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1 **Meeting Paris agreement objectives will temper seabird winter distribution**  
2 **shifts in the North Atlantic Ocean**

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68 **Abstract**

69 We explored the implications of reaching the Paris Agreement Objective of limiting  
70 global warming to <2°C for the future winter distribution of the North Atlantic seabird  
71 community. We predicted and quantified current and future winter habitats of five North  
72 Atlantic Ocean seabird species (*Alle alle*, *Fratercula arctica*, *Uria aalge*, *Uria lomvia* and  
73 *Rissa tridactyla*) using tracking data for ~1500 individuals through resource selection  
74 functions based on mechanistic modeling of seabird energy requirements, and a dynamic  
75 bioclimate envelope model of seabird prey. Future winter distributions were predicted to shift  
76 with climate change, especially when global warming exceed 2°C under a “no mitigation”  
77 scenario, modifying seabird wintering hotspots in the North Atlantic Ocean. Our findings  
78 suggest that meeting Paris agreement objectives, will limit changes in seabird selected habitat  
79 location and size in the North Atlantic Ocean during the 21<sup>st</sup> century. We thereby provide key  
80 information for the design of adaptive marine protected areas in a changing ocean.

81 **Keywords:** DBEM, Energy requirement, Mechanistic habitat selection, NicheMapper <sup>TM</sup>,  
82 Paris Agreement, RCP scenarios, Seabird migration, Seabird distributions

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90           The main target of the 2015 Paris Agreement under the United Nations Framework  
91 Convention on Climate Change (UNFCCC) is to limit temperature increase to less than 2°C  
92 above preindustrial levels at the global scale (United Nations Framework Convention on  
93 Climate Change (UNFCCC), 2015). Recent studies have demonstrated the potential benefits  
94 of this target for marine ecosystems (Sumaila et al., 2019; Trisos et al., 2020) but its relevance  
95 and our capacity to reach the Paris Agreement Objectives (PAO) are still being debated  
96 (Gasser, Guivarch, Tachiiri, Jones, & Ciais, 2015). Notably, there are few estimates of these  
97 benefits for marine top predators (but see Jenouvrier et al., 2020) despite their key roles in  
98 marine ecosystem functioning and their support to cultural ecosystem services  
99 (Hammerschlag et al., 2019). It is therefore essential to examine the possible effects of  
100 climate change on these species and the interest of avoiding such climate impacts.

101 Seabirds are among the most threatened of all bird groups (Dias et al., 2019), with  
102 demonstrated sensitivity to direct (through physiological modifications or change in extreme  
103 events exposure) and indirect (through trophic mechanisms or modifications of their critical  
104 habitats) climate change impacts (Sydeman, Poloczanska, Reed, & Thompson, 2015).  
105 Seabirds are also ecological sentinels of marine ecosystems across their life cycles (Durant et  
106 al., 2009; Lescroël et al., 2016), and the subject of long-term monitoring studies throughout  
107 the world (Paleczny, Hammill, Karpouzi, & Pauly, 2015). Yet, because of technological  
108 limitations and practical difficulties, most of these studies dealing with climate change  
109 impacts on seabirds focus on population processes (Descamps et al., 2017) or on their  
110 responses during the breeding season (Frederiksen, Anker-Nilssen, Beaugrand, & Wanless,  
111 2013), rather than climate change impacts on their at-sea distributions during the non-  
112 breeding period. This is critical since conditions encountered during the non-breeding period  
113 strongly shape seabird population dynamics (Alves et al., 2013). Knowledge of climate effects  
114 on seabird wintering distributions is therefore essential for global marine spatial planning and

115 conservation schemes. Community-wide analyses allowing direct comparison between  
116 species and providing a more complete picture of climate change impacts are then particularly  
117 valuable.

118 In this context, we explored the implications of succeeding or failing to reach the Paris  
119 Agreement Objective of limiting global warming to  $<2^{\circ}\text{C}$  on the North Atlantic Ocean seabird  
120 community distribution, during the non-breeding period (October-February). We used Global  
121 Location Sensors (GLS) to track the inter-breeding movements of five species across the  
122 North Atlantic Ocean and adjacent seas (see the map of the studied area in Supplemental  
123 materials I) and then modeled seabird energy requirement and seabird prey fields for each  
124 location. Mechanistic Resource Selection Functions (RSF) allowed us to determine how the  
125 balance between prey availability and energy requirements explained seabird winter habitat  
126 selection at the time of our investigations. Based on those mechanistic RSFs, we predicted  
127 current seabird community distributions during winter and determined the location and the  
128 size of selected habitats for each species before projecting them to the time periods 2045-2055  
129 and 2090-2100. To this aim, we used two greenhouse gas concentration pathways: the  
130 Representative Concentration Pathway RCP2.6 and RCP8.5, which correspond to low and  
131 high radiative forcing, respectively. While RCP8.5 is often qualified as a “no mitigation”  
132 scenario, RCP2.6 assumes strong mitigation policies under which global warming is projected  
133 to be on average  $<2^{\circ}\text{C}$  relative to preindustrial levels (Meinshausen et al., 2006; Vuuren et al.,  
134 2011). Overall, comparing current and future distributions and size of selected habitats, we  
135 tested the hypothesis that limiting greenhouse gas emissions will reduce community-level  
136 seabird winter habitat change in the North Atlantic Ocean.

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139 **Methods**

140 *Winter geolocation of the North Atlantic Ocean seabird community*

141 We focused on the five species which represent >75% of the total number of seabirds  
142 breeding in the North Atlantic Ocean and adjacent seas (Barrett et al., 2006): little auk (*Alle*  
143 *alle*), Atlantic puffin (*Fratercula arctica*), Brünnich's guillemot (*Uria lomvia*), common  
144 guillemot (*Uria aalge*) and black-legged kittiwake (*Rissa tridactyla*). Despite the major focus  
145 on the Alcidae seabird family and the Charadriiformes order, this sample included species  
146 with a wide range of prey species and foraging behaviors (del Hoyo, Elliott, & Sargatal,  
147 1996). Global Location Sensors (GLS) recording year-round locations were deployed and  
148 retrieved on 1532 individuals from 39 breeding colonies across the North Atlantic Ocean  
149 during summer fieldwork (see Supplemental materials XII for details). Each GLS tag  
150 recorded light levels, which were used to calculate two locations per day with an accuracy of  
151 +/- 200 km (Lisovski et al., 2012; Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004).  
152 Different models of GLS tags were used, and the raw light data were analyzed with  
153 corresponding software (see Supplemental materials XII for detail); some of these data were  
154 previously analyzed in other studies (Amélineau et al., 2018; Fayet et al., 2017; Fort et al.,  
155 2013; Fort et al., 2013; Frederiksen et al., 2016, 2011; Linnebjerg et al., 2013; McFarlane  
156 Tranquilla et al., 2015; Merkel, 2019; Montevecchi et al., 2012; Tranquilla et al., 2013). We  
157 kept locations acquired during the winter period (October-February) and erroneous locations  
158 obtained during the two weeks around either side of the equinoxes (Lisovski et al., 2012)  
159 and/or those falling on land or outside of the study area (100°W–100°E, 30°N–90°N) were  
160 removed.

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163 *Modeling current and future energyscapes*

164 We used the mechanistic model Niche Mapper <sup>TM</sup> (Porter & Mitchell, 2006) to model the  
165 current and future energy expenditures for each species across the North Atlantic Ocean basin  
166 for each wintering month (October-February). This model contains two sub-modules: a  
167 microclimate model, which provides environmental data for the near surroundings of the  
168 animal at each location, and an animal module, which uses outputs from the microclimate  
169 model, together with animal morphological, behavioral and physiological characteristics.  
170 These inputs are used to solve heat balance equations between the animal's body and its  
171 environment, and to find the metabolic rate needed for the animal to maintain its body  
172 temperature at the particular time with the considered behavior.

173 Environmental data (sea surface temperature, air temperature, wind speed, cloud cover and  
174 relative humidity) used to parameterize the microclimate model were selected from the  
175 outputs of the Earth system model HadGEM2-ES (Collins et al., 2011; Martin et al., 2011).  
176 This climatic model includes different components (troposphere, land surface and hydrology,  
177 aerosols, ocean, sea ice, terrestrial carbon cycle and ocean biogeochemistry) which are  
178 coupled on a 24h time-step with an atmospheric resolution of 1.875°x1.25° and an oceanic  
179 resolution of 1° (increasing to 1/3° at the equator) (Collins et al., 2011). We used HadGEM2-  
180 ES outputs because empirical data were not available for all of our study areas, precluding the  
181 calculation of global energyscapes (spatialized energy requirements). Also, HadGEM2-ES has  
182 been shown to perform well when simulating recent and past mechanisms such as deep  
183 convection in North Atlantic Ocean (Heuzé, 2017), North-West Atlantic Ocean physical  
184 process (Lavoie, Lambert, ben Mustapha, & Baaren, 2013), Arctic sea ice melt (Wang &  
185 Overland, 2012) and North-East Atlantic Ocean climatology (Perez, Menendez, Mendez, &  
186 Losada, 2014; Zappa, Shaffrey, & Odges, 2013). Relative humidity was calculated following

187 Nadeau & Puiggali (1995) and Nayar et al. (2016). Daily data were averaged to obtain  
188 monthly means and were interpolated in a 1° grid.

189 As Niche Mapper™ has already been parameterized to model energy expenditure in little  
190 auks, Brünnich's guillemots and common guillemots (Fort et al., 2013; Fort, Porter, &  
191 Grémillet, 2009), we re-used most Niche Mapper™ input values from these previous studies.  
192 Missing values and values required to parameterize Niche Mapper™ for black-legged  
193 kittiwakes and Atlantic puffins, were sourced from the literature (see Supplemental materials  
194 XIII) and supplemented with dedicated measurements. Notably, feather reflectivity was  
195 measured with a double beam spectrophotometer (CARY 5000 UV-VIS-NIR, Agilent, USA)  
196 with a deuterium-tungsten-mercury light source. We used an integrative sphere to measure  
197 spectral and diffuse reflectance with a 1 nm resolution across all wavelengths between 300  
198 and 2500 nm. This range covers approximately 98% of the solar spectrum that reaches the  
199 Earth's surface. Reflectance spectra relative to a Spectralon white standard were then  
200 computed with the Cary WinUV software. For each species, measurements were made on one  
201 ventral and dorsal patch for six individuals. We then calculated the reflectivity of each sample  
202 following the same method as in Medina et al (Medina et al., 2018). For each species the  
203 results were averaged across patches.

204 Other morphological properties such as leg length, as well as head and body diameters, were  
205 measured on bird carcasses of five Atlantic puffins and four black-legged kittiwakes. Since  
206 Niche Mapper has relatively low sensitivity with respect to the variables concerned by such  
207 measurements (Amélineau et al., 2018; Fort et al., 2009), potential biases induced by using  
208 such measurements on carcasses instead of live organisms had limited impacts on our results.

209 All input data are available in Supplemental materials XIII. Main drivers of the modeled  
210 energy requirements were identified through sensitivity analysis in previous studies  
211 (Amélineau et al., 2018; Fort et al., 2009).

212 *Modeling current and future seabird prey abundance*

213 We identified the main winter prey of each seabird species using bibliographic information  
214 (see Supplemental materials XIV for details). Little auks and black-legged kittiwakes are  
215 mainly zooplanktivorous during winter. Other studied species are assumed to lower their  
216 trophic level outside the breeding season but could still prey on Nereid worms and on various  
217 benthopelagic/pelagic fish such as Atlantic herring (*Clupea harengus*), capelin (*Mallotus*  
218 *villosus*), Atlantic cod (*Gadus morhua*) or lesser sand-eel (*Ammodytes marinus*).

219 We modeled the relative abundance of fish species to 1950 across the North Atlantic Ocean,  
220 using a Dynamic Bioclimate Envelope Model (DBEM) (Cheung et al., 2016, 2009). The  
221 DBEM simulates changes in abundance of marine fishes since 1950 according to  
222 oceanographic conditions. For each fish species considered, habitat suitability was modeled  
223 according to temperature, salinity, dissolved oxygen concentration, bathymetry and sea-ice  
224 extent. These environmental preferences were then linked to a population model which takes  
225 into account the carrying capacity of the habitat, growth, mortality, and larval and adult  
226 dispersion. DBEM outputs are annual averages but, considering the very large spatial scale  
227 and resolution of our study, we assumed that relative abundance patterns were maintained at  
228 the scale of months and that the winter period changes can be reflected in the annual  
229 projections.

230 Fish characteristics required as inputs to the DBEM model (see Cheung et al., 2016) for  
231 details) were obtained from the Sea Around Us catch database (<http://www.seaaroundus.org>)  
232 and from FishBase (<https://www.fishbase.se/search.php>). Environmental data needed for  
233 current and future modeling (see Supplemental materials XV for details) were obtained from  
234 the Earth system model HadGEM2-ES (Collins et al., 2008; Martin et al., 2011). We used  
235 HadGEM2-ES because empirical environmental data were not available at the right spatial  
236 and temporal scales. Equally, since empirical information on current and monthly spatial and

237 temporal abundances of each zooplankton species taken by seabirds was not available, we  
238 used the monthly total concentration of zooplankton provided by the ocean biogeochemical  
239 model, Diat-HadOCC, included within the Earth system model HadGEM2-ES to model the  
240 exchange of carbon dioxide between the atmosphere and the oceanic biosphere (Totterdell,  
241 2019). Zooplankton concentration is one of the 13 biogeochemical state variables represented  
242 by Diat-HadOCC, and is modeled as advected by ocean currents and mixed by physical  
243 processes. Zooplankton biomass is enhanced by grazing of miscellaneous phytoplankton,  
244 diatoms and detritus, and diminished by respiration and by density-dependent predation  
245 through higher trophic levels.

246 Finally, due to missing species-specific physiological data, the relative abundance of several  
247 fish species could not be calculated with DBEM (see Supplemental materials XIV for the list).  
248 According to FishBase, those fish are zooplanktivorous and are mainly benthopelagic. We  
249 therefore used bathymetry (using General Bathymetric Chart of the Oceans (GEBCO), 30 arc-  
250 second interval grid) and zooplankton concentration as a proxy of their availability to diving  
251 seabirds. All seabird prey data were interpolated in a 1° grid.

### 252 *Habitat selection of different seabird species*

253 To analyze seabird habitat use and predict current and future winter distributions, we used  
254 Resource Selection Functions (RSF) (Boyce & McDonald, 1999; Manly, McDonald, Thomas,  
255 McDonald, & Erickson, 2002). RSF compare environmental variables at locations used by the  
256 animal with those variables at a set of locations available to the animal (Manly, McDonald,  
257 Thomas, McDonald, & Erickson, 2007). In our case, RSF compared for each species the  
258 energy expenditure and prey availability at GLS locations with those expected at a set of  
259 random points generated in our study area (100°W–100°E, 30°N–90°N). The random points  
260 were created using the same temporal distribution as the GLS data. RSF were fitted using  
261 generalized linear mixed models with a binomial error distribution and a logit link. To take

262 into account individual heterogeneity and variation between colonies, we used a weighted  
263 logistic regression with random intercepts (individual and colony) and random slopes, with  
264 weight=1 for locations used and weight=1000 for available locations (Muff, Signer, &  
265 Fieberg, 2019). To avoid power issues that arise with random intercept, individuals with  
266 fewer than 100 locations (threshold obtained after a kernel stability analysis conducted with  
267 the BRB-MKDE software (Benhamou, 2011), March 2018 version) for the entire winter  
268 period were not included in the model.

269 For each species, we built a RSF model with month, energy expenditure and relative  
270 abundance of each prey as covariates. When computational issues or collinearity problems  
271 arose, we reduced model complexity by selecting the relative abundance of the prey most  
272 often eaten by the seabird species considered. We tested for the trade-off between main prey  
273 abundance and energy requirement by adding an interaction term between the two  
274 predictors. Moreover, when considered as seabird prey, zooplankton concentration was linked  
275 to sea surface temperature through an interaction term to allow selection of zooplankton  
276 species associated with cold or warm water. Finally, when bathymetry was considered as an  
277 availability proxy for some benthopelagic prey, we linked it to zooplankton concentration  
278 through an interaction term. We allowed non-linear effects for each covariate via a spline  
279 function. RSF models are detailed in Supplemental materials II.

280 Variables used in our final RSF analysis were scaled and were not correlated as tested with a  
281 Pearson pairwise correlation test and a variance inflation factor analysis ( $VIF < 3$  in all  
282 models). We evaluated each model using block cross-validation (Roberts et al., 2017) with  
283 80% of the data to fit the RSF and 20% to test it. The corresponding output (rated “k-fold rs”  
284 in Supplemental materials II) is based on the Spearman’s rank correlation (Boyce, Vernier,  
285 Nielsen, & Schmiegelow, 2002) and varies between 0 (low predictive performance) and 1

286 (good predictive performance). RSF analyses were performed in R (version 3.5) with the  
287 glmmTMB package (Brooks et al., 2017).

288 For each species, we mapped RSF results after splitting them in 10 quantile bins (Morris,  
289 Proffitt, & Blackburn, 2016). More than 60% of the GLS locations occurred in the 4 last bins,  
290 and we therefore defined selected habitat as pixels with a binned RSF score  $\geq 7$ . To identify  
291 wintering hotspots, we then summed, for each pixel of the map, the number of species for  
292 which the pixel considered was classified as a selected habitat. Finally, the area occupied by  
293 selected habitats were calculated.

#### 294 *Current and future predictions*

295 Current conditions were modeled with outputs from the HadGEM2-ES algorithm, according  
296 to the historical extended simulation (1950-2018). To assess the benefit of reaching the PAO  
297 and limiting temperature increase to the 2°C target at the global scale, environmental  
298 variables and models (see above) were considered under Intergovernmental Panel on Climate  
299 Change (IPCC)'s RCP2.6 and RCP8.5 scenarios at the medium term (2045-2055) and the  
300 longer term (2090-2100). The RCP2.6 scenario is based on a low radiative forcing and  
301 assumes that strong mitigation policies will limit global greenhouse gas emissions and reach  
302 the goal of negative emissions in the second half of the 21<sup>st</sup> century. Stabilization at this low  
303 level of emissions will limit global mean temperature increase to 2°C above preindustrial  
304 levels with high probability (Meinshausen et al., 2006). According to the HadGEM2-ES  
305 model, the global mean temperature increase will reach this 2°C threshold just before mid-  
306 century before slowly decreasing (Caesar et al., 2013). In contrast, the RCP8.5 scenario  
307 follows a high radiative forcing trajectory with a continuous increase in global greenhouse gas  
308 emissions across the 21st century. According to the HadGEM2-ES model, global mean  
309 temperature will increase  $>2.8^{\circ}\text{C}$  above preindustrial levels in 2050, and  $>6^{\circ}\text{C}$  in at the end of  
310 the 21<sup>st</sup> century (Caesar et al., 2013).

## 311 **Results**

### 312 Predictors of seabird distributions and current community wintering hotspots

313 All Resource Selection Functions (RSF) had high predictive power of species  
314 distributions (see “k-fold rs” in Supplemental materials II). Mechanistic RSF showed that  
315 seabirds selected winter habitat by balancing two major constraints: prey availability and their  
316 own energy requirements (see Figure 1 and Supplemental materials III). This trade-off was,  
317 nonetheless, best predicted by seabird energy requirements for all studied species (see  
318 Supplemental materials III).

319 **Figure 1:** The trade-off between zooplankton concentration and bird energy requirements predicts  
320 little auk habitat selection. An optimum was reached at a scaled energy requirement of -0.6 and a  
321 scaled zooplankton concentration of 1.3. See Supplemental materials III for other species.

322 Species-specific selected habitat was defined using a threshold approach on the developed  
323 RSF's (see Methods for details). These habitats were in turn combined to identify multi-  
324 species wintering hotspots (sensu (Fort, Beaugrand, Grémillet, & Phillips, 2012; Grecian et  
325 al., 2016)) by counting for each pixel of the map, the number of species for which the pixel  
326 considered was classified as a selected habitat. Given seabird energy requirements and prey  
327 availability (see Supplemental III and IV), birds were predicted to use areas off southwestern  
328 Iceland and along the Norwegian coast between October and November, while the Gulf of  
329 Maine was predicted to be a major wintering hotspot for the selected seabird community  
330 between December and February (Figure 2 and Supplemental materials V). At the beginning  
331 of the winter period, the southern coast of Greenland and the Barents Sea were predicted to be  
332 important areas for the seabird community. Yet, between December and February, the  
333 HadGEM2-ES climatic model showed scarce zooplankton resources to seabirds at those high-  
334 latitudes (see Supplemental materials IV), and the areas were then predicted to be used only  
335 by the two guillemot species (Figure 2 and Supplemental materials V). Further, the area off  
336 Newfoundland and Nova Scotia was predicted to be a wintering hotspot between October and

337 January, but the composition of the seabird community varied with the month considered:  
338 little auks and black-legged kittiwakes were joined by Atlantic puffins between October and  
339 December, and by Brünnich's guillemots between November and January (Figure 2 and  
340 Supplemental materials V). Finally, the Mid-Atlantic Ocean and the North Sea were predicted  
341 to be selected by black-legged kittiwakes, little auks and Atlantic puffins between November  
342 and February, but those species were also predicted to aggregate in the eastern Celtic Sea in  
343 January and in the Bay of Biscay in February (Figure 2 and Supplemental materials V).

344 **Figure 2:** Count of species for which the pixel considered was a selected habitat (RSF binned score  
345  $\geq 7$ ), in October (a), November (b), December (c), January (d) and February (e). Graticules are  
346 displayed at  $15^\circ$  intervals and the map is projected as North Pole Lambert Azimuthal Equal Area.

347 Climate change impacts on seabird distribution and selected habitat size

348 Modeled spatial trends of future selected habitats for seabird were generally similar under  
349 RCP2.6 and RCP8.5 scenarios. However, the magnitude of projected impacts on seabird  
350 biogeography was generally more pronounced under the higher CO<sub>2</sub> emission scenario  
351 (RCP8.5) and towards the end of the 21<sup>st</sup> century (Figure 3 and 4, Supplemental materials X  
352 and XI). Moreover, our projections showed that climate change is predicted to modify prey  
353 availability and seabird energy requirements (see Supplemental materials VI and VII),  
354 inducing loss and gain of selected habitats and resulting in a general northward shift of  
355 wintering areas (see Figure 3 and Supplemental materials VIII and IX).

356 **Figure 3:** Selected habitat (in purple) of Brünnich's guillemots predicted for January in 2006-2015  
357 (a) and in 2090-2100 according to the RCP2.6 scenario (b) and the RCP8.5 scenario (c). Maps for  
358 other months, species and time periods (2045-2055) are provided in Supplemental materials VIII and  
359 IX. Graticules are displayed at  $15^\circ$  intervals and the map is projected as North Pole Lambert  
360 Azimuthal Equal Area.

361 **Figure 4:** Count of species for which the pixel considered is predicted to be a selected habitat in  
362 January 2006-2015 (a) and in January 2090-2100 according to the RCP2.6 scenario (b) and the  
363 RCP8.5 scenario (c). Maps for other months and time periods (2045-2055) are provided in  
364 Supplemental materials X and XI. Graticules are displayed at  $15^\circ$  intervals and the map is projected as  
365 North Pole Lambert Azimuthal Equal Area.

366



367 In October, all five seabird species were predicted to be present in the Labrador Sea and south  
368 of Greenland. The Barents Sea was predicted to remain an important seabird wintering site in  
369 October, but its attractiveness for black-legged kittiwakes, Brünnich's guillemots and little  
370 auks was predicted to diminish as global warming intensifies. Further, in November, seabirds  
371 were projected to shift towards areas off southern Greenland and in the Labrador Sea, where  
372 conditions were predicted to improve in terms of energy requirements and prey availability  
373 (see Supplemental materials VI and VII). Thereby, black-legged kittiwakes and little auks  
374 were expected to progressively abandon the Norwegian coast. At the seabird community  
375 level, marine areas east off Newfoundland and the Gulf of St Lawrence were predicted to  
376 become increasingly important as wintering hotspots (see Figure 4 and Supplemental  
377 materials X and XI). All considered species were predicted to aggregate in these areas in  
378 December, January and February, where the birds will probably benefit from lower energy  
379 requirements relative to present (see Supplemental materials VI and VII). During these  
380 months black-legged kittiwakes, little auks and Atlantic puffins were predicted to continue to  
381 winter in the mid-Atlantic Ocean, but the corresponding hotspots were predicted to shift  
382 northward/westward. The North Sea was predicted to become a preferred habitat in January,  
383 except under the RCP8.5 scenario at the end of the 21<sup>st</sup> century. For this time period and  
384 scenario, seabird energy requirements were predicted to remain unchanged in the North Sea,  
385 but prey availability was predicted to diminish (see Supplemental materials VII), leading to a  
386 decrease in overall habitat quality.

387 The projected biogeographic shifts will significantly impact seabird winter habitat sizes (see  
388 Figure 5). Selected habitats size was predicted to increase for common guillemots (for  
389 example, by 21% and 47% by 2045-2055 and up to 38% and 102% by 2090-2100, in January  
390 according to RCP2.6 and RCP8.5 scenarios, respectively). Between 2045 and 2055, selected  
391 habitat of Brünnich's guillemots was predicted to increase slightly (up to 32% in October

392 according to the RCP2.6 scenario) but the persisting temperature increase will probably limit  
393 this expansion and even lead to a reduction of selected habitat size for the RCP8.5 scenario.  
394 Change in selected habitat size was predicted to be limited for the Atlantic puffin (+/- 9% or  
395 less regardless of the time period and climatic scenario). For black-legged kittiwakes,  
396 predicted selected winter habitat will initially show little change in size (+/- 9% or less)  
397 between 2045 and 2055, except in October, during which the range will expand by ca. 20%  
398 according to both scenarios. Later in the 21<sup>st</sup> century, our results nonetheless suggest a strong  
399 reduction (up to 63% in October but around 22% for the rest of the winter period) in kittiwake  
400 winter habitat for the RCP8.5 scenarios. Finally, for little auks, winter habitat range was  
401 generally predicted to decline as global warming increases, except in October between 2045  
402 and 2055 when it will increase slightly relative to today.

403 **Figure 5:** Variation relative to present (in %) of the size of predicted selected habitat for (a) little  
404 auks (b) black-legged kittiwakes (c) Atlantic puffins (d) common guillemots (e) Brünnich's  
405 guillemots. The y-axis scales are different between panels.

## 406 **Discussion**

407 To our knowledge, our study is the first to investigate climate change impacts on the  
408 winter distribution of a seabird community at an ocean basin scale with a mechanistic  
409 approach. Our work predicts that global warming will likely induce substantial changes in  
410 seabird prey field distributions and spatialized energy requirements (energyscapes, sensu  
411 Amélineau et al., 2018). These two predictors of seabird habitat selection are predicted to  
412 strongly shape the location and size of seabird selected habitats in the North Atlantic Ocean  
413 during winter. Thereby, global warming will result in northward distribution shifts of varying  
414 magnitude, depending on the seabird species and considered time period. More specifically,  
415 areas such as Newfoundland, the Gulf of St Lawrence, and southern Greenland will become  
416 increasingly attractive as seabird wintering hotspots because of diminishing seabird energy  
417 requirements. Crucially, our broad-scale analyses confirms that meeting Paris Agreement

418 Objectives will limit habitat range shifts of the North Atlantic Ocean seabird community in  
419 21<sup>st</sup> century in comparison with shifts induced by a “no-mitigation” scenarios.

420 Despite these advances, we recommend caution in interpreting our results. First, since direct  
421 measurements of seabird prey availability and energy requirements are lacking at the spatio-  
422 temporal scales needed for a community-wide, ocean-basin-scale study, we used a variety of  
423 modeling tools to gain this information. Those entail potential approximations and biases  
424 which could be difficult to assess. For example, as most commonly-used biogeochemical  
425 models (Arhonditsis & Brett, 2004), the Diat-HadOCC biogeochemical model included  
426 within HadGEM2-ES has not been evaluated on its ability to model zooplankton  
427 concentration. However, considering its ability to model chlorophyll concentration, this model  
428 seems to respect geographical distribution and seasonal cycle of the carbon cycle in the North  
429 Atlantic Ocean (Totterdell, 2019). Further, due to some lack of information about seabird  
430 winter diets, we extrapolated available dietary information, using those for birds from a  
431 subsample of all colonies. In the same line, the availability of seabird prey was modeled  
432 without taking into account the impacts of fisheries. By altering the difference in relative prey  
433 abundance between locations used by seabirds and random points, fisheries could diminish  
434 the role of prey availability in modelled seabird habitat selection. Moreover, the availability of  
435 seabird prey was modeled on an annual basis and future works should add seasonal resolution  
436 to the DBEM analysis. However, considering the very large spatial scale and resolution of our  
437 study, we assumed that relative prey abundance patterns were maintained at the scale of  
438 months, and that changes occurring during the winter period were adequately reflected by  
439 annual projections. Further, we limited the complexity of RSF models, by only considering  
440 seabird energy requirements and relative prey abundances, omitting the roles of abiotic factors  
441 such as sea ice concentration or day length as well as biotic factors like competition, predation  
442 or costs of transport (linked with migratory distance from the breeding ground). Notably, day

443 length may have an incidence on foraging times, although seabird have shown surprising  
444 abilities to cope with the polar night (Ostaszewska, Balazy, Berge, & Johnsen, 2017).  
445 Moreover, by modeling future distributions, we assume that the statistical link between  
446 seabird distributions, their energyscapes and prey fields will hold across time (Grémillet &  
447 Charmantier, 2010). Finally, our approach is based on model stacking, but allows a better  
448 understanding and representation of ecological processes, translating interactions of  
449 organismal functional traits with their environment into key fitness components throughout  
450 the inclusion of mechanistic models into correlative Habitat Suitability Models. RSF analyses  
451 yielded high predictive power and accuracy, providing support to this approach. In this  
452 context, limitations of studies based on DBEM and NicheMapper<sup>TM</sup> have been previously  
453 described and positively rated (Cheung et al., 2009; Fort, Porter, & Grémillet, 2011),  
454 suggesting that our work can indeed provide valuable predictions.

455 *A mechanistic framework to predict wildlife distribution hotspots in a changing world*

456 On the basis of mechanistic and biodynamic model outputs, Resource Selection Functions  
457 allowed us to predict seabird wintering habitats. We thereby elaborated a general  
458 methodological framework which may be applied to the spatial ecology of any animal  
459 tracking environmental gradients and resources. With respect to the North Atlantic Ocean  
460 seabird community, we confirmed the great importance of areas such as the mid-Atlantic  
461 Ocean (Afonso et al., 2020; Barrett et al., 2006; Bennison, Jessopp, Bennison, & Jessopp,  
462 2015), the Barents Sea (Gabrielsen, 2009), the North Sea (Harris, Daunt, Newell, Phillips, &  
463 Wanless, 2010), the Icelandic coast (Garðarsson, 1999) and southwest Greenland (Boertmann,  
464 Lyngs, Merkel, & Mosbech, 2004), for wintering seabirds. We highlighted the importance of  
465 seabird energy requirements as predictor of winter habitat selection (Figure 1). Prey  
466 availability contributed to shape seabird distributions at finer spatial scales (Amélineau et al.,  
467 2018), but we modeled that habitat choice generally resulted from a trade-off between energy

468 requirements and prey availability, and was predicted to be explained by the former (see  
469 Figure 1 and Supplemental materials III). This result is in agreement with recent  
470 macroecological studies (Somveille, Rodrigues, & Manica, 2018), and the magnitude of the  
471 energy requirement/prey availability trade-off may explain marked inter-species differences in  
472 seabird winter habitat dynamics under the influence of climate change. Yet, for all species  
473 considered, global warming was predicted to induce a significant decrease in seabird winter  
474 energy requirements following similar geographical features (see Supplemental materials VI  
475 and VII). Therefore, observed inter-species differences appeared to be related to variation in  
476 prey availability. For zooplanktivorous species, the decrease in energy requirements at high  
477 latitude was not predicted to be accompanied by a zooplankton concentration increase, thus  
478 limiting the northward expansion of their wintering habitat. However, as the northward shift  
479 of zooplankton was sufficient to decrease the relative probability of selection at the southern  
480 margin of their range, little auks and black-legged kittiwakes were predicted to experience an  
481 overall decrease in their selected habitat size. Conversely, for both species of guillemots, the  
482 decrease in energy requirements in the high Arctic was predicted to be accompanied by an  
483 increase in the abundance of cod and capelin, thus greatly increasing the probability of habitat  
484 selection in large areas such as the Russian Arctic. Further, decreases in the abundance of cod  
485 and capelin in the southern part of guillemot ranges seemed to remain within a range of  
486 favorable values. Those may not impact the relative probability of selection there, resulting in  
487 an overall gain of selected habitat. Further work will nonetheless be necessary to fully  
488 understand population consequences of these changes (Carneiro et al., 2020). Finally, the  
489 greater amplitude of latitudinal shifts in the abundance of fish species, relative to zooplankton  
490 concentration observed in our study, may be explained by the different temporal scales  
491 (annual versus monthly) considered, and/or by the impacts of other factors beyond  
492 temperature (such as day length or sea ice concentration) at high latitudes. Those factors may

493 have a greater impact on the northward expansion of zooplankton than on fish latitudinal  
494 shifts.

#### 495 *Seabirds tracking climate change*

496 Latitudinal shifts in response to climate change have been predicted and observed for many  
497 marine organisms, including top predators (Cristofari et al., 2018), small pelagic fish (Perry,  
498 Low, Ellis, & Reynolds, 2005) and zooplankton (Beaugrand et al., 2019). The High Arctic is  
499 already colonized by many organisms which currently occur at lower latitudes (Fosheim et  
500 al., 2015), and a series of endemic species might become extinct. Even though birds may  
501 adjust their migratory behavior in response to climate change (Visser, Perdeck, van Balen, &  
502 Both, 2009), seabirds generally seem to not shift their reproductive timing according to  
503 warmer ocean temperatures (Keogan et al., 2018), and remain extremely faithful to their  
504 breeding sites (Newton, 2010). Therefore, we speculate that the North Atlantic Ocean seabird  
505 community might be under pressure from climate change consequences through two main  
506 mechanisms. During the breeding season, site fidelity tends to expose seabird breeders to  
507 spatio-temporal mismatches with their food base and lead them into ecological traps (Durant,  
508 Hjernmann, Ottersen, & Stenseth, 2007; Grémillet et al., 2008). During the non-breeding  
509 season, even though there might be some fidelity to wintering sites, we might predict that  
510 seabirds will be more likely to track environmental conditions and shift spatio-temporally,  
511 following a trade-off between their energy requirements and prey availability. As a  
512 consequence, there is a strong potential for shifts in distances and/or directions between  
513 seabird breeding and wintering sites, which will reshape migratory corridors and locations of  
514 stopover sites (Newton, 2010; Clairbaux et al., 2019). Assessing and quantifying these  
515 changes in response to global warming for each colony will provide a better understanding of  
516 their magnitude, and of consequences for individual populations. Moreover, shifts in marine  
517 ecosystem composition and structure caused by global warming likely require seabirds to

518 change their diets and behaviours (Amélineau et al., 2019). The ability of seabirds to cope  
519 with such shifts, and the mechanisms (plasticity and/or microevolution) that underpin  
520 potential responses, are difficult to assess without long-term studies based on individual  
521 monitoring (Teplitsky & Charmantier, 2019). As long-lived organisms, we nonetheless expect  
522 that seabirds are more likely to respond through plasticity, rather than microevolution, when  
523 facing the consequences of climate change (Sauve, Divoky, & Friesen, 2019). Therefore,  
524 reaching Paris Agreement Objectives will decrease the risk that distribution discrepancies  
525 between seabirds and their prey arise and will also make it more likely that environmental  
526 shifts remain within the limits of seabird plastic responses (Descamps et al., 2017).

#### 527 *Conservation implications*

528 Global warming is one of the four most serious threats to seabirds, along with invasive  
529 species, bycatch, and overfishing of prey species (Dias et al., 2019; Grémillet et al., 2018). All  
530 of these challenges, which also compromise many other components of marine biodiversity,  
531 have to be urgently addressed. Restoring marine life may be feasible by 2050 if major  
532 pressures, such as global warming, are mitigated (Duarte et al., 2020) and, as our analysis  
533 shows, reaching PAO will be an effective way to mitigate climate change impacts on the  
534 North Atlantic Ocean seabird community. Our analyses provide new information and methods  
535 to identify seabird wintering hotspots in the North Atlantic Ocean, and allow modeling future  
536 spatio-temporal dynamics and community alteration under the threat of climate change. This  
537 is key to defining and managing marine protected areas (MPAs), which have emerged as  
538 powerful means to protect entire ecosystems from overfishing and effects of bycatch for  
539 which seabirds function as ecological indicators and umbrella species (Pichegru, Grémillet,  
540 Crawford, & Ryan, 2010). In practice, a first essential step towards defining MPAs using  
541 seabird at sea-movement data is to map marine Important Bird and Biodiversity Areas  
542 (Donald et al., 2019) (IBA). Several IBAs/MPAs have already been identified in the North

543 Atlantic Ocean (see, <http://datazone.birdlife.org/site/mapsearch> and  
544 <http://www.mpatlas.org/map/mpas/> for respective maps), most of them in coastal areas, with  
545 the exception of the MPAs recently established within the OSPAR Convention (Charlie  
546 Gibbs, north of the Azores and Milne seamount complex areas). In this context, our analysis  
547 features an important contribution to the upcoming marine IBA/MPA network, as we  
548 predicted currently unprotected community-level seabird wintering hotspots off  
549 Newfoundland, southern Greenland, Iceland and in the Barents Sea. Furthermore, our work  
550 emphasizes that marine spatial planning involving IBAs/MPAs will have to be adaptive, with  
551 protected areas adjusted according to species range shifts under the impact of global changes.  
552 MPA benefits will be negatively impacted by climate change (Bruno et al., 2018; Trisos et al.,  
553 2020), and thus reaching Paris Agreement Objectives will help to maintain their effectiveness  
554 in the future. Our modeling work is a clear example of how community-level winter  
555 distributions of marine top predators are likely to shift in the North Atlantic Ocean, and we  
556 provide a complete methodological framework allowing the forecasting of such range shifts  
557 according to different climate change scenarios. Overall, we emphasize the effectiveness of  
558 Paris Agreement Objectives for the spatial management of seabird community under the  
559 impact of climate change, and of dynamic MPAs defined using track-based data on at-sea  
560 movements of seabirds and other marine top predators (Péron, Authier, & Grémillet, 2018).

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#### 579 **Author Contributions**

580 Conceived and designed the project: D.G., J.F, M.C. Software developers and data providers:  
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584 the data: M.C, W.C, P.M, N.C. Wrote the paper: M.C., D.G. All authors reviewed the  
585 manuscript.

#### 586 **Competing Interests statement**

587 No competing interests.

#### 588 **Data availability statement**

589 The datasets analyzed during this study are available from the corresponding author on  
590 reasonable request.

591

592

593 **Code availability statement**

594 The different R codes used during this study are available from the corresponding author on  
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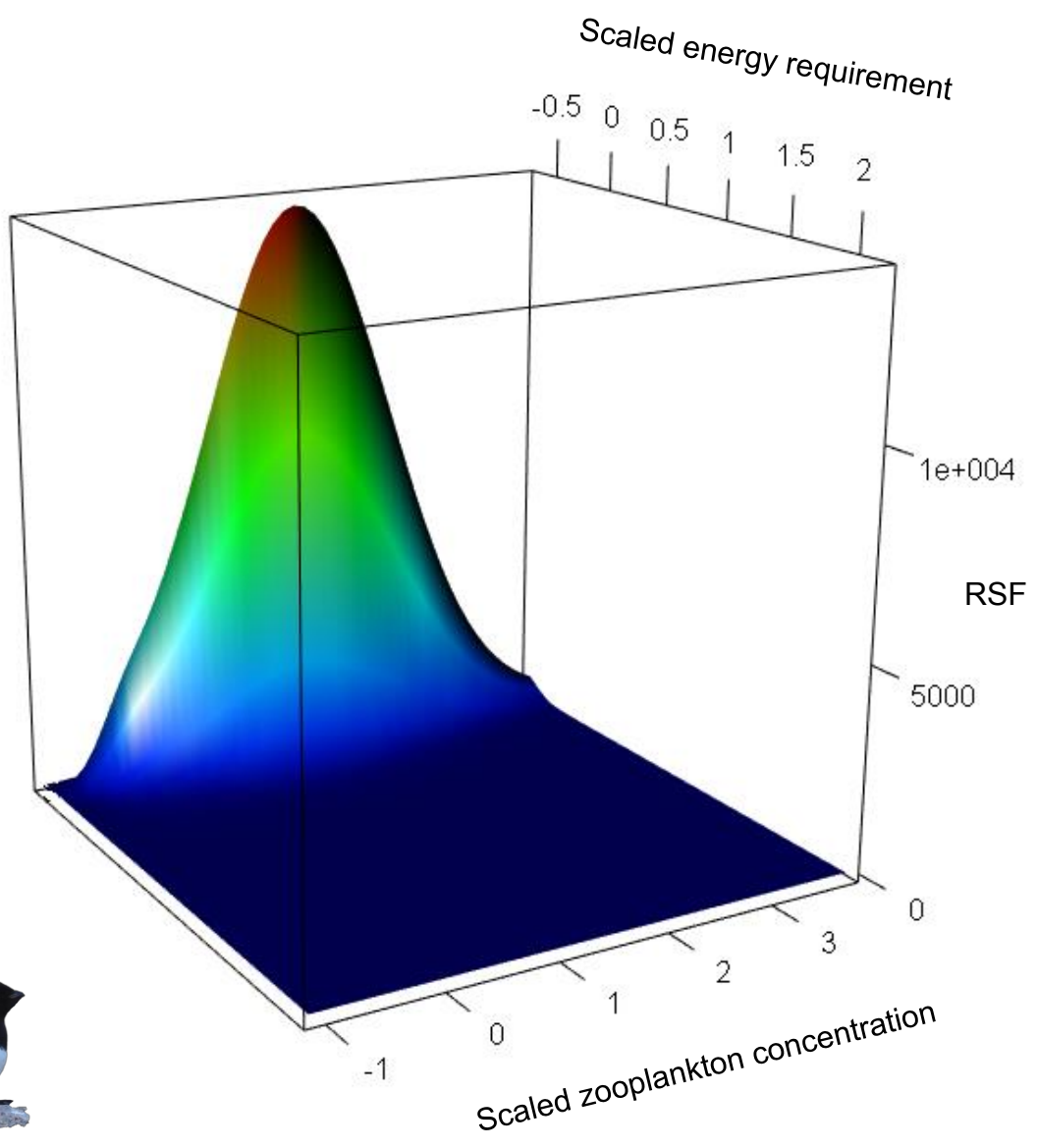
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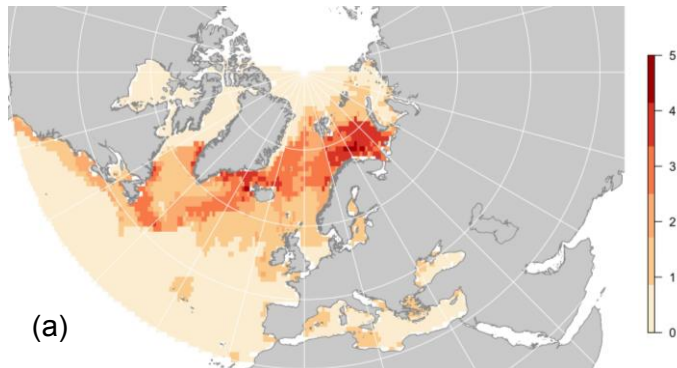
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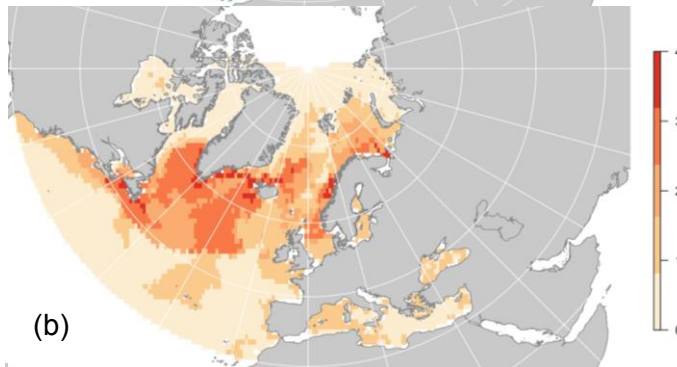
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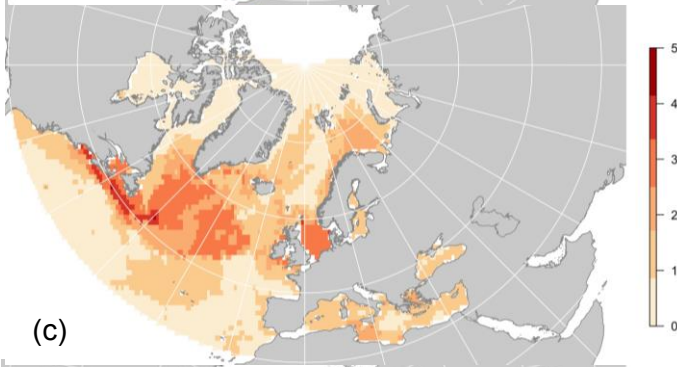
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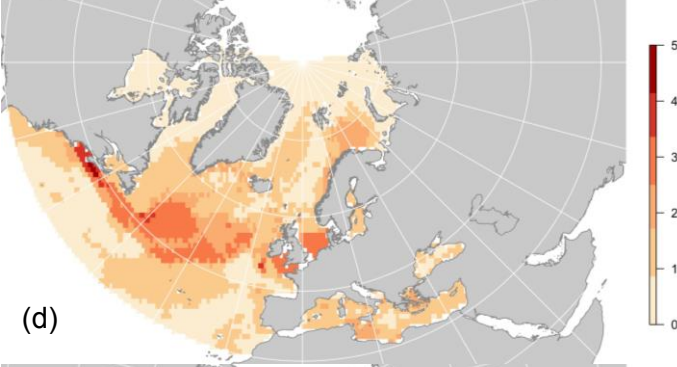
NOVEMBER



DECEMBER



JANUARY



FEBRUARY

