40°N to 62°N; all COGU from BI and 94% COGU SK tracks with 60°N to 77°N; 6% SK tracks with 50°N to 77°N
`day.around.spring.equinox & days.around.fall.equinox`	number of days before and after an equinox event in which a random latitude will be assigned	spring: 21 days before & 14 days after autumn: 14 days before & 21 days after
`speed.dry`	fastest most likely speed, speed sd and maximum speed allowed when the logger is not submerged in sea water	17/ 4/ 30 m/s[2]
`speed.wet`	fastest most likely speed, speed sd and maximum speed allowed when the logger is submerged in sea water	1/ 1.3/ 5 m/s[3]
`sst.sd`	logger-derived sea surface temperature (SST) sd	0.5°C[4]
`max.sst.diff`	maximum tolerance in SST variation	3°C
`east.west.comp`	compute longitudinal movement compensation for each set of twilight events (Biotrack, 2013)	used

[1] These parameters are chosen as they resemble the twilight error structure of open habitat species in Lisovski et al. (2012).
[2] inferred from GPS tracks (unpublished data) and (Elliott & Gaston, 2005)
[3] North Atlantic current speed up to fast current speeds (i.e. East Greenland current) (Lumpkin & Johnson, 2013) as the tagged animal is assumed to not actively move when the logger is immerged in seawater
[4] logger temperature accuracy

93 **Table S2.** Parameter chosen to describe the environmental space.

parameter	temporal resolution	spatial resolution	rational	data source
bathymetry	static	0.25°	predictable productivity on continental shelfs	ETOPO1 & IBCAO[1]
surface air temperature	daily	0.75°	influences energy requirements[2]	ECMWF[3]
sea surface temperature (SST)	daily	0.25°	water mass indicator & physiological constraint[2]	NOAA OI SST V2[4]
SST predictability (figure S2)	static	0.25°	identifier of spatially variable SST features across seasons and years (e.g. persistent frontal systems[5])	NOAA OI SST V2[4]
minimum distance to 15%, 50% & 90% sea ice concentrations	daily	0.25°	descriptor of marginal sea ice zone	NSIDC[6]
sea surface height (SSH)	daily	0.25°	descriptor of the locations of large scale features such as gyres and fronts	AVISO[7]
distance to SSH anomaly gradients	daily	0.25°	distance to mesoscale eddies as spatially dynamic sources of upwelling	AVISO[7]
distance to SST gradient	daily	0.25°	distance to mesoscale temperature fronts[5]	NOAA OI SST V2[4]

94 [1] (Amante & Eakins, 2009; Jakobsson et al., 2012), [2] (Fort, Porter, & Grémillet, 2009), [3] (Berrisford et al., 2011), [4] (Reynolds
95 et al., 2007), [5] (Scales et al., 2014), [6] (Cavalieri, Parkinson, Gloersen, Comiso, & Zwally, 1999), [7] Aviso, with support from
96 Cnes (http://www.aviso.altimetry.fr/)

97

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99
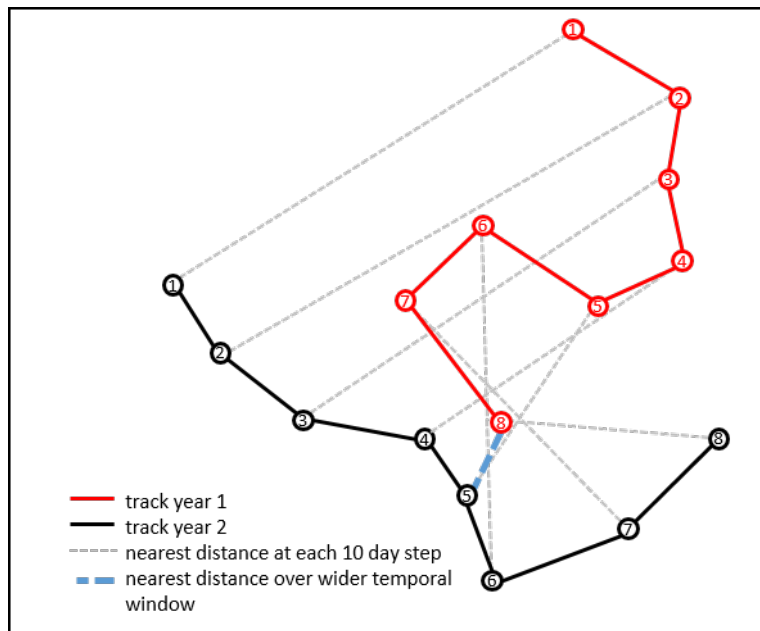
101 **Figure S1**. Schematic illustrating the calculation of NND at different time intervals
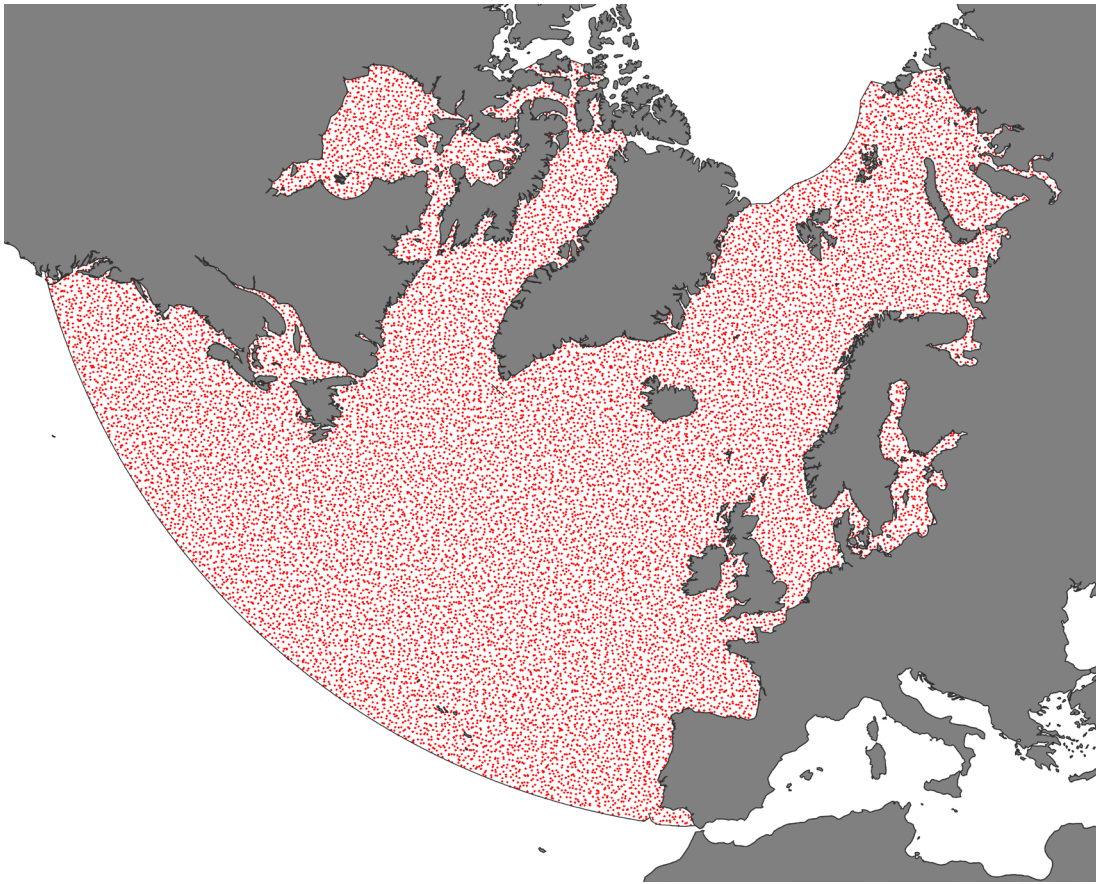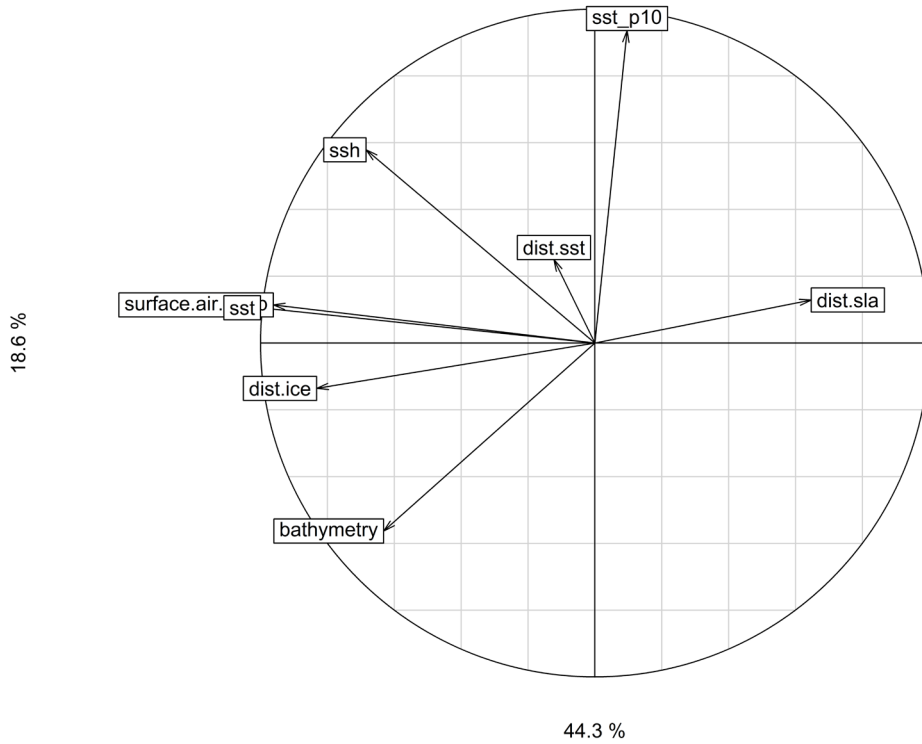
102

103   **Figure S2.** Map (in polar stereographic projection) displaying the study region including the 20000

104   points (in red) used to estimate the available environmental space.

105
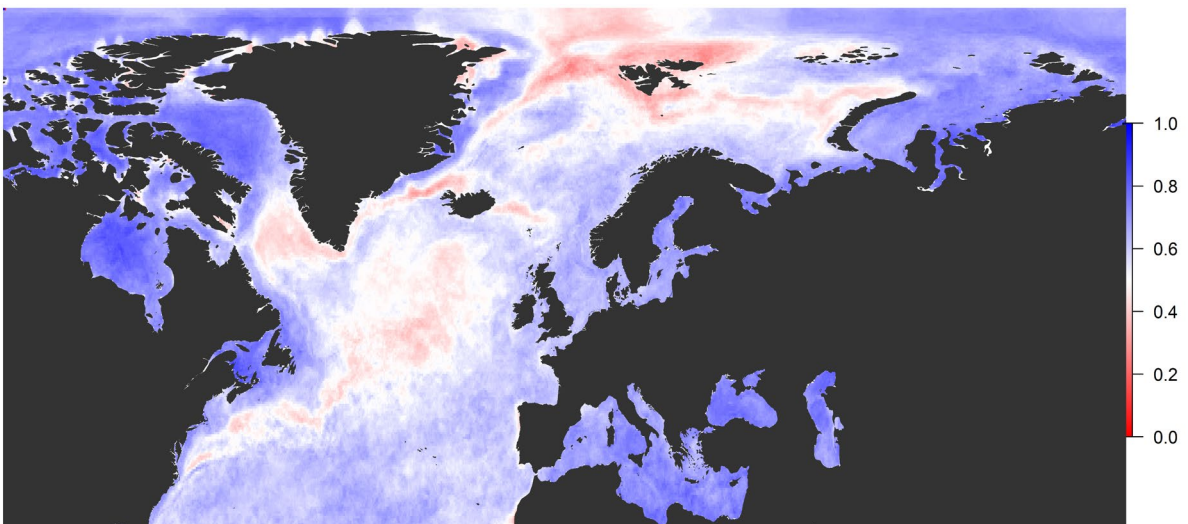
106
107

108   **Figure S3.** Distribution of SST predictability in the North Atlantic with a scale from 0 (no

109   predictability) to 1 (very predictable).

110

Figure S4. PCA correlation circle for the environmental space representing the North-Atlantic over the entire study period. dist.sla = distance to mesoscale eddies, dist.ice = distance to the marginal sea ice zone, surface.air.temp = surface air temperature, sst = sea surface temperature, ssh = sea surface height, dist.sst = distance to temperature fronts, sst_p10 = SST predictability

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116
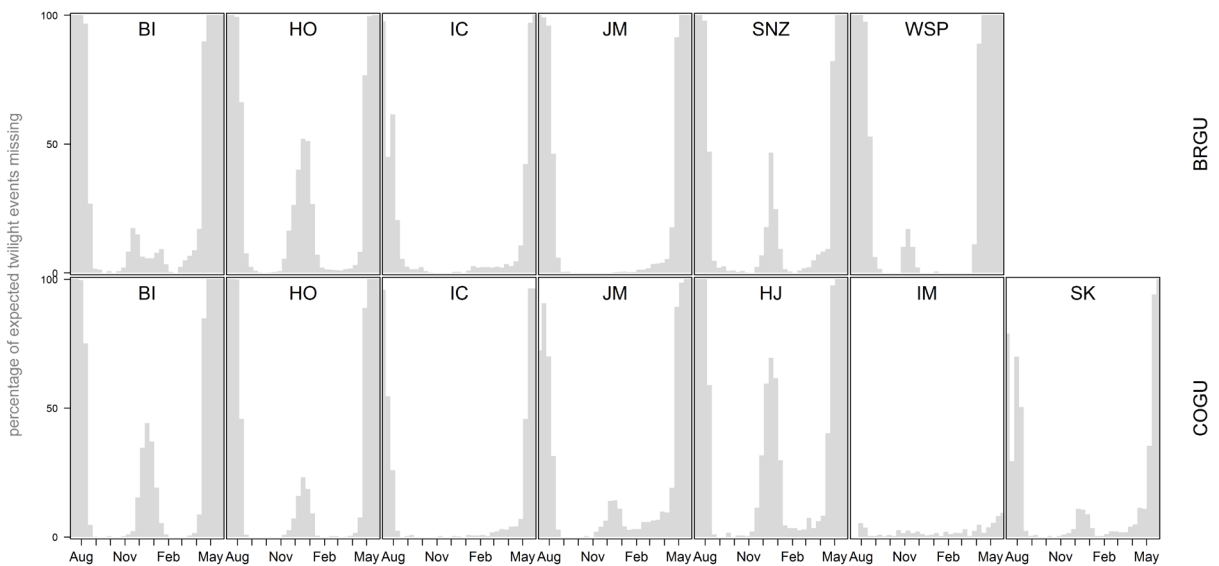
Figure S5. Species- and population-specific percentage of locations missing mainly due to lack of twilight (i.e. polar night or midnight sun).
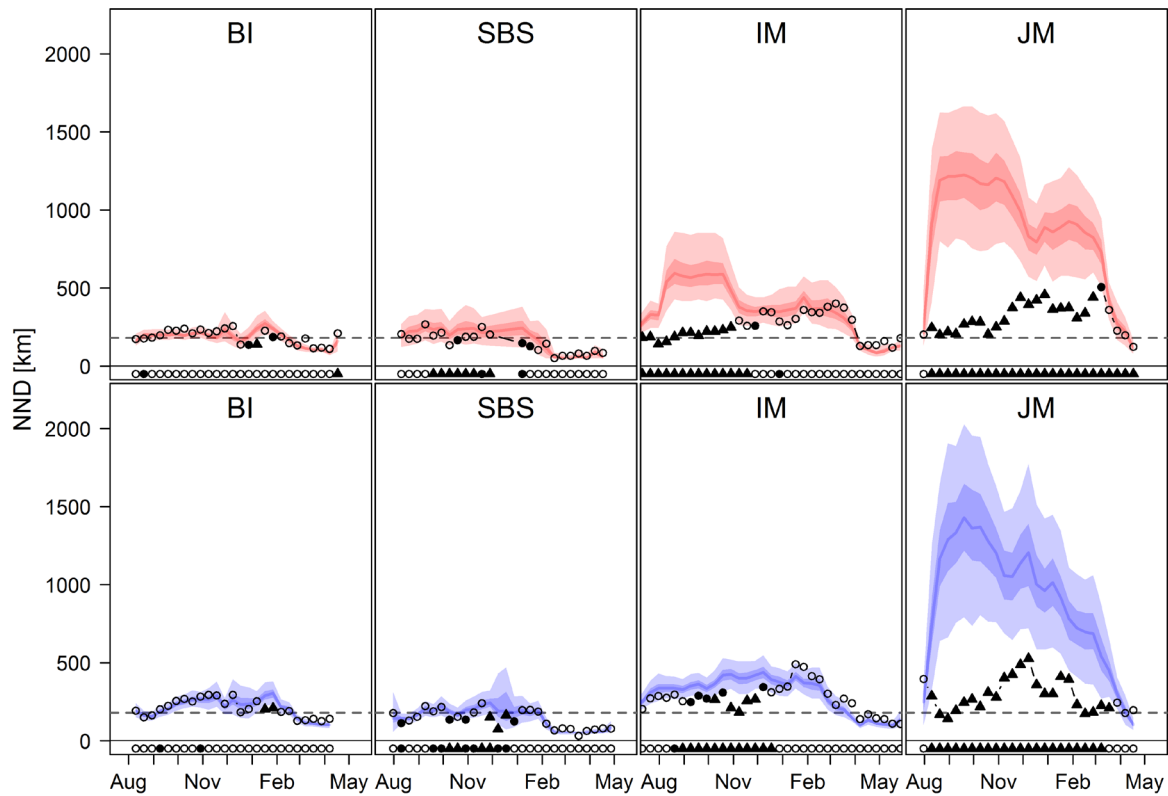
Figure S6. COGU mean sex- and breeding population-specific intra-individual nearest neighbour distance (NND, as measurement of spatial consistency) compared to the null distribution (light and dark shade indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black symbols correspond to a mean intra-individual NND significantly smaller than the null (white circle = ≥0.05, black circles =<0.05 & ≥0.01, black triangle = <0.01). Colours correspond to sex (red = female, blue = male). Bottom row in each panel depicts individual spatial consistency over a 70 day sliding window (with black symbols again corresponding to a mean intra-individual NND significantly smaller than the null).

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Figure S7. BRGU mean sex- and breeding population-specific intra-individual nearest neighbour distance (NND, as measurement of spatial consistency) compared to the null distribution (light and dark shade indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black symbols correspond to a mean intra-individual NND significantly smaller than the null (white circle = ≥0.05, black circles =<0.05 & ≥0.01, black triangle = <0.01). Colours correspond to sex (red = female, blue = male). Bottom row in each panel depicts individual spatial consistency over a 70 day sliding window (with black symbols again corresponding to a mean intra-individual NND significantly smaller than the null).

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138 **Figure S8.** Mean species- and breeding

139 population-specific intra-individual

140 nearest neighbour distance (NND, black

141 symbols) in environmental space

142 compared to the null distribution (red

143 and blue light and dark shades indicate

144 95% and 50% null distribution,

145 respectively; dark line denotes the

146 median). Black filled symbols

147 correspond to a mean species- and

148 breeding population-specific intra-

149 individual NND significantly smaller than

150 the null distribution (i.e. IMSF). Colours

151 correspond to species: BRGU in blue &

152 COGU in red.
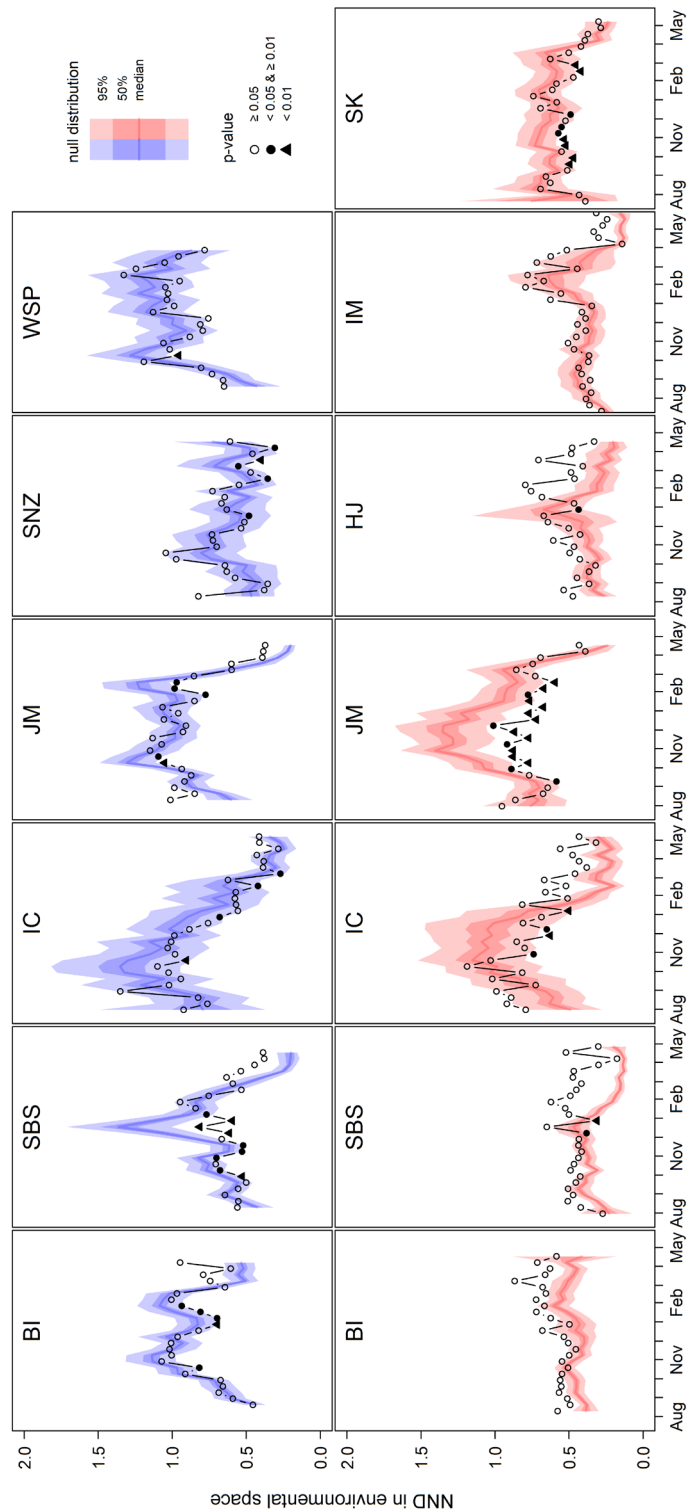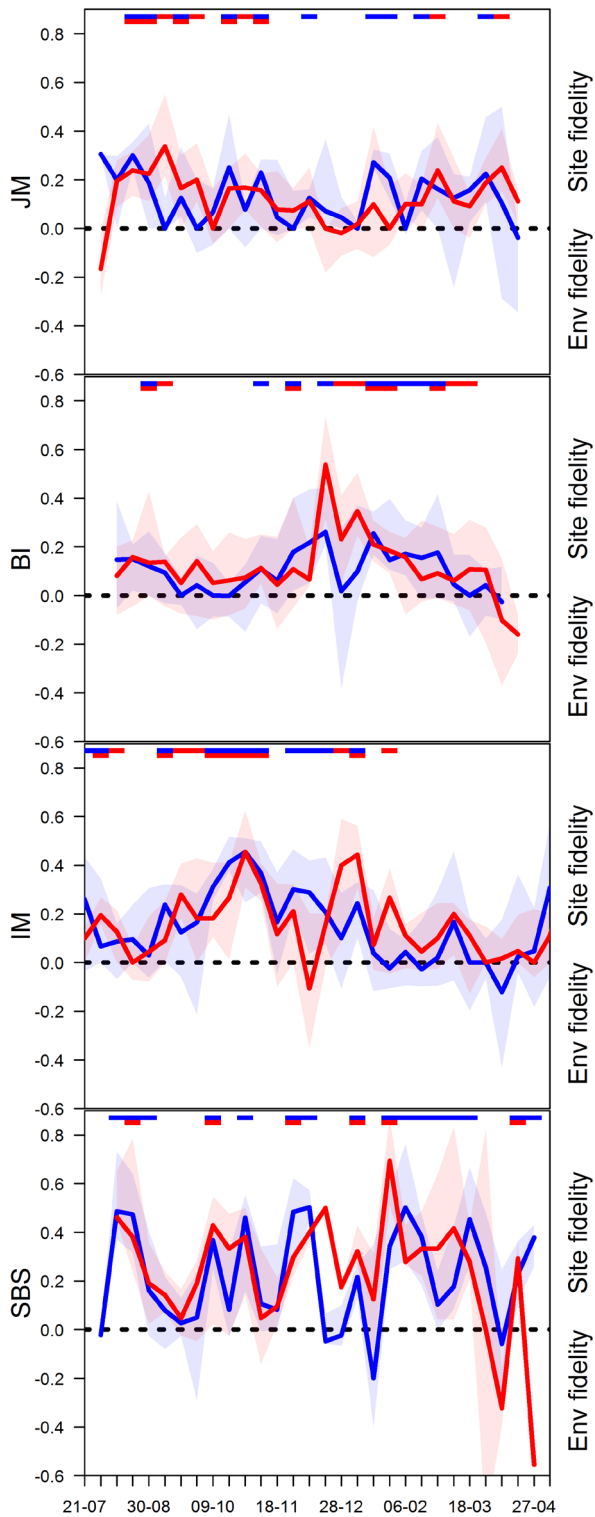
Figure S9. Sex- and population-specific similarity (ranging from -1 to 1) throughout the non-breeding period for COGUs (males in blue & females in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Lines represent the median fidelity for a given sex. Shaded areas illustrate the population-wide 25% to 75% quartile range in individual fidelity values. Bars at the top and bottom of each panel illustrate significant fidelity (i.e. significantly different from 0 at p = 0.05, scale on the right) to either sites (at the top) or habitat (at the bottom) during each ten day step.

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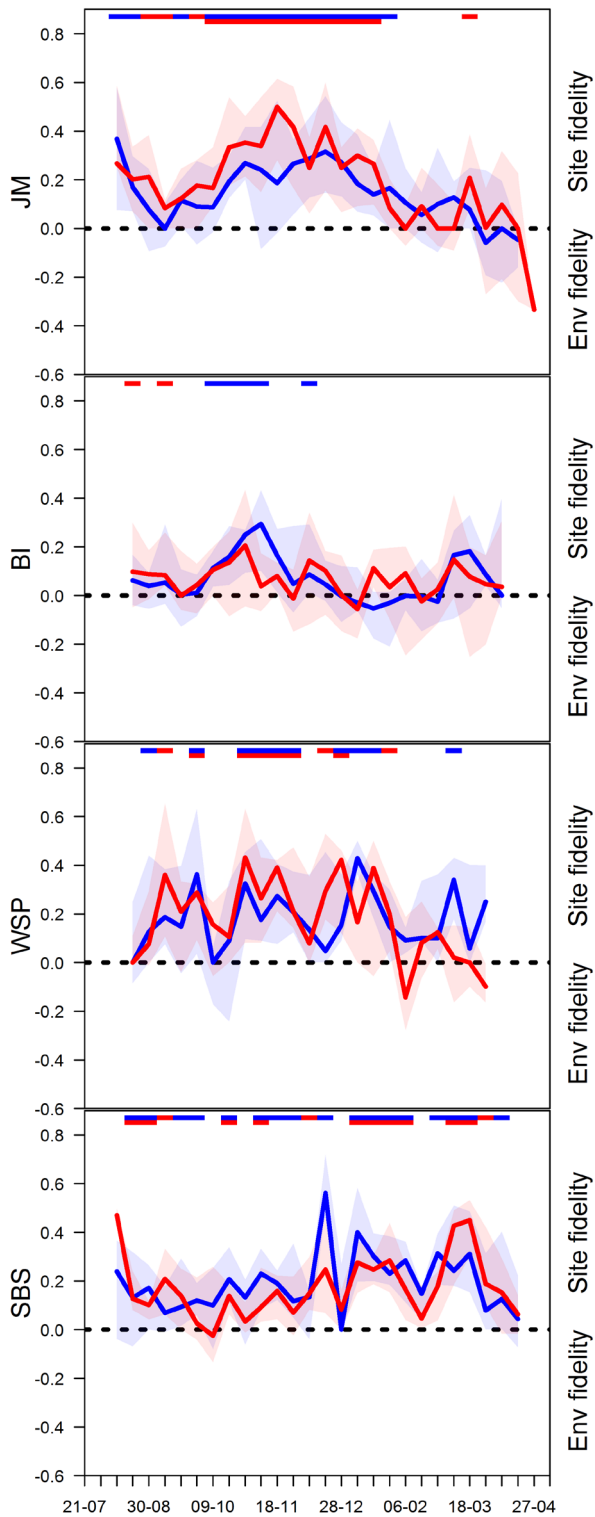
Figure S10. Sex- and population-specific similarity (ranging from -1 to 1) throughout the non-breeding period for BRGUs (males in blue & females in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Lines represent the median fidelity for a given sex. Shaded areas illustrate the population-wide 25% to 75% quartile range in individual fidelity values. Bars at the top and bottom of each panel illustrate significant fidelity (i.e. significantly different from 0 at p = 0.05, scale on the right) to either sites (at the top) or habitat (at the bottom) during each ten day step.
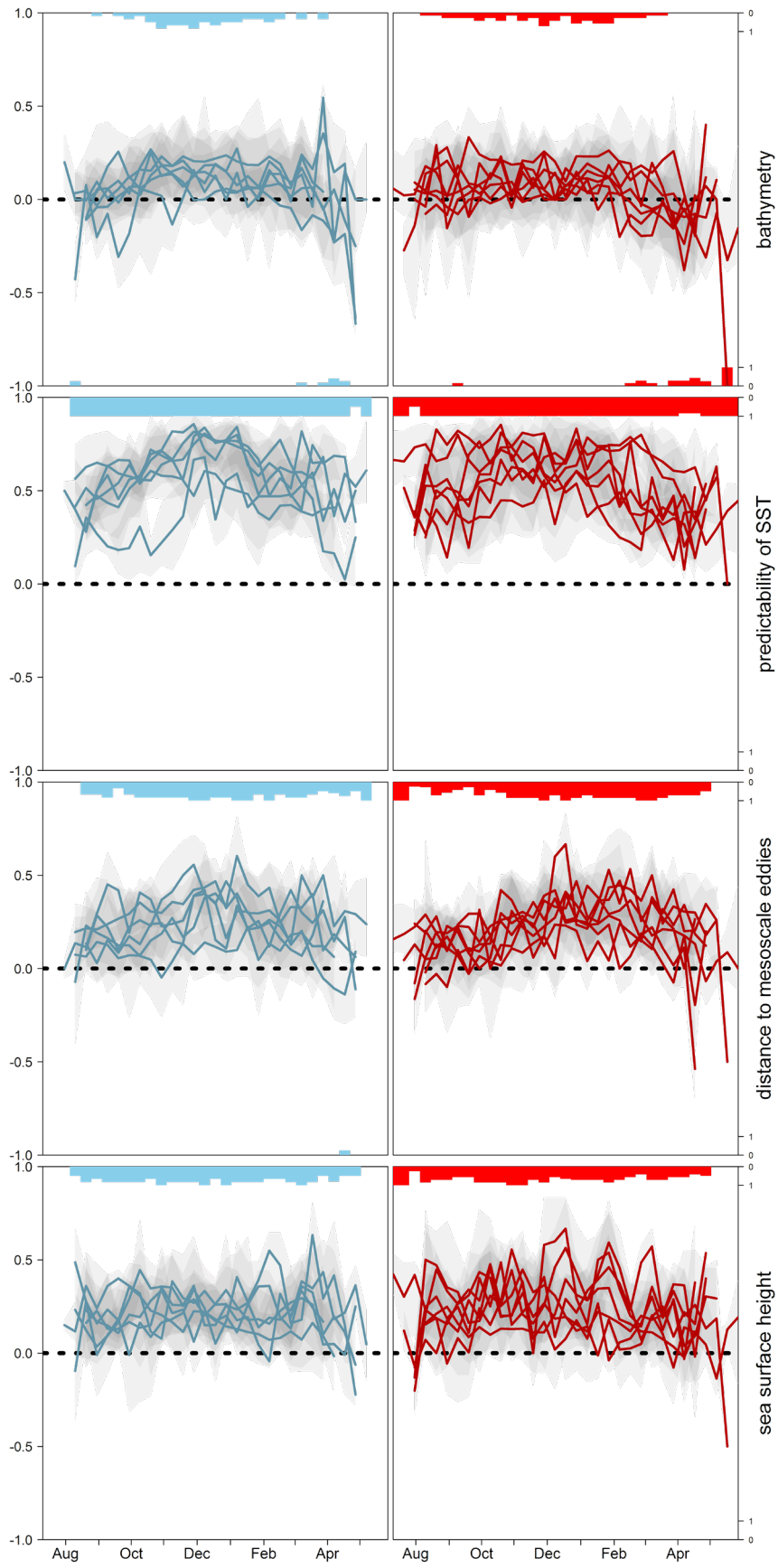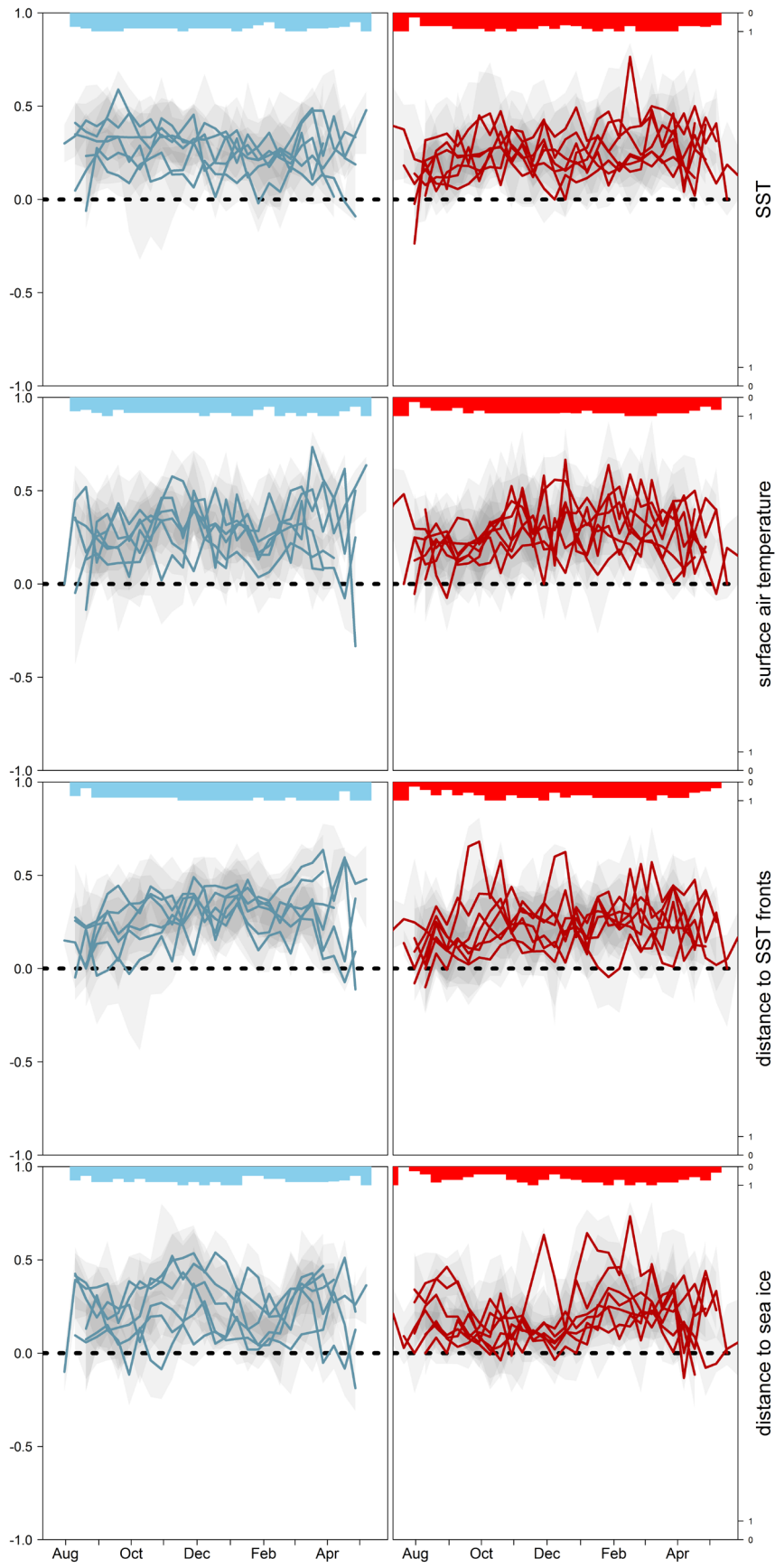
Figure S11. Species- and breeding population-specific similarity (ranging from -1 to 1) throughout the non-breeding period (Brünnich's guillemots in blue & common guillemots in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to the specified environmental parameter. Each line represents the median fidelity for a given population. Grey shaded areas illustrate the population-wide 25% to 75% quartile range 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 = 0.05, scale on the right) to either sites (at the top) or the specified environmental variable (at the bottom) during each ten day step. SST = sea surface temperature.