

# Meeting Paris agreement objectives will temper seabird winter distribution shifts in the North Atlantic Ocean

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#### Abstract

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

#### KEYWORDS

DBEM, energy requirement, mechanistic habitat selection, NicheMapper<sup>TM</sup>, Paris agreement, RCP scenarios, seabird distributions, seabird migration

## 1 | INTRODUCTION

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

Seabirds are among the most threatened of all bird groups (Dias et al., 2019), with demonstrated sensitivity to direct (through physiological modifications or change in extreme events exposure) and indirect (through trophic mechanisms or modifications of their critical habitats) climate change impacts (Sydeman et al., 2015). Seabirds are also ecological sentinels of marine ecosystems across their life cycles (Durant et al., 2009; Lescroël et al., 2016) and the subject of long-term monitoring studies throughout the world (Paleczny et al., 2015). Yet, because of technological limitations and practical

difficulties, most of these studies dealing with climate change impacts on seabirds focus on population processes (Descamps et al., 2017) or on their responses during the breeding season (Frederiksen et al., 2013), rather than climate change impacts on their at-sea distributions during the non-breeding period. This is critical since conditions encountered during the non-breeding period strongly shape seabird population dynamics (Alves et al., 2013). Knowledge of climate effects on seabird wintering distributions is therefore essential for global marine spatial planning and conservation schemes. Community-wide analyses allowing direct comparison between species and providing a more complete picture of climate change impacts are then particularly valuable.

In this context, we explored the implications of succeeding or failing to reach the Paris Agreement Objective of limiting global warming to  $<2^{\circ}\text{C}$  on the North Atlantic Ocean seabird community distribution, during the non-breeding period (October–February). We used Global Location Sensors (GLS) to track the inter-breeding movements of five species across the North Atlantic Ocean and adjacent seas (see the map of the studied area in Supplemental materials I) and then modeled seabird energy requirement and seabird prey fields for each location. Mechanistic Resource Selection Functions (RSF) allowed us to determine how the balance between prey availability and energy requirements explained seabird winter habitat selection at the time of our investigations. Based on those mechanistic RSFs, we predicted current seabird community distributions during winter and determined the location and the size of selected habitats for each species before

projecting them to the time periods 2045–2055 and 2090–2100. To this aim, we used two greenhouse gas concentration pathways: the Representative Concentration Pathway RCP2.6 and RCP8.5, which correspond to low and high radiative forcing, respectively. While RCP8.5 is often qualified as a “no mitigation” scenario, RCP2.6 assumes strong mitigation policies under which global warming is projected to be on average <2°C relative to preindustrial levels (Meinshausen et al., 2006; van Vuuren et al., 2011). Overall, comparing current and future distributions and size of selected habitats, we tested the hypothesis that limiting greenhouse gas emissions will reduce community-level seabird winter habitat change in the North Atlantic Ocean.

## 2 | METHODS

### 2.1 | Winter geolocation of the North Atlantic Ocean seabird community

We focused on the five species which represent >75% of the total number of seabirds breeding in the North Atlantic Ocean and adjacent seas (Barrett et al., 2006): little auk (*Alle alle*), Atlantic puffin (*Fratercula arctica*), Brünnich's guillemot (*Uria lomvia*), common guillemot (*Uria aalge*) and black-legged kittiwake (*Rissa tridactyla*). Despite the major focus on the Alcidae seabird family and the Charadriiformes order, this sample included species with a wide range of prey species and foraging behaviors (del Hoyo et al., 1996). Global Location Sensors (GLS) recording year-round locations were deployed and retrieved on 1532 individuals from 39 breeding colonies across the North Atlantic Ocean during summer fieldwork (see Supplemental materials XII for details). Each GLS tag recorded light levels, which were used to calculate two locations per day with an accuracy of ±200 km (Lisovski et al., 2012; Phillips et al., 2004). Different models of GLS tags were used, and the raw light data were analyzed with corresponding software (see Supplemental materials XII for detail); some of these data were previously analyzed in other studies (Amélineau et al., 2018; Fayet et al., 2017; Fort, Moe, et al., 2013; Fort, Steen, et al., 2013; Frederiksen et al., 2011, 2016; Linnebjerg et al., 2013; McFarlane Tranquilla et al., 2015; Merkel et al., 2019; Montevecchi et al., 2012; Tranquilla et al., 2013). We kept locations acquired during the winter period (October–February) and erroneous locations obtained during the 2 weeks around either side of the equinoxes (Lisovski et al., 2012) and/or those falling on land or outside of the study area (100°W–100°E, 30°N–90°N) were removed.

### 2.2 | Modeling current and future energyscapes

We used the mechanistic model Niche Mapper™ (Porter & Mitchell, 2006) to model the current and future energy expenditures for each species across the North Atlantic Ocean basin for each wintering month (October–February). This model contains two sub-modules: a microclimate model, which provides environmental data for the near surroundings of the animal at each location, and an animal module,

which uses outputs from the microclimate model, together with animal morphological, behavioral and physiological characteristics. These inputs are used to solve heat balance equations between the animal's body and its environment, and to find the metabolic rate needed for the animal to maintain its body temperature at the particular time with the considered behavior.

Environmental data (sea surface temperature, air temperature, wind speed, cloud cover and relative humidity) used to parameterize the microclimate model were selected from the outputs of the Earth system model HadGEM2-ES (Collins et al., 2011; Martin et al., 2011). This climatic model includes different components (troposphere, land surface and hydrology, aerosols, ocean, sea ice, terrestrial carbon cycle and ocean biogeochemistry) which are coupled on a 24 h time-step with an atmospheric resolution of 1.875° × 1.25° and an oceanic resolution of 1° (increasing to 1/3° at the equator; Collins et al., 2011). We used HadGEM2-ES outputs because empirical data were not available for all of our study areas, precluding the calculation of global energyscapes (spatialized energy requirements). Also, HadGEM2-ES has been shown to perform well when simulating recent and past mechanisms such as deep convection in North Atlantic Ocean (Heuzé, 2017), North-West Atlantic Ocean physical process (Lavoie et al., 2013), Arctic sea ice melt (Wang & Overland, 2012) and North-East Atlantic Ocean climatology (Perez et al., 2014; Zappa et al., 2013). Relative humidity was calculated following Nadeau and Puiggali (1995) and Nayar et al. (2016). Daily data were averaged to obtain monthly means and were interpolated in a 1° grid.

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

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

drivers of the modeled energy requirements were identified through sensitivity analysis in previous studies (Amélineau et al., 2018; Fort et al., 2009).

### 2.3 | Modeling current and future seabird prey abundance

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

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

Fish characteristics required as inputs to the DBEM model (see Cheung et al., 2016 for details) were obtained from the Sea Around Us catch database (<http://www.seaaroundus.org>) and from FishBase (<https://www.fishbase.se/search.php>). Environmental data needed for current and future modeling (see Supplemental materials XV for details) were obtained from the Earth system model HadGEM2-ES (Collins et al., 2008; Martin et al., 2011). We used HadGEM2-ES because empirical environmental data were not available at the right spatial and temporal scales. Equally, since empirical information on current and monthly spatial and temporal abundances of each zooplankton species taken by seabirds was not available, we used the monthly total concentration of zooplankton provided by the ocean biogeochemical model, Diat-HadOCC, included within the Earth system model HadGEM2-ES to model the exchange of carbon dioxide between the atmosphere and the oceanic biosphere (Totterdell, 2019). Zooplankton concentration is one of the 13 biogeochemical state variables represented by Diat-HadOCC, and is modeled as advected by ocean currents and mixed by physical processes. Zooplankton biomass is enhanced by grazing of miscellaneous phytoplankton, diatoms and detritus, and diminished by respiration and by density-dependent predation through higher trophic levels.

Finally, due to missing species-specific physiological data, the relative abundance of several fish species could not be calculated

with DBEM (see Supplemental materials XIV for the list). According to FishBase, those fish are zooplanktivorous and are mainly benthopelagic. We therefore used bathymetry (using General Bathymetric Chart of the Oceans [GEBCO], 30 arc-second interval grid) and zooplankton concentration as a proxy of their availability to diving seabirds. All seabird prey data were interpolated in a 1° grid.

### 2.4 | Habitat selection of different seabird species

To analyze seabird habitat use and predict current and future winter distributions, we used Resource Selection Functions (RSF; Boyce & McDonald, 1999; Manly et al., 2002). RSF compare environmental variables at locations used by the animal with those variables at a set of locations available to the animal (Manly et al., 2007). In our case, RSF compared for each species the energy expenditure and prey availability at GLS locations with those expected at a set of random points generated in our study area (100°W–100°E, 30°N–90°N). The random points were created using the same temporal distribution as the GLS data. RSF were fitted using generalized linear mixed models with a binomial error distribution and a logit link. To take into account individual heterogeneity and variation between colonies, we used a weighted logistic regression with random intercepts (individual and colony) and random slopes, with weight = 1 for locations used and weight = 1000 for available locations (Muff et al., 2019). To avoid power issues that arise with random intercept, individuals with fewer than 100 locations (threshold obtained after a kernel stability analysis conducted with the BRB-MKDE software (Benhamou, 2011; March 2018 version) for the entire winter period were not included in the model.

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

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

RSF analyses were performed in R (version 3.5) with the *glmmTMB* package (Brooks et al., 2017).

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

## 2.5 | Current and future predictions

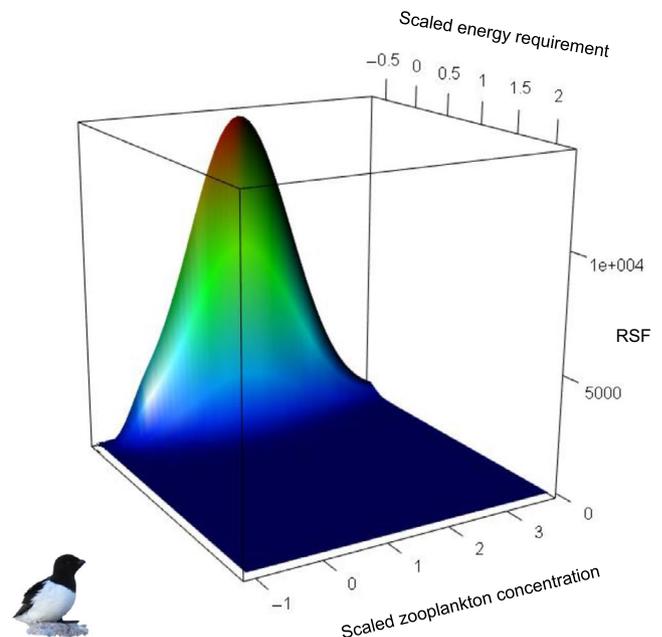
Current conditions were modeled with outputs from the HadGEM2-ES algorithm, according to the historical extended simulation (1950–2018). To assess the benefit of reaching the PAO and limiting temperature increase to the 2°C target at the global scale, environmental variables and models (see above) were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

## 3 | RESULTS

### 3.1 | Predictors of seabird distributions and current community wintering hotspots

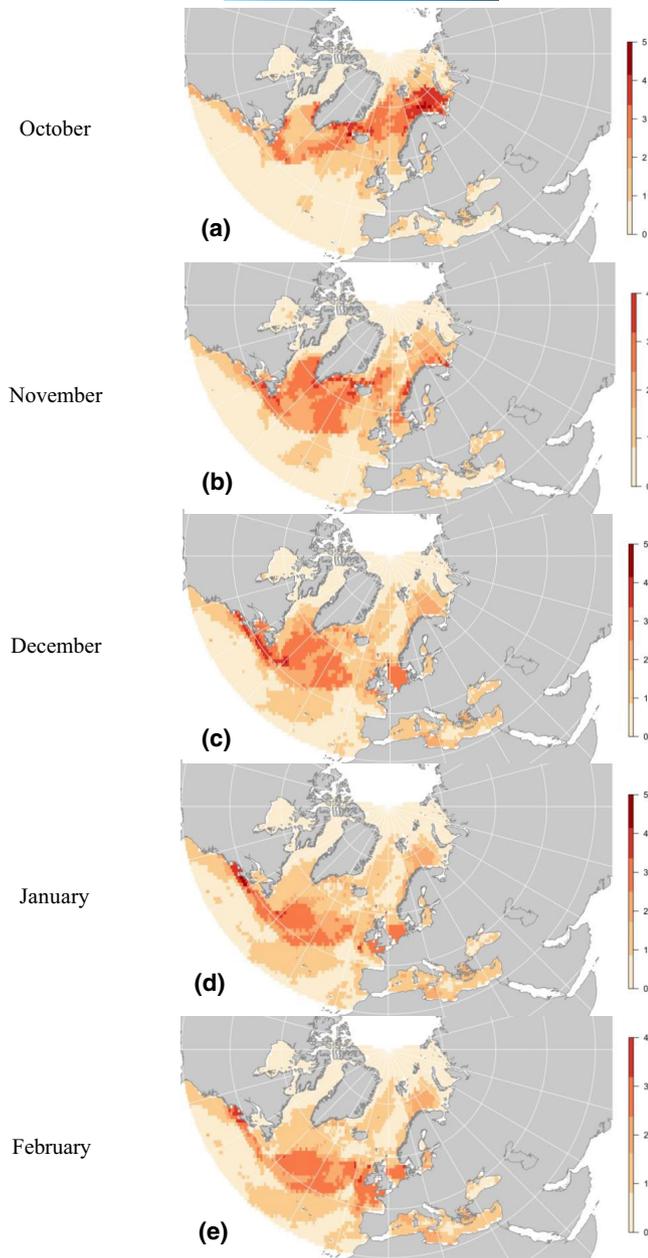
All Resource Selection Functions (RSF) had high predictive power of species distributions (see “k-fold rs” in Supplemental materials II). Mechanistic RSF showed that seabirds selected winter habitat by balancing two major constraints: prey availability and their own energy requirements (see Figure 1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

Species-specific selected habitat was defined using a threshold approach on the developed RSFs (see Section 2 for details). These



**FIGURE 1** The trade-off between zooplankton concentration and bird energy requirements predicts little auk habitat selection. An optimum was reached at a scaled energy requirement of  $-0.6$  and a scaled zooplankton concentration of  $1.3$ . See Supplemental materials III for other species [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

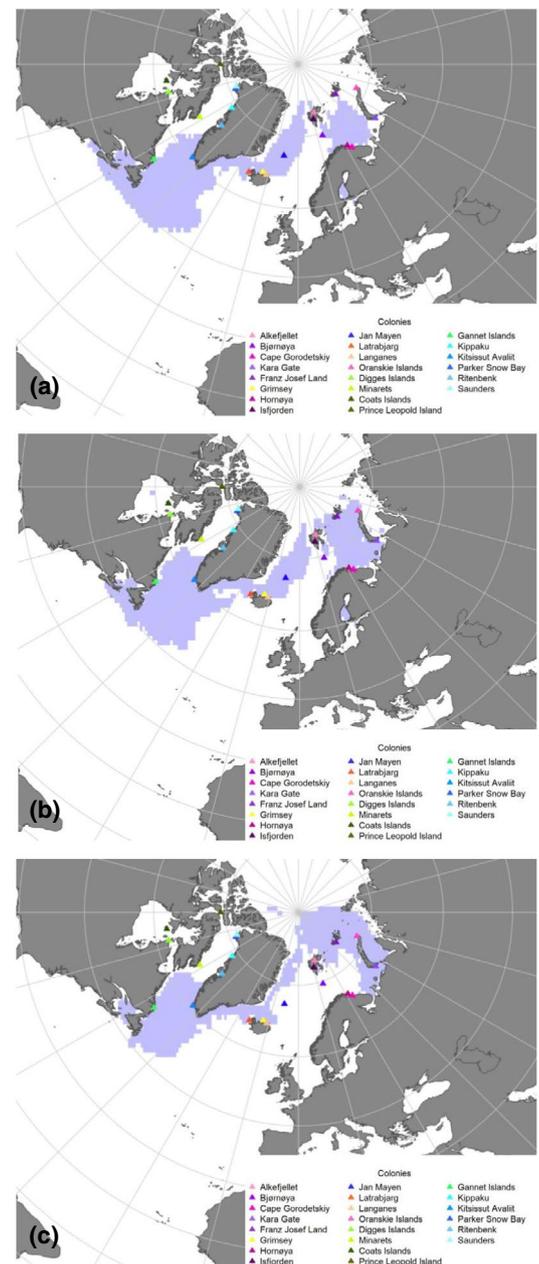
habitats were, in turn, combined to identify multi-species wintering hotspots (sensu Fort et al., 2012; Grecian et al., 2016)) by counting for each pixel of the map, the number of species for which the pixel considered was classified as a selected habitat. Given seabird energy requirements and prey availability (see Supplemental III and IV), birds were predicted to use areas off southwestern Iceland and along the Norwegian coast between October and November, while the Gulf of Maine was predicted to be a major wintering hotspot for the selected seabird community between December and February (Figure 2 and Supplemental materials V). At the beginning of the winter period, the southern coast of Greenland and the Barents Sea was predicted to be important areas for the seabird community. Yet, between December and February, the HadGEM2-ES climatic model showed scarce zooplankton resources to seabirds at those high latitudes (see Supplemental materials IV), and the areas were then predicted to be used only by the two guillemot species (Figure 2 and Supplemental materials V). Furthermore, the area off Newfoundland and Nova Scotia was predicted to be a wintering hotspot between October and January, but the composition of the seabird community varied with the month considered: little auks and black-legged kittiwakes were joined by Atlantic puffins between October and December, and by Brünnich's guillemots between November and January (Figure 2 and Supplemental materials V). Finally, the Mid-Atlantic Ocean and the North Sea were predicted to be selected by black-legged kittiwakes, little auks and Atlantic puffins between November and February, but those species were also predicted to aggregate in the eastern Celtic Sea in January and in the Bay of Biscay in February (Figure 2 and Supplemental materials V).



**FIGURE 2** Count of species for which the pixel considered was a selected habitat (RSF binned score  $\geq 7$ ), in October (a), November (b), December (c), January (d) and February (e). Graticules are displayed at  $15^\circ$  intervals and the map is projected as North Pole Lambert Azimuthal Equal Area [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3.2 | Climate change impacts on seabird distribution and selected habitat size

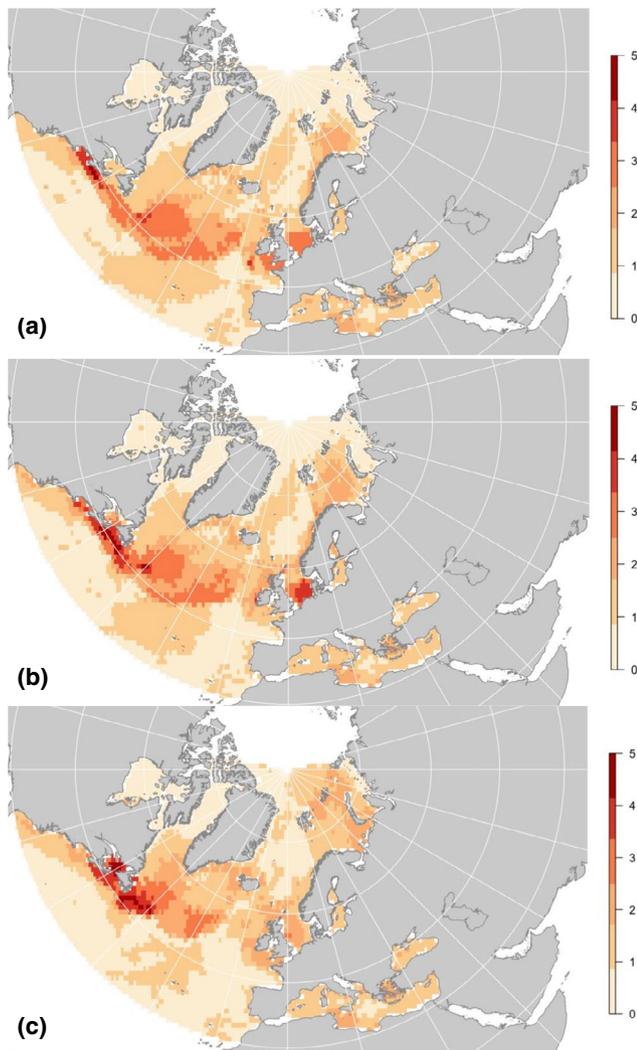
Modeled spatial trends of future selected habitats for seabird were generally similar under RCP2.6 and RCP8.5 scenarios. However, the magnitude of projected impacts on seabird biogeography was generally more pronounced under the higher  $\text{CO}_2$  emission scenario (RCP8.5) and toward the end of the 21st century (Figures 3 and 4; Supplemental materials X and XI). Moreover, our projections showed that climate change is predicted to modify prey availability



**FIGURE 3** Selected habitat (in purple) of Brünnich's guillemots predicted for January in 2006–2015 (a) and in 2090–2100 according to the RCP2.6 scenario (b) and the RCP8.5 scenario (c). Maps for other months, species and time periods (2045–2055) are provided in Supplemental materials VIII and IX. Graticules are displayed at  $15^\circ$  intervals and the map is projected as North Pole Lambert Azimuthal Equal Area [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

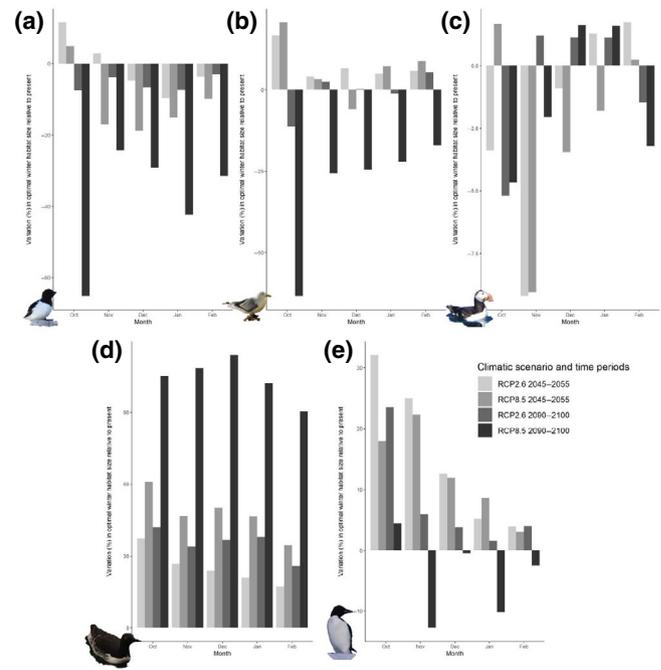
and seabird energy requirements (see Supplemental materials VI and VII), inducing loss and gain of selected habitats and resulting in a general northward shift of wintering areas (see Figure 3 and Supplemental materials VIII and IX).

In October, all five seabird species were predicted to be present in the Labrador Sea and south of Greenland. The Barents Sea was predicted to remain an important seabird wintering site in October, but its attractiveness for black-legged kittiwakes, Brünnich's guillemots and little auks was predicted to diminish as global warming



**FIGURE 4** Count of species for which the pixel considered is predicted to be a selected habitat in January 2006–2015 (a) and in January 2090–2100 according to the RCP2.6 scenario (b) and the RCP8.5 scenario (c). Maps for other months and time periods (2045–2055) are provided in Supplemental materials X and XI. Graticules are displayed at 15° intervals and the map is projected as North Pole Lambert Azimuthal Equal Area [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

intensifies. Furthermore, in November, seabirds were projected to shift toward areas off southern Greenland and in the Labrador Sea, where conditions were predicted to improve in terms of energy requirements and prey availability (see Supplemental materials VI and VII). Thereby, black-legged kittiwakes and little auks were expected to progressively abandon the Norwegian coast. At the seabird community level, marine areas east off Newfoundland and the Gulf of St Lawrence were predicted to become increasingly important as wintering hotspots (see Figure 4 and Supplemental materials X and XI). All considered species were predicted to aggregate in these areas in December, January and February, where the birds will probably benefit from lower energy requirements relative to present (see Supplemental materials VI and VII). During these months, black-legged kittiwakes, little auks and Atlantic puffins were predicted to



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

continue to winter in the mid-Atlantic Ocean, but the corresponding hotspots were predicted to shift northward/westward. The North Sea was predicted to become a preferred habitat in January, except under the RCP8.5 scenario at the end of the 21st century. For this time period and scenario, seabird energy requirements were predicted to remain unchanged in the North Sea, but prey availability was predicted to diminish (see Supplemental materials VII), leading to a decrease in overall habitat quality.

The projected biogeographic shifts will significantly impact seabird winter habitat sizes (see Figure 5). Selected habitats size was predicted to increase for common guillemots (e.g., by 21% and 47% by 2045–2055 and up to 38% and 102% by 2090–2100, in January according to RCP2.6 and RCP8.5 scenarios, respectively). Between 2045 and 2055, selected habitat of Brünnich's guillemots was predicted to increase slightly (up to 32% in October according to the RCP2.6 scenario) but the persisting temperature increase will probably limit this expansion and even lead to a reduction of selected habitat size for the RCP8.5 scenario. Change in selected habitat size was predicted to be limited for the Atlantic puffin ( $\pm 9\%$  or less regardless of the time period and climatic scenario). For black-legged kittiwakes, predicted selected winter habitat will initially show little change in size ( $\pm 9\%$  or less) between 2045 and 2055, except in October, during which the range will expand by ca. 20% according to both scenarios. Later in the 21st century, our results nonetheless suggest a strong reduction (up to 63% in October but around 22% for the rest of the winter period) in kittiwake winter habitat for the RCP8.5 scenarios. Finally, for little auks, winter habitat range was generally predicted to decline as global warming increases, except in October between 2045 and 2055 when it will increase slightly relative to today.

## 4 | DISCUSSION

To our knowledge, our study is the first to investigate climate change impacts on the winter distribution of a seabird community at an ocean basin scale with a mechanistic approach. Our work predicts that global warming will likely induce substantial changes in seabird prey field distributions and spatialized energy requirements (energyscapes, sensu Amélineau et al., 2018). These two predictors of seabird habitat selection are predicted to strongly shape the location and size of seabird selected habitats in the North Atlantic Ocean during winter. Thereby, global warming will result in northward distribution shifts of varying magnitude, depending on the seabird species and considered time period. More specifically, areas such as Newfoundland, the Gulf of St Lawrence and southern Greenland will become increasingly attractive as seabird wintering hotspots because of diminishing seabird energy requirements. Crucially, our broad-scale analyses confirm that meeting Paris Agreement Objectives will limit habitat range shifts of the North Atlantic Ocean seabird community in 21st century in comparison with shifts induced by a “no-mitigation” scenarios.

Despite these advances, we recommend caution in interpreting our results. First, since direct measurements of seabird prey availability and energy requirements are lacking at the spatiotemporal scales needed for a community-wide, ocean-basin-scale study, we used a variety of modeling tools to gain this information. Those entail potential approximations and biases which could be difficult to assess. For example, as most commonly used biogeochemical models (Arhonditsis & Brett, 2004), the Diat-HadOCC biogeochemical model included within HadGEM2-ES has not been evaluated on its ability to model zooplankton concentration. However, considering its ability to model chlorophyll concentration, this model seems to respect geographic distribution and seasonal cycle of the carbon cycle in the North Atlantic Ocean (Totterdell, 2019). Furthermore, due to some lack of information about seabird winter diets, we extrapolated available dietary information, using those for birds from a subsample of all colonies. In the same line, the availability of seabird prey was modeled without taking into account the impacts of fisheries. By altering the difference in relative prey abundance between locations used by seabirds and random points, fisheries could diminish the role of prey availability in modeled seabird habitat selection. Moreover, the availability of seabird prey was modeled on an annual basis and future works should add seasonal resolution to the DBEM analysis. However, considering the very large spatial scale and resolution of our study, we assumed that relative prey abundance patterns were maintained at the scale of months, and that changes occurring during the winter period were adequately reflected by annual projections. Furthermore, we limited the complexity of RSF models, by only considering seabird energy requirements and relative prey abundances, omitting the roles of abiotic factors such as sea ice concentration or day length as well as biotic factors like competition, predation or costs of transport (linked with migratory distance from the breeding ground). Notably, day length may have an incidence on foraging times, although seabird have shown surprising abilities to cope with the polar night (Ostaszewska et al., 2017). Moreover, by modeling future distributions, we assume that the statistical link between

seabird distributions, their energyscapes and prey fields will hold across time (Grémillet & Charmantier, 2010). Finally, our approach is based on model stacking, but allows a better understanding and representation of ecological processes, translating interactions of organismal functional traits with their environment into key fitness components throughout the inclusion of mechanistic models into correlative Habitat Suitability Models. RSF analyses yielded high predictive power and accuracy, providing support to this approach. In this context, limitations of studies based on DBEM and NicheMapper™ have been previously described and positively rated (Cheung et al., 2009; Fort et al., 2011), suggesting that our work can indeed provide valuable predictions.

### 4.1 | A mechanistic framework to predict wildlife distribution hotspots in a changing world

On the basis of mechanistic and biodynamic model outputs, Resource Selection Functions allowed us to predict seabird wintering habitats. We thereby elaborated a general methodological framework which may be applied to the spatial ecology of any animal tracking environmental gradients and resources. With respect to the North Atlantic Ocean seabird community, we confirmed the great importance of areas such as the mid-Atlantic Ocean (Afonso et al., 2020; Barrett et al., 2006; Bennison et al., 2015), the Barents Sea (Gabrielsen, 2009), the North Sea (Harris et al., 2010), the Icelandic coast (Garðarsson, 1999) and southwest Greenland (Boertmann et al., 2004), for wintering seabirds. We highlighted the importance of seabird energy requirements as predictor of winter habitat selection (Figure 1). Prey availability contributed to shape seabird distributions at finer spatial scales (Amélineau et al., 2018), but we modeled that habitat choice generally resulted from a trade-off between energy requirements and prey availability, and was predicted to be explained by the former (see Figure 1 and Supplemental materials III). This result is in agreement with recent macroecological studies (Somveille et al., 2018), and the magnitude of the energy requirement/prey availability trade-off may explain marked inter-species differences in seabird winter habitat dynamics under the influence of climate change. Yet, for all species considered, global warming was predicted to induce a significant decrease in seabird winter energy requirements following similar geographic features (see Supplemental materials VI and VII). Therefore, observed inter-species differences appeared to be related to variation in prey availability. For zooplanktivorous species, the decrease in energy requirements at high latitude was not predicted to be accompanied by a zooplankton concentration increase, thus limiting the northward expansion of their wintering habitat. However, as the northward shift of zooplankton was sufficient to decrease the relative probability of selection at the southern margin of their range, little auks and black-legged kittiwakes were predicted to experience an overall decrease in their selected habitat size. Conversely, for both species of guillemots, the decrease in energy requirements in the high Arctic was predicted to be accompanied by an increase in the abundance of cod and capelin, thus greatly increasing the probability of habitat selection in large areas such as the Russian Arctic. Furthermore, decreases in the abundance

of cod and capelin in the southern part of guillemot ranges seemed to remain within a range of favorable values. Those may not impact the relative probability of selection there, resulting in an overall gain of selected habitat. Further work will nonetheless be necessary to fully understand population consequences of these changes (Carneiro et al., 2020). Finally, the greater amplitude of latitudinal shifts in the abundance of fish species, relative to zooplankton concentration observed in our study, may be explained by the different temporal scales (annual versus monthly) considered, and/or by the impacts of other factors beyond temperature (such as day length or sea ice concentration) at high latitudes. Those factors may have a greater impact on the northward expansion of zooplankton than on fish latitudinal shifts.

## 4.2 | Seabirds tracking climate change

Latitudinal shifts in response to climate change have been predicted and observed for many marine organisms, including top predators (Cristofari et al., 2018), small pelagic fish (Perry et al., 2005) and zooplankton (Beaugrand et al., 2019). The High Arctic is already colonized by many organisms which currently occur at lower latitudes (Fossheim et al., 2015), and a series of endemic species might become extinct. Even though birds may adjust their migratory behavior in response to climate change (Visser et al., 2009), seabirds generally seem to not shift their reproductive timing according to warmer ocean temperatures (Keogan et al., 2018), and remain extremely faithful to their breeding sites (Newton, 2010). Therefore, we speculate that the North Atlantic Ocean seabird community might be under pressure from climate change consequences through two main mechanisms. During the breeding season, site fidelity tends to expose seabird breeders to spatiotemporal mismatches with their food base and lead them into ecological traps (Durant et al., 2007; Grémillet et al., 2008). During the non-breeding season, even though there might be some fidelity to wintering sites, we might predict that seabirds will be more likely to track environmental conditions and shift spatiotemporally, following a trade-off between their energy requirements and prey availability. As a consequence, there is a strong potential for shifts in distances and/or directions between seabird breeding and wintering sites, which will reshape migratory corridors and locations of stopover sites (Clairbaux et al., 2019; Newton, 2010). Assessing and quantifying these changes in response to global warming for each colony will provide a better understanding of their magnitude, and of consequences for individual populations. Moreover, shifts in marine ecosystem composition and structure caused by global warming likely require seabirds to change their diets and behaviors (Amélineau et al., 2019). The ability of seabirds to cope with such shifts, and the mechanisms (plasticity and/or microevolution) that underpin potential responses are difficult to assess without long-term studies based on individual monitoring (Teplitsky & Charmantier, 2019). As long-lived organisms, we nonetheless expect that seabirds are more likely to respond through plasticity, rather than microevolution, when facing the consequences of climate change (Sauve et al., 2019). Therefore, reaching Paris Agreement Objectives will decrease the risk that distribution discrepancies between seabirds and their prey

arise and will also make it more likely that environmental shifts remain within the limits of seabird plastic responses (Descamps et al., 2017).

## 4.3 | Conservation implications

Global warming is one of the four most serious threats to seabirds, along with invasive species, bycatch and overfishing of prey species (Dias et al., 2019; Grémillet et al., 2018). All of these challenges, which also compromise many other components of marine biodiversity, have to be urgently addressed. Restoring marine life may be feasible by 2050 if major pressures, such as global warming, are mitigated (Duarte et al., 2020) and, as our analysis shows, reaching PAO will be an effective way to mitigate climate change impacts on the North Atlantic Ocean seabird community. Our analyses provide new information and methods to identify seabird wintering hotspots in the North Atlantic Ocean, and allow modeling future spatiotemporal dynamics and community alteration under the threat of climate change. This is key to defining and managing marine-protected areas (MPAs), which have emerged as powerful means to protect entire ecosystems from overfishing and effects of bycatch for which seabirds function as ecological indicators and umbrella species (Pichegru et al., 2010). In practice, a first essential step toward defining MPAs using seabird at sea-movement data is to map marine Important Bird and Biodiversity Areas (Donald et al., 2019; IBA). Several IBAs/MPAs have already been identified in the North Atlantic Ocean (see <http://datazone.birdlife.org/site/mapsearch> and <http://www.mpatlas.org/map/mpas/> for respective maps), most of them in coastal areas, with the exception of the MPAs recently established within the OSPAR Convention (Charlie Gibbs, north of the Azores and Milne seamount complex areas). In this context, our analysis features an important contribution to the upcoming marine IBA/MPA network, as we predicted currently unprotected community-level seabird wintering hotspots off Newfoundland, southern Greenland, Iceland and in the Barents Sea. Furthermore, our work emphasizes that marine spatial planning involving IBAs/MPAs will have to be adaptive, with protected areas adjusted according to species range shifts under the impact of global changes. MPA benefits will be negatively impacted by climate change (Bruno et al., 2018; Trisos et al., 2020), and thus reaching Paris Agreement Objectives will help to maintain their effectiveness in the future. Our modeling work is a clear example of how community-level winter distributions of marine top predators are likely to shift in the North Atlantic Ocean, and we provide a complete methodological framework allowing the forecasting of such range shifts according to different climate change scenarios. Overall, we emphasize the effectiveness of Paris Agreement Objectives for the spatial management of seabird community under the impact of climate change, and of dynamic MPAs defined using track-based data on at-sea movements of seabirds and other marine top predators (Péron et al., 2018).

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#### CONFLICT OF INTEREST

No competing interests.

#### AUTHOR CONTRIBUTION

Conceived and designed the project: D.G., J.F. and M.C. Software developers and data providers: W.P., P.M., J.F., H.S., B.M., P.F., S.D., H.H., V.S.B., B.M., T.A.-N., I.S.B., O.C., S.C.-D., J.D., F.D., N.D., K.E.E., A.E., M.G., Y.K., M.L., S.H.L., M.N., B.O., T.K.R., G.S., T.L.T., M.B., T.D., A.L.F., M.G.F., M.F., H.G.G., T.G., N.P.H., M.J., K.L.J., A.L.K., J.F.L., L.M.T., M.M., F.R.M., W.M., A.M., A.P. and D.G. Analyzed the data: M.C., W.C., P.M. and N.C. Wrote the paper: M.C. and D.G. All authors reviewed the manuscript.

#### DATA AVAILABILITY STATEMENT

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

#### CODE AVAILABILITY STATEMENT

The different R codes used during this study are available from the corresponding author on reasonable request.

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## SUPPORTING INFORMATION

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

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