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No evidence that seasonal changes in large-scale environmental conditions drive migration in seabirds

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Abstract

1. Seasonal variability is one of the main drivers of seasonal movements like migration. The literature has suggested that bird migration is often driven by poor environmental conditions during one season and permits avoidance of resource shortage or harsh weather by tracking the more favourable conditions.
2. We tested at the global scale, and focusing on seabirds, whether this pattern exists in the marine realm. Specifically, we tested the hypothesis that seabird migration permits achieving stability in niche occupancy, and that it is triggered by seasonal variations in niche availability.
3. We collated data on monthly presence of species over marine ecoregions from literature and expert knowledge. First, we quantified niche occupancy during breeding and non-breeding periods from environmental conditions encountered in ecoregions in which species were present at each periods and compared seasonal dynamics across migratory strategies. Second, we quantified the seasonal niche dynamics from simulated residency in breeding and non-breeding grounds to quantify the seasonality in niche availability and to test its effect on seabird migratory strategies.
4. We demonstrated that all seabirds are niche trackers, yet resident and dispersive seabirds displayed higher levels of niche tracking throughout the year, regardless of the environmental seasonality, while migrants exhibited more divergent seasonal niches. In most cases, migratory status was not related to the unavailability of favourable conditions at the breeding or non-breeding grounds, suggesting that the availability of the favourable niche is not the main driver of migration.
5. We hypothesize that this unexpected pattern might arise from strong constraints imposed on seabirds by the scarcity of suitable breeding sites which constrain the range of environments available for optimizing reproductive success. This work sheds new light on the ecological drivers of migration.

Keywords: Biogeography; Ecological niche; Marine Ecoregions of the World; Niche dislocation; Niche dynamics; Niche overlap; Niche stability; Seasonality

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1 Introduction

Environmental conditions faced by living organisms are highly variable in space and time, from hours to decades. Seasonal variability is one of the most predictable dimensions of temporal variability, and is considered one of the main drivers of seasonal movements such as migration (Alerstam et al., 2003; Winger et al., 2019; Dufour et al., 2020). Migration is an adaptation strategy ensuring persistence in face of climate or resources fluctuations through optimisation of fitness. Its evolution might be driven by fidelity to reproductive and wintering sites, increasing both reproductive success (breeding sites) and survival (non-breeding sites; Shaw & Couzin, 2013; Winger et al., 2019). Although today we have a good understanding of many aspects of migration, our general knowledge of how migratory strategy affects the realized ecological niche of species (Hutchinson, 1957), and in particular the temporal dynamics of species occupancy within their niche, is still limited.

Many birds are thought to engage in seasonal migration from high latitude breeding grounds to avoid resource shortage or bad weather during the unfavourable season, optimising survival by tracking the spatial displacement of optimal energetic conditions (the Green Wave Surfing; Somveille et al., 2019; Winger et al., 2019). For example, common cuckoo (*Cuculus canorus*) tracked the peak in vegetation greenness and adjusted the timing and direction of migration to fit seasonal changes in resources across its range (Thorup et al., 2017; Williams et al., 2017). Such patterns have been supported by recent efforts suggesting that resident species display more pronounced fluctuations in their ecological niche across seasons (Gómez et al., 2016), while migrants preferentially track the same niche (Thorup et al., 2017; Williams et al., 2017; Zúñiga et al., 2017; Zurell et al., 2018; Somveille et al., 2019).

Yet, most of the research on the relationship between niche characteristics and migration has focused on terrestrial systems (e.g. Gómez et al., 2016; Thorup et al., 2017; Zurell et al., 2018), and whether niche-tracking tends to characterise migrant species in marine systems is still unknown. Marine pelagic systems are characterised by a strong spatio-temporal structuring (Hunt & Schneider, 1987) with their seasonal fluctuations peaking at temperate latitudes and in large upwellings, but being lower at equatorial latitudes (Figure 1). Seabirds are among the best known groups of mobile marine species at the global scale, with diversified ecological strategies and a wide array of seasonal movements (Box 1). Some species are resident year-round, some disperse widely during the non-breeding period, others engage in basin-scale or pole to pole migrations (Hunt & Schneider, 1987; Gaston, 2004), supposedly to track favourable environmental conditions (Shaffer et al., 2009; Block et al., 2011; Péron & Grémillet, 2013). Seabirds perform some of the longest known migrations, as the 70,900 km of arctic terns (*Sterna paradisaea*; Egevang et al., 2010) or the 64,000 km of sooty shearwaters (*Ardenna grisea*; Shaffer et al., 2006).

One of the main characteristics of seabirds that may impact the relationship between niche dynamics and migratory strategy is their particular relationship to land (Gaston, 2004). While feeding within marine waters, seabirds have to go back to land to breed (Schreiber & Burger, 2002). Yet, sites with the physical and environmental conditions requested to ensure successful breeding (e.g. nest substrate, wind, rain, predation, disturbance, food availability) are relatively rare for many species (Coulson, 2002). This low availability of breeding sites is a major constraint, and probably one of the factors favouring colonial breeding for most of seabird species (Siegel-Causey & Kharitonov, 1990). This enhances competition for resources and increases constraints on habitats where sufficient resources should be available to sustain the very high energetic demands of densely aggregated breeding individuals (Hamer et al., 2002; Gaston, 2004). When released from reproductive duties, seabirds are also released from the necessity of remaining close to shore (central-place foraging; Gaston, 2004) and are free to move to virtually any favourable habitat (free-ranging foraging), thanks to their exceptional flight capabilities. Furthermore, seabirds have a broad thermal tolerance range (Schreiber & Burger, 2002), permitting them to live in polar areas and to cross the equatorial regions without harm. Several polar species are also able to cope with the polar night and adverse weather of the highest latitudes (some Alcid species for example; Fort et al., 2013), as well as extreme winds associated with storm and cyclones (Weimerskirch & Prudor, 2019; Clairbaux et al., 2021).

This work had two objectives which we fulfilled at global scale using the monthly distribution of 62 seabird species across marine ecoregions. First, we quantified the niche occupancy during the breeding and non-breeding periods for all species, and compared the niche dynamics between groups of species with different seasonal movement patterns to test the hypothesis that migrants track their ecological niche throughout the year, while residents switch their niche seasonally. Second, we tested the hypothesis that the niche used by migrants during one season becomes unavailable during the other,

49 as would be if niche availability triggered niche occupancy dynamics through avoidance of adverse conditions. Here, the
50 ecological niche was characterised as the realized part of the fundamental niche resulting from the restrictions imposed
51 on the species distribution in geographical space by the interaction between abiotic, biotic, dispersal and historical factors
52 (Peterson, 2011). Although knowledge regarding seabird distribution and migration has accumulated at the species level,
53 there has been, to our knowledge, no attempt to concurrently describe the global-scale ecological niches of a wide array
54 of seabird species, ranging from polar to tropical waters. As such, this study is the first integrated analysis drawing
55 perspectives on the link between the seasonal dynamics of the ecological niche of seabirds and migratory status.

56 **2 Materials and methods**

57 **2.1 Species seasonal distributions and species phenology**

58 For this study, we focused on the species for which extensive knowledge exists on seasonal movements during both the
59 breeding and non-breeding periods over a set of colonies representative of the entire distribution range. This resulted in
60 the inclusion of 62 species of flying seabirds from seven families distributed worldwide (Supporting Information S1): 10
61 *Alcidae* species, 10 *Diomedeidae*, four *Fregatidae*, two *Laridae*, three *Phaethontidae*, 23 *Procellaridae* and 10 species of
62 *Sulidae*. This set of species represents 21% of the total number of seabird species, including 40% of *Alcidae* species, 45%
63 of *Diomedeidae*, 80% of *Fregatidae*, 100% of *Phaethontidae* and *Sulidae*, 25% of *Procellaridae*, and 2% of *Laridae*. For
64 this latter family, the two included species represented 50% of the species with an exclusively pelagic marine distribution
65 year-round. No *Stercoraridae* species were included, due to the relatively poor knowledge on the global scale distribution
66 ranges and its dynamics across season and populations. Similarly, we were not able to incorporate any *Oceanitidae*,
67 *Hydrobatidae* or *Pelecanoididae* as they are small and elusive species, for which knowledge of their at-sea distributions and
68 seasonal movements remains very scarce.

69 We compiled validated information from the literature and from the BirdLife database (see Supporting Information S1
70 for detailed references; Supporting Information S2 for the maps) to build the breeding and non-breeding distributions of
71 seabird species at the scale the Marine Ecoregions of the World. This publicly available dataset (Figure 2 and Supporting
72 Information S2; Spalding et al., 2007, 2012) classifies the coastal, shelf and surface pelagic waters into biogeographic
73 ecoregions. Their scale matched the one of seabird distribution: all studied species had ranges wider than the ecoregions
74 and always encompassed more than one ecoregion, without species ranging at a smaller scale. As such, this approach did
75 not blur the seasonal variations in distribution through an over-representation of unused areas.

76 We also assessed the species migratory strategies from the literature and the BirdLife database (see Supporting Infor-
77 mation S1). Four seasonal movement patterns were considered: migrant, partial migrant, dispersive, resident (Box 1).
78 44% of species were migratory (27 species), 26% dispersive (16 species), 16% resident (10 species) and 16% partially
79 migratory (10 species), with species ranging in tropical, temperate and polar areas in each category.

80 This work did not require ethical approval.

81 **2.2 Environmental space**

82 The environmental space is the representation of the environmental conditions (climate, resource) available to the species
83 when removing all geographical and temporal attributes, so that contiguous points in that space are not necessarily
84 contiguous in the geographical space, nor in time (Peterson, 2011). The niche of species is then described as the volume
85 used by the species within this environmental space, which corresponds to the so-called "multi-dimensional hypervolume"
86 defined by Hutchinson (1957). Here, we built the environmental space by summarizing monthly climatologies (*i.e.*, long-
87 term averages) of 29 variables characterizing the pelagic ecosystem at the global scale by means of a Principal Component
88 Analysis (PCA; Husson et al., 2016, Supporting Information S3).

89 Dynamic environmental variables were derived from GLObal ReanalYSIS (GLORYS) of environmental conditions, using
90 the "GLORYS Phys" dataset for sea surface temperature (SST), sea surface salinity (SSS), sea surface current (SSC), sea
91 surface height (SSH), sea ice fraction (SIF), mixed layer depth (MLD); and the "GLORYS Bio" dataset for chlorophyll
92 *a* surface concentration (CHL) and plankton concentration in carbon (PKN). For each month, the mean, minimum and
93 maximum values of SST, SSS, SSC, SSH, SIF, MLD, CHL and PKN were summarised over the complete available period

94 (2007-2017) to compute monthly climatologies. Minimum and maximum were considered in addition to the mean to take
95 into account the temporal variability of environmental conditions within each month. The mean solar radiance (UVB) was
96 used as a proxy for day length. UVB was extracted from the "Global UV-B radiation dataset for macro-ecological studies",
97 using the monthly climatologies constructed from daily measurements summarised into monthly means over the period of
98 2004-2013. As UVB is null over polar areas during winter, we set all pixels with no values to zero, to avoid removing these
99 areas from the analysis. Similarly, SIF values were set to zero in all pixels without sea ice. Two static variables, bathymetry
100 and roughness, were extracted from the BioORACLE database. Monthly maps and detailed sources for each variables can
101 be found in the Supporting Information S3.

102 All variables were resampled at a 1° resolution, centred and scaled before being included in the PCA. CHL and PKN
103 were logged. Each 1° cell was considered 12 times in the analysis (one per month). The PCA was computed in R version
104 3.5.1 with the FactoMineR package (Husson et al., 2016; R Core Team, 2021). A single PCA was performed to ensure
105 comparison of niche dynamics across species.

106 One inherent risk in characterizing the realised niche is the use of uninformative or irrelevant environmental gradients,
107 *i.e.* with very small effects on species fitness, thereby impairing relevant assessment of niche dynamics. To reduce this
108 risk, we considered only environmental variables with recognized importance to seabird ecology. They can have direct
109 effects on bird physiology (temperature, salinity, solar radiance) or diet (plankton concentration), or be proxies of either
110 prey availability (MLD, chlorophyll and plankton concentration) or oceanographic processes favouring prey aggregation
111 (upwellings, eddies, river plumes, tidal fronts, described by roughness, SST, SSS, SSC and SSH; Weimerskirch, 2007;
112 Wakefield et al., 2009). We incorporated minimum and maximum monthly values to include a full description of temporal
113 variability and potential effects of extremes in the analysis: the monthly mean of one environmental parameter might not
114 constrain the presence of a species at a given time, but its maximum value might impair species survival through threshold
115 effects (e.g. Šímová et al., 2011). Although we took great care in using only relevant ecological parameters, we were not
116 able to include wind patterns in our analysis, despite its importance to seabird migration flyways (Felicísimo et al., 2008)
117 due to large gaps in high latitude data.

118 2.3 Niche dynamics under true distribution

119 The ecological niche of seabirds during the breeding period is composed of two subniches: the at-sea and the nesting
120 subniches. The at-sea subniche is characterised by the set of environmental conditions occurring at sea that conditions
121 the survival of immatures and adults, and indirectly that of chicks (through food supply by adults), so the at-sea subniche
122 have a large effect on the overall species growth rate. The nesting subniche is characterised by the set of environmental
123 conditions occurring at the reproductive sites on land (wind, rain, snow, predatory pressure), and impacts the species
124 growth rate by directly conditioning the survival of the brood (but not that of adults). This terrestrial subniche being
125 by definition deserted during the non-breeding period, the breeding and non-breeding niches are always partially different.
126 The overall reduced availability of this nesting subniche in the geographical space combined with central-place foraging
127 constraints makes large portions of the ocean inaccessible that would otherwise be included in the fundamental or potential
128 niche. Here, we focused on the at-sea subniche resulting from these accessibility limitations, and did not consider the
129 nesting subniche (which would be quantified at a finer scale than the one considered here).

130 We analysed the seasonal niche dynamics of seabirds following four steps and using the R package ecospat (Broenni-
131 mann et al., 2012; R Core Team, 2021). (1) Species presences in ecoregions during the breeding vs non-breeding months
132 were projected over the environmental space depicted by the first two PCA dimensions (see Supporting Information S1
133 for species-specific periods) for the respective periods. (2) For each period, occurrences on the environmental space were
134 smoothed using a kernel function, then the space occupied by the species in the environmental space (its niche) was
135 described by dividing the species' density of occurrence by the density of occurrence of the entire environment. (3) Niche
136 dynamics were quantified with four metrics (Figure 3a): (A) the niche overlap between seasons was estimated using the
137 Schoener's D, as $1 - \frac{1}{2}(\sum(|z_b - z_{nb}|))$, where z_b is the breeding niche and z_{nb} the non-breeding niche (see Broennimann
138 et al., 2012); (B) the breeding specificity was quantified as the proportion of occurrences in the breeding niche located
139 in environmental conditions not occupied during the non-breeding season (Petitpierre et al., 2012); (C) the non-breeding
140 specificity was the proportion of occurrences in the non-breeding distribution located in environmental conditions not
141 occupied during the breeding season; (D) the stability of the non-breeding niche was the proportion of occurrences in the

142 non-breeding distribution located in environmental conditions also occupied during the breeding season. The four metrics
143 ranged from 0 to 1.

144 We formulated five theoretical patterns that could characterise seasonal niche dynamics (Figure 3), from near-complete
145 overlap (*i.e.*, niche tracking) to complete dislocation (*i.e.*, niche switching). Extreme niche tracking behaviour would result
146 in a strong overlap between seasonal niches, low breeding and non-breeding specificity but high stability (Figure 3B).
147 Extreme niche switching behaviour would result in low to no overlap, with high breeding and non-breeding specificity but
148 low stability (Figure 3B). We tested for the equality of medians across seasonal movement types using a Kruskal-Wallis
149 test, as variances were non-normal and non-homogeneous. The comparison was done for each metric, comparing all types
150 together and then each pair separately if the first test was significant.

151 Finally, we computed the difference between the average position of species occurrences across PCA dimensions during
152 the breeding and non-breeding periods to investigate any changes in niche positions and the orientation of such changes.
153 We also computed the difference in niche breadth between periods (niche breadth was the difference between the minimum
154 and maximum positions of species occurrences on the PCA dimensions).

155 2.4 Niche dynamics under simulated residency

156 To test if migration was triggered by the avoidance of adverse conditions during the non-breeding period, we simulated
157 (1) species residency at the breeding grounds by considering species to range only in the breeding grounds during the non-
158 breeding period, and (2) residency in the non-breeding grounds by considering species to range only in the non-breeding
159 grounds during the breeding period. If the assumption that migration is driven by avoidance of adverse conditions was
160 true, there should be strong seasonal differences due to changing environmental conditions between the two periods.

161 Overlap, breeding specificity, non-breeding specificity and stability were computed for the two simulated residencies.
162 We then compared the metrics obtained with the true distribution and the two simulated residencies separately for each
163 movement type using a paired Wilcoxon test, and visually inspected the deviation of observed niches from simulated
164 residencies for each species.

165 3 Results

166 3.1 Environmental space

167 The first two PCA dimensions were retained to define the environmental space, explaining 56.3% of the total variance of
168 the dataset (Supporting Information S4). The first dimension, explaining 34.8% of the variance, represented a gradient
169 from areas of high temperature, high plankton concentration and high sea surface height to polar areas with an important
170 sea ice fraction. The second dimension was a productivity gradient (21.5% of the variance).

171 3.2 Niche dynamics under true distribution

172 All theoretical patterns of seasonal niche dynamics except for complete dislocation (Figure 3B) were identified in at least
173 one of the 62 studied species. The overlap between seasonal niches of all species was high, with an average of 0.68 ± 0.21
174 (mean \pm standard deviation; range: 0.24–1.00). Overall, breeding specificity and non-breeding specificity were low,
175 averaging 0.05 ± 0.08 (from 0.00 to 0.37) and 0.06 ± 0.11 (from 0.00 to 0.59), respectively. Niche stability was strong
176 with an average of 0.94 ± 0.11 (from 0.41 to 1.00).

177 Kruskal-Wallis tests confirmed that niche dynamics strongly depended on the migratory status (Figure 4 and Supporting
178 Information S4), as at least one of the statuses had a median differing from the others for each of the four metrics (overlap:
179 $p < 0.01$; breeding specificity : $p = 0.04$, stability and non-breeding specificity: $p < 0.01$). Pairwise tests showed that
180 migrant species had a significantly lower overlap between niches than resident, partial migrant and dispersive species
181 ($p < 0.01$, $p = 0.03$, $p < 0.01$, respectively; Figure 4A). Migrants also had higher breeding specificity than dispersive
182 species ($p < 0.01$; Figure 4B). Migrant and partial migrants exhibited lower stability and higher non-breeding specificity
183 than resident and dispersive species (Figures 4C, D): $p < 0.01$ for migrant-dispersive and migrant-resident comparisons,
184 $p < 0.01$ for partial migrant-dispersive and $p < 0.01$ for partial migrant-resident.

185 The difference in niche positioning and breadth between the two seasons also varied according to migratory status
186 (Figure 5A and Supporting Information S4). Dispersive species did not shift their niches between seasons (null differences
187 for the two dimensions, Figure 5A) but exhibited wider niches on the second dimension during the breeding period (Figure
188 5B). Resident species experienced, on average, warmer and saltier (dimension 1) but also more productive waters (dimension
189 2) during the breeding period compared to the non-breeding one (positive differences for both dimensions; Figure 5A).
190 They displayed no difference in niche breadth between breeding and non-breeding niches on the second dimension, but
191 wider breeding niches on the first one (Figure 5B). Migrant and partial migrant species experienced more productive waters
192 during the breeding period (dimension 2, Figure 5A). They shifted positioning between season for the first dimension as
193 well, but in both directions with species experiencing warmer and saltier waters during the breeding season or the opposite.
194 Both groups exhibited non-breeding niche wider than the breeding one (Figure 5B), on both dimensions for migrants but
195 mostly on the first dimension for partial migrants.

196 3.3 Niche dynamics under simulated residency

197 Niche dynamics were similar when residency was simulated in the breeding and non-breeding ranges for resident and disper-
198 sive species (non-significant differences; Figure 4 and Supporting Information S4). Partial migrants exhibited similar niche
199 overlap and breeding specificity if remaining resident in the breeding or non-breeding areas (non-significant differences),
200 but exhibited smaller ranges of niche stability and non-breeding specificity under simulated residency than for the true
201 distribution ($p = 0.03$ and 0.02 for stability and non-breeding specificity under the two simulations, respectively; Figure
202 4). Simulated seasonal niches for migrants resident in either the breeding or non-breeding ranges were more similar across
203 seasons than the observed seasonal niches of migrants (Figure 4). For migrants, the overlap increased to values similar
204 to that of the other groups for both simulated residencies ($p < 0.01$ for residency in breeding areas and in non-breeding
205 areas), while breeding specificity was strongly reduced compared to the true distribution (difference only significant for
206 residency in non-breeding area, $p = 0.02$). Stability and non-breeding specificity remained the same in the case of residency
207 in the breeding range ($p > 0.05$), but stability was larger and non-breeding specificity smaller in the case of residency in
208 the non-breeding range ($p < 0.01$ in both cases).

209 Visual inspection of the relationships between metrics obtained from the true distribution and simulated residency
210 (Figure 6) confirmed that migrants deviated more from equivalence (1:1 line) than others species (except for two partial
211 migrant species, the yelkouan (*Puffinus yelkouan*) and Balearic (*P. mauretanicus*) shearwaters). The overlap between true
212 breeding and non-breeding niches was lower for migrants than when residency was simulated in the breeding and non-
213 breeding ranges (the largest deviations were observed for the Antarctic (*Pachyptila desolata*) and slender-billed (*P. belcheri*)
214 prions; Figure 6A). Yet, some species (including dispersive and partial migrants) exhibited the opposite pattern, with a
215 true overlap larger than under simulated residency, such as the yelkouan shearwater, the Chatham albatross (*Thalassarche*
216 *eremita*), the black-footed albatross (*Phoebastria nigripes*) and the Barolo shearwater (*Puffinus baroli*). The majority of
217 species had breeding specificity similar to the one obtained from simulated residency in the breeding and non-breeding
218 ranges (Figure 6B), but a set of species exhibited strong deviations from simulated residency: breeding niches were either
219 more different (higher breeding specificity; in particular the sooty and short-tailed (*Ardenna tenuirostris*) shearwaters) or
220 more similar (lower breeding specificity; yelkouan and Balearic shearwaters) than non-breeding niches. There was less
221 deviation from what would occur under simulated residency for stability and specificity of non-breeding niches (Figures
222 6C, D), but niche stability was still lower and specificity higher for migrants (*i.e.*, non-breeding niches differed more from
223 breeding niches than under simulated residency). A set of three species stood out, exhibiting much lower stability and much
224 higher expansion than under simulated residency (higher dissimilarity in seasonal niches): the Antarctic and slender-billed
225 prions (migrants) and the Balearic shearwater (partial migrant).

226 4 Discussion

227 This study represents the first investigation of the seasonal dynamics of seabird ecological niches at the global, ecoregion
228 and inter-specific scales, by analysing the up-to-date knowledge about their spatial distribution. The comparison of
229 the niche dynamics among the four existing seasonal movement patterns highlighted that, contrary to our predictions,

230 migratory species tracked less their ecological niche across seasons than resident and dispersive ones. Achieved with a
231 macro-ecological perspective, both spatially (global) and temporally (climatological), it hence provides new insights as
232 to what processes could drive seabird migratory strategy at the species scale. Yet, such a macro-ecological scale limits
233 interpretations at individual or population levels (e.g. drivers of specific trajectories or of distribution at specific sites) as
234 it does not investigate conditions tracked by individuals, but rather the conditions experienced by the species as a whole.
235 Therefore, the present study opens new perspectives and calls for further down-scaling investigations, exploring the niche
236 dynamics at the population and individual levels as to further disentangle the drivers of migration and understand their
237 consequences on the temporal variations of the ecological niche. Thanks to the rapid increase in individual tracking for
238 more and more seabirds species and in various environments, we are confident that such approaches should become possible
239 in a near future.

240 4.1 Seasonal dynamics of ecological niches

241 Our quantification of the ecological niche dynamics of 62 seabird species demonstrated that they all tracked their ecological
242 niche between seasons to some extent, with strong niche overlap (68% on average) between the breeding and non-breeding
243 periods. Thus, there was a high stability of environmental conditions between the two niches: on average, 94% of the
244 non-breeding niche was included in the breeding niche and only 5% of conditions encountered in the breeding niche were
245 not encountered in the non-breeding niche (breeding specificity).

246 Seasonal niche dynamics nonetheless varied between species with different migratory status. Resident and dispersive
247 species had an average overlap >80% between their seasonal niches, with almost complete stability of environmental
248 conditions between the breeding and non-breeding niches. Resident and dispersive species were distributed mainly at
249 low latitudes (boobies, tropicbirds and frigatebirds) in the least seasonal environments, where encountered environmental
250 conditions barely change across the year, explaining this strong stability. However, some resident and dispersive species
251 exhibiting niche tracking were also distributed in highly seasonal subpolar to polar waters. This was the case for the black
252 guillemot (*Cephus grylle*), the marbled murrelet (*Brachyramphus marmoratus*), the light-mantled albatross (*Phoebetria*
253 *palpebrata*), the sooty albatross (*Phoebetria fusca*), the Indian yellow-nosed albatross (*Thalassarche carteri*), the northern
254 fulmar (*Fulmarus glacialis*), the Barolo shearwater and the blue petrel (*Halobaena caerulea*). These species exhibited
255 similar breeding and non-breeding niche contours, but their highest densities were located in different parts of their niches
256 due to environmental seasonality. We can thus propose that these species have developed strategies other than migration
257 to cope with unfavourable environmental conditions (Shaffer et al., 2001; Fort et al., 2013; Winger et al., 2019).

258 Partial migrant species exhibited an intermediate pattern between resident/dispersive and migrant species, as found
259 for the thermal niche by Dufour et al. (2020). The seasonal niche overlap of partial migrants was lower than in resident
260 and dispersive species but larger than in migrants. Stability and non-breeding niche specificity of partial migrants were
261 similar to that of migrants, but their breeding specificity was similar to resident and dispersive species. This pattern
262 indicates that the non-breeding niche incorporates and expands the breeding one, as confirmed by the difference in niche
263 breadth between seasons. As a result, partial migrants do not switch, but rather expand, their ecological niche during the
264 non-breeding period (third theoretical niche dynamics in Figure 3B). The intermediate pattern observed in partial migrants
265 might originate in the migratory portions of the population exhibiting niche switching, while the resident portions track
266 the same niche year-round, although testing this hypothesis would require examining the niche dynamics of the migrant
267 and resident portions of the population separately.

268 Contrary to studies showing niche-tracking migrants (Gómez et al., 2016; Zurell et al., 2018; Somveille et al., 2019),
269 the migratory species included in our study displayed more divergent breeding and non-breeding niches than other species
270 (Dufour et al., 2020). They exhibited the lowest overlap coupled with the lowest stability of the environmental conditions
271 between seasonal niches, and the largest breeding niche specificity. Migrants also exhibited the largest differences in niche
272 breadth between seasons. These species engaged in short to long-range migrations, including basin-scale, trans-equatorial
273 migrations. It has previously been suggested that long-range migration in seabirds might be linked to niche tracking,
274 allowing individuals to follow an endless summer, such as in sooty shearwaters in the Pacific Ocean (Shaffer et al., 2006) or
275 in Scopoli shearwaters (*Calonectris diomedea*) from the Mediterranean Sea to the equatorial Atlantic (Péron & Grémillet,
276 2013). This result cautions against considering niche tracking a golden rule for marine migrants, given the stronger
277 level of niche divergence observed in migrant species when considering a large set of environmental conditions, rather than

278 productivity only, as has previously been done. Some trans-equatorial migrants did exhibit similar (but not identical) niches
279 between the breeding and non-breeding seasons, despite performing long-range, basin-scale migrations: Chatham albatross,
280 Buller's albatross (*Thalassarche bulleri*), Cook's petrel (*Pterodroma cooki*), Deserta's petrel (*Pterodroma deserta*). Yet,
281 others species performing similar basin-scale migrations exhibited some of the most divergent seasonal niches among studied
282 species: sooty shearwater, great shearwater (*Ardenna gravis*, unlike in [Shaffer et al., 2006](#)), and short-tailed shearwater.

283 4.2 Environmental drivers of seabird migration

284 Migrant species exhibiting some variation in their niche occupancy across seasons points towards a more complex pattern
285 than migrant tracking favourable conditions. However, the question remains open as to whether migration is triggered
286 by avoidance of unfavourable conditions, which could optimise the individual survival during the non-breeding period
287 ([Alerstam et al., 2003](#); [Shaw & Couzin, 2013](#); [Somveille et al., 2019](#); [Winger et al., 2019](#)). Here, we tested this hypothesis
288 by simulating the residency of seabirds in their breeding and non-breeding grounds. If migration was triggered by favourable
289 conditions becoming unavailable, simulated residency should show important variations in niche occupancy.

290 This was, however, found for two partial migrant species only, the yelkouan and the Balearic shearwaters. Both species
291 breed in the Mediterranean Sea from October to May/July ([Guilford et al., 2012](#); [Raine et al., 2013](#)). Environmental con-
292 ditions encountered during this higher productivity period changed drastically during the non-breeding period (Supporting
293 Information S4), and both species cope with this change by performing short and medium scale migrations to track their
294 niche, to the eastern Mediterranean, Black Sea (yelkouan shearwater; [Raine et al., 2013](#)) and the Bay of Biscay (Balearic
295 shearwater [Guilford et al., 2012](#)). The environmental envelop ensuring individual survival became too scarce to ensure the
296 maintenance of the complete population within the breeding range, eventually driving the migration of a large portion of
297 the populations.

298 Conversely, the stand-out result arising from this work is that, for all other species and whatever their migratory
299 strategies, environmental conditions used during the breeding and non-breeding periods remained available during the
300 other period. Migrants exhibited stronger seasonal variations in niche occupancy when migrating than if they stayed in
301 either the breeding or non-breeding grounds. Thus, our results suggest that the unavailability of favourable conditions is
302 not a primary driver of migration, contrary to what was hypothesized.

303 This striking result is opposite to what was found in terrestrial birds ([Gómez et al., 2016](#); [Thorup et al., 2017](#); [Zurell
304 et al., 2018](#)) and opens the question as to why seabirds engage in migration if favourable conditions remain available
305 from one season to the other? For a migratory strategy to be viable, it must come with a fitness benefit, either through
306 enhanced survival or through an improved reproductive success ([Zúñiga et al., 2017](#)). As mentioned above, one of the
307 main characteristics of seabirds is their reliance on land for reproduction. This characteristic entails strong constraints on
308 species distribution as it induces central-place foraging behaviour, and requires breeding sites suitable enough to support
309 reproduction in densely aggregated colonies and ensure the survival of both adults and their chicks.

310 During the breeding season, the most energy demanding period in seabirds, aggregations of individuals around colonies
311 induce the strongest level of competition faced by seabirds during their phenological cycle ([Gaston, 2004](#)). However, once
312 the breeding duties are completed, seabird energy requirements drop and the central-place foraging constraint disappears.
313 This results in a dilution of intra-specific competition during the non-breeding period ([Pettex et al., 2019](#)), but also in the
314 possibility for individuals to move to more favourable areas otherwise inaccessible during the breeding period.

315 We can then reasonably suggest that the larger shift observed in the seasonal niches of migrating seabirds reflects the
316 fact that large-scale seasonal movements of seabirds are not driven by niche availability alone but rather by a combination
317 of biological (reproductive duty) and environmental (breeding site availability and fidelity) constraints imposed during the
318 breeding period ([Gaston, 2004](#); [Shaw & Couzin, 2013](#); [Winger et al., 2019](#)). This combination eventually leads species
319 to switch their niche between seasons, where individuals move between areas offering an environment that optimises their
320 reproductive success (as exemplified by the more productive systems used in average by migrants during the breeding
321 period) and areas that are optimal for the survival during the free-ranging period.

322 However, while all species have to cope with strong levels of competition during the breeding period, they do not all
323 migrate or disperse. Migration is only one of the many strategies available to animals to cope with environmental seasonal
324 fluctuations ([Winger et al., 2019](#)), and resident species must chose alternative strategies to cope with the unfavourable
325 period (low temperature, polar night or extreme winds). Several seabirds have been shown to sustain their needs in seasonal

326 environments by adjusting other parameters than spatial distribution, such as their energy budget, their foraging effort, or
327 their diet (Fort et al., 2013). Those alternative strategies are less common than migration in seabirds, as in birds in general
328 (see Figure (a) in Box 1), because birds are characterised by exceptional flight capabilities (Gaston, 2004; Winger et al.,
329 2019). Yet, alternative strategies are necessary to ensure species maintenance in seasonally fluctuating environments in
330 the absence of migration. As a result, a needful extension to the present work is to better describe the strategies used
331 by resident species to face fluctuating conditions (e.g. activity budgets, diets). Thanks to the increasing availability of
332 tracking dataset and biological information for a large amount of species and populations, it would become possible to
333 complement this work in that direction in a near future, to more precisely quantify seasonal niches of seabirds at a finer
334 scale, and ultimately to better understand what triggers seabird migration.

335 Finally, other factors not considered in the present study might also influence seabird seasonal movements. In particular,
336 we did not control for phylogenetic relationships among species, nor for past evolutionary constraints on bird spatial
337 distributions: some species might engage in migration through inheritance processes although current environmental
338 conditions do not favour such a strategy (Pulido, 2007). Migratory strategies might also be influenced by morphological
339 characteristics (the bird capacity to carry out long-range migration; Dias et al., 2012), foraging tactics, and life history
340 parameters (e.g. maturity, life expectancy; Péron & Grémillet, 2013). These factors might interact with the effect of
341 the environmental availability to condition the extent of niche tracking exhibited by seabird species. The present work
342 thus opens several research avenues to further investigate underlying drivers of seabird migratory movements and to better
343 understand the evolution of migration.

344 To conclude, we, for the first time, described the global seasonal dynamics of a wide array of seabird species, ranging
345 from polar to tropical waters. We demonstrated that all seabirds are niche trackers, yet contrasting dynamics occurred
346 depending on seasonal movement types. Resident and dispersive seabirds displayed high levels of niche tracking throughout
347 the year, regardless of the environmental seasonality, while migrants exhibited more divergent seasonal niches. In most
348 cases, breeding and non-breeding niches of migrants were still available during the other period, suggesting that migration
349 is not primarily driven by the availability of the favourable niche. This result contrasts with previous results obtained on
350 terrestrial systems, and might originate from the particular biological constraints experienced by seabirds. Specifically,
351 seabird migration might in part be driven by the scarcity of breeding sites, which may force individuals to move between
352 areas where the environment allows for optimization of reproductive success and non-breeding grounds that are optimal
353 for survival during the free-ranging period.

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358 **Conflict of interest**

359 We have no conflict of interest to declare.

360 **Author contributions**

361 Charlotte Lambert conceived the ideas and designed the methodology; Charlotte Lambert collected and analysed the data;
362 Charlotte Lambert and Jérôme Fort wrote the manuscript. Both authors contributed critically to the drafts and gave final
363 approval for publication.

364 **Data Accessibility Statement**

365 Codes available from the Zenodo repository <https://doi.org/10.5281/zenodo.6617889> (Lambert & Fort, 2022).

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Box 1. The four types of seasonal movement patterns in seabirds: Four movement types were considered in this work:

Residency: the population remains sedentary within a similar area along the year; e.g. Cape gannet *Morus capensis* (Sabarros et al., 2014).

Dispersal: the population disperses using non-directed movements during the non-breeding period over a large range often including the breeding range, without a clearly defined non-breeding "residency area"; e.g. white-tailed tropicbird (*Phaethon lepturus*; Mejías et al., 2017).

Partial migration: one fraction of the population is sedentary, another migrant; e.g. Balearic and yelkouan shearwaters (*Puffinus mauretanicus* and *yelkouan*), wandering albatross (*Diomedea exulans*; Raine et al., 2013; Guilford et al., 2012; Weimerskirch et al., 2015).

Migration: populations completely desert their breeding grounds during the non-breeding period with directed movements and precise schedules.

Direct migration: individuals perform direct trips from breeding to non-breeding grounds, optionally with some stop-over sites; e.g. sooty shearwater (*Ardenna grisea*; Shaffer et al., 2006).

Leap-frog migration: individuals from northerly colonies migrate further south than those from southerly colonies; e.g. Bulwer's petrel (*Bulweria bulwerii*; Ramos et al., 2015).

Chain migration: populations from all colonies migrate the same distance, resulting in a sequential displacement where a colony breeding ground becomes the non-breeding ground for another colony during the non-breeding period; e.g. northern gannet (*Morus bassanus*; Fort et al., 2012).

A majority of the studied species were migrant or dispersive (70%), a minority resident (16%; Figure S2-1, Supporting Information S1). *Alcidae*, *Diomedeidae* and *Procellariidae* families included all four movement types, *Fregatidae* two types, *Laridae* and *Phaethontidae* only one.

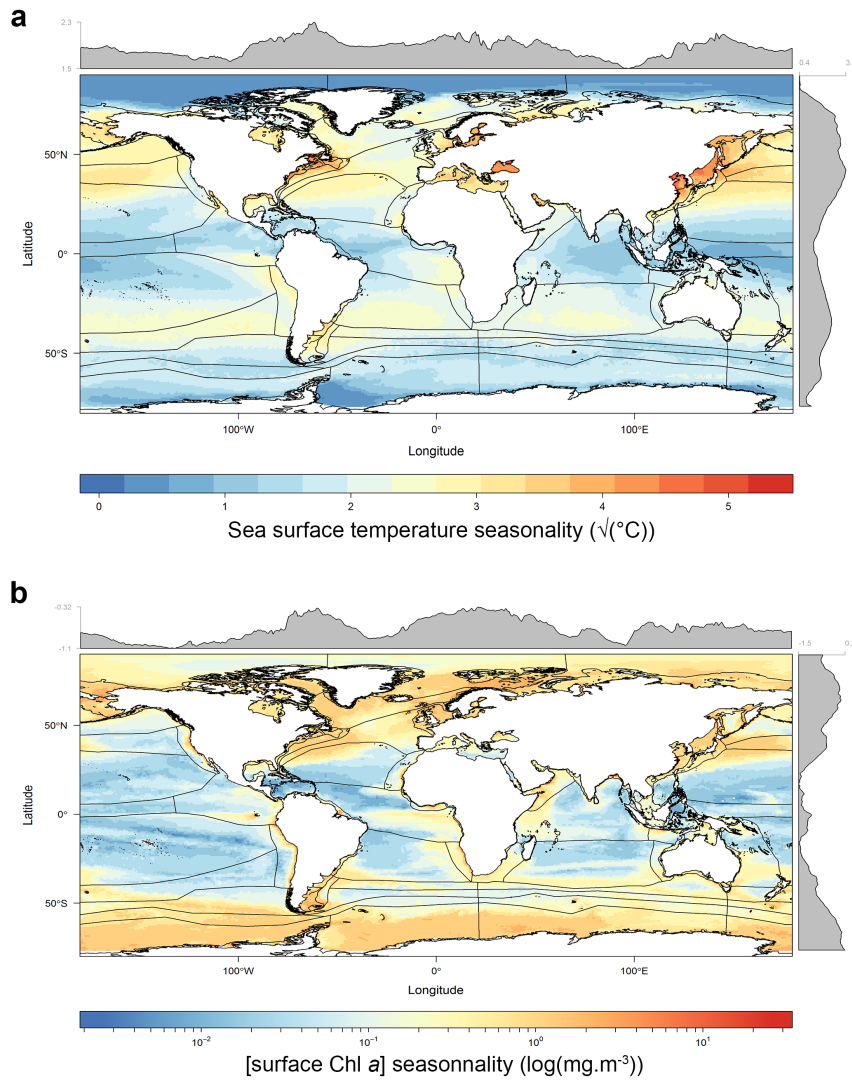


Figure 1. The seasonality of (A) the sea surface temperature and (B) the surface concentration in chlorophyll a. The seasonality is calculated as the difference between the largest and the smallest values from monthly climatologies (computed from GLORYS reanalysis for the period 2007–2017). The seasonality is represented as square root of SST and log of Chl a concentration for a better visualisation. The black contours are the Marine Ecoregions of the World (Spalding et al., 2007, 2012).

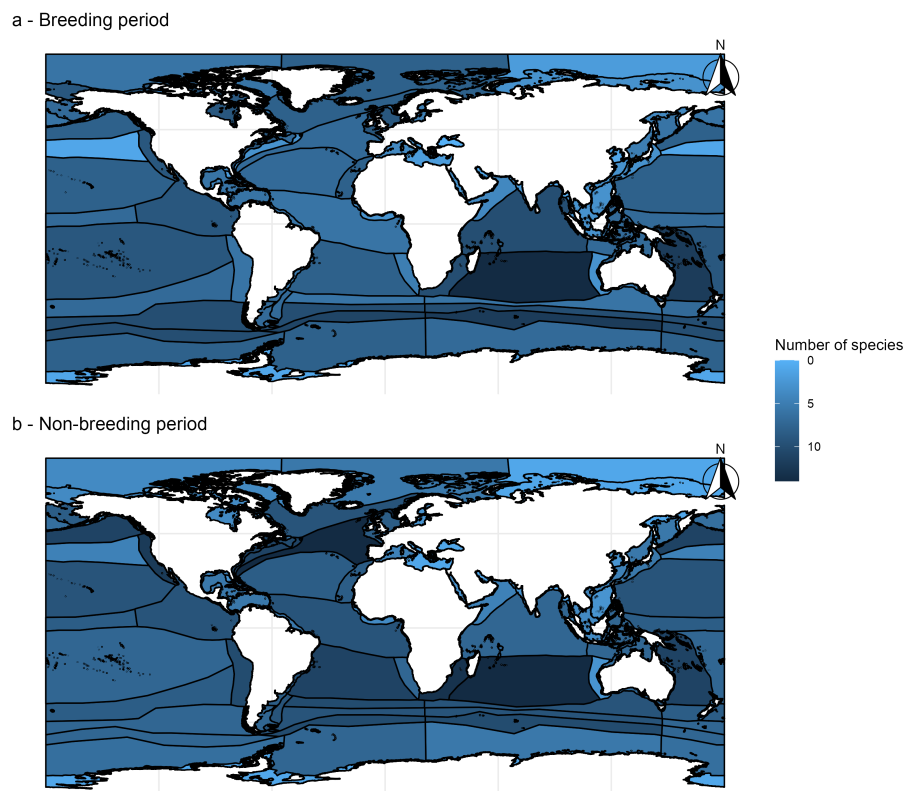


Figure 2. Number of species present in each Marine Ecoregion of the World (Spalding et al., 2007, 2012) during (a) their breeding and (b) non-breeding periods. Note that breeding and non-breeding periods do not necessarily overlap among species present in similar ecoregions, meaning they are not necessarily present at the same time.

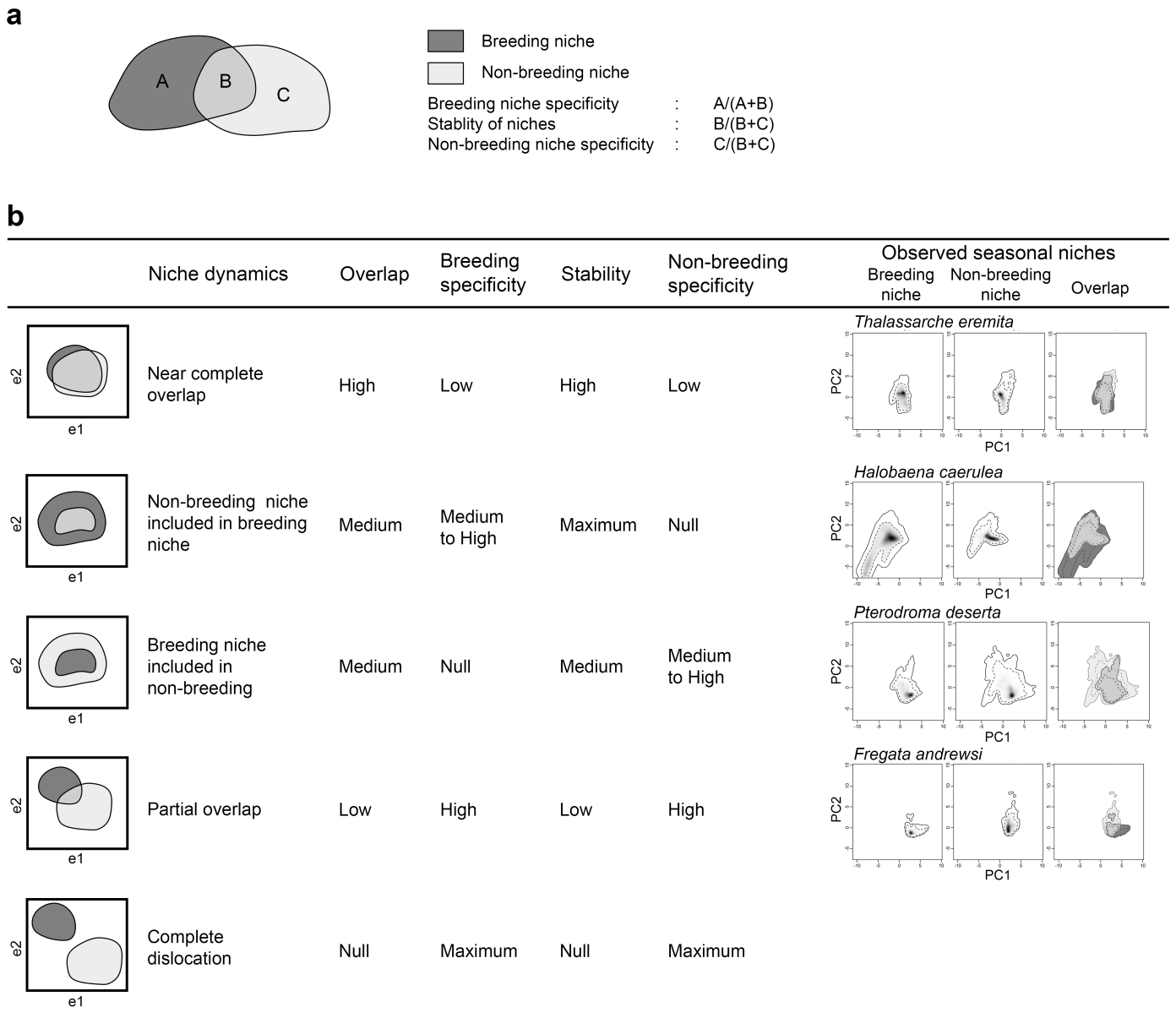


Figure 3. (a) - Seasonal niches projected on environmental spaces and the four metrics derived from their comparisons: niche overlap, breeding specificity (portion of the niche occupied only during the breeding season), niche stability (portion of the niche occupied in both seasons) and non-breeding specificity (portion of the niche occupied only during the non-breeding season); (b) - Five different possible niche dynamics along the continuum from niche tracking to niche switching, and their resulting comparison metrics (overlap, breeding specificity, stability and non-breeding specificity), with examples from observed seabird seasonal niches. One species is shown as an example for each category (Chatham albatross *Thalassarche eremita*, blue petrel *Halobaena caerulea*, Desertas petrel *Pterodroma deserta* and Antarctic prion *Pachyptila desolata*). The breeding (left panel) and non-breeding (centre panel) niches are shown displaying the densities of presence inside the niche as shaded grey. The overlap between the two niches is shown in the right panel, with breeding niche in dark grey, non-breeding niche in light grey and overlap in mid-tone grey. The solid contour lines depict 100% of the available environment, the dashed contour lines 50% of the most common background environment. There was no seabird species exhibiting complete dislocation of seasonal niches.

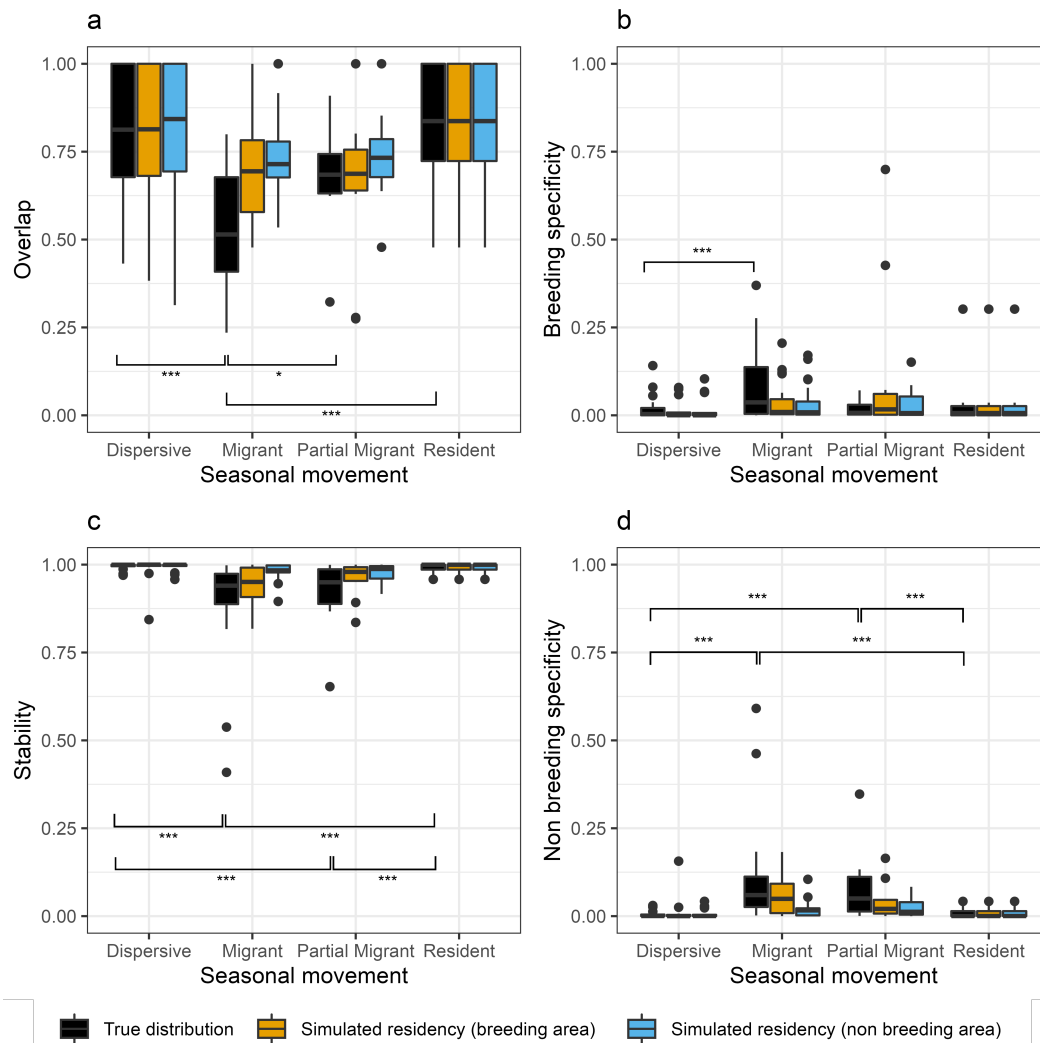


Figure 4. (a) - Species niche overlap, (b) - breeding niche specificity, (c) - stability of niches and (d) - non-breeding niche specificity for each type of seasonal movement pattern for the true distribution (observed niche, in black), simulated residency in breeding area (orange) and simulated residency in non-breeding area (blue). The highlighted pairs of seasonal movement patterns are those exhibiting significantly different medians (for true distributions only) as determined by Kruskal-Wallis tests, with the corresponding significance levels below.

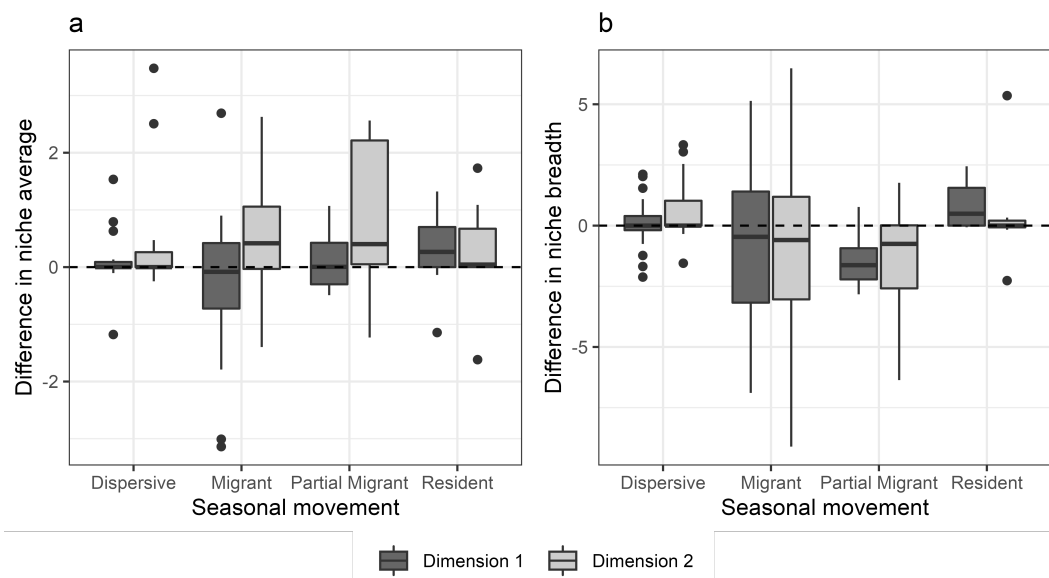


Figure 5. (a) - Differences in averaged position of species occurrences on PCA dimensions 1 and 2 between the breeding and non-breeding periods. Positive differences correspond to warmer, saltier and shallower waters (dimension 1) or more productive waters (dimension 2) during the breeding period compared to the non-breeding one. (b) - Differences in niche breadth between the breeding and non-breeding periods. Positive differences indicate a wider breeding niche compared to the non-breeding one.

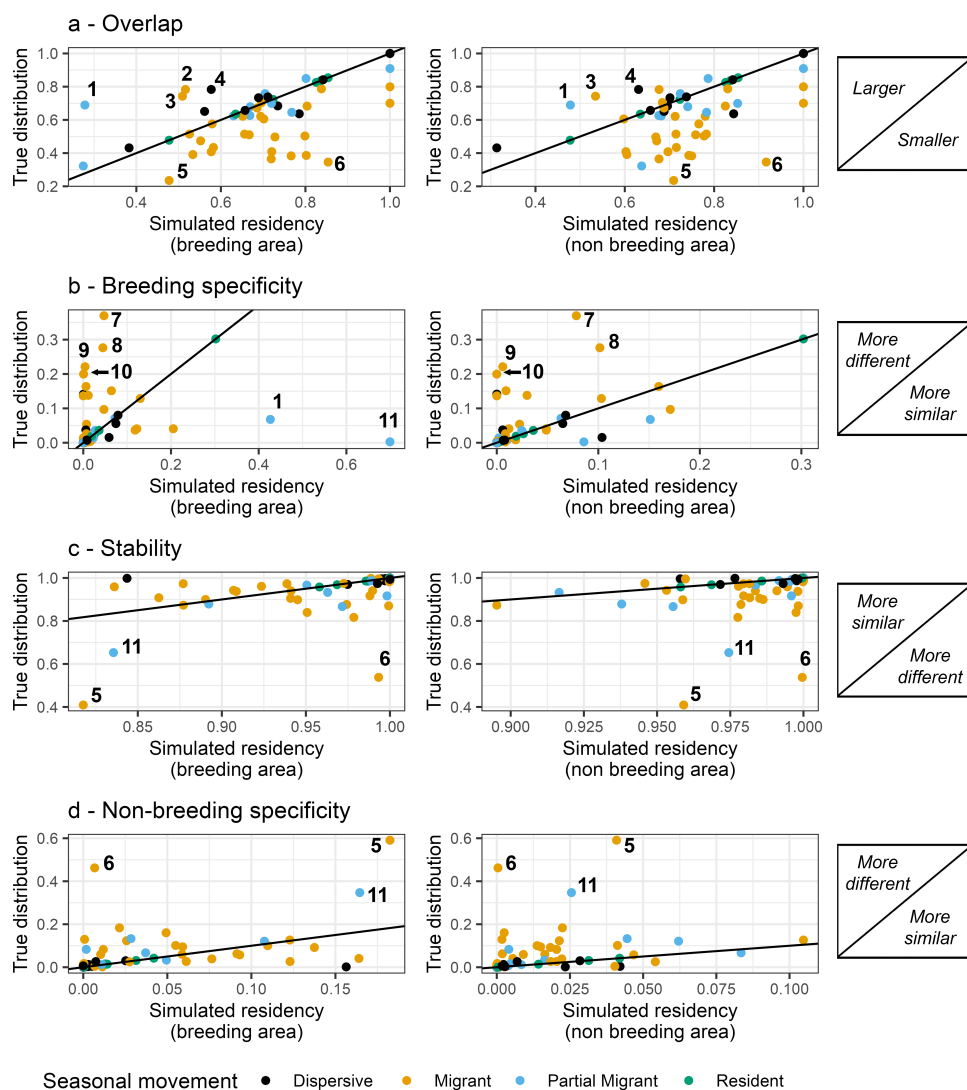


Figure 6. Relationship between observed niche (true distribution) and simulated niche (left: simulated residency in breeding area; centre: simulated residency in non-breeding area). (a) - Overlap of seasonal niches: species occurring above the line display stronger overlap in the observed distribution than under simulated residency (right panel). (b) - Breeding niche specificity: species occurring above the line have conditions encountered during the breeding period that differ more from conditions encountered during the non-breeding period than under simulated residency (right panel). (c) - Stability of seasonal niches: species occurring below the line have conditions encountered during the non-breeding period that differ more from conditions encountered during the breeding period than under simulated residency (right panel). (d) - Non-breeding niche specificity: species occurring above the line have conditions encountered during the non-breeding period that differ more from conditions encountered during the breeding period than under simulated residency (right panel). Some species displaying contrasting behaviours are specified: 1 - Yelkouan shearwater (*Puffinus yelkouan*); 2 - Chatham albatross (*Thalassarche eremita*); 3 - Black-footed albatross (*Phoebastria nigripes*); 4 - Barolo shearwater (*Puffinus baroli*); 5 - Antarctic prion (*Pachyptila desolata*); 6 - Slender-billed prion (*Pachyptila belcheri*); 7 - Sooty shearwater (*Ardenna grisea*); 8 - Short-tailed shearwater (*Ardenna tenuirostris*); 9 - Black-legged kittiwake (*Rissa tridactyla*); 10 - Christmas frigatebird (*Fregata andrewsi*); 11 - Balearic shearwater (*Puffinus mauretanicus*).