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**THESE POUR OBTENIR LE GRADE DE DOCTEUR
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**Filière EFSA - Écologie Fonctionnelle et Sciences Agronomiques
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**ENERGETIC LANDSCAPES OF MIGRATORY SEABIRDS IN
THE NORTH ATLANTIC OCEAN IN A CONTEXT OF CLIMATE
CHANGE**

**Présentée par Manon CLAIRBAUX
Le 04 décembre 2020**

Sous la direction de David GREMILLET

Devant le jury composé de

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Børge MOE, Senior Research Scientist, NINA, Norway
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**UNIVERSITÉ
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“The irony is that just as the phenomenon of migration is slipping away, we are entering a golden age to study it”

David S. Wilcove

Abstract

Seabirds are particularly vulnerable to the direct and indirect effects of climate change, however little is known about those impacts outside of the breeding season. This lack of knowledge is problematic because the conditions encountered during migration and wintering strongly shape seabird population dynamics. It is therefore essential to understand the effects of climate on their winter distribution and migration routes. Linking the distribution of organisms to environmental factors is therefore a primary task benefiting from the concept of energyscapes (defined as the variation of an organism's energy requirements across space according to environmental conditions) which has recently provided a mechanistic explanation for the distribution of many animals. In this context, we have predicted the current and future winter habitats of five species representing 75% of the seabird community in the North Atlantic (*Alle alle*, *Fratercula arctica*, *Uria aalge*, *Uria lomvia* and *Rissa tridactyla*). To this aim, we monitored the movements of more than 1500 individuals to identify the birds' preferred habitats through resource selection functions based on the modeling of their energy expenditure and prey availability. Electronic tracking data were also overlaid with cyclone locations to map areas of high exposure for the seabird community across the North Atlantic. In addition, we explored the energetic consequences of seabird exposure to storms using a mechanistic bioenergetic model (Niche Mapper™). Finally, we examined the impact of total summer sea ice melt from 2050 on Arctic bird migration. Our analyses predict a northward shift in the preferred wintering areas of the North Atlantic seabird community, especially if global warming exceeds 2°C. Our results suggest that cyclonic conditions do not increase the energy requirements of seabirds, implying that they die from the unavailability of prey and/or inability to feed during cyclones. Finally, the melting sea ice at the North Pole may soon allow 29 species of Arctic birds to make new trans-Arctic migrations between the Atlantic and the Pacific. We also estimate that an additional 26 currently migratory species could remain in the Arctic year-round. This work illustrates how climate change could radically alter the biogeography of migratory species and we provide a methodological toolbox to assess and predict these changes by combining movement ecology and energetic physiology.

Keywords: Energyscape, Global change biology, Habitat selection, Marine birds, Migration, Oceanography, Spatial ecology

Résumé

Les oiseaux marins sont particulièrement vulnérables aux effets directs et indirects du changement climatique, cependant on sait peu de choses sur ces impacts en dehors de la période de reproduction. Ce manque de connaissances est problématique car les conditions rencontrées pendant la migration et l'hivernage déterminent fortement les dynamiques populationnelles des oiseaux marins. Il est donc essentiel de comprendre les effets du climat sur leurs distributions hivernales et leurs itinéraires de migration. Lier distribution des organismes et facteurs environnementaux est une tâche primordiale bénéficiant du concept de paysages énergétiques (défini comme la variation des besoins énergétiques d'un organisme dans l'espace en fonction de l'environnement) qui a récemment permis de fournir une explication mécaniste à la distribution de nombreux animaux. Dans ce contexte, nous avons déterminé les habitats hivernaux actuels et futurs de cinq espèces représentant 75% de la communauté d'oiseaux marins en Atlantique Nord (*Alle alle*, *Fratercula arctica*, *Uria aalge*, *Uria lomvia* and *Rissa tridactyla*). Pour cela, nous avons suivi électroniquement les mouvements de plus de 1500 individus afin d'identifier leurs habitats préférentiels par le biais de fonctions de sélection de ressources basées sur la modélisation de leurs dépenses énergétiques et de la disponibilité de leurs proies. Les données de suivi électroniques ont également été recoupées avec les emplacements des cyclones afin de cartographier les zones d'exposition pour la communauté d'oiseaux marins à l'échelle de l'Atlantique Nord. De plus, nous avons exploré les conséquences énergétiques de l'exposition des oiseaux marins aux tempêtes en utilisant un modèle bioénergétique mécaniste (Niche MapperTM). Enfin, nous avons examiné l'impact de la fonte totale de la banquise estivale à partir de 2050 sur la migration des oiseaux de l'Arctique. Nos analyses prévoient un déplacement vers le nord des zones préférentielles d'hivernage des oiseaux marins en Atlantique Nord, surtout si le réchauffement climatique mondial dépasse 2°C. Nos résultats suggèrent que les conditions cycloniques n'augmentent pas les besoins énergétiques des oiseaux marins, ce qui implique que l'indisponibilité des proies et/ou l'incapacité à se nourrir pendant les cyclones causeraient leur mort. Enfin, la fonte de la banquise au pôle nord pourrait permettre à 29 espèces d'oiseaux arctiques de bientôt effectuer de nouvelles migrations transarctiques entre l'Atlantique et le Pacifique. Nous estimons également que 26 autres espèces actuellement migratrices pourraient rester en Arctique toute l'année. Ce travail illustre comment les changements climatiques pourraient modifier radicalement la biogéographie des espèces migratrices et fournit une boîte à outils méthodologique permettant d'évaluer et de prévoir ces modifications en mariant écologie du mouvement et physiologie énergétique.

Mots-clés: Dépenses énergétiques, Biologie du changement global, Sélection d'habitat, Oiseaux marins, Migration, Océanographie, Ecologie spatiale

Papers, conferences and outreach

This thesis is based on the following papers:

Clairbaux M, Cheung W, Mathewson P, Porter W, Courbin N, Fort J, Strøm H, Moe B, Fauchald P, Descamps S, Helgason H, Bråthen V.S, Merkel B, Anker-Nilssen T, Bringsvor I.S, Chastel O, Christensen-Dalsgaard S, Danielsen J, Daunt F, Dehnhard N, Erikstad K.E, Ezhov A, Gavrilov M, Krasnov Y, Langset M, Lorentsen S.H, Newell M, Olsen B, Reiertsen T.K, Systad G, Thórarinnsson T.L, Baran M, Diamond T, Fayet A.L, Fitzsimmons M.G, Frederiksen M, Gilchrist H.G, Guilford T, Huffeldt N.P, Jessopp M, Johansen K.L, Kouwenberg A.L, Linnebjerg J.F, McFarlane Tranquilla L, Mallory M, Merkel F.R, Montevecchi W, Mosbech A, Petersen A, Grémillet D. **Meeting Paris agreement objectives will temper seabird winter distribution shifts in the North Atlantic Ocean.** Under Review in *Global Change Biology* . (Chapter II)

Clairbaux M, Fort J, Mathewson P, Porter W, Strøm H, Grémillet D. (2019). **Climate change could overturn bird migration: Transarctic flights and high-latitude residency in a sea ice free Arctic.** *Scientific Reports*, 9(1), 17767. doi:10.1038/s41598-019-54228-5 (Chapter III)

Clairbaux M, Mathewson P, Porter W, Fort J, Strøm H, Moe B, Fauchald P, Descamps S, Helgason H, Bråthen V.S, Merkel B, Anker-Nilssen T, Bringsvor I.S, Chastel O, Christensen-Dalsgaard S, Danielsen J, Daunt F, Dehnhard N, Erikstad K.E, Ezhov A, Gavrilov M, Krasnov Y, Langset M, Lorentsen S.H, Newell M, Olsen B, Reiertsen T.K, Systad G, Thórarinnsson T.L, Baran M, Diamond T, Fayet A.L, Fitzsimmons M.G, Frederiksen M, Gilchrist H.G, Guilford T, Huffeldt N.P, Jessopp M, Johansen K.L, Kouwenberg A.L, Linnebjerg J.F, McFarlane Tranquilla L, Mallory M, Merkel F.R, Montevecchi W, Mosbech A, Petersen A, Grémillet D. **North Atlantic Ocean winter storms starve seabirds.** In prep. (Chapter IV)

Ste Marie E, Grémillet D, Fort J, Brisson-Curadeau E, **Clairbaux M**, Perret S, Speakman J, Elliott K.H. **High dive costs in a small seabird disrupt the dynamic body acceleration – energy expenditure relationship.** Submitted to *Journal of Experimental Biology*. (Appendix I)

Conference and congresses:

Effets du changement climatique sur la migration et l'hivernage de la communauté d'oiseaux marins d'Atlantique Nord. **Clairbaux M**, Cheung W, Mathewson P, Porter W, Courbin N, Fort J, Strøm H, Moe B, Fauchald P, Descamps S, Helgason H, Bråthen V.S, Merkel B, Anker-Nilssen T, Bringsvor I.S, Chastel O, Christensen-Dalsgaard S, Danielsen J, Daunt F, Dehnhard N, Erikstad K.E, Ezhov A, Gavrilov M, Krasnov Y, Langset M, Lorentsen S.H, Newell M, Olsen B, Reiertsen T.K, Systad G, Thórarinnsson T.L, Baran M, Diamond T, Fayet A.L, Fitzsimmons M.G, Frederiksen M, Gilchrist H.G, Guilford T, Huffeldt N.P, Jessopp M, Johansen K.L, Kouwenberg A.L, Linnebjerg J.F, McFarlane Tranquilla L, Mallory M, Merkel F.R, Montevecchi W, Mosbech A, Petersen A, Grémillet D. November 2020. Colloque Migration. Visioconference

Climate change impacts on multi-species seabird wintering hotspots in the North Atlantic Ocean- An energyscape approach. **Clairbaux M**, Cheung W, Mathewson P, Porter W, Courbin N, Fort J, Strøm H, Moe B, Fauchald P, Descamps S, Helgason H, Bråthen V.S, Merkel B, Anker-Nilssen T, Bringsvor I.S, Chastel O, Christensen-Dalsgaard S, Danielsen J, Daunt F, Dehnhard N, Erikstad K.E, Ezhov A, Gavrilov M, Krasnov Y, Langset M, Lorentsen S.H, Newell M, Olsen B, Reiertsen T.K, Systad G, Thórarinnsson T.L, Baran M, Diamond T, Fayet A.L, Fitzsimmons M.G, Frederiksen M, Gilchrist H.G, Guilford T, Huffeldt N.P, Jessopp M, Johansen K.L, Kouwenberg A.L, Linnebjerg J.F, McFarlane Tranquilla L, Mallory M, Merkel F.R, Montevecchi W, Mosbech A, Petersen A, Grémillet D. Novembre 2019. SEATRACK Workshop. Visioconference

Future flights across the Arctic basin: Will climate change overturn bird migration? **Clairbaux M**, Fort J, Mathewson P, Porter W, Strøm H, Grémillet D. October 2018. International Conference on Ecological Science, SFE2, Rennes

Others activities: Teaching and science outreach

Reviewer for Marine Ecology Progress Series and PlosOne

Teaching integrative biology to first-year bachelor students through directed studies and practical works, University of Montpellier, (32h between October and December 2018)

Presentation of my thesis work to children during the French Polar week, APECS France (May 2019)

Presentation of my thesis work to a large audience during the "Fête de la Science" event (October 2019 / October 2020)

Participation to the "My thesis in comics" workshop organized by the doctoral college of Montpellier (November 2020)

Vanishing sea ice in the Arctic could shake up seabird migrations:
<https://news.mongabay.com/2019/12/vanishingsea-ice-could-shake-up-bird-migrations/>

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Samuel Perret

INTRODUCTION

I. Importance of migration and wintering periods for avian life cycles

1. Definition and overview

Animal migration usually refers to a regular round trip between two distinct locations, on a daily, seasonal or annual basis in response to temporal or geographic variations of resources availability and/ or predation risk (Dingle & Drake, 2007). Migrants take advantage of spaced and temporary suitable niches in order to maximize their fitness by increasing safety, as well as foraging and reproductive opportunities (Alerstam, Hedenström, & Åkesson, 2003; Avgar, Street, & Fryxell, 2014; Somveille, Rodrigues, & Manica, 2015). It concerns all branches of the animal kingdom (see Figure 1), from insects (Chapman, Reynolds, & Wilson, 2015), to large terrestrial or marine mammals (Naidoo et al., 2016; Stern, 2009), including birds (Newton, 2010), fish (Righton et al., 2016), crustaceans (Last et al., 2016), amphibians and reptiles (Russell, Bauer, & Johnson, 2005) as well as humans (Clark, 2020). Resulting trips often involve thousands of organisms, shaping the biogeography of ecological community networks on local, regional or global scales (Somveille, 2016). Moreover, along their routes, migrants modify consumers-resources interactions and play an important part in the transfers of nutrients, seeds and pathogens across widely spaced areas, altering community structure and ecosystem functions (Bauer & Hoye, 2014). Due to their ability to fly, birds are the most pre-adapted organisms for long distance migration (up to 30 000 km for the Arctic Tern (*Sterna paradisaea*) (Egevang et al., 2010)), making possible impressive journeys (see Figure 1) across oceans, deserts, sea ice and highest mountains (Adamík et al., 2016; Alerstam et al., 2007; Gill et al., 2009; Hawkes et al., 2011).

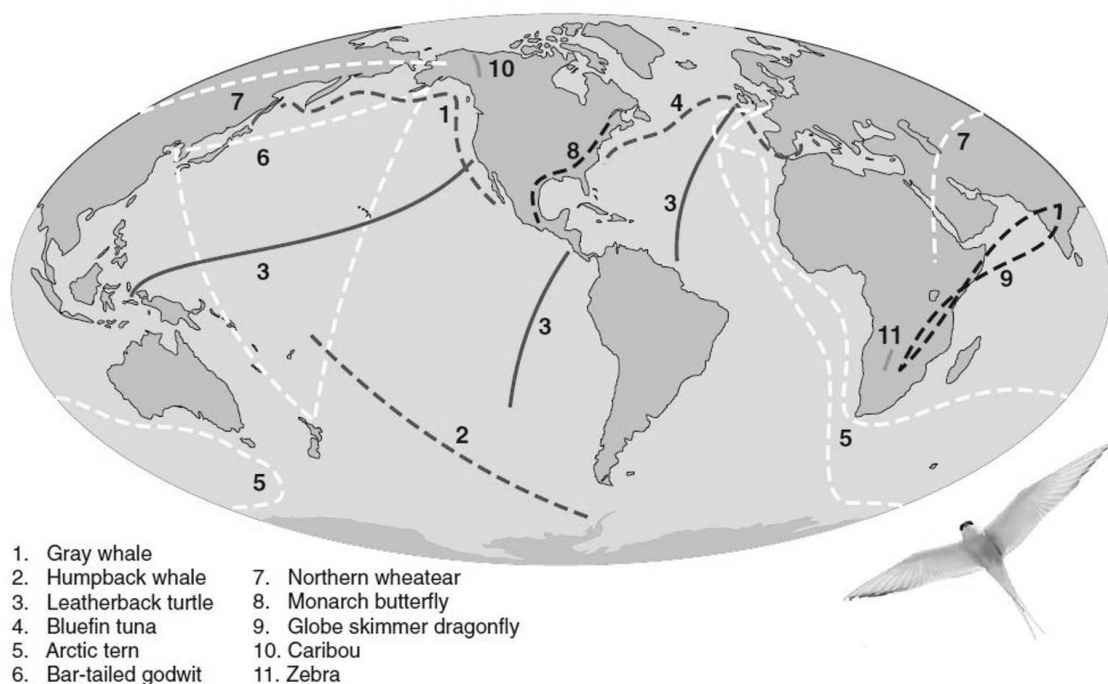


Figure 1. Record long-distance migrations. Source: Alerstam, T., & Bäckman, J. (2018). Ecology of animal migration. *Current Biology*, 28, 968–972. <https://doi.org/10.1016/j.cub.2018.04.043>

2. Bird migration

Bird migration generally corresponds to a regular movement between breeding and wintering grounds (Newton, 2010) that birds perform each year to maximize their fitness, being present at their breeding ground during the peak of resources abundance and absent in periods of scarcity (Somveille et al., 2015). As the breeding period is usually constrained in time by resources, the non-breeding period represents the bigger part of the avian annual cycle.

Seasonal appearances/disappearances of bird flocks has fascinated people for thousands of years (Aristotle, Book VIII, section 12; written 350 BCE and translated by Thompson, 1907). Migration was initially studied through direct observations and, since 1899, by ringing (Preuss, 2001): By individually marking birds and retrieving them at different places around the world, this technique provided first insights on movement patterns. Thereupon, migration research continued to progress along with new technological advances. After the Second World War, radars provided information regarding migration timing, speed, direction of flights, and on the influence of weather on bird migration (Alerstam & Gudmundsson, 1999; Anderson, 2013; Bruderer, 1997; Gauthreaux & Belser, 2003). In recent decades, miniaturization of radio/satellite transmitters and geolocation sensors allowed the massive equipment of specific individuals, providing data on migration routes, annual schedules and wintering grounds/stopovers locations for a growing number of species/populations (see for example Delmore, Fox, & Irwin, 2012). Therefore researchers widely used tracking data to study migratory connectivity (Finch, Butler, Franco, & Cresswell, 2017) and breeding/wintering sites fidelity (Wijk, Bauer, & Schaub, 2016), to identify hotspots where different species and/or populations aggregate (Yurkowski et al., 2018) and to define at the community level broad-scale movements patterns and flyways (see Figure 2).

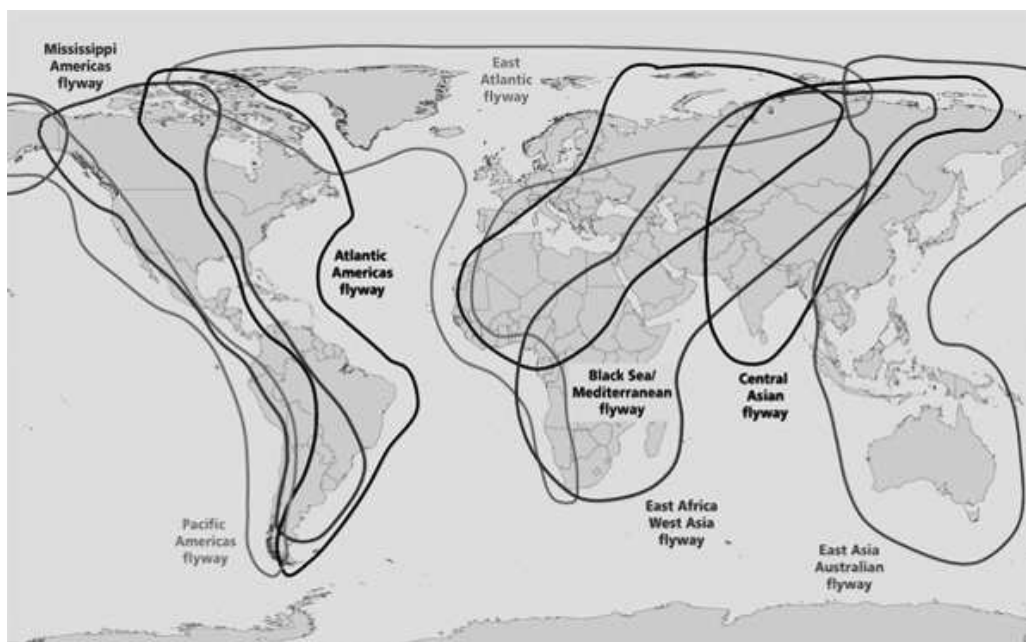


Figure 2. General flyways used by migratory shorebird species. Source: FAO/Wetlands International

Finally, laboratory experiments conducted on caged birds allowed a better understanding of migratory physiology, orientation and the importance of genetics for the migratory behavior (Åkesson, 2003). For example, manipulating day length and observing bird behavior, William Rowan concluded that the photoperiod triggers migration timing (1926) whereas recent studies shown that it is under both endogenous and extrinsic controls (Sokolov & Tsvey, 2016). Moving celestial sphere and geomagnetic field in cages confirmed the importance of such cues in bird orientation during migration (Åkesson & Bianco, 2017). Overall, these studies provide the opportunity to link migratory birds to their environment.

3. Vulnerability of migratory birds to environmental constraints

Migratory birds are currently declining at a faster rate than the sedentary ones (Robbins, Sauer, Greenberg, & Droege, 1989; Sanderson, Donald, Pain, Burfield, & Bommel, 2006). Contrary to their resident counterparts, migrants have to cope with environmental constraints across all their range, on their breeding and wintering grounds but also during their journeys and on molting and stopovers sites increasing the number of potential threats (Runge et al., 2015).

Seasonal variations of temperature, precipitations, day length, resources and habitats drive bird migrations (Newton, 2010) and natural selection favors individuals fitting the most with those drivers during their annual life cycle (see for example Reed, Jenouvrier, & Visser, 2013). Acting at both spatial and temporary scales, environmental constraints could change bird phenology (Cotton, 2003), distance of migration (Visser, Perdeck, van Balen, & Both, 2009) and population demography: Indeed, migratory strategies and environmental conditions experienced during winter, affecting adult survival and body conditions, could impact the following breeding success through carry-over effects (Alves et al., 2013). Conversely, breeding success could impact subsequent migration (Bogdanova et al., 2011). Moreover, many migrants are faithful to their breeding and/or wintering grounds, which could become ecological traps if the suitability of the areas changes across time (Mettke-Hofmann, 2016).

Most of the migratory birds mortality occurs during the non-breeding period (see for example Harris & Wanless, 1996), and identifying the different threats which occur during this time, and understand their effects is therefore crucial to protect migrants, especially when corridors, stopovers and wintering sites aggregate populations in few areas: Those areas are therefore particularly important and sometime irreplaceable for conservation purposes (Le Saout et al., 2013). Migratory birds are then particularly sensitive to loss of high-quality habitat (Bairlein, 2016), anthropogenic infrastructure (Loss, Will, & Marra, 2015), hunting pressure (Jiguet et al., 2019), extreme weather events (Newton, 2007) and climate change impacts (Robinson et al., 2009) which affect them simultaneously or at different spatial and temporary scales across their life cycle, potentially leading to deleterious cocktail effects.

II. Climate change, a supplementary threat to living organisms

1. Climate change at a global scale

The earth's climate has fluctuated between warming and glaciation eras, with a 100 000 years periodicity, linked to volcanic activities, plates tectonics, the earth's orbital position and solar activity (Zachos, Pagani, Sloan, Thomas, & Billups, 2001). However, since mid-19th century and the industrial revolution, the global temperatures increased at an alarming pace: According to the Intergovernmental Panel on Climate Change (IPCC), the global average surface temperature was $0.87 \pm 0.12^\circ\text{C}$ higher for the decade 2006-2015 than across the 1850-1900 time period (Masson-Delmotte et al., 2018). Surface temperatures observed during each of the last three decades were successively higher than any preceding decade since 1850 (Stocker et al., 2013). The global ocean has also warmed up since 1970, thereby storing >90% of the heat accumulated between 1971 and 2010 (Pörtner et al., 2019). Since 1993, it is likely that the rate of ocean warming has more than doubled (Pörtner et al., 2019). The ocean plays an important role in carbon cycle absorbing atmospheric CO₂ (Marinov & Sarmiento, 2004): With the increase in CO₂ emissions and the subsequent ocean absorption, the surface pH of the open ocean declined by a range of 0.017-0.027 per decade since 1990 (Pörtner et al., 2019). Further, the open oceans lost oxygen (between 0.5 and 3.3%) since 1970 (Pörtner et al., 2019) and sea level rose for 2006-2015 at an unprecedented rate of 3.6 mm.yr⁻¹ (Pörtner et al., 2019) mainly due to ice loss from the Greenland and Antarctic ice sheets (Pörtner et al., 2019). Arctic sea ice is also thinner and younger and decreased in volume for all months of the year between 1979 and 2018, with a maximal reduction of 12.8 ± 2.3 % per decade in September (Pörtner et al., 2019). Finally, changes in extreme weather events have been recorded since 1950: For example, the frequency of heat waves and heavy precipitation events increased in some regions and it is virtually certain that tropical cyclone activity has increased in the North Atlantic since 1970 (IPCC, 2014). Northern mid-latitude westerly winds also increase from the 1950s to the 1990s.

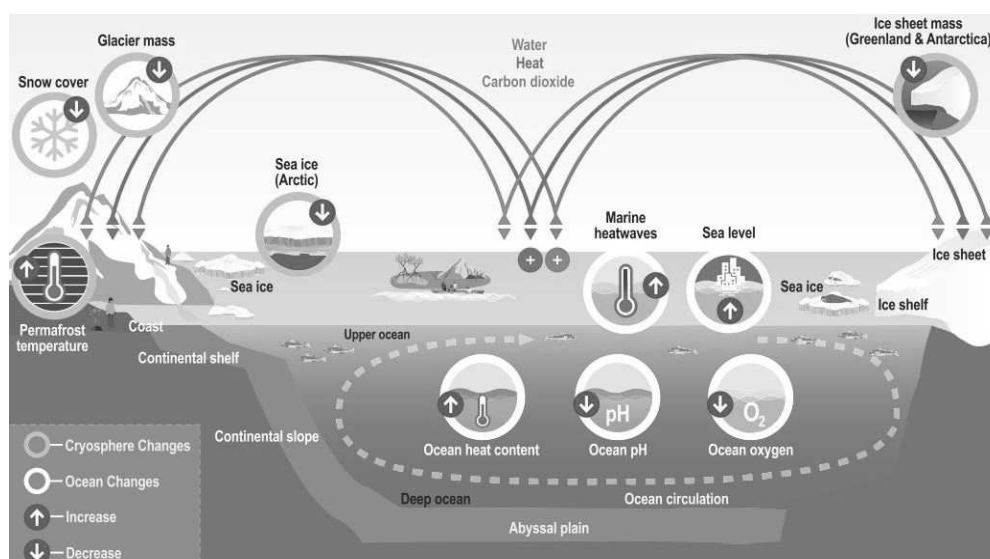


Figure 3. Schematic illustration of key components and changes occurring on ocean and cryosphere at a global scale. Source: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. 2019

2. Causes and future predictions

Changes in greenhouse gas and aerosols emissions, modifications in land uses but also natural variations in volcanic or solar activity alter the Earth's energy budget (IPCC, 2014). Perturbation of energy intake into the Earth system caused by those drivers is quantified by radiative forcing. Currently, this radiative budget is positive (3.1 W.m^{-2} in 2018, (see Annual Greenhouse Gas Index developed by Butler & Montzka (2013)), mainly caused by the increase in the atmospheric concentrations of CO_2 since 1750, leading to a global surface warming (IPCC, 2014). Indeed, anthropogenic emissions of gas and aerosols have increased since the pre-industrial period, to reach the highest level ever recorded from 2000 to 2010, due to economic and population growth (IPCC, 2014). Particularly, the total anthropogenic radiative forcing has increased more rapidly since 1970 than during prior decades (IPCC, 2014). This global positive radiative forcing is mainly due to anthropogenic activities and it is extremely likely that human influence is the dominant cause of observed warming since 1950 (IPCC, 2014). Further, roles of human activities have been detected in most of the climate changes described previously, such as ocean warming, reductions in snow and ice and global sea level rise (IPCC, 2014). Moreover, the warming caused by anthropogenic emissions since 1750 and its effects are predicted to persist for centuries to millennia (Masson-Delmotte et al., 2018). Anthropogenic impacts on climate are part of drastic modifications of the biosphere (Diaz et al., 2019) caused by humans since the industrial revolution in 1850, defining a new era, "the Anthropocene". Finally, to prevent climate change impacts on ecosystems (see below) and human societies, 190 policy-makers adopted the Paris Agreement Objectives in 2015, aiming to limit global warming under 2°C below pre-industrial level by 2100 (UNFCCC, 2015).

Climatic research progresses steadily, allowing a better understanding of the Earth's climate systems, and climatic models are more and more able to depict accurately climatic phenomena. Last generation models are Earth System Models (ESM) that simulate climate, taking into account physical, chemical and biological process (Heavens, Ward, & Natalie, 2013). Models are evaluated by assessing their ability to reproduce past or current conditions (Stocker et al., 2013): Some patterns such as global mean surface temperature are generally well described but some uncertainty remain for others variables (Stocker et al., 2013). Those models are particularly useful to predict future climate and the potential impact of those changes on ecosystems. Future predictions are currently based on Representative Concentration Pathways (RCPs) which correspond to four different scenarios that hypothesize future land uses, greenhouse gas and air pollutant emissions during the 21st century (see Figure 4) (IPCC, 2014). There is one mitigation scenario (RCP2.6) under which the Paris Agreement Objectives will be reached, two intermediate scenarios (RCP4.5 and RCP6.0) and a last one, implemented with very high greenhouse gas emissions (RCP8.5) (see Figure 4). The number included in the RCP's name, refers to the corresponding radiative forcing (in W.m^{-2}) for 2100 relative to 1750.

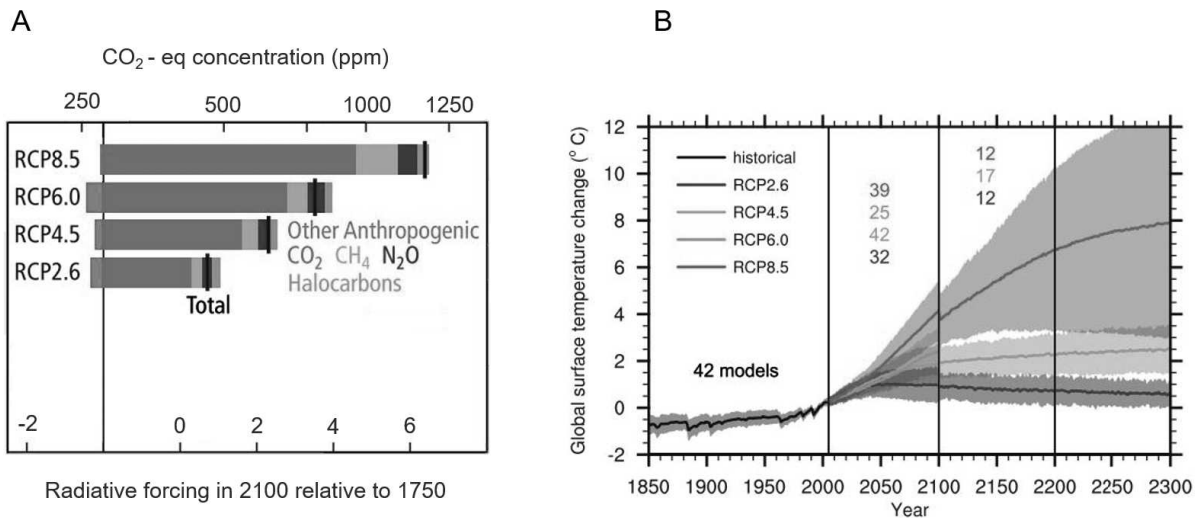


Figure 4. (A) Future radiative forcing levels for the RCP scenarios. **(B)** Time series of global annual mean surface air anomalies relative to 1986-2005. Projections are shown for each RCP scenario for each multi-model (solid lines) \pm 1.64 standard deviation (shading). For each periods the number of model considered is provided for each RCP scenario. Adapted from IPCC Climate Change 2014: Synthesis Report (2014) and IPCC Climate Change 2013: Physical Science Basis Report (2013)

At short-term, the global mean surface temperature is predicted to increase under the four RCP scenarios (between 0.3° and 0.7°C relative to 1986-2005) (IPCC, 2014). From 2050, trends are predicted to diverge according to the pathway considered: Relative to 1986-2005, the temperature will increase on average by 1°C for the RCP2.6 scenario and 3.7°C for the RCP8.5 scenario in 2081-2100 (see Figure 5) (IPCC, 2014). The oceans are also predicted to warm under the four pathways (Pörtner et al., 2019). Prolonged periods of much warmer than usual sea temperature (marine heatwaves) are predicted to increase in frequency, duration, intensity and spatial extent (Pörtner et al., 2019). For example, heatwaves will be 20 or 50 times more frequent by 2081-2100 than in 1850-1900 under the RCP2.6 and RCP8.5 scenarios respectively (see Figure 5) (Pörtner et al., 2019). Further, ocean acidification is predicted to persist by 2100 for the four scenarios even if a slight improvement is likely from 2050, under the RCP2.6 scenarios (Pörtner et al., 2019). There is no consensus regarding the dissolved oxygen concentration, but regarding to the future warming trends predicted, a future decrease is likely (IPCC, 2014; Pörtner et al., 2019). Moreover, the global mean sea level is expected to continue raising at a rate which could reach 15 mm.y⁻¹ in 2100 under the RCP8.5 scenario (Pörtner et al., 2019). Finally, glaciers are projected to lose 18 \pm 7% or 36 \pm 8.5% of their mass between 2015 and 2100 for the RCP2.6 and RCP8.5 scenarios, respectively (see Figure 5) (Pörtner et al., 2019). All pathways project an Arctic sea ice loss but the RCP8.5 scenarios is particularly alarming, predicting an Arctic free of sea ice at the end of each summer from 2050 (IPCC, 2014; Wang & Overland, 2012). Reaching the Paris Agreement Objective of keeping global warming below 2°C will drop the probability of such an event to 10-35 % (Pörtner et al., 2019).

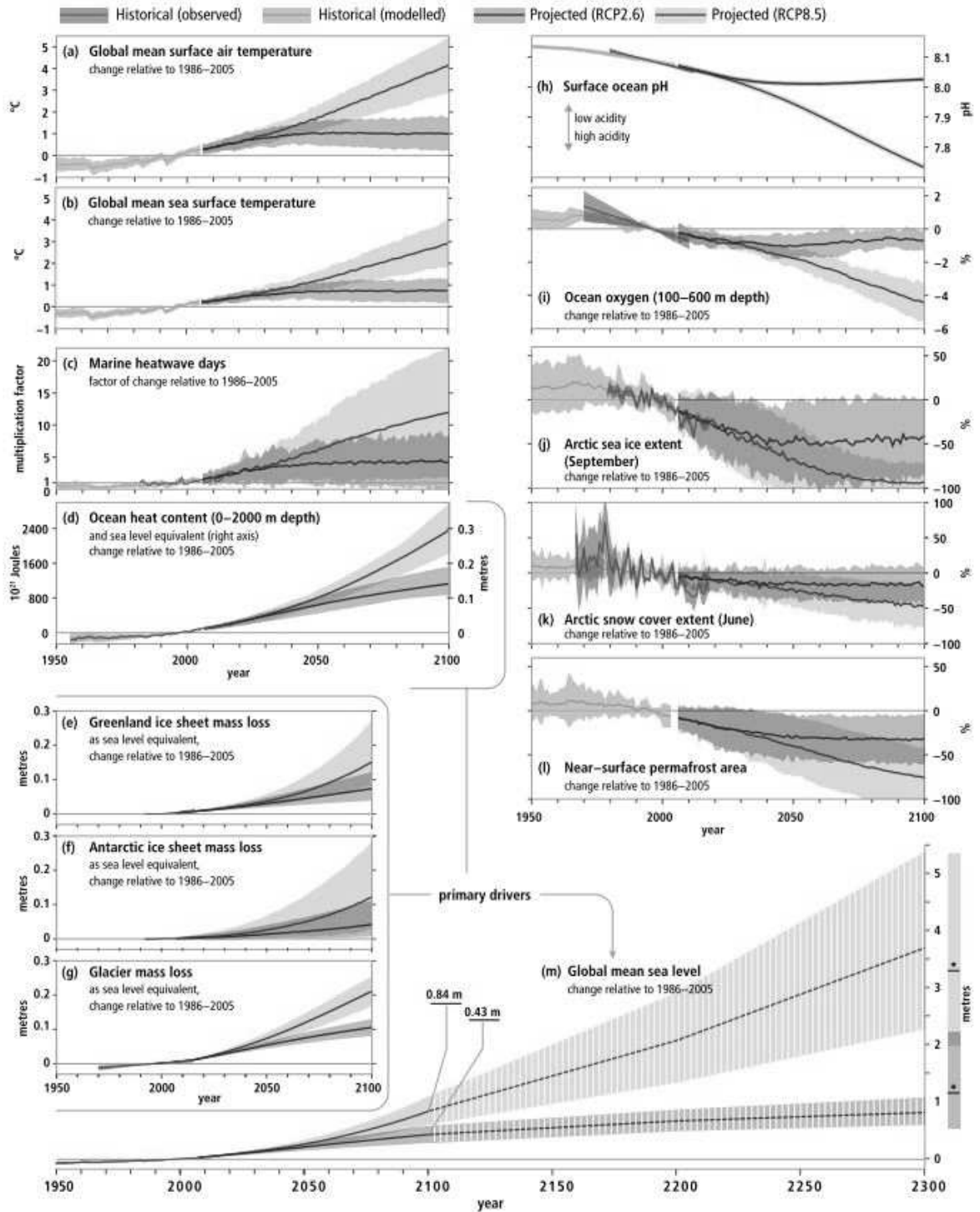


Figure 5. Observed and modelled historical changes in the ocean and cryosphere since 1950, and projected future changes under low (RCP2.6) and high (RCP8.5) greenhouse gas emissions scenarios. Source: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. 2019

3. Impacts of climate change on ecosystems

3.1 Spatial heterogeneity of climate change

The observed and future climatic changes previously listed were described at a global scale, hiding large heterogeneity between the world's regions (see Figure 6) (IPCC, 2014). For example, global warming is stronger on land, particularly in the Northern hemisphere, and the Arctic warms twice faster than the rest of the world (IPCC, 2014). Moreover, the North Atlantic Ocean warmed more than other oceans between 1971 and 2010 (Stocker et al., 2013), and it will be the case for its northern adjacent seas in the future (see Figure 6) (Pörtner et al., 2019). Local effects on the ecosystems could therefore diverge between regions, even though they are influenced by general atmospheric and oceanographic circulation patterns.

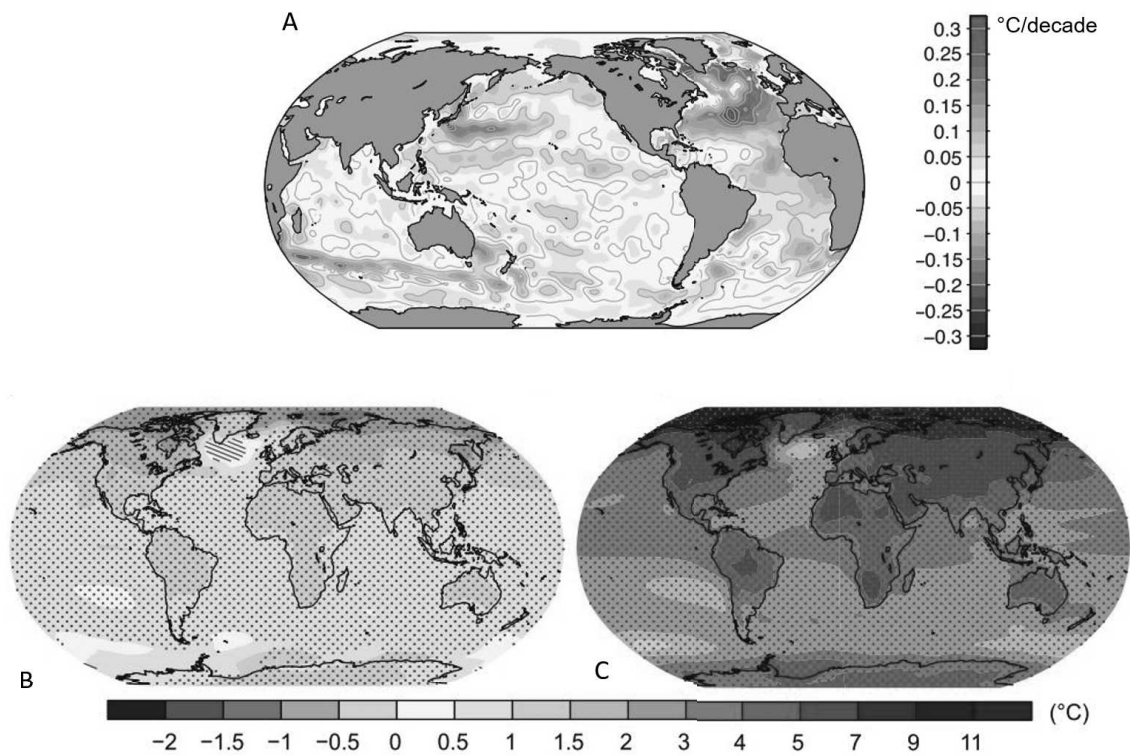


Figure 6. (A) Ocean (depth comprised between 0-700m) temperature trend for 1971-2010 in degrees Celsius per decade. (B) and (C) Annual mean surface temperature change (in degrees Celsius) in 2081-2100 relative to 1986-2005 according to two scenarios, the RCP2.6 and RCP 8.5, respectively. Source: IPCC Climate Change 2013: Physical Science Basis Report. 2013

3.2 Marine ecosystems: the particular case of the North Atlantic Ocean and adjacent seas

The Atlantic Ocean is, after the Pacific Ocean, the second-largest ocean of our planet. The North Atlantic Ocean plays a key role in the global ocean circulation and the climatic regulation (Ottersen, Stenseth, & Hurrell, 2004). Natural climate variability of the North Atlantic Ocean is essentially driven by the North Atlantic Oscillation (NAO) (Hurrell & Dickson, 2004): Jet stream location, winds and storms regimes, as well as temperatures and precipitations on the North American and European continents are closely linked to the state of the NAO. During positive NAO phases, subarctic temperatures are low, storms are more frequent and westerly winds are stronger (Hurrell, 2003). These features are opposite during negative NAO phases. Although climatic models do not link trends of the NAO with anthropogenic climate change (Stocker et al., 2013), its effects will modify regional climates and have to be taken in account.

The North Atlantic Ocean is intensively exploited by humans (Pauly & Maclean, 2003) and global warming is only one of the numerous anthropogenic threats which looms over its ecosystems and each compartment of its food webs (Halpern et al., 2008). Notably, it could impact organisms through physiological and phenological modifications (see Figure 9), changes in their abundance and distribution resulting in shifts in community structure (Hughes, 2000). Impacts of climate change on organisms are therefore direct or indirect (see Figure 9) (e.g. through the predators-prey interactions for example) (Ottersen et al., 2004) and the vulnerability of species will depend on their ability to adapt, their sensitivity and the degree of exposure to climate change effects (Beaugrand, 2015).

3.2.1. Direct impacts of climate change on primary productivity

The marine food web is based on autotroph organisms which constitute the phytoplankton: Through photosynthesis, those small unicellular algae release 50% of the annual oxygen produced at the global scale (Beaugrand, 2015) and constitute an important biological carbon pump (Field, Behrenfeld, Randerson, & Falkowski, 1998; Sabine et al., 2004). The abundance of those organisms and their photosynthetic activity drive the primary productivity of marine ecosystems. However, this productivity is not homogeneous in space and time; it depends on temperature, light and nutrient concentrations (Cloern, 1999; Edwards, Thomas, Klausmeier, & Litchman, 2016). Accordingly, in the North Atlantic Ocean, spring and early summer are favorable periods for explosive phytoplankton population growths, called blooms (Yoder, Mcclain, Feldman, & Esaias, 1993). Indeed, higher temperatures shorten the growth cycle of algae and induce sea ice melt at high latitudes, favoring light absorption. Blooms are also favored by extending day length. In the North Atlantic Ocean, diatoms are the most abundant taxa during blooms, followed by coccolithophores, dinoflagellates, and pico-phytoplankton (Lochte, Ducklow, Fasham, & Stienen, 1993).

Areas supporting a high primary productivity are very localized because of particularly suitable environmental conditions, such as upwelling of deep and cold water, particularly rich in nutrients.

Highly dependent on temperature, primary productivity is impacted by global warming (see Figure 7): It induces Arctic sea ice melt, increasing Arctic primary productivity (Yool, Popova, & Coward, 2015) but diminishes the duration of blooms by reducing the life cycle of algae (Beaugrand, 2015) and advances the peak of primary productivity at high latitudes (Karhu, Brotas, Manzano-Sarabia, & Mitchell, 2011). Decreasing ocean pH and the Atlantic meridional overturning circulation (Cheng, Chiang, & Zhang, 2013; Pörtner et al., 2019) such as modifying winds regimes, climate change dramatically affects phytoplankton: It deadly impacts species which produce calcareous shell such as coccolithophores (Meyer & Riebesell, 2015), increases ocean stratification, limits the mixing of nutrients from deep, nutrient-rich water (Pörtner et al., 2019) and finally modifies currents and the resulting upwelling, changing the locations of high productive areas.

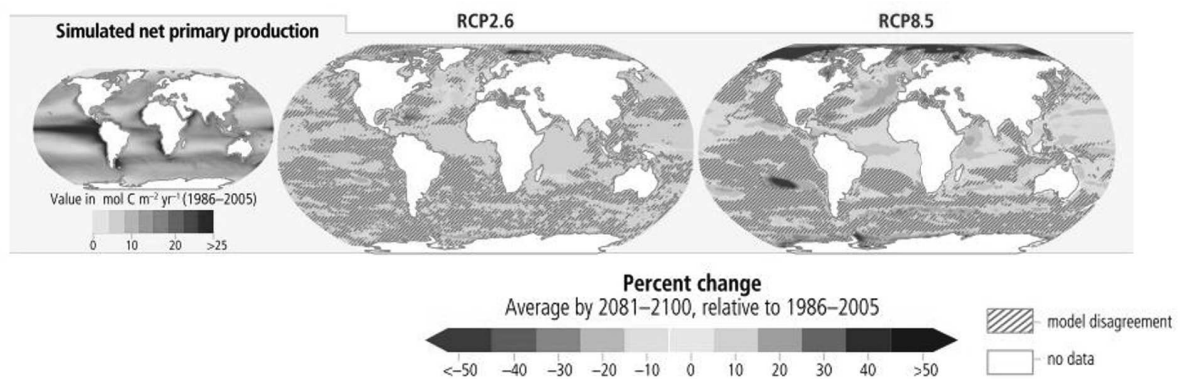


Figure 7. Changes in net primary production between 2081-2100 relative to 1986-2005 for the RCP2.6 and the RCP8.5 scenarios. Source: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. 2019

3.2.2 Direct impacts of climate change on intermediate levels of the trophic chain

Zooplankton grazes on phytoplankton, and constitutes primary consumers in marine ecosystem. The first 200 meters of the water column (corresponding to the euphotic zone) usually contain most zooplankton biomass, whereas biodiversity is greater at 800-900 meters (Angel, 1993). Across the North Atlantic Ocean, copepods dominate the mesozooplankton (Ciannelli et al., 2005), especially *Calanus finmarchicus*, which constitutes most of the copepod biomass during summer (Planque & Batten, 2000) and are among the most abundant multicellular organisms on earth. Zooplankton is the main prey of small pelagic fish but also of some top predators such as seabirds and whales. Fish and their larvae also feed predators of higher trophic level and represent more than 1100 species in the North Atlantic Ocean (Merrett, 1994).

Among them, capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), polar and Atlantic cod (*Boreogadus saida* and *Gadus morhua* respectively), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), European sprat (*Sprattus sprattus*) and lesser sand eel (*Ammodytes marinus*) are key prey items for seabirds and others predators and an important resource for Atlantic fisheries (Pauly, Zeller, & Palomares, 2020).

Zooplankton and most fish are ectotherms, meaning that their body temperature is relatively close to that of the near environment. Therefore, changes in sea temperature directly impact their metabolism, having negative effects on their physiology when moving away from their optimal temperature range. For example, ocean warming increases the metabolism and the oxygen demand of fish (Schulte, 2015). Also, zooplankton living at high latitude migrate towards deeper and colder waters in winter to reduce its metabolism and save energy during this period of food scarcity (diapause phenomenon): Global warming reduces the duration of this diapause, increases zooplankton metabolism and reserves consumption, and then diminishes its ability to produce eggs in the subsequent spring (Wilson, Banas, Heath, & Speirs, 2016). Moreover, as colder waters are richer in dissolved oxygen, global warming reduces the availability of dissolved oxygen for fish, and decrease their body size (see Figure 8) (Cheung et al., 2012). Additionally, climate change impacts the reproduction and development of marine organisms: For example, ocean warming shortens gonadal development of fish, potentially leading to an earlier reproduction (Ottersen et al., 2004). Larvae development is also shortened in warmer water, due to metabolic increase, and results smaller-sized juveniles (Beaugrand, 2015). Finally, dispersion and recruitment of larvae and juveniles will be affected by potential changes of currents according to oceanic and atmospheric circulation (Wilson et al., 2016).

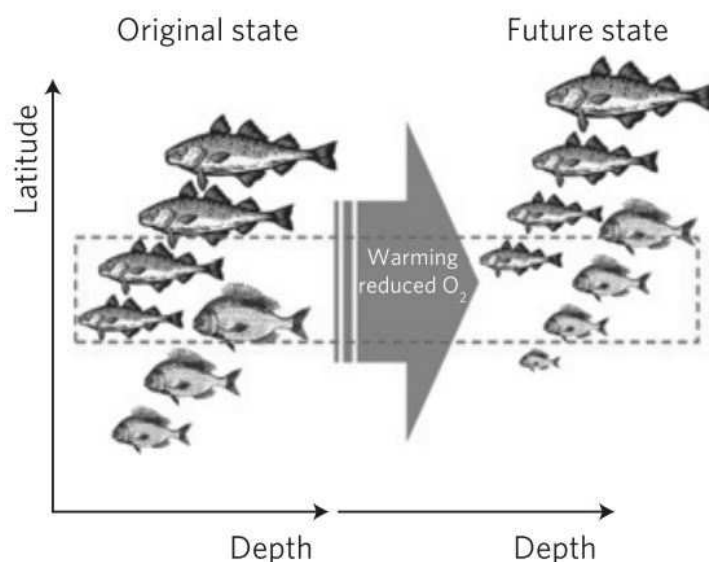


Figure 8. Schematic illustrating the expected changes in body size at individual and assemblage levels in a specific region (area enclosed by dashed red line). Source: Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Palomares, M. L. D., ... Pauly, D. (2012). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258. <https://doi.org/10.1038/nclimate1691>

3.2.3. Direct impacts of climate change on top predators

The last level of the trophic chain is constituted by top predators which prey upon the lower levels. The North Atlantic Ocean and adjacent seas host polar bears, six of the seven marine turtle species (Poloczanska, Limpus, & Hays, 2009), 84 sharks species (FAO, 2012), 8 species of pinnipeds, 10 whales species, 32 small cetaceans (Waring, Palka, & Evans, 2009) and 21 genus of seabirds during summer (Gaston, 2004). Those animals are charismatic and often used as flagship species in conservation (Sergio et al., 2008).

As previously described, ectotherms such as fish and marine turtles are impacted by global warming through the modifications of their metabolism. However some sharks and big fish perform inertial homeothermy thank to their large bodies and could maintain their muscle at a temperature 10-15°C above field temperatures (Beaugrand, 2015). Seabirds and marine mammals are less vulnerable to temperatures variations, even if they also have a range of thermal preferences (Beaugrand, 2015). Specifically, ocean warming may decrease their energy requirements for thermoregulation, especially during winter when conditions are harsh at high latitude (Amélineau et al., 2018). Conversely, temperature increase could lead to hyperthermia for seabirds during summer (Oswald & Arnold, 2012). Further, the sex ratios of marine turtles are temperature-dependent, with eggs exposed to higher temperature producing more female than male (Poloczanska et al., 2009): Global warming is therefore likely to modify the sex ratios of marine turtle populations nesting in the most impacted beaches (see for example Glen & Mrosovsky, 2004). Moreover, an increase in temperature could advance the nesting of marine turtles (see for example Mazaris, Kallimanis, Sgardelis, & Pantis, 2008; Weishampel, Bagley, Ehrhart, & Weishampel, 2010 but see Neeman et al., 2015) and Arctic seabirds (Descamps et al., 2019). However, this result seems to be highly variable at the seabird species level, and was not found at a global scale (Keogan et al., 2018). Seabird and marine turtle movements (Collins et al., 2020; Furness & Bryant, 1996; Navarro & González-solís, 2009; Poloczanska et al., 2009) are dependent upon winds and currents, respectively, suggesting that climate change modifies reachable areas. Finally, higher temperatures increase the sensitivity of marine mammals to diseases (Sanderson & Alexander, 2020) and diminish their reproductive success (Schumann, Gales, Harcourt, & Arnould, 2013).

3.2.4. Indirect impacts of climate change on organisms

Climate change could also impact marine organisms indirectly through modifications of their habitats and changes in predators-prey and/or host-parasites interactions. Indeed, climate change could drastically impact habitat suitability: for example, the sea level rise reduces the availability of beaches needed by marine turtles and seabirds to breed (Mainwaring et al., 2017). Beaches and coastal habitats are also particularly vulnerable to extreme events, which could destroy or flood nests and burrows, with negative consequences for breeding success (Poloczanska et al., 2009).

Ocean warming and acidification equally damage coral reefs to which many organisms belong (Hoegh-Guldberg, Poloczanska, Skirving, & Dove, 2017). Arctic sea ice melt is also particularly alarming for animals linked to this frozen environment, such as polar bears, some seals and seabirds but also zooplankton and primary producers (Post, 2013). Further, bioaccumulation rates of certain contaminants may be affected by global warming, through alteration in their transport, persistence and exposure (Krabbenhoft & Sunderland, 2013), potentially leading to negative impacts for marine organisms (Amélineau et al., 2019). Moreover, organisms are interdependent through the food webs they belong to: the abundance of primary producers influences higher levels of the trophic chain (bottom-up control) and the top predators act upon the abundance of lower components of the trophic network (top-down control). Additionally, fluctuations of organisms belonging to intermediate levels of the food web affect both upper and lower levels through wasp-waist control (Cury et al., 2000), especially when few species composed those intermediate levels. Consequently, climate change effects on one trophic level percolate through the entire food web. Climate change could also directly impact the predation phenomenon through modifications in water mixing, affecting the encounter rates between phyto and zooplankton (Behrenfeld, 2014). Further, prey and predators interactions are linked to their own performances (for example escapement capabilities, swimming performances) which are impacted by ocean warming, acidification and hypoxia (Domenici, Allan, Lefrançois, & McCormick, 2019).

In response to climate change, species could track favorable conditions in time (shift in their phenology, (Parmesan, 2007), but also across space: Some species shift their range towards higher latitudes or deeper waters to stay within their thermal preferences, modifying their global distributions (Perry, Low, Ellis, & Reynolds, 2005). Due to a less constrained physical environment and a thinner thermal safety margin, marine species are more capable of tracking climate warming than their terrestrial counterparts (Lenoir et al., 2020). Sensibility to climate change is nonetheless species dependent (for example difference in thermal niche between endo- and ectotherms), inducing different responses and then creating mismatches in space and time between prey and predators (Burthe et al., 2012). Species migrating using local cues to trigger their journey and benefit from peak of abundance resources several hundred kilometers away are particularly sensitive to those mismatch. Finally, those desynchronizations modify structure and functioning of entire communities (Beaugrand et al., 2019). Species which were previously not in contact could also meet through those shifts, potentially forming new interactions (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010) or host-parasites relationships (Gehman, Hall, & Byers, 2018). Finally, species could also adapt to climate change through their behavioral or physiological plasticity or microevolution but disentangle and understand the mechanisms behind those processes requires rigorous long-term studies based on individual monitoring (Teplitsky & Charmantier, 2019).

As the North Atlantic Ocean provides important ecosystems services, better understanding and monitoring of the effects of climate change on marine ecosystems and organisms ranks particularly high on the research and management agenda (Bindoff et al., 2019).

Top predators are key species of marine ecosystems which integrate the state of underlying trophic chains (Hammerschlag et al., 2019). Among North Atlantic Ocean predators, seabirds are highly mobile, conspicuous and well-studied, making them ideal organisms to study the impacts of climate change on marine migratory species (Lescroël et al., 2016).

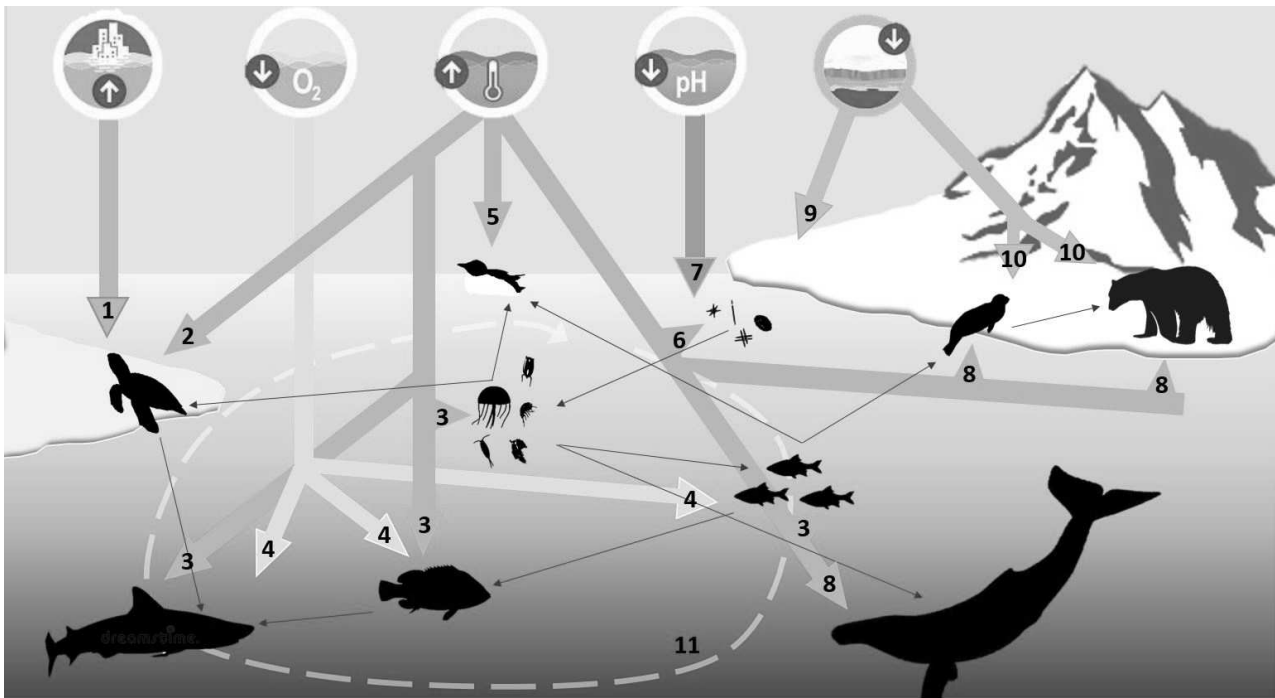


Figure 9. Schematic summing the main impacts of climate change on the marine food web.

The black, thin arrows represent the trophic interaction and mean “is eaten by”. Grey-blue, light blue, orange, green, blue and white arrows represent respectively the effect on organisms of sea level rise, oxygen concentration decrease, temperature increase, pH decrease, sea-ice melt and current modifications. Those effects are the following:

- 1) Sea level rise will limit the availability of nesting grounds.
- 2) Temperature increase will change the sex-ratios of turtle litters on exposed beaches.
- 3) Ocean warming will increase fish and zooplankton metabolism.
- 4) Oxygen concentration decrease will induce a decrease in fish size.
- 5) Temperature increase will lead to a diminution in seabird energy requirement and potentially to hyperthermia.
- 6) Ocean warming will increase primary productivity in Arctic, advance peak abundance of phytoplankton and decrease bloom duration.
- 7) pH decrease will deadly impact calcareous species.
- 8) Ocean warming will increase disease sensitivity and decrease reproductive success of marine mammals
- 9) Arctic sea ice melt, favoring light absorption, will increase Arctic primary productivity.
- 10) Arctic sea ice melt will be problematic for species linked to this frozen environment such as seals and polar bear.
- 11) Modifications of deep-water mixing and currents will impact nutrient, larvae and juveniles dispersion.

For clarity reason, spatial and/or temporal shifts as well as their potential resulting mismatch are not represented.

III. Seabirds in a changing ocean

Seabirds are charismatic top predators living in all of the world's oceans and classified in 369 species (BirdLife International). As they are mainly dependent on marine resources to feed, seabirds spend 90% of their life cycle at sea, only regularly visiting land during the few months dedicated to reproduction within often dense colonies (Schreiber & Burger, 2002). The non-breeding period is spent at-sea or on the wing, often far offshore. During the breeding period, seabirds' movements are limited around the colonies to regularly feed chicks: seabirds are then qualified as "central place foragers" (Orians & Pearson, 1979) and the distance travelled in each round trip between the colony and the foraging areas varies according to the environment and the flight ability of the species considered (Elliott & Gaston, 2005; Weimerskirch, Zimmermann, & Prince, 2001).

Through those round trips, seabirds provide marine nutrients to the colony surroundings, drastically modifying flora and fauna and are therefore considered as environmental engineers (González-Bergonzoni et al., 2017). Marine resources used by seabirds are located in patches where oceanographic conditions (such as upwelling, eddies, polar fronts or polynias) enhance primary productivity and concentrate seabird prey (Boertmann, Lyngs, Merkel, & Mosbech, 2004; Grecian et al., 2016; Stirling, 1995). Those patches are often predictable in space and time at a global scale (Weimerskirch, 2007) and seabirds evolved to detect accurately prey aggregations across the seascape (Boyd et al., 2016; Nevitt & Bonadonna, 2005). In the North Atlantic Ocean, they mainly rely on a limited number of prey species (Ciannelli et al., 2005), and changes in their abundances significantly impact seabird populations (see for example (Reiertsen et al., 2014)). Therefore, they are often used as ecological sentinels of marine ecosystem state across their life cycle (Durant et al., 2009), in particular to assess impacts of fishing pressure on prey stocks (see for example Barrett, 2002).

Seabirds are among the most threatened of all birds groups (Dias et al., 2019) and their migratory status make them particularly vulnerable. They are particularly sensitive to invasive species (Jones et al., 2016), bycatch (Lewison et al., 2014; Žydelis, Small, & French, 2013), overfishing of their prey (Grémillet et al., 2018) and to direct and indirect effects of climate change (see previous section). All of these challenges, which also compromise many other components of marine biodiversity, have to be urgently addressed. Most of the 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, Anker-Nilssen, Beaugrand, & Wanless, 2013). Indeed, seabirds are easily reachable on land during this period, and as most of them are philopatric (Schreiber & Burger, 2002), they can be monitored year after year at the same colony. With the miniaturization of tracking devices, the non-breeding period received more and more attention across the last decade (Fort, Moe, et al., 2013; Frederiksen et al., 2012), but there is a lack of knowledge on climate change impacts on seabirds during this period.

As seabirds are long-lived organisms (Schreiber & Burger, 2002), such information and understanding are critical since conditions encountered during the non-breeding period may strongly shape seabird population dynamics (Alves et al., 2013): For example, the limited knowledge currently available strongly suggests that winter is energetically challenging for seabirds (Fort, Porter, & Grémillet, 2009) and storms occurring during this period may be responsible of the death of thousands of individuals each year (Camphuysen, Wright, Leopold, Hüppop, & Reid, 1999). Knowledge of climate effects on seabird wintering distributions is therefore essential for global marine spatial planning and conservation schemes.

Along these lines, Grémillet and Boulinier (2009) stressed that determining the drivers of seabird winter at-sea distributions is a research priority, such as the prediction of future climate change impacts onto seabird spatial dynamics. Therefore, study several populations of one species is important to fully depict the ecological niche of the species considered, to better understand the meta-population functioning outside the breeding season and to have an overview of climate change impacts. Moreover, focus on several species brings global insight of ecosystems and ecological patterns, free of particular species specificity. Finally, as (sea)bird migrations generally take place at large extent, the concept of “macroecology” (Smith, Lyons, Ernest, & Brown, 2008) is a powerful tool to reveal the general mechanism underlying bird distribution across their life cycle (Somveille, Rodrigues, & Manica, 2018).

IV. Energyscapes for the study of animal migration

The balance between energy intake, body reserves and energy expenditure conditions the survival of all organisms, related to morphological, physiological and/or behavioral mechanisms (Brown, Gilgooly, Allen, Savage, & West, 2004). In the field of movement ecology, optimal foraging theory predicts that organisms will tend to minimize their energy expenditure during foraging trips, and to maximize their rates of energy gain (Stephens, Brown, & Ydenberg, 2007).

Therefore, the costs of transport in a particular landscape may explain why and how animals distribute. Recently, Shepard (2013), Wilson (2012) and their colleagues defined “energyscapes” as variation in the costs of transport according to environment characteristics, such as vegetation, incline, ocean currents speed or direction. As the energyscape does not account for variations in speed employed by an animal affecting its movement costs, Halsey (2016) developed the concept of “individual energy landscape” which must reflect animal chosen locomotion speeds across that landscape (see Figure 10). Mapping those energyscapes/ individual energy landscapes while tracking animal movements with bio-logging opens new perspectives for the study of movement and migration ecology. This approach notably helps understanding how environmental heterogeneity shapes behavioral strategies. It also provides valuable insights on other drivers of animal movement such as predation or food abundance, notably when movements are not only determined by transport costs (Shepard et al., 2013).

In this context, Amélineau and colleagues (2018) broadened the concept of energyscape, which they defined as variations of the energy balance (expenses versus yield) of an organism across geographical space according to environmental conditions, providing a framework to compare spatial profitability and a mechanistic framework to study animal distributions. This notably applies to animal migrations, yet there are challenges linked to determining the energy balance of wild species on the move, especially in the case of oceanic seabirds which winter far offshore. Fortunately, bio-logging now allows tracking animal movements anywhere on the planet. This information blends in a powerful manner with outputs from mechanistic models, to yield energyscapes even for the most elusive migratory creatures. The potential of this approach has been recently demonstrated for single seabird species migrating and wintering in the North Atlantic (Amélineau et al., 2018), providing a conceptual and methodological framework which can now be expanded at the community level across the North Atlantic basin.

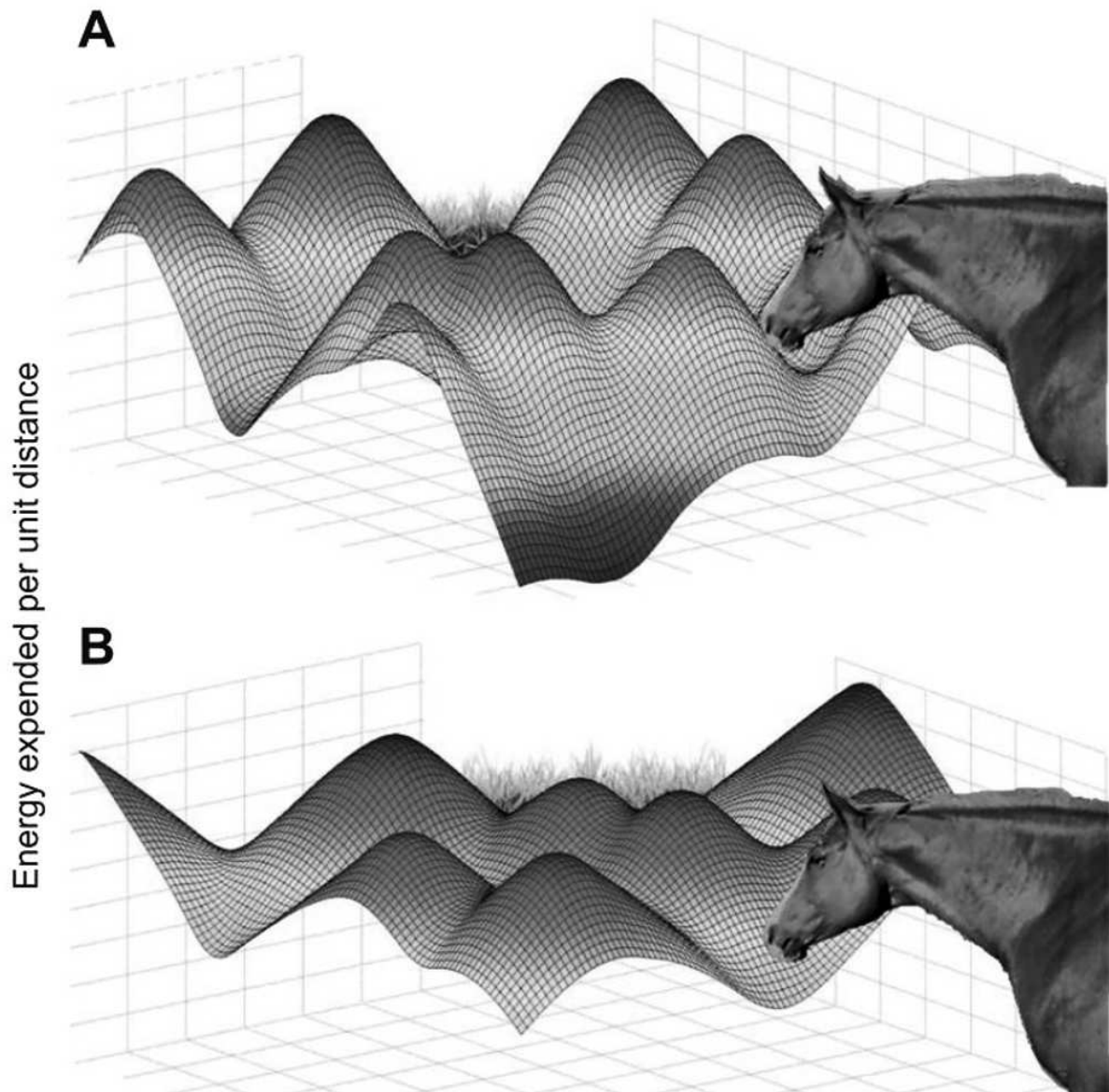


Figure 10. Schematic illustrating the concept of individual energy landscape.

This landscape represents variation in space in the energy cost to move a unit distance; reds indicate high costs and blues represent low costs.

“The minimum energy costs that can be incurred by an animal to move across a geographical landscape by a given route are defined by physical factors such as the substrate and slope of the terrain. However, the energy costs actually incurred by that animal can differ depending upon the decisions it makes predominantly about the speeds at which to traverse the landscape. For example, if a horse intends to move to a food patch but is not under a time constraint, it may opt to walk at an average walking speed, which is likely to be energetically economical for the given terrain (A). It may also choose an indirect route across its individual landscape that is nonetheless energetically more economic than the most direct route such that the energy spent to reach the food patch is further reduced. (B) In contrast, if, for example, the horse opts to trot at a high speed in order to reach the food patch quickly, then all routes to cross the landscape, at least on average, become more energetically expensive. Because of possible interactions between, movement speed, slope angle and the substrate underfoot, we would typically expect the energy landscape to vary in response to movement speed in a more nuanced fashion than simply raising or lowering a consistent amount across the surface. For instance, in the present example, although the majority of the landscape is raised in B, indicating higher energy costs to cross the landscape at a high trotting speed, there are nonetheless a number of peaks in A where that point on the landscape cannot be traversed more economically by moving at slower speeds. This could be the case, for instance, when moving into high winds or travelling downhill.”

Adapted from Halsey, L. G. (2016). Terrestrial movement energetics : current knowledge and its application to the optimising animal, *Journal of Experimental Biology*, 219, 1424–1431. <https://doi.org/10.1242/jeb.133256>

V. Study aims

The overall objective of this thesis work is to investigate climate change impacts on the seabird community migration in the North Atlantic Ocean, focusing on their winter distribution through an energetics approach. More precisely, the aims were:

- To identify current wintering hotspots for the North Atlantic seabird community, and to determine their environmental drivers at an Ocean basin scale (Chapter II).
- To determine and forecast North Atlantic climate change impacts on seabird distributions, to then assess the potential for new migratory and wintering strategies induced by those impacts (Chapter II and III).
- To determine current North Atlantic seabird exposure to winter storms, to better understand their future vulnerability to such events (Chapter IV).

After a short description of the methods used (Chapter I), this thesis contains three main chapters corresponding to published and submitted articles. Those tested the following hypotheses:

I. Energyscapes and prey availability shape the current wintering distribution of the North Atlantic seabird community. By diminishing seabird energy requirements and modifying the distribution of their prey, global warming will shift seabird community distributions during winter, especially if we fail to reach the Paris Agreement Objective of limiting global warming to $<2^{\circ}\text{C}$. These hypotheses are tested in Chapter II, which determines the current drivers of the North Atlantic Ocean seabird community before projecting its distributions under different climatic scenarios. Current seabird wintering hotspots are thereby identified, and their future locations projected.

II. The Arctic is predicted to be sea ice free each summer from 2050 under IPCC's RCP8.5 scenario. We hypothesize that this melt will lead to new migratory strategies of Arctic birds, such as future trans-arctic migrations and high Arctic year-round residency. We determine in Chapter III which bird species could switch their migratory behavior towards those new strategies, and then assess the adequacy and energetic benefits of trans-arctic migration and high Arctic residency, using little auks as an example.

III. Thousands of seabirds are killed each year during winter storms and washed ashore. We hypothesize that extreme conditions experienced during such events are energetically challenging, leading to the death of wintering seabirds. We therefore determine current seabird storm exposure in the North Atlantic Ocean in Chapter IV, and estimate seabird energy requirements during these extreme events, to better understand their energetic consequences for seabirds in the context of climate change.

To conclude, results obtained during this thesis are discussed in a general conclusion, leading to perspectives for future work.

CHAPTER I
METHODS

I. Study species

The seabird community of the North Atlantic Ocean is mainly represented by five key species which are severely hit by winter storms (Camphuysen et al., 1999; Morley et al., 2016) and account for 75% of the total number of seabirds breeding in this Ocean (Barrett et al., 2006): Little auk (*Alle alle*), Atlantic puffin (*Fratercula arctica*), common guillemot (*Uria aalge*), Brunnich's guillemot (*Uria lomvia*) and black-legged kittiwake (*Rissa tridactyla*). During the breeding period, those species are key components of marine and terrestrial Arctic ecosystems, fertilizing the near surroundings of their colony with marine nutrients, exerting top-down and bottom-up control on aquatic and terrestrial food web, and providing socio-economic services (Mosbech et al., 2018; Plazas-jiménez & Cianciaruso, 2020). As those species display contrasting diets and foraging behaviors, we anticipate that climate change may impact them differently. Chapter II and Chapter IV focused on those species, while Chapter III investigated which Arctic bird species are potentially impacted by Arctic sea ice melt, before using little auk as a methodological example.

1. Little auk

The little auk is one of the smallest Atlantic seabird (ca. 150g), belongs to the Alcids family and is the most numerous bird in the North Atlantic Ocean, with 40 to 80 million individuals (Egevang, Boertmann, Mosbech, & Tamstorf, 2003). During summer, little auks reproduce in the high Arctic, between Eastern Canada and Severnaya Zemlya in the Northern Russian Federation (see Figure 11) (Gaston & Jones, 1998), within colonies hidden in steep screes. Major colonies are in West and East Greenland, Svalbard as well as in Franz Josef Land whereas few individuals nest in Jan Mayen, Bjørnøya and in the Bering Sea (Stempniewicz, 2001). Little auks deserted Icelandic colonies in the 20th century and only rare individuals seem to visit the island during the breeding season (Frédéric Vautrin, personal observation).

Little auks are sub-surface feeders capturing their prey in the first meters of the water column by visually-guided suction feeding (Enstipp, Descamps, Fort, & Grémillet, 2018). As others Alcids, little auks are shaped to dive and pursue their prey efficiently under water, implying high flight costs (Elliott et al., 2013). During summer, they select their prey among copepods, amphipods and euphausiids according to local conditions affecting the abundance of these organisms (Harding et al., 2009; Karnovsky, Hobson, Iverson, & Hunt, 2008; Karnovsky, Kwaśniewski, Węśławski, Walkusz, & Beszczyńska-Möller, 2003). During the breeding period, little auks use extensively areas where prey aggregate such as the continental slope, marginal ice zone and polynias (Amélineau, Grémillet, Bonnet, Bot, & Fort, 2016; Karnovsky, Hobson, Iverson, & Hunt, 2008). They are major contributors to the carbon cycle of some regions, and may consume up to 24% of local copepods stock (Karnovsky & Hunt, 2002).

During winter, their ecology is less known due to their inaccessibility. However, descriptions of little auks diet benefited from stable isotopic analyses (Fort et al., 2010), and the development of miniaturized tracking devices allowed the identification of molting and wintering grounds. For example, little auks from East Greenland molt off eastern Svalbard (Mosbech et al., 2012) before wintering off Newfoundland (Fort, Moe, et al., 2013), showing a trade-off between their energy expenditure and the concentration of their main winter prey, *Calanus finmarchicus* (Amélineau et al., 2018). Little auks breeding in Svalbard and Russia winter off Jan Mayen and in the Barents Seas (see the SEATRACK project's website with online maps: <http://www.seapop.no/en/seatrack/>). They were also monitored to study Arctic pollutants (mercury and plastics) exposure (Amélineau et al., 2016; Fort, Grémillet, Traisnel, Amélineau, & Bustamante, 2016), and to identify impacts of climate change on Arctic ecosystems (Grémillet et al., 2015).

They show an important plasticity in response to environmental changes: Shifts in the composition of foraging behavior and chick diet were for example observed following changes in sea surface temperature or sea-ice cover (Amélineau et al., 2016; Grémillet et al., 2012), and little auks are supposed to spend less energy to thermoregulate in the future because of global warming (Amélineau et al., 2018). As their main prey items are predicted to shift Northward with climate change (Reygondeau & Beaugrand, 2011), little auk ability to cope with new environmental conditions will therefore depend on their capacity to track global warming by going northward or their possibility to ensure their energy requirements with new prey, probably less rich in lipids (Karnovsky et al., 2010).

2. *Atlantic puffin*

The Atlantic puffin is one of four species of puffins belonging to the Alcid family, but the only one breeding in the North Atlantic (Harris & Wanless, 2011). Its body mass (350-600g) is intermediate among auks, and the species nests in burrows or crevices between Eastern Canada and Northern Norway, including the Gulf of Maine, Iceland, Greenland, Ireland, the British Isles, Faeroe Islands, France and Svalbard (see Figure 11). They are around 6-7 million breeding pairs of Atlantic puffins in total, with some declines among European colonies in the last decades (Harris & Wanless, 2011). Determining the causes of such declines is difficult but environmental conditions could impact Atlantic puffins breeding success through direct or indirect effects: For example it is negatively correlated to sea surface temperature (Kress, Shannon, & O'Neal, 2016) and positively correlated to *Calanus finmarchicus* habitat suitability (Frederiksen et al., 2013).

Atlantic puffins are excellent divers which can pursue their prey as deep as 75 meters (Burger & Simpson, 1986), but like others Alcid, have high flight costs (Elliott et al., 2013). Little is known about the diet of adults but chicks are fed with sandeels, sprats, Atlantic herrings, whittings, capelins, and cods, whereas adults probably eat fish but also worms and squids (Harris & Wanless, 2011). Dissections of carcasses suggested that Atlantic puffins prey on sandeels, silvery lightfishes, rocklings,

Norway pouts, whittings, squids and nereids during winter (Falk, Jensen, & Kampp, 1992; Harris, Leopold, Jensen, Meesters, & Wanless, 2015). Moreover, stable isotope analysis revealed that zooplankton might be an important part of the winter diet (Hedd et al., 2010).

Atlantic puffins from the Western Atlantic winter near the Gulf of Maine but also off Newfoundland. Birds from Iceland, Ireland and the Celtic Sea often aggregate near the Charlie-Gibbs Fracture Zone in the mid-North Atlantic, but can also be found in the Labrador Sea, south of Iceland and off Ireland respectively (Fayet et al., 2017) (see Figure 11). Atlantic puffins from Britain usually stay in the North Sea whereas birds from Norway winter off Iceland or in the Barents Sea (Fayet et al., 2017).

Fayet and colleagues (2017) demonstrated that colony size, local resource availability and latitude drive migratory patterns, ultimately impacting colony productivity: birds from larger colonies tend to migrate farther than those from smaller ones. Moreover, birds wintering at higher latitudes and experiencing poorer quality habitats have higher winter energy expenditure, leading to lower colony productivity, which demonstrates a cost of migration at a species' range level. Shifts in water productivity during winter could therefore affect demographic processes. Finally, Harris and colleagues (2005) hypothesized that the worsening conditions encountered during winter in the North Sea induced a shift towards Atlantic waters, making birds more vulnerable to hunting pressure there, affecting adult survival.

3. Common and Brunnich's guillemots

Common and Brunnich's guillemots form the genus *Uria* and are the largest living species (ca. 1kg) belonging to the Alcid family. They are morphologically similar, and relatively to their size, present the highest flight cost of any animal (Elliott, Ricklefs, et al., 2013). They often breed in sympatry on high cliffs (Gaston & Jones, 1998), relying on the same local prey during the breeding period. Their breeding distribution is circumpolar (see Figure 11), but both species are more represented in the North Atlantic Ocean which hosts 6-8 million common guillemots and 10-15 million Brunnich's guillemots (Gaston & Jones, 1998), even if populations declined in recent decades in many parts of the Atlantic Arctic (Fauchald et al., 2015).

Common and Brunnich's guillemots are deep divers (down to 250m) (Chimienti et al., 2017), and then more likely impacted by horizontal changes in prey abundance than by vertical shifts. During summer, they prey on various schooling fish such as capelins, cods, herrings, sprats and sand eels according to locally available resources. Common guillemots are nonetheless strictly piscivorous, whereas Brunnich's guillemots are more generalist and feed on zooplankton and squids (Gaston & Jones, 1998). The winter diet of those species is less known and mainly based on stomach content analyses of hunted guillemots or stable isotopic studies, concluding that guillemots probably prey on lower trophic levels during the non-breeding period (Lilliendahl, 2009; Moody & Hobson, 2007).

Brunnich's guillemots from Canada and North-West Greenland winter in the Baffin Bay, in the Labrador Sea and off Newfoundland whereas birds from Svalbard, Norway and Iceland preferably stay off South Greenland, around Iceland and in the Barents Sea during winter (see Figure 11) (Frederiksen et al., 2016). Brunnich's guillemots may therefore travel thousands of kilometers during the non-breeding period in spite of the high flight costs induced (Fort, Steen, et al., 2013). Conversely, common guillemots stay close to their breeding colony during winter, saving travel costs but facing harsh climatic conditions in the high-Arctic (see Figure 11) (Fort, Steen, et al., 2013).

Frederiksen and colleagues (2016) showed a strong association between population status of Brunnich's guillemots and their wintering area. However, causal links between threats occurring in the different areas and population status are not obvious. Both guillemots species are hunted during the non-breeding period, are vulnerable to bycatch and oiling (Frederiksen, Linnebjerg, Merkel, Wilhelm, & Robertson, 2019; Österblom, Fransson, & Olsson, 2002) and are highly impacted by fluctuations in oceanic conditions (Descamps, Strøm, & Steen, 2013) and in prey abundance (Erikstad, Reiertsen, Barrett, Vikebø, & Sandvik, 2013). The magnitude of such threats could explain the difference in their impacts on local populations and have to be taken into account when establishing conservation measure across the guillemots' range.

4. Black-legged kittiwake

Black-legged kittiwakes belong to the Larid family. The species has a circumpolar distribution (see Figure 11) and the majority of the global population breeds in the North Atlantic, with 4.5 million of individuals (Frederiksen et al., 2012) nesting on Atlantic cliffs.

Black-legged kittiwakes are surface feeders, which mainly prey in summer on zooplankton and fish such as sand eels, Atlantic herrings and capelins, according to local abundance of each prey in the near surroundings of the colony (Barrett, 2007; Carscadden, Montevecchi, Davoren, & Nakashima, 2002; Lewis et al., 2001). As their breeding success is particularly dependent on prey abundance (which could be negatively impacted by fisheries) and environmental conditions, black-legged kittiwakes are good indicators of environmental changes through long-term monitoring (Frederiksen, Wanless, Harris, Rothery, & Wilson, 2004; Vihtakari et al., 2018; Wanless, Frederiksen, Daunt, Scott, & Harris, 2007). Especially, recent studies linked global warming rate with steep kittiwakes population decline in the 1990's (Descamps et al., 2017).

Moreover, breeding success affects subsequent migration timing and wintering destinations, with unsuccessful breeders leaving the colony earlier and moving farther than successful breeders (Bogdanova et al., 2011; 2017). Additionally, food supplementation experiments conducted in summer established that successful fed breeders departed the colony earlier and move less during winter than unfed controls, suggesting that they have greater tolerance of harsh winter conditions (Whelan et al., 2020). Multicolony tracking revealed that most of Atlantic kittiwakes aggregate in the western part of

the ocean basin in winter, between Newfoundland and the Mid-Atlantic Ridge, whereas some birds from the British Isles stay on the European side in the North Sea (see Figure 11) (Frederiksen et al., 2012). During winter, black-legged kittiwakes are assumed to feed on lower trophic level than during the breeding season, mainly preying on crustaceans such as copepods, amphipods, euphausiids and pteropods (González-Solís et al., 2011; Karnovsky et al., 2008). As the density of those prey during the non-breeding period affects the adult survival of kittiwakes (Reiertsen et al., 2014), future oceanic conditions may radically impact their demography and winter distribution even if they demonstrated foraging plasticity (Vihtakari et al., 2018).

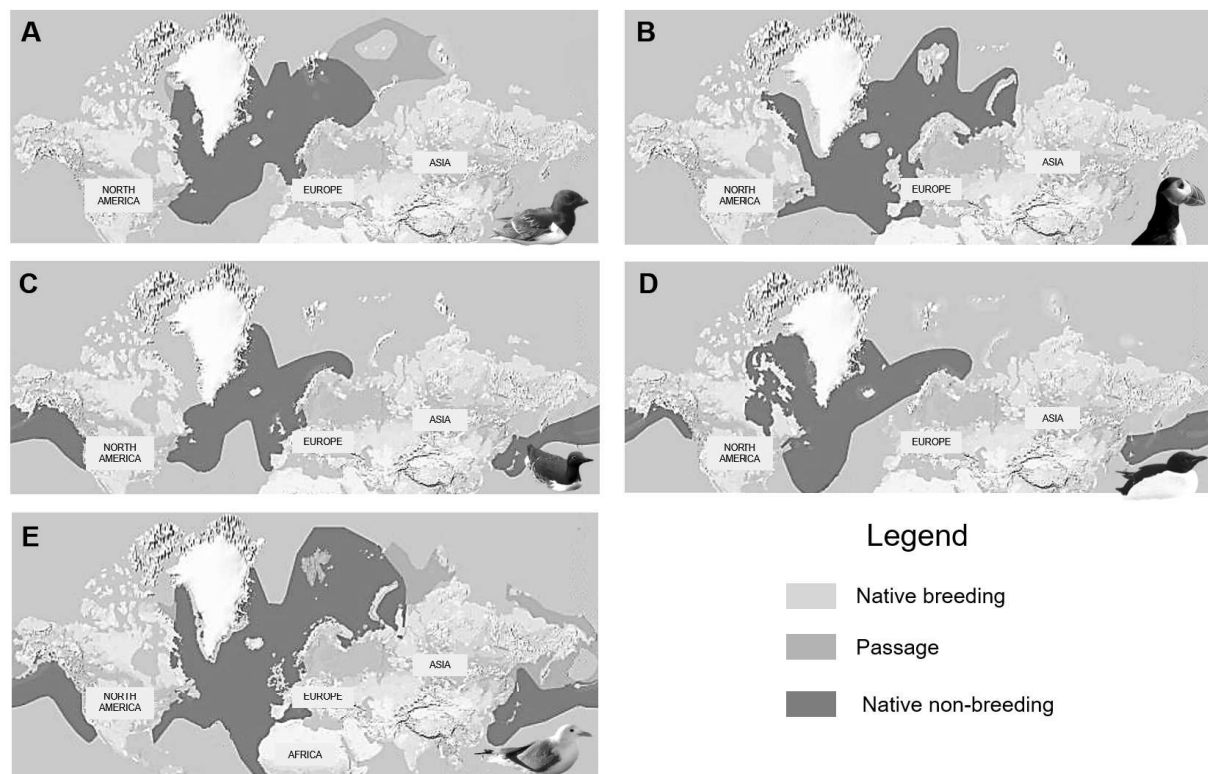


Figure 11. Distribution maps of the five species considered: (A) Little auk, (B) Atlantic puffin, (C) Common guillemot, (D) Brunnich’s guillemot, (E) Black-legged kittiwake. Source: BirdLife. Bird pictures from Tornos.J and Clairbaux.M

II. Locating seabirds at-sea during the non-breeding period

Locating seabirds is the first step when investigating the impacts of climate change on their winter distributions. However, seabirds usually winter far offshore and/or are unreachable during most of the year, strongly limiting data acquisition needed to better understand their winter ecology. Some species migrating near the coast are observed and/or hunted legally, providing information on their migratory pathways and winter diet (Karnovsky et al., 2008). Moreover, location data for numerous species may be recorded during boat journeys/transects and could be provided online in open access (see GBIF website for example). However such data could suffer from misidentification and biases

towards areas which are more accessible (Guillera-Arroita et al., 2015), especially in winter when sea-ice conditions and/or winter storms could preclude marine navigation.

Seabird studies therefore widely benefitted from technological advances: For example Argos and GPS (Global Positioning System) devices locate seabirds with high accuracy worldwide (Ryan, Petersen, Peters, & Grémillet, 2004), and miniaturization of accelerometer and TDR (Temperature Depth Recorder) provide useful additional behavioral data (Harding et al., 2009). However, deploying such devices for several months is often not possible on small species due to heavy batteries needed. Tracking small animals all year-round is however possible since early 1990s through lightweight geolocators (less than 2g) called GLS (Global Location Sensors) invented by Rory P. Wilson and Roger Hill (Grémillet, 2015). Their low weight and drag limit their impact on bird behavior, physiology and survival in comparison with heavier tracking devices such as GPS (Brlík et al., 2019; Vandenabeele, Shepard, Grogan, & Wilson, 2012 but see Costantini & Møller, 2013). Those loggers record ambient light-level and time (see Figure 12), providing 2 locations per day using day length as a proxy for latitude and timing of noon as proxy for longitude (Hill, 1994; Wilson, Ducamp, Rees, Culik, & Niekamp, 1992). Recently, conductivity and temperature recorders have been added to GLS, providing information on bird behavior (flying or diving/resting on water) and on their bird surrounding environment, allowing scientists to assess and correct bird locations (Teo et al., 2004). GLS are comparatively light, cheap and easy to use, however, birds equipped with such loggers still have to be recaptured to download stored data. Moreover, GLS have a low accuracy (186km +/- 114 km, Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004) highly dependent on weather, animal's behavior, habitat and time of the year (Lisovski et al., 2012). Additionally, birds cannot be located with GLS around the equinoxes, when day and night durations are equal, precluding the latitude calculation (Hill, 1994 but see Merkel et al., 2016). GLS data used in this thesis work were obtained through a massive deployment and collaborative effort, allowing to track more than 1500 individuals of the five species from 39 colonies.

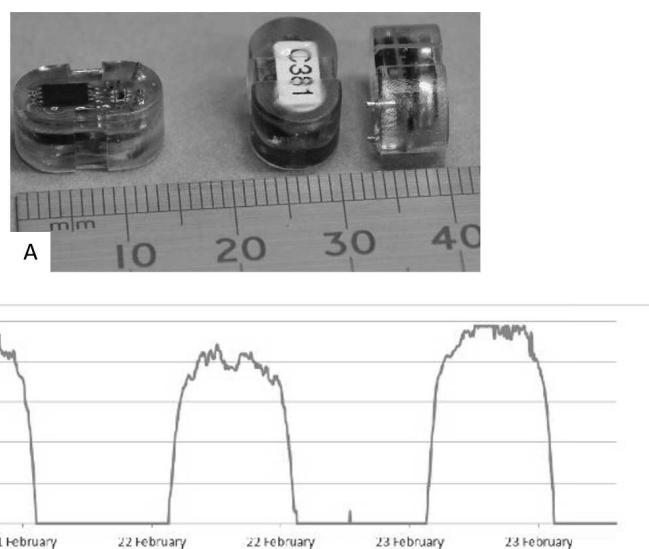


Figure 12. (A) An example of GLS used during this thesis: the Intigeo-C65 model, 14*8*6mm for 1g, insuring 1 to 2 year of battery. (B) An example of 3 days light data obtained from an Intigeo. Source: ® Migrate technology

III. Modelling current and future seabird distributions

Once seabirds have been located, determining the current drivers of their distributions is important, to better understand their ecology, assess the effects of environmental conditions, and project future impacts of climate change.

To occupy a site and maintain populations, species have to reach the considered site, and abiotic and biotic conditions experienced there have to be suitable for the species (Lortie et al., 2004; Pulliam, 2000; Soberón, 2007). The overall combinations of abiotic variables values within which the physiological needs of the species are satisfied corresponds to its ‘fundamental niche’ (*sensu* Hutchinson, 1957). However, determine the fundamental niche of a species in natural conditions is nearly impossible because of biotic interactions such as predation and competition acting on organismal distribution. Therefore, the observed distribution of a species corresponds to its “realized niche”, i.e. its fundamental niche constrained by biotic interactions and dispersal limitations (Soberón, 2007). Quantifying this realized niche allows to determine the drivers of species distributions to assess current habitat suitability of any areas and, under several hypotheses, to project it across time and space as long as associated environmental variables needed are known (Elith & Leathwick, 2009).

Habitat suitability models (HSM) have been developed to this aim during the previous decades, and have been widely used to predict climate change impacts on species distributions but also in biogeography, conservation ecology and invasive species management (Guisan et al., 2013). HSM include many techniques such as species Distribution Models (SDM) or Resource Selection Functions (RSF) but all are correlative models, linking mathematically species occurrences to environmental conditions experienced at those locations (see Figure 13) (Elith & Leathwick, 2009). It allows the determination of important variables and once it is assessed positively having a high predictive power, one could extrapolate it to predict species distribution under new conditions. Many methods were used to fit HSM such as convex hulls, regression models (GLM, GAM) or more recently machine learning techniques (ANN, BRT, Random Forest etc.) and those techniques may be combined to build robust ensemble models (Guisan, Thuillier, & Zimmermann, 2017).

Usually, HSM capitalize on climatic variables such as temperature or precipitation, as well as physical ones (bathymetry, elevation, substrates etc.), shortlisted because considered relevant as predictors of species distributions. Therefore, distribution models widely benefitted from geographic information systems and satellite remote sensing advances allowing the use of environmental data at global scales in both marine and terrestrial realms (Leitão, Santos, & Morgan, 2019). With the new generations of climatic models (see II.2 section in the Introduction) more and more variables were available at finer spatial and temporal scales allowing future species distribution projections with more accuracy under different climatic scenarios.

Some HSM include biotic processes such as facilitation (see for example Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007) but most of the time biotic variables are difficult to obtain at the scale needed, and scientists usually used proxy to investigate their influence on species locations choices. For example, chlorophyll A concentration is generally used as a proxy of marine primary productivity (Huot et al., 2007), but such proxy could hide mismatch in the marine food web and therefore lead to misinterpretation when assessing the drivers of top-predator distributions (Grémillet et al., 2008). Empiric variables providing information on fish and zooplankton abundance and distribution at global scales are particularly scarce (but see Continuous Plankton Recorder) and most of the time have to be modeled before being integrated in HSM of its predators, adding complexity, especially when temporal predictions are aimed. In this thesis work, we considered zooplankton concentration obtained from Earth System Models and current and future fish abundances were obtained from Dynamic Bioclimatic Envelope Model (DBEM, Cheung et al., 2009) outputs. The DBEM simulates changes in the 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, larval and adult dispersion.

Indeed, combining HSM with dispersal, population and/or mechanistic models allows better representation of ecological processes within correlative models (see for example Meineri, Deville, Grémillet, Gautier-Clerc, & Béchet, 2015): Along this line, we therefore integrated a novel energyscape approach when modeling seabird distributions.

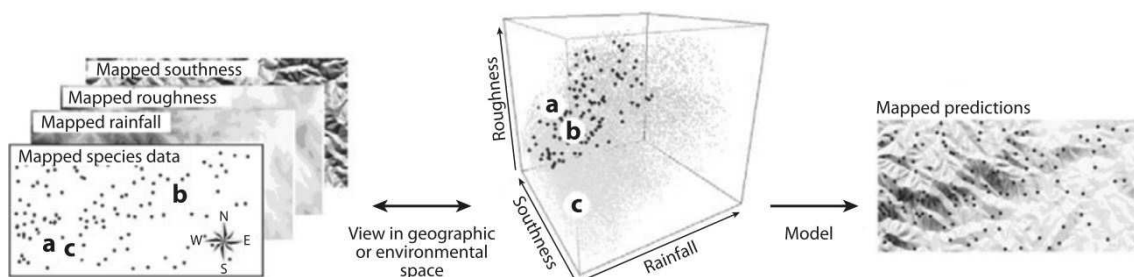


Figure 13. The relationship between mapped species and environmental data (left), environmental space (center), and mapped predictions from a model only using environmental predictors (right). Source: Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>

IV. A bio-mechanistic model: Niche Mapper™

Calculating the energy requirements of seabirds across geographical space according to environmental conditions (energyscape, Amélineau et al., 2018) is a powerful tool to mechanistically explain their distribution and to compare environmental profitability across space and time. Several approaches exist to measure and calculate the energy expenditure of free-living animals (Fort, Porter, & Grémillet, 2011) such as allometric equations (White, 2011), heart rate measurements (Green, 2011), time-energy budget analyses (Dunn, Wanless, Daunt, Harris, & Green, 2020), overall dynamic body acceleration (ODBA) (Elliott, Vaillant, Kato, Speakman, & Ropert-coudert, 2013) or the doubly-labeled water technique (Welcker, Harding, Kitaysky, Speakman, & Gabrielsen, 2009).

These different techniques all have strengths and weaknesses. For example, the accuracy of allometric equations and of ODBA calculation suffer some exceptions at the species level, and we showed that ODBA is not appropriate when calculating little auk energy expenditure due to its high-buoyancy and ability to hold its breath when diving (see Appendix I). Moreover, energetic calculations from heart rate recorders, accelerometers (ODBA) or doubly-labeled water require the bird to be recaptured in a short period of time and calculations of time-energy budget are time- and cost intensive as the energy requirements and time spent for each activities have to be recorded. Therefore, when seabirds are unreachable during the non-breeding period, those methods are unsuitable for our purpose. Additionally, when modeling energyscapes, one has to calculate energy requirements for the overall landscape considered, taking into account variability and effects of environmental conditions. All these requirements point to energetics modeling as the adequate approach to study seabird winter energyscapes.

Despite limited knowledge available on seabird winter ecology, such modeling was successfully conducted on several seabird species (Amélineau et al., 2018; Fort et al., 2009; 2013), by using the mechanistic model, Niche Mapper™. This algorithm contains two sub-modules: a microclimate model, which provides environmental data (sea surface temperature, air temperature, wind speed, cloud cover and relative humidity) 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 (see Chapter II, Supplemental material XIII for the list of input data). These inputs are used to solve heat balance equations between the animal's body and its environment, and to estimate the metabolic rate needed for the animal to maintain its body temperature at a particular time with the considered behavior. Sea surface and air temperature as well as body temperature, feather characteristics and wind speed are identified as main drivers of seabird energy requirements modeled with Niche Mapper™ (Amélineau et al., 2018; Fort et al., 2009).

CHAPTER II

**MEETING PARIS AGREEMENT OBJECTIVES WILL
TEMPER SEABIRD WINTER DISTRIBUTION SHIFTS
IN THE NORTH ATLANTIC OCEAN**

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 succeeding or failing to reach 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 the 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°C under a “no mitigation” scenario, modifying seabird wintering hotspots in the North Atlantic Ocean. Our findings suggest that limiting global warming to less than 2°C above preindustrial levels, will limit changes on the location and size of seabird habitats in the 21st century.

Keywords: DBEM, Energy requirement, Mechanistic habitat selection, Niche MapperTM, Paris Agreement, RCP scenarios, Seabird migration, Seabird distributions

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°C above preindustrial levels at the global scale (United Nations Framework Convention on Climate Change, 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, Guivarch, Tachiiri, Jones, & Ciais, 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, Poloczanska, Reed, & Thompson, 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 (Palczyński, Hammill, Karpouzi, & Pauly, 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 breeding season (Frederiksen, Anker-Nilssen, Beaugrand, & Wanless, 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°C on the North Atlantic Ocean seabird community distribution, during the non-breeding period (October-February). We focused on five key species which represent 75% of the total number of seabirds breeding in the North Atlantic Ocean: little auk (*Alle alle*), Atlantic puffin (*Fratercula arctica*), common guillemot (*Uria aalge*), Brünnich's guillemot (*Uria lomvia*) and the black-legged kittiwake (*Rissa tridactyla*) (Barrett et al., 2006). We used Global Location Sensors (GLS) to track the inter-breeding movements of 1532 birds from 39 breeding colonies spread 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 $<2^{\circ}\text{C}$ relative to preindustrial levels (Meinshausen et al., 2006; 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.

Methods

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, Elliott, & Sargatal, 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, Silk, Croxall, Afanasyev, & Briggs, 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 et al., 2013; Frederiksen et al., 2016, 2011; Linnebjerg et al., 2013; McFarlane Tranquilla et al., 2015; Merkel, 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 two 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. 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). 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, Lambert, ben Mustapha, & Baaren, 2013), Arctic sea ice melt (Wang & Overland, 2012) and North-East Atlantic Ocean climatology (Perez, Menendez, Mendez, & Losada, 2014; Zappa, Shaffrey, & Odges, 2013). The HadGEM2-ES model provided the information required to model present and future seabird energetics, as well as seabird prey fields (see below). Relative humidity was calculated following Nadeau & 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., 2013; Fort, Porter, & Grémillet, 2009), 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, USA) 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 (Medina et al., 2018). For each species the results were averaged across patches.

Other morphological properties such as body dimensions were measured on bird carcasses of five Atlantic puffins and four black-legged kittiwakes. 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).

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., 2016, 2009). 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 abundance of each zooplankton species taken by seabirds wasn't available, we used the monthly total concentration of zooplankton provided by the Earth system model HadGEM2-ES (Totterdell, 2019).

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.

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, McDonald, Thomas, McDonald, & Erickson, 2002). RSF compare environmental variables at locations used by the animal with those variables at a set of locations available to the animal (Manly, McDonald, Thomas, McDonald, & Erickson, 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, Signer, & Fieberg, 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 non-linear 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, Vernier, Nielsen, & Schmiegelow, 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, Proffitt, & Blackburn, 2016). More than 60% of the GLS locations occurred in the 4 last bins, and we therefore defined selected habitat as pixels with a binned RSF score ≥ 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 were calculated.

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). 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 IPCC, the global mean temperature will increase >2°C above preindustrial levels between 2045 and 2065 and >4.2°C at the end of the 21st century following this scenario (IPCC, 2014).

Results

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).

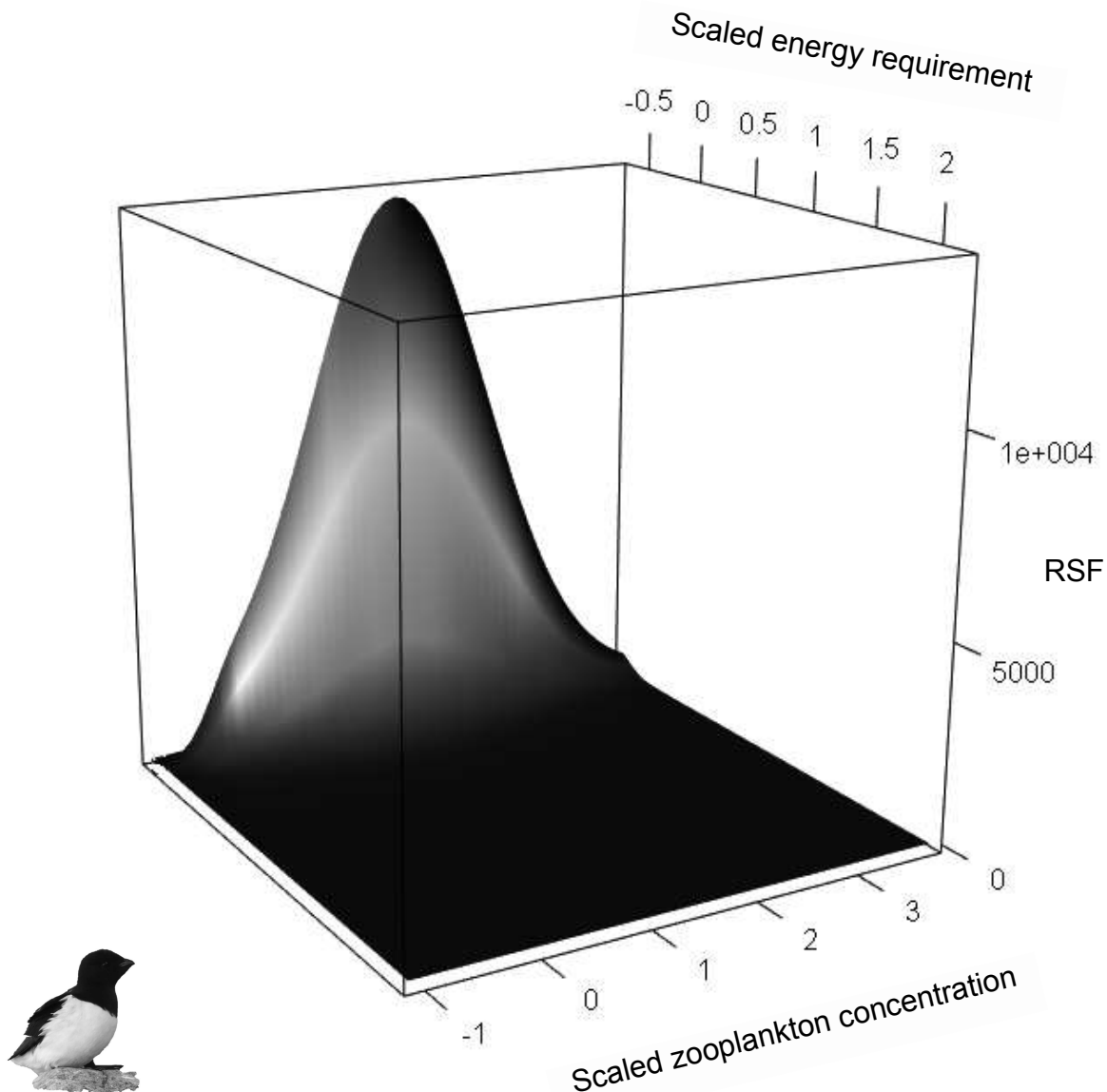
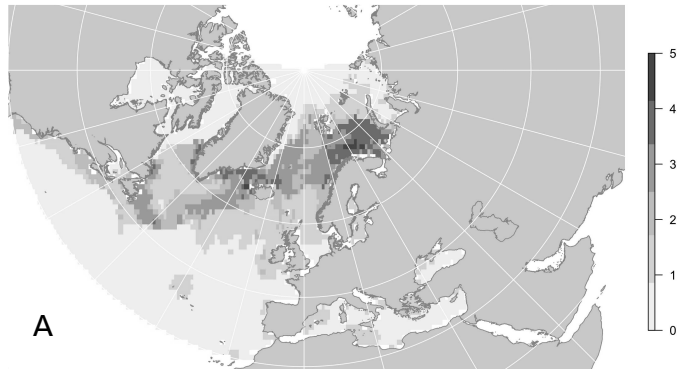


Figure 1. The trade-off between zooplankton concentration and bird energy requirements predicts little auk habitat selection. An optimum was reached at a scaled energy requirement of -0.6 and a scaled zooplankton concentration of 1.3. See Supplemental materials III for other species.

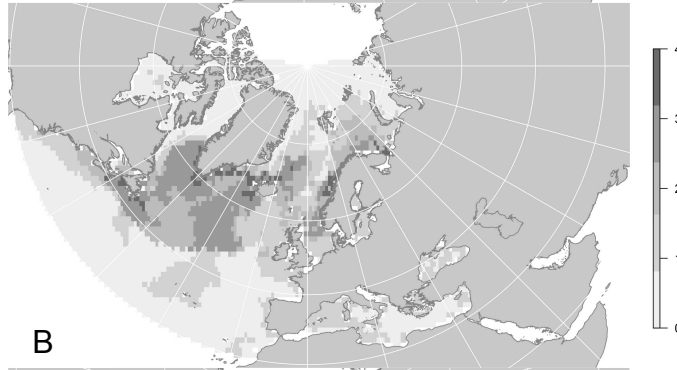
Species-specific selected habitat was defined using a threshold approach on the developed RSF's (see Methods for details). These habitats were in turn combined to identify multi-species wintering hotspots (*sensu* Fort, Beaugrand, Grémillet, & Phillips, 2012; Grecian et al., 2016) by counting for each 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 were 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). Further, 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 ≥ 7), in October (**A**), November (**B**), December (**C**), January (**D**) and February (**E**). Graticules are displayed at 15° intervals and the map is projected as North Pole Lambert Azimuthal Equal Area.

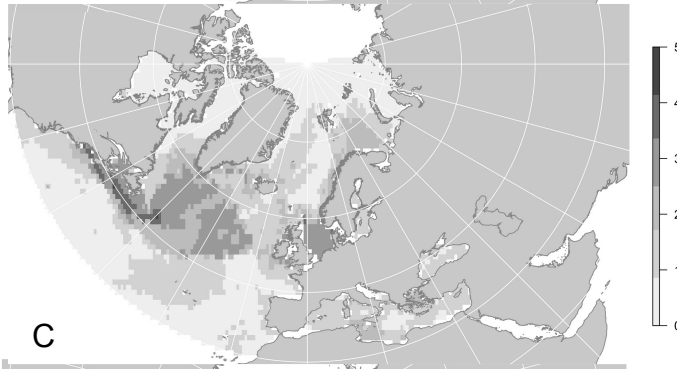
OCTOBER



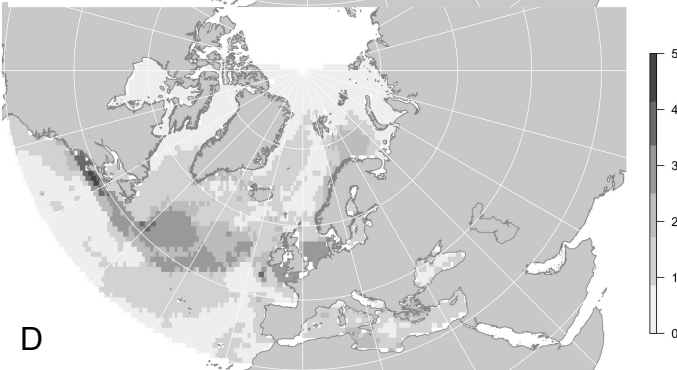
NOVEMBER



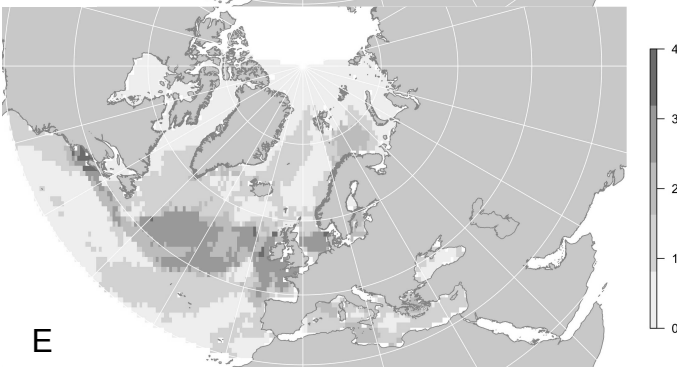
DECEMBER



JANUARY



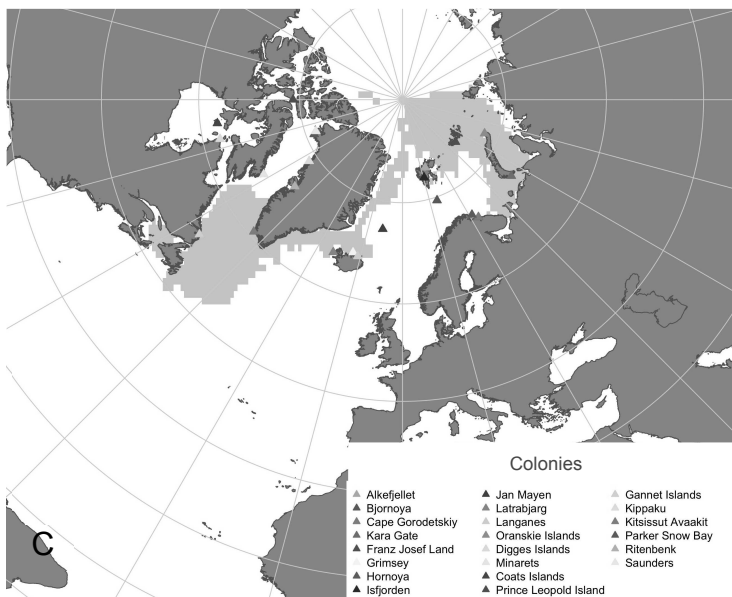
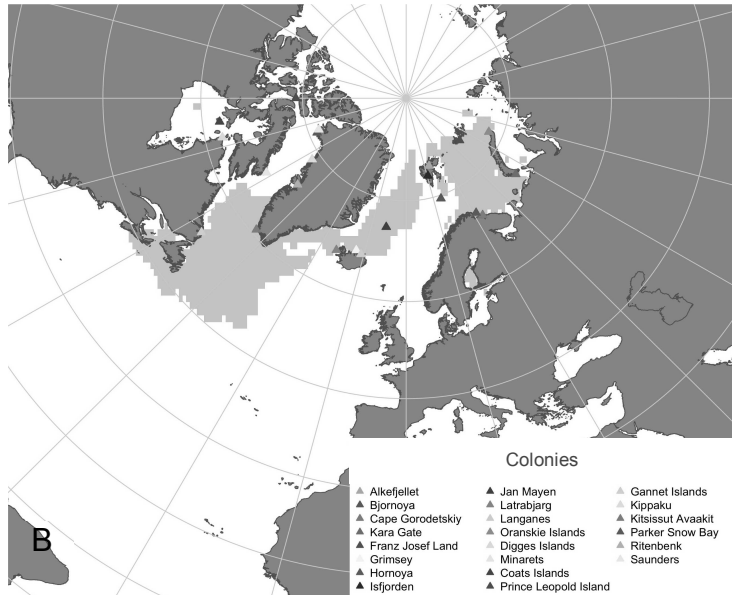
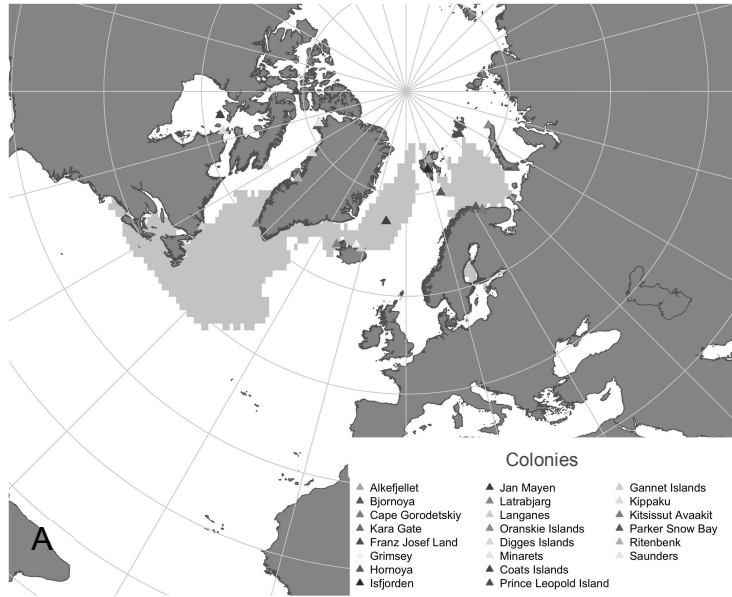
FEBRUARY



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 CO₂ emission scenario (RCP8.5) and towards the end of the 21st century (Figure 3 and 4, Supplemental materials X and XI). Moreover, our projections showed that climate change is predicted to modify prey availability 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).

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° intervals and the map is projected as North Pole Lambert Azimuthal Equal Area.



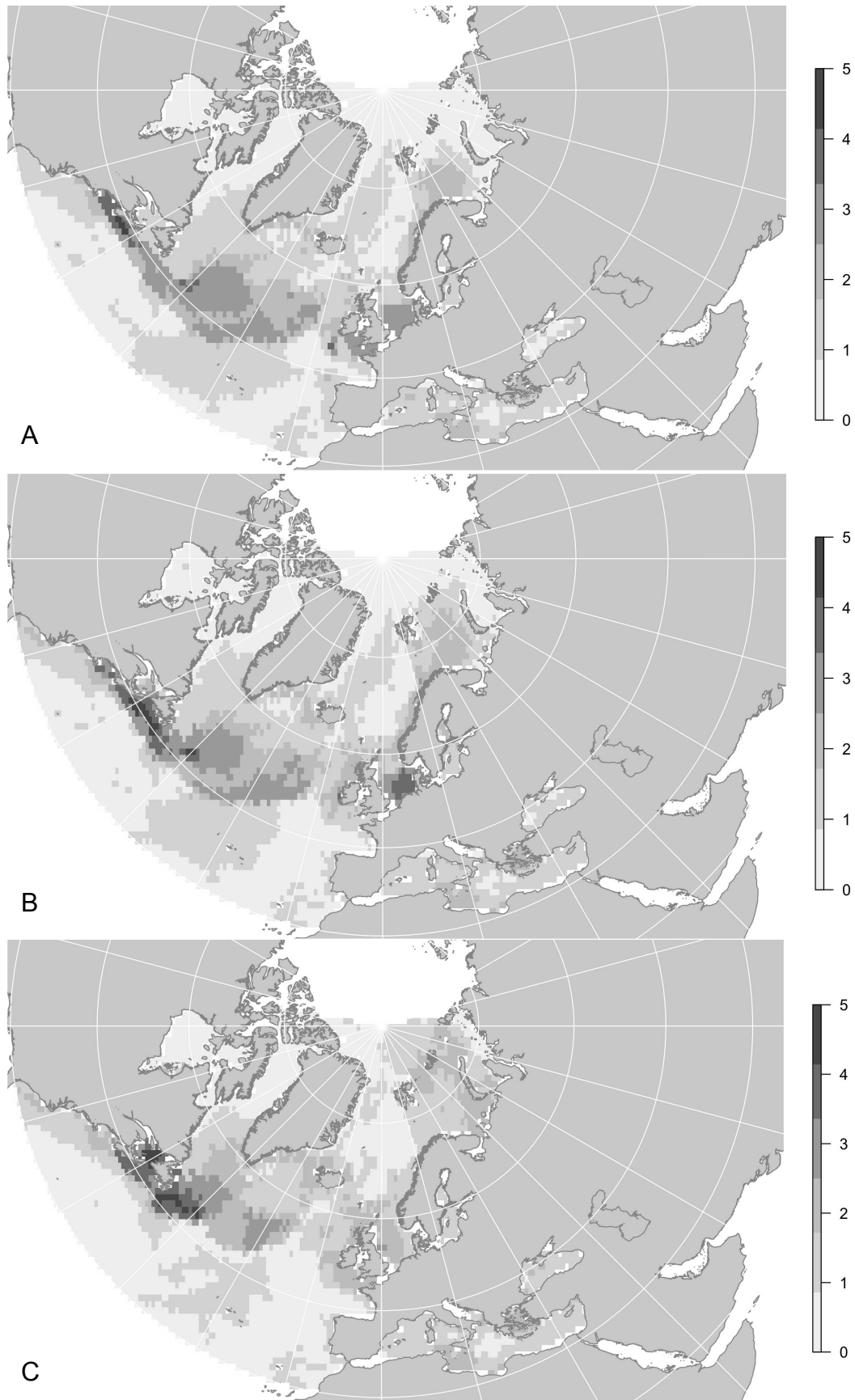


Figure 4. Count of species for which the pixel considered is predicted to be a selected habitat in January 2006-2015 (A) and in January 2090-2100 according to the RCP2.6 scenario (B) and the RCP8.5 scenario (C). Maps for other months and time periods (2045-2055) are provided in Supplemental materials X and XI. Graticules are displayed at 15° intervals and the map is projected as North Pole Lambert Azimuthal Equal Area.

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 intensifies. Further, in November, seabirds were projected to shift towards 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 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 Table 1). Selected habitats size was predicted to increase for common guillemots (for example, 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 (+/- 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 (+/- 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.

	October				November				December				January				February			
	2045-2055		2090-2100		2045-2055		2090-2100		2045-2055		2090-2100		2045-2055		2090-2100		2045-2055		2090-2100	
	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP	RCP
Little auks	11.5	4.8	-7.5	-65.2	2.9	-16.9	-3.8	-24.3	-4.7	-18.7	-6.6	-29.1	-9.7	-15.2	-7.4	-42.3	-3.6	-9.9	-3.0	-31.4
Black-legged kittiwakes	16.7	20.7	-11.3	-63.6	4.1	3.2	2.4	-25.7	6.7	-5.9	0.3	-24.5	5.0	7.2	-1.2	-22.1	5.8	8.8	5.5	-17.1
Atlantic puffins	-3.4	1.7	-5.2	-4.7	-9.2	-9.1	1.2	-2.0	-0.9	-3.4	1.1	1.6	1.3	-1.8	1.1	1.6	1.7	0.2	-1.5	-3.2
Common guillemots	37.3	61.0	42.1	105.2	26.8	46.8	34.0	108.5	24.0	50.2	36.8	113.9	21.1	46.7	38.1	102.0	17.3	34.8	25.9	90.4
Brünnich's guillemots	32.1	18.0	23.5	4.4	25.0	22.3	5.9	-12.8	12.6	11.9	3.8	-0.49	5.2	8.6	1.6	-10.2	3.9	3.1	4.0	-2.5

Table 1. Variation relative to present (in %) of the size of predicted selected habitat.

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 confirms that meeting Paris Agreement Objectives will limit habitat range shifts of the North Atlantic Ocean seabird community in 21st century in comparison with shifts induce 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 spatio-temporal 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. For example, due to some lack of information about seabird winter diet, we extrapolated the diets, using those for birds from a subsample of all colonies. In the same line, 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. Further, we limited the complexity of RSF models, by only considering energy requirements and relative prey abundances, omitting the roles of abiotic factors such as day length or biotic factors like competition, predation or cost of transport (linked with migratory distance). Notably, day length may have an incidence on foraging times, although seabirds have shown surprising abilities to cope with the polar night (Ostaszewska, Balazy, Berge, & Johnsen, 2017). Moreover, by modeling future distributions, we assume that the statistical link between seabird distributions, their energyscapes and prey fields will hold across time (Gremillet & Charmantier, 2010). Finally, our predictions result from model stacking, but RSF analyses yielded high predictive power and accuracy, providing support to our approach. In this context, limitations of studies based on DBEM, Niche MapperTM and HadGEM2-ES climatic models have been previously described and positively rated (Cheung et al., 2009; Collins et al., 2011; Fort, Porter, & Grémillet, 2011), suggesting that our work can indeed provide valuable predictions.

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, Jessopp, Bennison, & Jessopp, 2015), the Barents Sea (Gabrielsen, 2009), the North Sea (Harris, Daunt, Newell, Phillips, & Wanless, 2010), the Icelandic coast (Garðarsson, 1999) and southwest Greenland (Boertmann, Lyngs, Merkel, & Mosbech, 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, Rodrigues, & Manica, 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 (see Supplemental materials VI and VII), with impacts on their distributions (see Supplemental materials VIII and IX). Further work will be necessary to fully understand population consequences of these changes (Carneiro et al., 2020).

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, Low, Ellis, & Reynolds, 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, Perdeck, van Balen, & Both, 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 spatio-temporal mismatches with their food base and lead them into ecological traps (Durant, Hjernann, Ottersen, & Stenseth, 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 spatio-temporally, 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 (Newton, 2010; Clairbaux et al., 2019). Moreover, shifts in marine ecosystem composition and structure caused by global warming likely require seabirds to change their diets and behaviours (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, Divoky, & Friesen, 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).

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 provides new information and methods to identify seabird wintering hotspots in the North Atlantic Ocean, and allow modeling future spatio-temporal 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, Grémillet, Crawford, & Ryan, 2010). In practice, a first essential step towards 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, Authier, & Grémillet, 2018).

Supplementary materials

Available at: <https://osf.io/qbx25>

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CHAPTER III

**CLIMATE CHANGE COULD OVERTURN BIRD
MIGRATION: TRANSARCTIC FLIGHTS AND HIGH-
LATITUDE RESIDENCY IN A SEA ICE FREE ARCTIC**

Climate change could overturn bird migration: Transarctic flights and high-latitude residency in a sea ice free Arctic

Manon Clairbaux, Jérôme Fort, Paul Mathewson, Warren Porter, Hallvard Strøm, David Grémillet

Abstract

Climate models predict that by 2050 the Arctic Ocean will be sea ice free each summer. Removing this barrier between the Atlantic and the Pacific will modify a wide range of ecological processes, including bird migration. Using published information, we identified 29 arctic-breeding seabird species, which currently migrate in the North Atlantic and could shift to a transarctic migration towards the North Pacific. We also identified 24 arctic-breeding seabird species which may shift from a migratory strategy to high-arctic year-round residency.

To illustrate the biogeographical consequences of such drastic migratory shifts, we performed an in-depth study of little auks (*Alle alle*), the most numerous arctic seabird. Coupling species distribution models and climatic models, we assessed the adequacy of future wintering and breeding areas for transarctic migrants and high-arctic year-round residents. Further, we used a mechanistic bioenergetics model (Niche MapperTM), to compare the energetic costs of current little auk migration in the North Atlantic with potential transarctic and high-arctic residency strategies.

Surprisingly, our results indicate that transarctic little auk migration, from the North Atlantic towards the North Pacific, may only be half as costly, energetically, than high-arctic residency or migration to the North Atlantic.

Our study illustrates how global warming may radically modify the biogeography of migratory species, and provides a general methodological framework linking migratory energetics and spatial ecology.

Keywords: Arctic birds, Cryosphere, Energy requirements, Migratory flyway, Niche MapperTM, SDM

Introduction

The Arctic environment is highly seasonal and bird breeding phenologies closely match enhanced spring and summer resource availability (Dingle & Drake, 2007). Most species subsequently leave the Arctic to winter at lower latitudes, resulting in the migration of billions of individuals. Migration and overwintering are periods during which high mortality occurs (Harris, Daunt, Newell, Phillips, & Wanless, 2010; Newton, 2010). Long-distance flights and winter habitat quality may also have carry-over effects on subsequent breeding success (Bogdanova et al., 2017; Sorensen, Hipfner, Kyser, & Norris, 2009). Overall, migration greatly contributes to shaping bird population dynamics (Newton, 2010; Somveille, 2016). Studying arctic bird migration at the individual, population, species and community levels is therefore a major research objective, which has greatly benefited from recent developments in migration tracking technologies. These technologies allow a better understanding of how birds might choose migratory routes and wintering areas, and help analyze the interplay between genetic and phenotypic plasticity in shaping bird responses to geographical and ecological barriers (Wang et al., 2018), intra- and interspecific competition (Fort et al., 2013), as well as the consequences of environmental change (Lameris et al., 2018).

Climate change has direct and indirect effects on birds (Durant et al., 2004) and migratory species are particularly sensitive. Notably, altered climatic conditions can modify migratory phenologies (Both & te Marvelde, 2007; Rubolini, Møller, Rainio, & Lehikoinen, 2007) and result in shifting wintering and/or breeding areas, with consequences for migratory distances (Newton, 2010; Visser, Perdeck, van Balen, & Both, 2009). Global changes may even result in species/populations switching from a migratory to a resident strategy, and *vice versa* (Newton, 2010; Pulido & Berthold, 2010).

Global warming is fastest in the Arctic, with a temperature increase more than twice the world's average (IPCC, 2014). This has marked impacts on the arctic cryosphere: The central part of the Arctic Basin, where some areas have been permanently covered by multi-year sea ice for at least the last 5,500 years (England et al., 2008), is supposed to become completely sea ice free each summer before the mid-21st-century (IPCC, 2014; Wang & Overland, 2012). Such a drastic habitat modification will have major consequences for large scale ocean circulation (Holland, Bitz, Eby, & Weaver, 2001; Polyak et al., 2010) but also for Arctic Ocean acidity (Steinacher, Joos, Frölicher, Plattner, & Doney, 2009) and productivity (Vancoppenolle et al., 2013; Yool, Popova, & Coward, 2015), with impacts on ecological processes (Meier et al., 2014; Moline et al., 2008; Post et al., 2013).

Former glacial cycles governed transarctic exchanges between Pacific and Atlantic biota across time, leading to population mixing or isolation, and shaping evolution (Polyak et al., 2010). Thereby, colonization from the Pacific into the high Arctic and the North Atlantic already occurred in the mid/end Pliocene, induced by mild arctic conditions and ended by sea ice expansion (Vermeij & Roopnarine, 2008).

Currently, Arctic sea ice is an ecological barrier for migratory birds. Henningsson and Alerstam (Henningsson & Alerstam, 2005) also rated transarctic migration as particularly difficult for birds because of navigational issues (but see Alerstam et al., 2007; Åkesson, Morin, Muheim, & Ottosson, 2001) and of the lack of stop-over sites. With sea ice constraining the availability of stop-over sites, more costly and risky non-stop transarctic flights are therefore unlikely. Conversely, migration along sea ice edges at the periphery of the Arctic Basin seems much more widespread (Alerstam et al., 2007). Also, radar studies and direct observations demonstrated that several species of seabirds are capable of crossing the Arctic Basin (Alerstam & Gudmundsson, 1999; Mckeon et al., 2016) as already observed in fishes (Wisz et al., 2015) and marine mammals (Mckeon et al., 2016).

Re-creating sea ice free conditions favorable for transarctic exchanges (Vermeij & Roopnarine, 2008), climate change is in the process of drastically modifying constraints set upon arctic bird migration by sea ice. Indeed, Vermeij and Roopnarine (2008) predicted that a sea ice free Arctic Basin in summer will lead to enhanced transarctic migrations between the Atlantic and the Pacific oceans. Concomitantly with shifting migratory routes and wintering areas, some arctic-breeding bird species may also become year-round residents. High latitudes and the associated polar night has long been thought to impose a major constraint upon such a strategy, yet a series of recent studies demonstrated that birds may cope surprisingly well with very low light levels (Berge et al., 2015; Grémillet et al., 2005; Ostaszewska, Balazy, Berge, & Johnsen, 2017).

In this context, the objectives of this study were to: 1) Determine which birds species could switch to transarctic bird migration and/or arctic year-round residency as a result of a decreasing sea ice cover within the Arctic Basin. 2) Assess the adequacy of future wintering and breeding habitats in the context of these two new migratory strategies. 3) Compare the energetics of current bird migration in the North Atlantic, with those linked to potential transarctic and high-arctic residency strategies.

As our aim was to study the impact of reduced sea ice cover on the propensity of birds to become transarctic migrants and/or year round residents, we focused on coastal and marine species. We thereby assumed that they are more directly impacted by a vanishing arctic sea ice cover. With respect to transarctic migration, we narrowed the range of studied species by selecting those which are pelagic during winter.

Indeed, those species will benefit the most from a sea ice free Arctic Basin in future summers, and we assumed that they would consequently be the most prone to engage in new transarctic migrations. We assumed that for terrestrial or coastal birds with land based feeding habits, the sea would represent the same ecological barrier as an un-melted Arctic Basin.

Even if species are ecophysiologicaly capable of engaging in new migratory strategies, shifting to residency or to new transarctic migration induces the use of new breeding and/or wintering areas. Modeling of those future habitats is needed to assess their adequacy with potential new migratory strategies, for each species concerned. To this aim, we propose a methodological framework based on a mechanistic bioenergetics modelling (Niche MapperTM), which we applied to little auks (*Alle alle*) as an example.

This species was chosen because the little auk is the most numerous seabird in the North Atlantic Arctic (population estimated at 40-80 million individuals (Egevang, Boertmann, Mosbech, & Tamstorf, 2003)), with significant impact on terrestrial and marine trophic networks (González-Bergonzoni et al., 2017) and an acknowledged sensitivity to environmental changes (Amélineau et al., 2019; Grémillet et al., 2012; Jakubas, Iliszko, Wojczulanis-Jakubas, & Stempniewicz, 2012; Welcker et al., 2009). On the basis of its morphological and ecophysiological traits, we short-listed the little auk as a likely candidate for future year-round residency in the high Arctic, and/or for new transarctic migration (see Methods), from the North Atlantic into the Pacific.

Methods

1. Species selections

We defined the Arctic according to boundaries set by the Arctic Council and its working groups, notably the Conservation of Arctic Fauna and Flora (CAFF; <https://www.caff.is>) (Scott, 1998). Following CAFF (Scott, 1998), we selected coastal and marine birds among 316 migratory/partially migratory bird species whose breeding ranges overlapped by at least 5% with the arctic region. We assumed that bird species which are currently year-round residents of the Arctic would remain so. Indeed, shifting from a residency to a migratory strategy is far less frequent than the opposite shift (Newton, 2010). Finally, even though poleward shifts in bird distributions do occur in response to climate change (Brommer, Lehikoinen, & Valkama, 2012; Pearce-Higgins & Green, 2014) we did not include new species that may migrate into the Arctic in summer as a consequence of global warming. This would go beyond the scope of our current analysis, but would certainly be a valid target for future work.

1.1. Selection of potential new resident arctic bird species

We narrowed the range of studied species, by selecting those which primarily use coastal and marine habitats. Even in a climate change context high latitude photoperiods will remain unchanged and arctic winter residents will always have to cope with the polar night. We therefore further reduced our sample to species, or family of species, for which nocturnal activities (in particular foraging) have been described in literature, indicating that the considered species are potentially anatomically and ecophysiologicaly capable of surviving the polar night.

1.2. Selection of bird species susceptible to shift to a transarctic migration

We used the CAFF list of migrant arctic breeding birds (see above), and selected species with a primarily pelagic habitat during winter.

2. Predicting little auk's future habitats with ecological niche modeling

Little auks mainly breed (May to August) in Greenland, Svalbard and the Russian Western Arctic, and currently migrate southwards into the Atlantic, with at-sea wintering areas (October to February) ranging from the Barents Sea to Newfoundland (Fort et al., 2013) (See supplemental materials I). Following the aforementioned species selection, we short-listed the little auk as a likely candidate for future year-round residency in the high Arctic, and/or for new transarctic migration, from the North Atlantic into the Pacific (Figure 1).

Current and future little auk nesting, summer foraging and wintering habitat distributions were modelled with 'biomod2' (Thuiller, Georges, Engler, & Breiner, 2016), which draws from current occurrences to predict suitable habitats in space and time, on the basis of environmental conditions.

2.1. Little auk occurrence data

Current occurrence data were direct observations drawn from three open access databases, the Global Biodiversity Information Facility (<https://www.gbif.org/>), the Ocean Biogeographic Information System-Spatial Ecological Analysis of Megavertebrate Population (<http://seamap.env.duke.edu/>) and the North Pacific Pelagic Seabird Database (https://www.usgs.gov/centers/asc/science/north-pacific-pelagic-seabird-database?qt-science_center_objects=0#qt-science_center_objects), and complemented with information on breeding locations from the literature (Fort, Beaugrand, Grémillet, & Phillips, 2012; Fort et al., 2013; Karnovsky, Kwaśniewski, Węśławski, Walkusz, & Beszczyńska-Möller, 2003) and from the Norwegian Polar Institute (Strøm, Descamps, & Bakken, 2008) (Russian data excluded). Only dated and located data for which environmental variables were available (see below), were conserved and duplicates deleted. Museum data weren't considered.

Overall, we used respectively 67, 68 and 580 occurrences to model nesting, summer foraging and wintering habitats.

2.2. Environmental data

To predict nest site distributions, we used monthly mean air surface temperatures from 1948 to 2018 retrieved from National Oceanic and Atmospheric Administration (NOAA)'s 0.5° Global Historical Climatology Network version 2/Climate Anomaly Monitoring System. Since little auks breed underground and are limited by snow cover in their access to nest cavities, we calculated the percentage of time during which the ground was covered by snow two months before, and during the breeding period using the National Snow and Ice Data Center (NSIDC)'s IMS 4 km Daily Northern Hemisphere Snow and Ice Analysis between 2006 and 2017. Also, since little auks are central-place foragers during the breeding season, and have a constrained foraging range during that period, we created a discrete variable to deal with the distance from the coast (<10 km, <20 km, <50 km, <100km, <200km or >=200km).

Previous work showed that wintering little auks are significantly constrained by air temperatures (Fort et al., 2012). For marine areas, we therefore used monthly mean air surface temperature data from 1960 to 2017 retrieved from NOAA 1° International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Since bathymetry and sea ice constrain little auk foraging (Amélineau, Grémillet, Bonnet, Bot, & Fort, 2016; Wojczulanis-Jakubas et al., 2014), we calculated the slope of the bathymetry using General Bathymetric Chart of the Oceans (GEBCO) 30 arc-second interval grid and used monthly sea ice concentration data (1978-2017) from the 25km*25km NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration. Used variables were not correlated as tested with a 0.8 threshold in a Pearson pairwise correlation test (Menard, 2002) and a threshold of 10 for the variance inflation factor analysis. All environmental data were interpolated linearly on a 0.1° spatial grid, in the Northern Hemisphere. Environmental values were extracted for the year and month corresponding to each occurrence data.

2.3. Climate models

To make future predictions, environmental variables (see above) were considered under Intergovernmental Panel on Climate Change (IPCC)'s RCP8.5 scenario using four climatic models (HadGEM2-CC, HadGEM2-ES, ACCESS1.0 and ACCESS1.3) considered as performant (reasonably simulating recent past climate) when predicting future Arctic climates, in particular the cryosphere (Wang & Overland, 2012).

2.4. Modeling Little auk distributions

We used a model averaging approach in the ‘biomod2’ package in R (Thuiller et al., 2016) with Boosted Regression Tree (BRT), Random Forest (RF), Classification Tree Analysis (CTA) and Flexible Discriminant Analysis (FDA) algorithms which deal in the same way with pseudo-absences parametrization (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). Beyond existing presence data, we generated five sets of 1000 random pseudo-absences outside of current range (SRE method) and ten sets of 100 random pseudo-absences outside of a 2° area around each presence data, for wintering and for summer nesting/foraging distribution modeling, respectively. Pseudo-absences were time-stamped using the same temporal distribution as occurrence data, and environmental variables were extracted according to each location and date. We performed three runs for each set of pseudo-absences, with each distribution modeling and each ‘biomod2’ algorithm. For each run, outputs were assessed with the True Skill Statistic (TSS) and the importance of each environmental variables was calculated. Finally, for each distribution model, all obtained models (number of algorithms *3*number of pseudo-absence data sets) were weighted with TSS, and averaged to yield a single ensemble model. Those final models were evaluated with the continuous Boyce index (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006), which assess presence-only predictions and vary between -1 and 1, with 1 indicating good to perfect predictions (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). Each final distribution model was then projected across space and time to map little auk potential distribution. For each future distribution projection, we calculated the coefficient of variation between climatic models.

We considered an area suitable for little auks when its probability of suitability (habitat suitability index) was higher than 0.9 (a high conservative threshold set with ‘biomod2’ (Thuiller et al., 2016)). For distributions related to each climatic model, we assumed that suitable nesting sites within 200 km of suitable foraging areas were potential breeding areas. Indeed, the maximum foraging range for little auks during the breeding period rarely exceed 200 km (Amélineau et al., 2016; Jakubas et al., 2016; Welcker et al., 2009). Because environmental variables available in ACCESS 1.0 and ACCESS1.3 climatic models did not allow nesting distribution predictions, we used nesting sites obtained with the HadGEM2-CC and HadGEM2-ES climatic models. Further, we assumed that resident wintering little auks would remain in marine areas within 250 km of potential or known breeding sites.

3. Energetic consequences of future migratory strategies

To calculate present and future little auk energy requirements according to each migratory strategy (current migration, residency or transarctic migration), we used Niche Mapper™ (see (Fort, 2009; Kearney & Porter, 2009; Porter & Mitchell, 2006)). This mechanistic model contains a microclimate module, which provides environmental data for the immediate surroundings of the animal, and an animal module, which integrates outputs from the microclimate model with animal morphological, behavioral and physiological characteristics. Those modules are used to solve heat balance equations between the animal's body and its surroundings, and estimate the metabolic rate required for the animal to remain in a thermal steady-state. Niche Mapper™ simulations were performed for the little auks population breeding in Franz Josef Land (Russian Federation), because both winter residency and transarctic migration are plausible for birds from this locality (see Results below) and their current wintering areas are known (Figure 1). Niche Mapper™ has been previously used to model little auk wintering energetics (Amélineau et al., 2018; Fort, Porter, & Grémillet, 2009), and we built up on this prior work, notably using a majority of the same input values for bird morphological and physiological characteristics.

We modelled current and future little auk energy requirements during their migratory journey (in September and March) and wintering phase (October to February) according to three scenarios: 1) Current migration: At their current wintering areas in the North Atlantic (defined as the centroid of kernel distribution available on the SEATRACK website, see also Figure 1). 2) Transarctic migration: At potential future wintering locations in the North Pacific, corresponding to the closer area predicted as suitable for the four climatic models using 'biomod2' (see previous section and results) (Figure 1). 3) Residency: Within 250 km of their potential future breeding site in Franz Josef Land, in areas predicted as suitable using 'biomod2' (Figure 1). For each strategy, the migratory flyway used in September was considered as the straight line between the colony and the wintering location, avoiding flights >100 consecutive km across land (Figure 1). In the spring, the Arctic Basin is predicted to remain iced until much later in the 21st century, and it is unclear whether little auks would engage in a direct flight to the Atlantic, or will perform a loop migration, whereby the return journey will use polynyas peripheral to the Arctic Basin as stop-over sites. Both cases were studied, by considering a direct flyway (the same as in September) or a peripheral one, the latter corresponding to a path minimizing the time spent flying above areas dense in sea-ice (Figure 1). For the current and residency strategies, the spring return journey is supposed to be the same as in September.

All required current and future environmental variables were retrieved from climatic models previously described. Outputs from climatic models were averaged on a 0.1° spatial grid for each environmental variable across 2006-2017 for the current scenario and across 2050-2059 for future predictions. Environmental values between October and February were then extracted for each strategy at the wintering location. Environmental conditions experienced during the migratory journey

(in September and March) were calculated as the average of environmental values encountered during the trip for those months. Percentage of time spent flying per day during this travel was calculated assuming that birds migrated in one month, with an average flight speed of 13 m.s^{-1} (Nettleship & Birkhead, 1985). For each scenario, energetic costs obtained were averaged for the four climatic models and standard deviations between them were calculated.

All input data are available in Supplemental materials II.

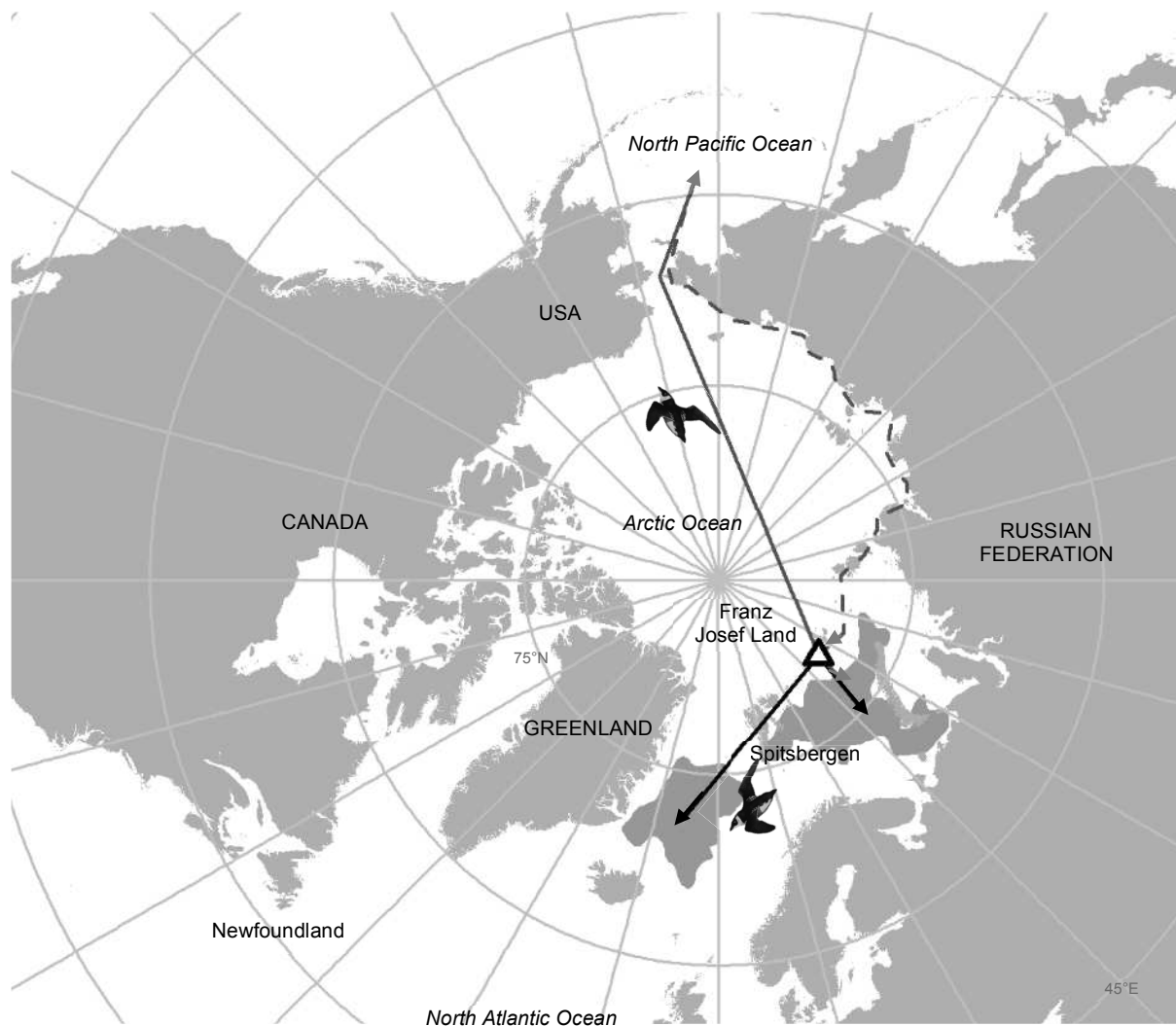


Figure 14. Current (black arrows) and future (grey arrows) migratory strategies of little auks breeding in Franz Josef Land (white triangle). In March, the return journey from Pacific could be made directly (grey arrows) or by a peripheral flyway (grey dashed arrows). Their current known wintering areas (<http://www.seapop.no/en/seatrack/>) are in blue. Graticules are set at a 15° interval and the map is projected as North Pole Lambert Azimuthal Equal Area.

Little auks drawings used in this figures were extracted from Richard Crossley's picture (available online under CC-BY-SA license <https://creativecommons.org/licenses/by-sa/2.0/legalcode> at https://commons.wikimedia.org/wiki/File:Little_Auk_from_the_Crossley_ID_Guide_Britain_and_Ireland.jpg).

Results

1. Species selections

Among the 449 species which breed or have bred in the Arctic (Scott, 1998), 359 (80%) have a breeding range which overlaps to >5% with the Arctic as defined by CAFF (Scott, 1998). Among those, 316 (88 %) are migrants or partial migrants (see Supplemental materials III), and belong to 44 families (see Supplemental materials III). During winter, 29 of those species are pelagic (essentially alcids, gulls and skuas) and another 37 (mainly ducks and gulls) utilize costal marine habitats (see Supplemental materials III). Only 24 (see Supplemental materials IV) of those 66 species are likely to remain active during the polar night, and may become year-round residents to the Arctic in the future. Alcids and gulls represent 42% of those species but some ducks, cormorants, petrels, shearwaters and loons, are potential future residents. Overall, our bibliography study indicated that only 29 pelagic species (6.5% of all arctic breeding species) are potential candidates for future transarctic migrations (see Supplemental materials III).

2. Predicting current and future little auk habitats

Modelled current little auk habitats are presented in Figure 2 and Supplemental materials V. All averaging models concerning the breeding and wintering periods had a continuous Boyce Index close to 1 (0.823 and 0.769 for nesting and foraging areas respectively and 0.936 for winter area). According to 'biomod2', air temperature was the main driver of little auk marine distributions, whereas distance from the coast was the main driver of nesting distributions during the breeding season. During winter, highest suitability likelihoods were recorded both in the North Atlantic and in the North Pacific with some potential wintering hotspots in the North Sea and the Labrador Sea, which are in agreement with observed occurrences. During summer, predicted foraging areas seem to follow the sea ice edge, especially off East Greenland. Most known colonies were adequately predicted by model outputs, but the model seems to overfit in eastern Canada, by predicting suitable little auk habitat in regions where little auks do not breed. Future little auk habitats assessed according to the four climatic models are presented in Figure 2 and Supplemental materials V. The coefficient of variation map (Supplemental materials VI) comparing model outputs shows their general concurrence.

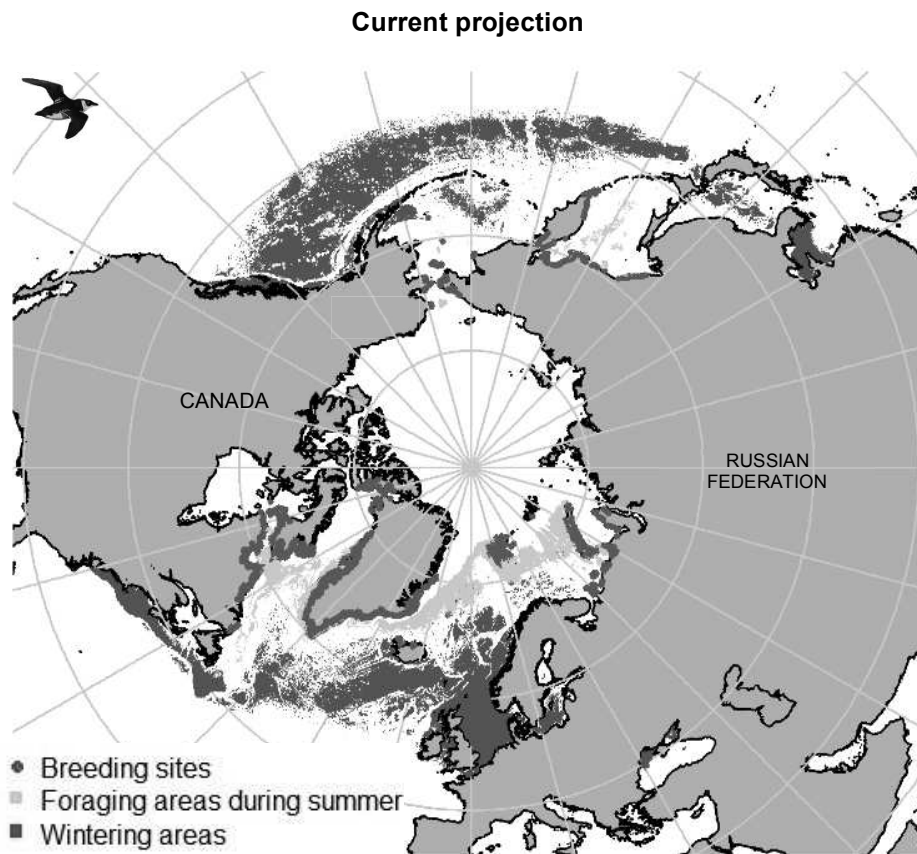
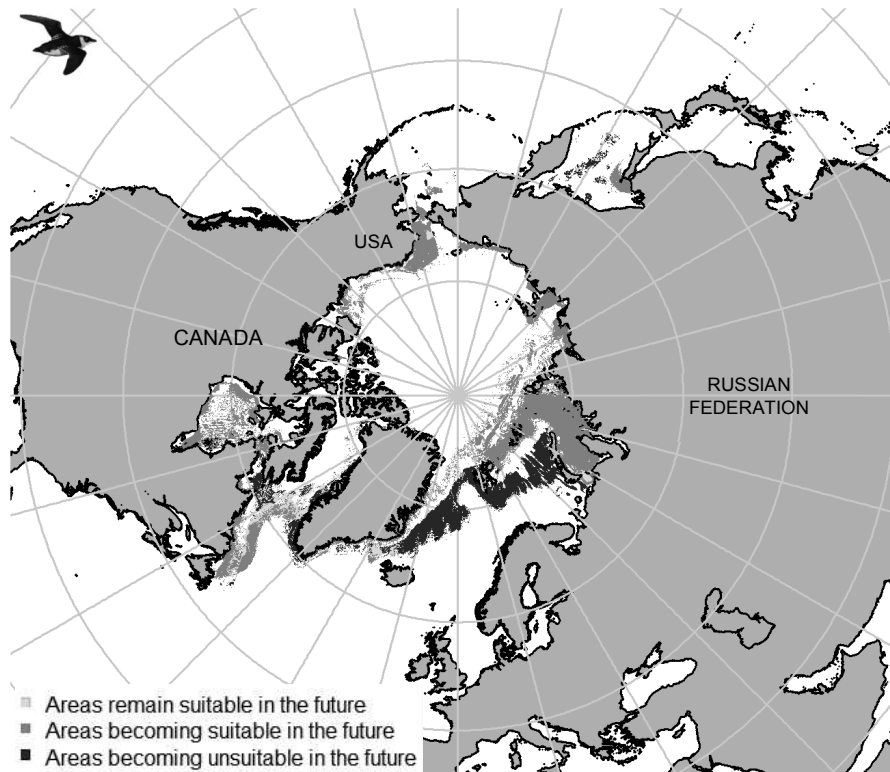


Figure 2. Potential suitable (suitability likelihood > 0.9) little auk habitats for present (2000-2017) and future (2050-2059, HadGEM2-ES climatic model, RCP 8.5 scenario) projections).

Overall, climate change is predicted to cause loss or gain of suitable little auk habitats, depending on the region (see Figure 3 and Supplemental materials V): For example, the Pacific Ocean off British Columbia (Canada) will become unsuitable for overwintering little auks, whereas the Barents Sea will become increasingly suitable. During summer, suitable foraging areas are predicted to shift northward, both in the Atlantic and in the Pacific. On land, breeding distributions are also predicted to shift northwards in response to climate change.

Crucially, the main breeding area of Thule in Northwest Greenland, which currently hosts half of the little auk world population, is predicted to become unsuitable according the climatic model HadGEM2-CC. Finally, model outputs suggested that shifting to transarctic migration towards the Pacific is a potential option for North Atlantic little auks. However, predicted migratory distance varied considerably, depending on the climatic model considered. Year-round high-arctic residency is also predicted to occur in the future, close to some nesting sites (Supplemental materials V and Figure 4).

Changes in the distribution of suitable foraging areas in summer between present and future



Changes in the distribution of suitable wintering areas between present and future

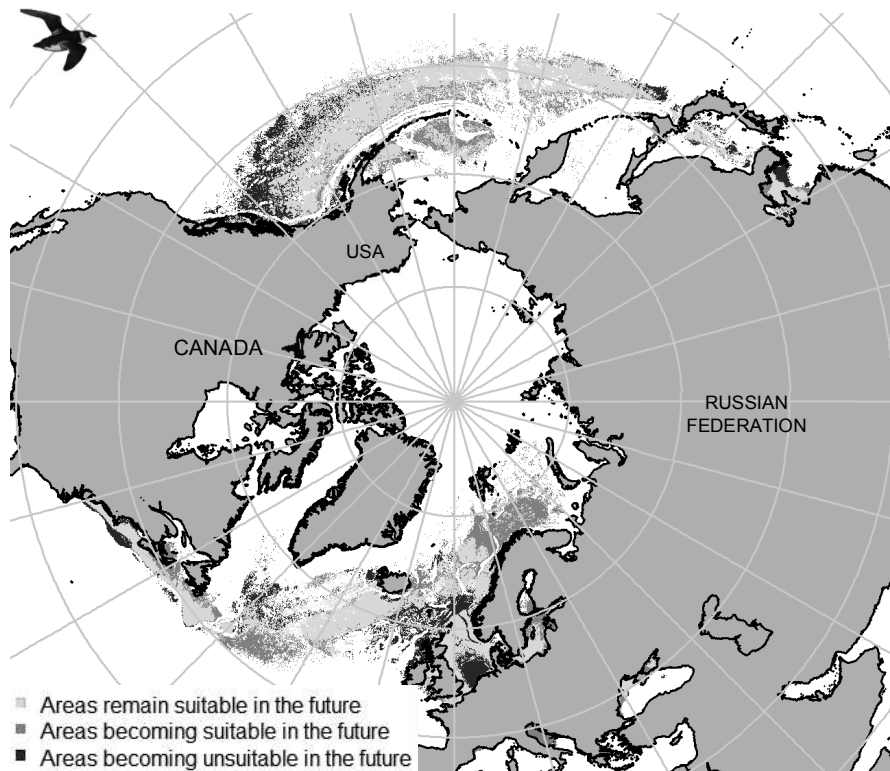


Figure 3. Changes in the potential distribution of suitable foraging and wintering habitats between present (2000-2017) and future (2050-2059, HadGEM2-ES climatic model, RCP 8.5 scenario) projections.

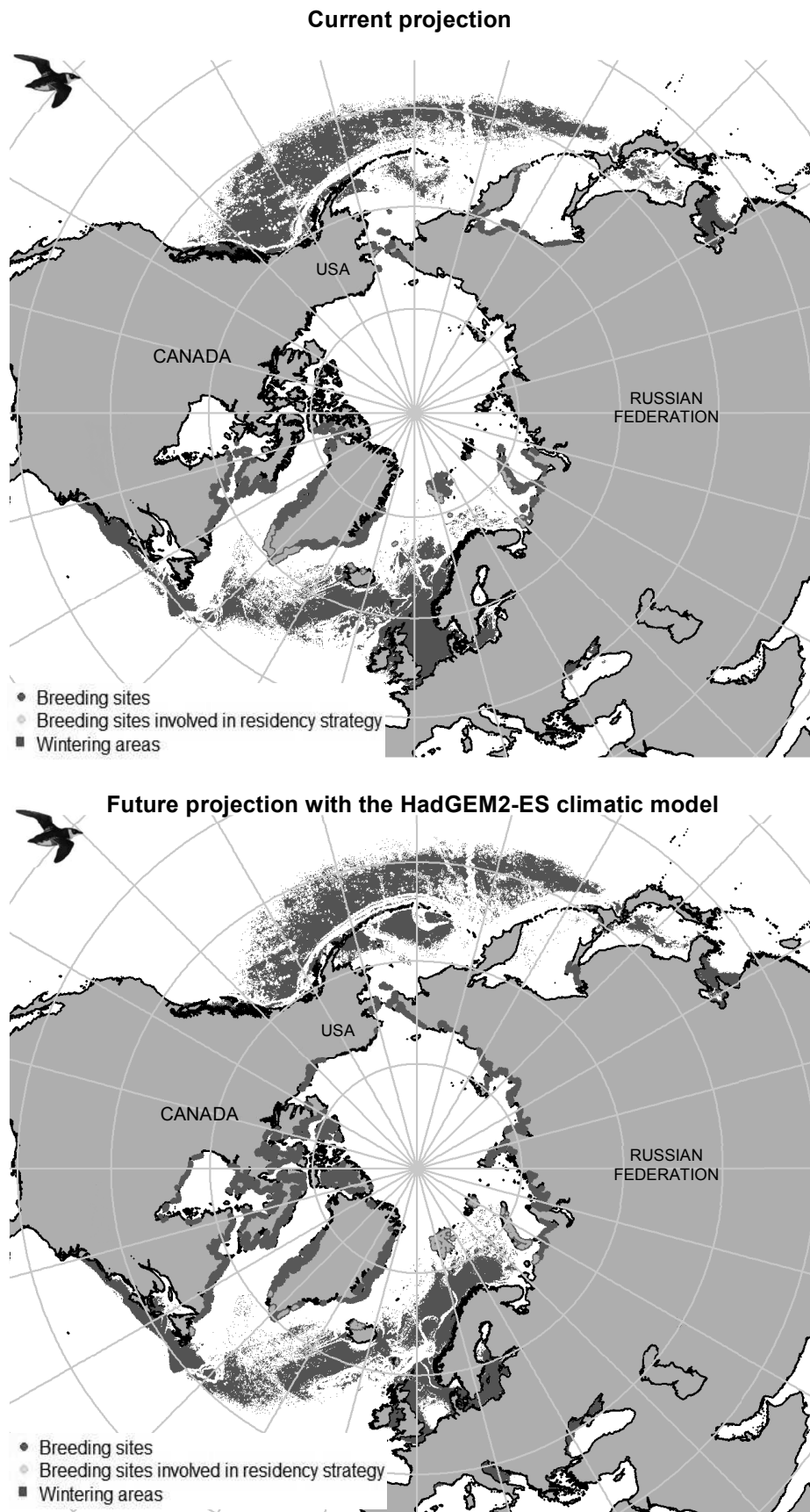


Figure 4. Potential suitable (suitability likelihood > 0.9) little auk breeding habitats involved in the residency strategy, currently (2000-2017) and in the future (2050-2059, HadGEM2-ES climatic model, RCP 8.5 scenario).

3. Energy requirements linked to future migratory strategies

Little auks breeding in Franz Josef Land currently winter predominantly in the Barents Sea and off Jan Mayen (North Atlantic). In these areas, their current daily energy requirements are predicted to increase throughout the non-breeding period (September to March), from 449 +/- 57 to 760 +/- 6 kJday⁻¹ off Jan Mayen and from 732 +/- 2 to 772 +/- 8 kJday⁻¹ in the Barents Sea. Rising winter energy requirements has already been observed in the Atlantic for little auks overwintering off Newfoundland, and is explained by the decreasing air temperatures (Fort et al., 2012). Across the winter period, birds were predicted to require a total of 138 +/- 3 MJ off Jan Mayen and 161 +/- 1 MJ in the Barents Sea. According to the four climatic models considered, winter energy requirements linked to the little auks' current migratory strategy are predicted to decrease slightly in the future (Figure 5). Their future total energy requirements may therefore decrease to 119 +/- 4 MJ off Jan Mayen and to 158 +/- 0.1 MJ in the Barents Sea. In comparison, predicted daily requirements of little auks wintering in the North Pacific are considerably lower, and range, on average, from 267 +/- 2 kJday⁻¹ in September to 323 +/- 6 kJday⁻¹ or 322 +/- 5.8 kJday⁻¹ in March according to the migratory flyway considered (direct or peripheral, respectively). Indeed, favorable thermal conditions encountered along the peripheral route offset the enhanced flight costs due to the greater travelling distance. Overall wintering costs (accounting for flights across the arctic basin) are 59 +/- 0.7 MJ for this transarctic strategy according to the four climatic models. Sea surface and air temperature are main drivers of little auk winter energy requirements (Amélineau et al., 2018; Fort et al., 2012), and since those temperatures are higher in the North Pacific in winter, they explain lower overall energy requirements for little auks engaging in transarctic migration, despite higher flight costs. Little auks from Franz Josef Land are predicted to become year-round residents only under the ACCESS 1.3 and HadGEM2-ES climatic models: Under these conditions, their energy requirements are predicted to range between 737 +/- 2 kJday⁻¹ in September and 761 +/- 2 kJday⁻¹ in March. Little auk overall winter energy requirements for this residency strategy are then estimated to 159 +/- 0.3 MJ, similar to those of birds remaining in the Barents Sea in the future.

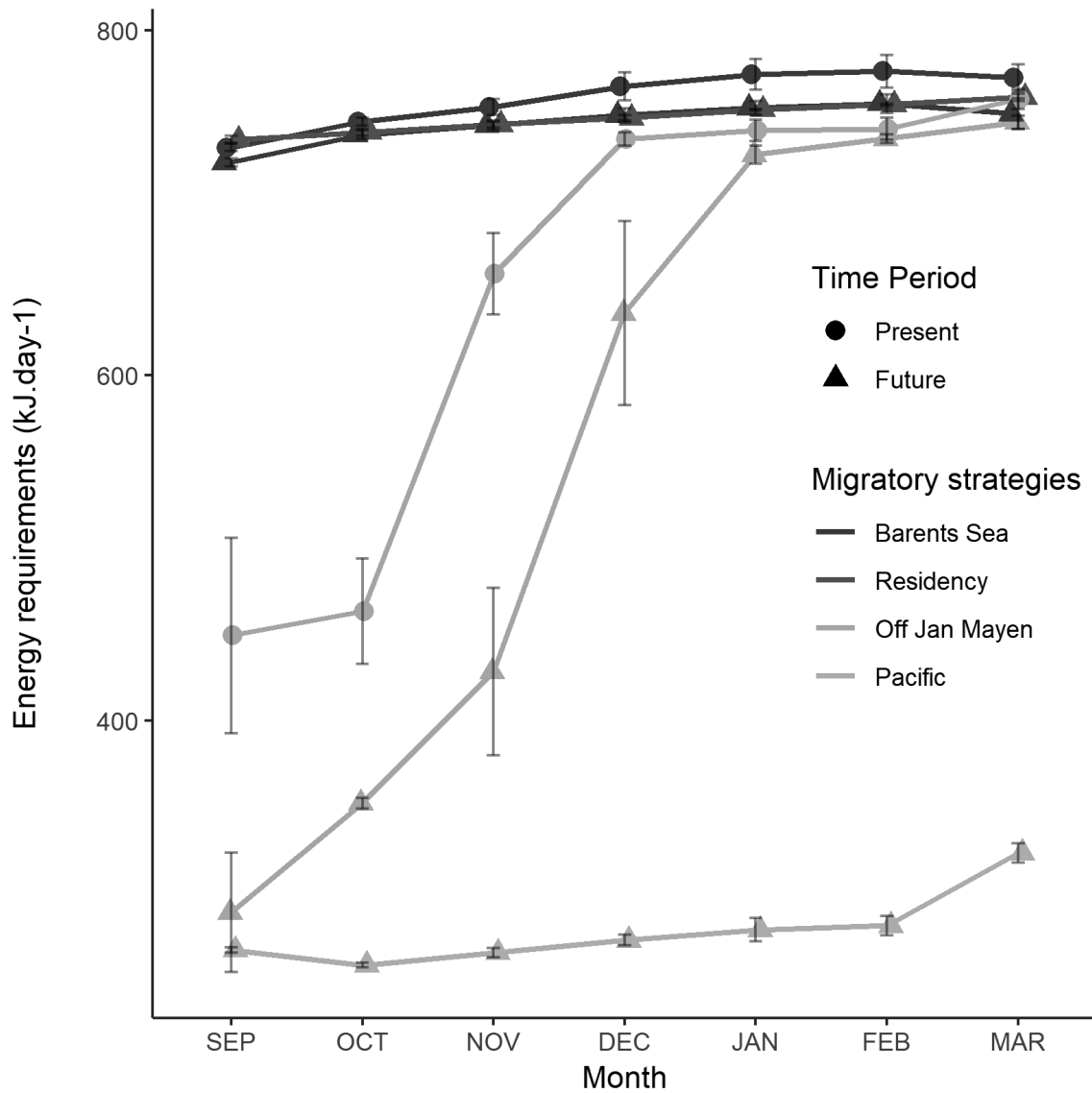


Figure 5. Average daily energy requirements (in $\text{kJ}\cdot\text{day}^{-1}$) for each month along the winter period according to different migratory strategies (see Figure 1). ‘Barents Sea’ is for birds wintering in the Barents Sea, just South of their breeding areas, ‘Residency’ for birds wintering close to their breeding site on Franz-Josef Land, ‘Off Jan Mayen’ for birds migrating away from Franz-Josef Land to winter close to Jan Mayen in the Western North Atlantic, and ‘Pacific’ for birds engaging in transarctic migration from the North Atlantic into the North Pacific. In the latter case return migration from the Pacific towards the Atlantic might cross the central arctic basin, or follow the periphery. Since both return strategies induce similar costs (see results), we only present one data set. Error bars correspond to standard deviations capturing the variation between climatic models

Discussion

Our study is, to the best of our knowledge, the first to address the impact of global change on arctic seabird migratory ecology, focusing both on a multi-species synthesis and on detailed statistical and mechanistic modelling of eco-energetics in a spatial context. Crucially, our work strongly suggests that arctic cryosphere loss may overturn migration patterns from the Atlantic into the Pacific, at least in some species. Also, as a consequence of global warming, other species may stop migrating, to become year-round residents of the high-Arctic. Beyond these surprising results, our analyses provide a conceptual framework which may be useful to understand and predict future bird migration in other regions of the world.

1. Potential limitations

Despite these advances, our results have limitations which should be examined carefully. First, even if we identified a suite of species for which migration may change radically in the near future, those remain a minority at the scale of the arctic seabird community. Selection criteria for future trans-arctic migrants or high-arctic residents were mainly morphological and physiological, and linked to their capacity to benefit from a sea ice free Arctic Ocean, and to feed on marine prey during the polar night. Thanks to new tracking technologies and winter expeditions, there is information available for some species (Berge et al., 2015; Orben et al., 2015). Yet, the migratory biology and the nocturnal behavior of many arctic seabird species still has not been subjected to detailed work. As results from biotelemetry studies typically reveal unexpected animal performances (Egevang et al., 2010; Hawkes et al., 2011) we speculate that future investigations will lead to expanding the list of potential transarctic migrants or year-round high-arctic residents.

Second, a strong assumption of our modelling work is that migratory ecology is primarily driven by environmental factors. This ignores the evolutionary and cultural history of studied populations. Indeed, past distributions (Newton, 2010), as well as local culture (Grémillet et al., 2004) have been demonstrated to shape animal distributions and migratory pathways, beyond current biotic and abiotic forcing factors. Nevertheless, there is also strong evidence that migratory birds do adjust their migratory ecology following global change, even at small spatio-temporal scales (Pearce-Higgins & Green, 2014). Further, migratory divides occurring within populations, and sometimes even within the same pair of breeding adults, may lead conspecifics to display radically different migratory strategies, towards different ocean basins (Davis, Maftai, & Mallory, 2016).

Third, and along the same lines, we used species distribution models (SDM) and a mechanistic model (Niche MapperTM), and our results are subjected to assumptions and limitations specific to these techniques (Elith & Leathwick, 2009; Guillera-Aroita et al., 2015; Guisan, Thuillier, & Zimmermann, 2017). The accuracy of Niche MapperTM predictions has been discussed and rated positively (Fort et

al., 2009) and we will not reiterate this information here. With respect to SDMs, we assumed that little auks are (i) at equilibrium with their environment, (ii) that statistical links between bird distributions and environmental data will still hold in the future and that (iii) we characterized the whole Hutchinsonian ecological niche for this species. The little auk is a long-lived seabird with low fecundity and high adult inter-annual survival (Stempniewicz, 2001), showing phenotypic plasticity (Grémillet et al., 2012) at small temporal and spatial scales. Nevertheless, its sensitivity to environmental changes (Amélineau et al., 2019; Grémillet et al., 2012) and the time scale chosen for our analysis allowed us to assume a steady state between little auks and their environment. Further, we also had to face some potential biases contained in the opportunistic occurrence data which we used, such as misidentification, geographical bias (data collected in places with easier access) and or/climatic bias (missing data from an area with different climatic characteristics). In our case, we reduced geographical and climatic biases impacts by choosing modelling procedures which minimize them when creating sets of pseudo-absences (Barbet-Massin et al., 2012).

Fourth, SDMs do not take into account biotic factors, such as trophic interactions, predation or competition (Elith & Leathwick, 2009). This might explain why our model overfitted current distributions in Eastern Canada, notably by predicting suitable breeding habitat where little auks do not currently breed (with the exception of a single colony on Baffin Island). Such discrepancies might be explained by potential mismatches between seabird observed occurrences, biotic and abiotic factors. For example, shaping the suitability of future habitats, the availability of food will put strong constraints on future birds' migration. By affecting the temperature, salinity, acidity and productivity of Arctic Ocean, sea ice melt will also drastically change the distribution of all marine taxa including fishes and zooplankton. Current and future prey fields are difficult to obtain at the scale considered, but should allow to better access the likelihood of future distribution and behavior of birds. Moreover, further information on rare but extreme events or on small scale conditions would be useful to increase our model performance when predicting suitable habitats: For example, if available, the presence of crevices for nesting would have been a practical factor to predict suitable breeding grounds and potentially avoid overfitting where strong slopes occur in the absence of scree.

Despite these limitations, SDMs presented in this study had high continuous Boyce indexes. Also, model outputs for current little auk distributions are in agreement with available bibliographic information (del Hoyo, Elliott, & Sargatal, 1996; Stempniewicz, 2001). For example, predicted suitable little auk breeding, foraging, and wintering habitats for the North Pacific are in agreement with the fact that individual little auks (typically less than five) are often observed on/near Saint Laurence Island in the Bering Sea (Day, DeGange, Divojy, & Troy, 1988) but also near Japan (Nakumura et al., 2003; Takada, 2001) or British Columbia (Halpin & Willie, 2014). Moreover, predicted current winter residency in Svalbard or South Greenland is also supported by observations of little auks off Spitsbergen during the polar night (Berge et al., 2015; Ostaszewska et al., 2017).

Finally, northwards shifts of suitable habitats predicted by our models are in agreement with others studies of marine top predators (Hazen et al., 2012) and on their prey (Ottersen et al., 2004; Reygondeau & Beaugrand, 2011).

2. From vagrancy to dispersal and migration

Beyond migration, seabird large-scale movements may also include vagrancy and dispersal (Newton, 2010). These principles apply to all organisms on the move but, to remain in an arctic context, we will illustrate them using our case study of little auks. In this species, vagrants (as defined by Newton (2010)) may leave North Atlantic breeding colonies, to fly across the Arctic Basin and reach the North Pacific, but without breeding there or ever returning to the Atlantic. Dispersing individuals (*sensu* Clobert (2001)) may show the same behavior, but are predicted to settle and breed (or at least attempt to) in the North Pacific. This might well be the case for the very few little auk individuals which are sighted on St Lawrence Island in the Bering Sea (Day et al., 1988). Under current and near future sea ice conditions, vagrancy and dispersal into the North Pacific are more likely to occur in little auks, than complete migration as hypothesized in our study. Indeed, in the case of a full migration between a North Atlantic breeding site and the North Pacific, the returning journey in spring will have to be peripheral to avoid dense sea ice and the presence and quality of future stop-over sites (as polynyas) will be major constraints. Indeed, polynyas have long been established as key feeding and resting sites for a wide range of polar organisms (Alaska Audubon, Conservancy Ocean, Oceana Pew Charitable Trusts, & (WWF) World Wildlife Fund, 2016; Heide-Jorgensen, Laidre, Quakenbush, & Citta, 2012; Stirling, 1995), especially during the winter period. Where and when polynyas will occur in the arctic in the future is nonetheless difficult to predict, but they are predicted to be impacted negatively by global warming (Smith & Barber, 2007). Vagrants, and dispersing individuals, which do not travel back to the Atlantic, will not be affected by spring sea ice conditions in the Arctic Basin, and are therefore more likely to engage in a one way transarctic flight to the North Pacific. Finally, those movements to the opposite side of the Arctic could lead to genetic mixing between previously-isolated populations, and encourage transmission of diseases/parasites.

3. Global relevance

The Arctic is subjected to drastic environmental changes and, at the request of arctic peoples, there is much research on the fate of species emblematic to this vast region, including birds (see (Wheeler et al., 2018)). Understanding current and future arctic bird distribution and migration has therefore been identified as a key objective by the Arctic Council and its working groups (in particular through the AMBI project <https://www.caff.is/arctic-migratory-birds-initiative-ambi>) and are the aim of recent studies (Amélineau et al., 2018; Fort et al., 2013; Frederiksen et al., 2016; Huettmann, Artukhin, Gilg, & Humphries, 2011). With sea ice melt, the Arctic will be more and more exposed to human pressures such as gas/oil extraction, fisheries, marine traffic or tourism.

Detailed ecological knowledge is therefore essential for the design of adaptive conservation strategies, within advanced marine spatial planning (Fort et al., 2013; Montevecchi et al., 2012; Yurkowski et al., 2018). Marine Protected Areas (see <http://www.mpatlas.org/> for detailed maps) already exist in the Arctic, but are lacking in some key areas such as the Bering Sea or along the Northern Canadian coast. Even though our conclusions have to be taken with all necessary caution, as detailed across the previous sections, our work suggests that arctic bird distribution and migratory pathways may shift radically within the next few decades. Overall, the establishment of future Marine Protected Area have to evolve with those shifts, preserving wintering and breeding grounds but also stop-over sites needed by the vast majority of migratory arctic birds. The modalities and likelihood of forthcoming major changes will thereby be investigated, both theoretically when studying migration ecology (Somveille, Rodrigues, & Manica, 2015), during winter field expeditions (Berge et al., 2015) and via biotelemetry studies (Fayet et al., 2017; Frederiksen et al., 2012).

On a worldwide scale, we speculate that other migratory pathways may be shifted by global change. Notably, there are strong signals that Pacific seabirds may also migrate into the Atlantic via the North Pole (Mckeon et al., 2016). Transcontinental bird migrations currently occur on eight flyways which all run North-South along the Americas, Africa-Eurasia, and Australasia (Galbraith, Jones, Kirby, & Taej, 2014). Whether populations of migratory birds using these flyways will go extinct following global change impacts, or will radically shift migratory pathways and/or strategies, will be the subject of some exciting research in the near-future.

Supplementary materials

Available at: https://static-content.springer.com/esm/art%3A10.1038%2Fs41598-019-54228-5/MediaObjects/41598_2019_54228_MOESM1_ESM.pdf or at <https://osf.io/bwv3u>

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CHAPTER IV
NORTH ATLANTIC OCEAN WINTER STORMS
STARVE SEABIRDS

North Atlantic Ocean winter storms starve seabirds

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Abstract

Each winter the North Atlantic Ocean is the stage for spectacular cyclones, some leading to seabird mass-mortality events called ‘winter wrecks’. Thousands of emaciated dead or dying seabirds are washed ashore along the European and North American coasts, but most often their geographic origins and the causes of their deaths remain unclear. Coupling winter tracking data for ~1500 individuals of five key North Atlantic seabird species (*Alle alle*, *Fraterecula arctica*, *Uria aalge*, *Uria lomvia* and *Rissa tridactyla*) and cyclone locations obtained from climatic reanalysis data, we determined high cyclone exposure areas for the seabird community on an ocean basin scale. Furthermore, we explored the energetic consequences of storm exposure for seabirds using a mechanistic bioenergetics model (Niche MapperTM) under various cyclone intensities. Our study indicates that seabirds wintering off Iceland and South Greenland, and in the Labrador Sea, or the Barents Sea, can experience cyclones of high intensity. Our model-based results suggest that cyclonic conditions do not increase seabirds’ energy requirements, implying that they die because of unavailability of their prey and/or their inability to feed during cyclones. Our study provides essential information on seabird cyclone exposure in a context of marked storm regime changes under global warming.

Keywords: At-sea distribution, Cyclones, Energy expenditure, GLS tracking, Seabird migration

Introduction

Each winter, numerous storms abound across the North Atlantic Ocean. The most severe one lead to seabird mass-mortality events called “winter wrecks”, during which thousands of emaciated seabird carcasses are washed ashore along European and North American coasts (Anker-Nilssen, Harris, Kleven, & Langset, 2017; Camphuysen, Wright, Leopold, Hüppop, & Reid, 1999; Farque, 2014). Winter storms can therefore shape seabird population dynamics (Frederiksen et al., 2009; Guéry et al., 2019), by affecting survival rates, as well as the body condition of surviving individuals. Storm-induced winter mortality adds to other threats such as habitat loss, invasive species or competition with fisheries, contributing to the general downward trend of the global seabird community (Grémillet et al., 2018) and making them one of the most threatened bird groups (Dias et al., 2019). The frequency of high-intensity storms coming from the North Atlantic tropical zone is forecasted to increase in the near future (Christensen et al., 2013), and North Atlantic storm tracks are predicted to shift northward with climate change. These increasing storms off Western Europe (Wolf, Woolf, & Bricheno, 2020) may lead to increased catastrophic seabird mortality events. It is therefore essential to understand the causes of seabird mortality during storms, and to identify factors contributing to contrasting spatio-temporal mortality patterns at the seabird-community level. Since multiple seabird species from different breeding colonies may inhabit different wintering areas (Fayet et al., 2017; Frederiksen et al., 2016), it may strongly affect the composition of seabird winter wrecks.

Community-wide analyses are lacking due to the technical difficulties of studying seabirds wintering far out at sea under storm conditions. Importantly, previous studies have focused on beach surveys (e.g. Morley et al., 2016), probably greatly underestimate the total number of seabird casualties. Those studies also struggle to infer the geographic origin of the birds and the cause of their death (but see Morley et al., 2016). The actual cause of seabird mortality in winter wrecks therefore remains unknown. Necropsies suggest that seabirds starve during storms (Jones, Barrett, Mudge, & Harris, 1984; Morley et al., 2016) and that the resulting mortality can be aggravated by mercury contamination (Fort et al., 2015). Questions remain whether seabirds starve due to abnormally high-energy expenditure (Fort, Porter, & Grémillet, 2009), reduced foraging profitability and energy inputs, or because both these constraints affect their energy balance at the same time. Recent research has shown that seabirds wintering in the North Atlantic Ocean track environmental gradients to remain in an energetic steady state (Amélineau et al., 2018; Fort, Beaugrand, Grémillet, & Phillips, 2012), but how winter storms affect this delicate balance is unknown.

In this study, we explored the energetic consequences of storm exposure for the North Atlantic Ocean seabird community during the non-breeding period (October-February). We focused on five key species (little auk *Alle alle*, Atlantic puffin *Fratercula arctica*, common guillemot *Uria aalge*, Brünnich's guillemot *Uria lomvia* and the black-legged kittiwake *Rissa tridactyla*). These species which account for ca. 75% of the total number of seabirds breeding along the North Atlantic Ocean (Barrett et al., 2006) are also among the most severely hit by winter storms (Camphuysen et al., 1999; Farque, 2014). Using tracking data of 1532 birds from 39 breeding colonies spread across the North Atlantic Ocean and adjacent seas (see map in Supplemental material I), we defined core use areas for each species/colony during winter months. By mapping these areas against the locations of cyclones occurring in the North Atlantic Ocean, we determined high cyclone exposure areas for this vast seabird community on an ocean-basin scale. We then modeled the energy requirements of each species under different cyclonic conditions using a mechanistic bioenergetics model (Niche MapperTM, Porter & Mitchell, 2006), to investigate storm effects on seabird energy balance. Overall, by comparing North Atlantic Ocean seabird energy requirements under cyclonic and non-cyclonic conditions, we tested the hypothesis that storms dramatically increase seabird energy requirements.

Material and methods

1. Locations and characteristics of North Atlantic cyclones during winter

Cyclone locations were obtained from the 'Northern Hemisphere Cyclone Locations and Characteristics from NCEP/NCAR Reanalysis Data, Version 1' online dataset (Serreze, 2009). Locations were calculated using the updated Serreze (1997) (Serreze, Carse, Barry, & Rogers, 1997) algorithm on daily Sea Level Pressure from the National Center for Environmental Prediction (NCEP) and National Center for Atmospheric Research (NCAR) Reanalysis data set in a 250km grid. We focused on winter cyclones (October to February) in the North Atlantic and adjacent seas (100°W–100°E, 0°N–90°N) between 2000 and 2016. Using the Dvorak storm classification (Dvorak, 1984) on the cyclone central pressure we defined four classes of cyclone intensity (> 1009 hPa = Class 1; 1005-1009 hPa = Class 2; 987-1005 hPa = Class 3; < 987 hPa = Class 4) then classified each cyclone in the studied area across its duration. Finally, for each month, we calculated the average number of cyclones of each category that occurred between 2000 and 2016 for each 250 km grid cell.

2. Winter distribution of seabirds

We focused on the winter distribution of five seabird species (little auk, Atlantic puffin, Brünnich's guillemot, common guillemot and black-legged kittiwake). Bird locations were obtained from Global Location Sensors (GLS) deployed and retrieved during the breeding season for 1532 individuals from 39 breeding colonies across the North Atlantic Ocean (see Supplemental material II). Two locations per day were obtained through the recorded light levels for each individual with an accuracy of +/- 200 km (Lisovski et al., 2012; Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004). We focused on locations acquired during the winter period (October to February) and removed locations obtained during the two weeks on either side of the equinoxes (Lisovski et al., 2012) as well as spurious locations and those falling on land.

For each species, we then calculated monthly utilization distributions (UD) for each individual using the BRB-MKDE software (Benhamou, (2011), March 2018 version for location in decimal degrees with $h_{min}=250$ km) before averaging by seabird colony and species. To avoid some individuals disproportionately driving the colony's UDs, we performed a kernel stability analysis and for each month, we only considered individuals, which had enough locations to satisfy this stability criteria (see Supplemental materials III). We then used the 25% utilization kernels to approximate areas of core use for each colony and species during the winter months.

3. Modeling seabird energy requirements under non-cyclonic and cyclonic conditions

We used the mechanistic model Niche MapperTM (Porter & Mitchell, 2006) to calculate energy requirements for each species under cyclonic and non-cyclonic conditions for each wintering month. This model is based on a microclimate model and an animal module: the microclimate model calculates hourly environmental conditions for the near surroundings of the bird and the animal module uses the resulting outputs together with bird morphological, behavioural and physiological properties to estimate the metabolic rate needed by the bird to maintain its body temperature at a given time with a specific behavioral time budget. Variables having the strongest influence upon the modeled energy requirements were identified through sensitivity analyses in previous studies (Amélineau et al., 2018; Fort et al., 2009).

We focused on a 1000km*1000km area off North Newfoundland (see Supplemental materials I) where the five seabird species aggregate during winter (see Results). For this area, we used environmental characteristics (sea surface temperature, air temperature, wind speed, and relative humidity) of cyclonic and non-cyclonic conditions to parameterize the microclimate module of Niche MapperTM. The study area experienced numerous cyclones during the winter months between 2000 and 2016 (see Supplemental materials IV) and for each of them, we extracted corresponding sea surface temperatures using the NOAA High Resolution SST dataset provided by the NOAA/OAR/ESRL PSL (<https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html#detail>)

(Reynolds et al., 2007). The corresponding air temperature and relative humidity were extracted from the NCEP/NCAR Reanalysis dataset previously used to define cyclone locations (see above). We set the wind speed of each cyclone according to its intensity ($5-13 \text{ m.s}^{-1}$ = Class 1; $13.1-17 \text{ m.s}^{-1}$ = Class 2; $17.1-32.5 \text{ m.s}^{-1}$ = Class 3; $> 32.6 \text{ m.s}^{-1}$ = Class 4) using the Dvorak classification (Dvorak, 1984). We then averaged the values obtained by intensity class to calculate mean environmental characteristic of each class for each winter month between 2000 and 2016. Finally, for each year, non-cyclonic conditions were defined by calculating the daily mean characteristics of each month using the same environmental dataset after excluding cyclone days. Wind speeds were obtained from the NCEP/NCAR Reanalysis data set. All environmental data used were interpolated in a 250km grid. Mean environmental conditions encountered during cyclonic and non-cyclonic events are presented in Figure 1 and Supplemental materials V.

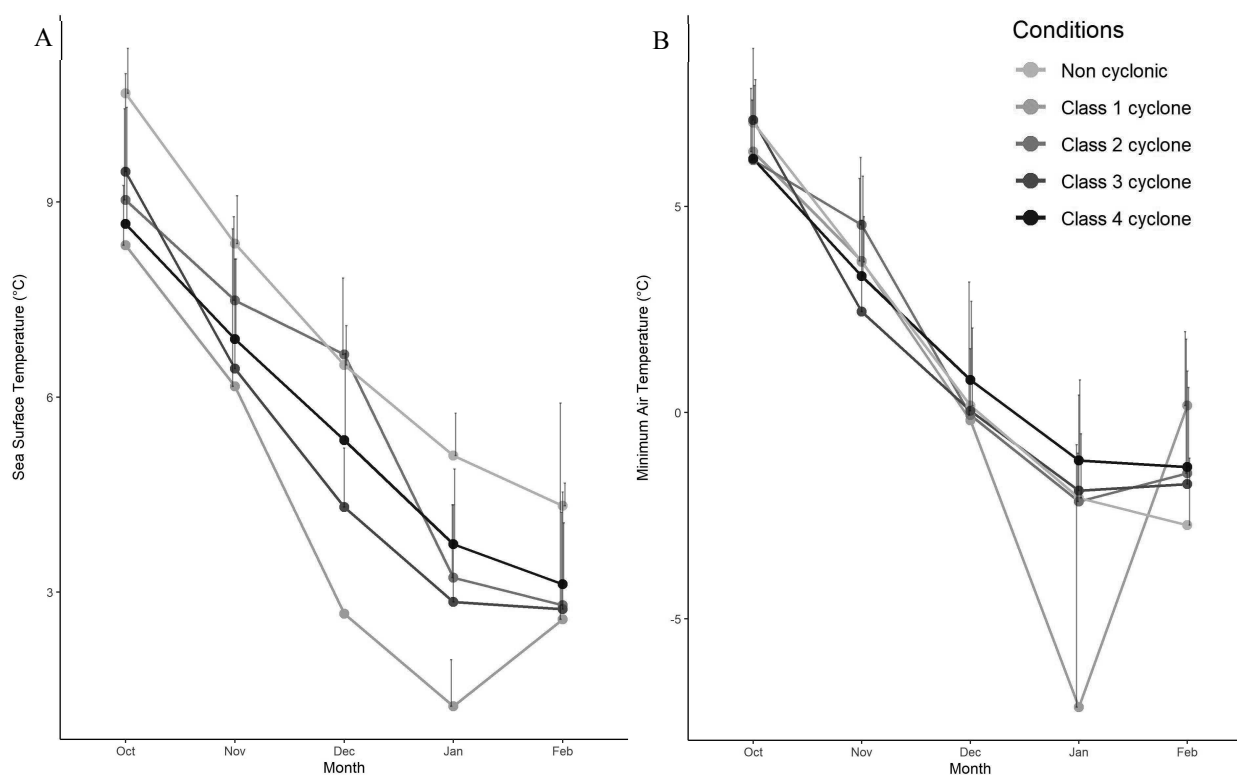


Figure 1. Average sea surface temperature (A) and minimum air temperature (B) between 2000 and 2016 for each winter month under cyclonic and non-cyclonic conditions in the studied area off Newfoundland. Error bars were halved for clarity reasons and correspond to standard deviations capturing the variation between years. Average minimum and maximum relative humidity such as maximum air temperature are provided in Supplementary materials V.

Once we had parametrized the microclimate model of Niche MapperTM, we parametrized its animal module to obtain seabird daily energy requirements. As this module had already been parameterized to model energy expenditure in little auks, Brünnich's guillemots and common guillemots (Fort et al., 2009, 2013), we re-used most Niche MapperTM input values. Missing values and values required to parameterize Niche MapperTM for black-legged kittiwakes and Atlantic puffins, were sourced from the literature (see Supplemental materials VI) and obtained through dedicated measurements. Notably, feather reflectivity was measured with a double beam spectrophotometer (CARY 5000 UV-VIS-NIR, Agilent, USA) 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 methods of Medina et al. (Medina et al., 2018). For each species the results were averaged across patches. Other morphological properties such as body dimensions were measured on adult bird carcasses of five Atlantic puffins and four black-legged kittiwakes collected on Ré Island (France) during February 2014. All Niche Mapper input data are available in Supplemental materials VI.

Very little is known about the behavior of seabirds under storm conditions. Through personal observations performed by a wide range of North Atlantic seabird experts (e.g. many authors of this publication, as well as Dr. Kyle Elliott) we assumed that the seabird species considered react to winter storms by reducing their flight activity to zero when wind speeds exceed 15 m.s^{-1} (corresponding to cyclones of Class 2, 3 and 4). As black-legged kittiwakes are surface feeders we assumed that conditions experienced when wind speeds exceed this threshold precluded them to dive and feed. Further, diving in the first thirty meters of the water column (Amélineau, Grémillet, Bonnet, Bot, & Fort, 2016), we assumed that little auks are also severely impacted by those cyclonic conditions, which are too perturbed for them to dive and prey on zooplankton. In contrast, deeper diving species such as puffins and guillemots, which could dive up to 75 and 250 meters respectively (Burger & Simpson, 1986; Chimienti et al., 2017), may still manage to dive (Finney, Wanless, & Harris, 1999). Flight and diving activities were assumed to be the same as usual under cyclone of Class 1 (for which wind speeds are below 13 m.s^{-1} , see above).

Using climatic, morphological and behavioural information as stated above, we modeled species-specific, monthly energy requirements for each winter between 2000 and 2016, under four intensities of cyclones and under non-cyclonic conditions. To disentangle the effects of changes in behaviour (decreased flight/diving activities) and of weather conditions on the birds' energy requirements during cyclones, we also calculated those requirements for each species under non-cyclonic conditions,

setting behavioural parameters as those displayed during a cyclone with wind speed higher than 15 m.s⁻¹.

Results

1. Winter storm exposure of the North Atlantic Ocean seabird community

The occurrences and strengths of storms in our study area varied in time and space, thereby also their overlap with core areas of different seabird species and populations (Figure 2 and Supplemental materials VII). A limited number of localized low intensity cyclones (Class 1 and 2) occurred mainly in Baffin Bay, Gulf of Maine and Mediterranean Sea regions. Those cyclones encountered Atlantic puffins from Skomer Island, but their overlap with the seabird community was limited. Class 3 cyclones were more numerous and widespread, particularly in October and November, and mainly occurred in Baffin and Hudson bays, the Davis Strait, Labrador Sea, east off Newfoundland, around Iceland and in the Barents Sea. Finally, Class 4 cyclones were observed in all winters off west Iceland, off the Norwegian coast and in the Barents Sea, whereas the Davis Strait and the Labrador Sea were only affected by Class 4 cyclones between December and February.

Accordingly, Brünnich's guillemots from Canadian, Greenlandic and Icelandic colonies encountered with Class 3 and 4 cyclones in the Davis Strait, the Labrador Sea and off Newfoundland. Little auks and black-legged kittiwakes from all tracked colonies and Atlantic puffins from North-West Iceland also aggregated off Newfoundland and experienced the same events. Icelandic common and Brünnich's guillemots, black-legged kittiwakes from North-East Iceland and Brünnich's guillemots from Svalbard colonies were exposed to Class 3 and 4 cyclones off-Iceland during winter. In October, this area also hosted little auks from East Greenland, Atlantic puffins from South-West Ireland and Wales as well as black-legged kittiwakes from Norway, Svalbard and Russia. Norwegian kittiwakes aggregating off western Norwegian coasts between October and December were impacted by Class 4 cyclones. Class 3 and 4 cyclones occurring in the Barents Sea also likely impacted Norwegian and Russian common guillemots, Brünnich's guillemots and black-legged kittiwakes (except in November and December for the latter). Finally, Class 3 cyclones were fewer in the mid-west Atlantic Ocean and were more likely to spare seabirds wintering there, such as Atlantic puffins from South-West Ireland and Wales (except in October). In January and February, black-legged kittiwakes from North-East Iceland, Faroe Islands, East Scotland, Norway and Svalbard also wintered in the mid-west Atlantic Ocean, avoiding some cyclonic events. Seabirds wintering in the Gulf of Maine and off Newfoundland were spared from Class 4 cyclones at the beginning of the non-breeding period.

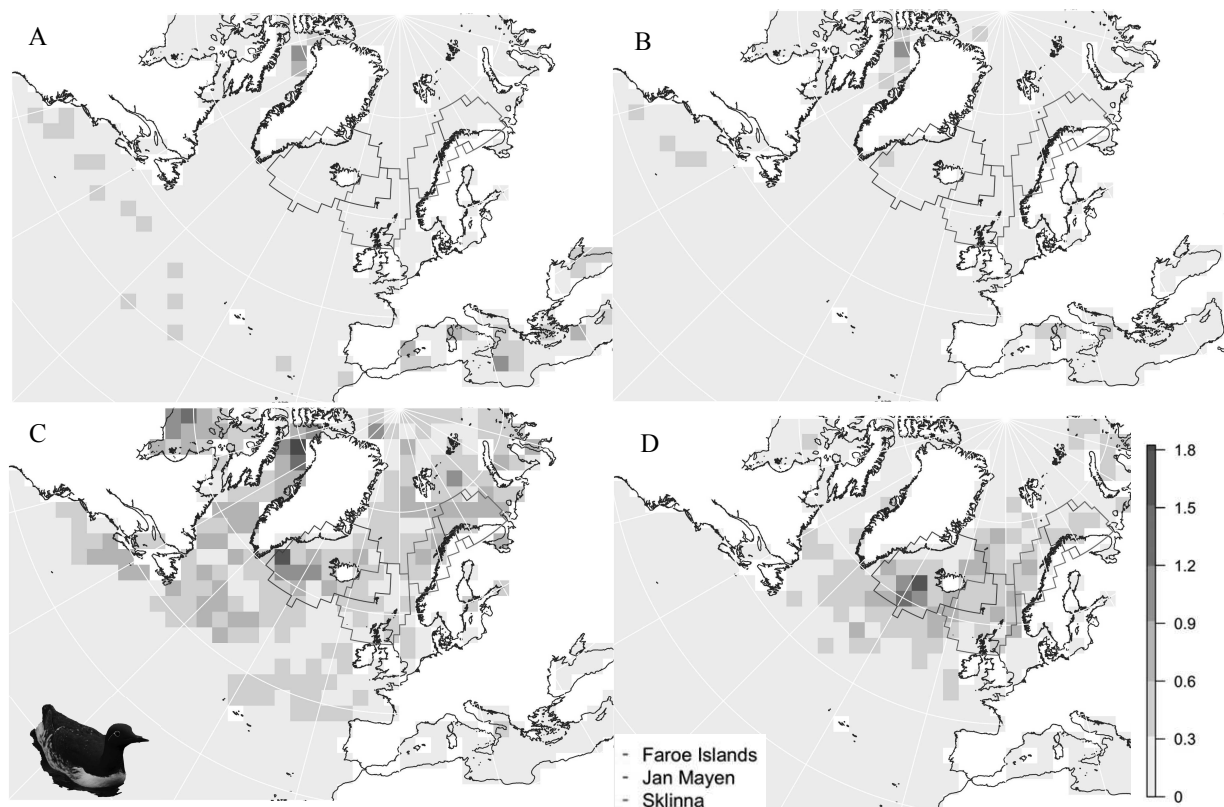


Figure 2. Overlap between core use areas of common guillemots from three colonies (Faroe Islands in pink, Jan Mayen in purple and Sklinna in red) and average number of Class 1 (A), Class 2 (B), Class 3 (C), Class 4 (D) cyclones in October between 2000 and 2016. Graticules are set at 15° intervals and the map is projected as NSIDC EASE (Equal-Area Scalable Earth) grid for the northern hemisphere. Maps for other species, colonies and months are provided in Supplemental materials VII.

2. Seabird energy requirements under cyclonic and non-cyclonic conditions

Seabird energy requirements under cyclonic and non-cyclonic conditions are presented in Figure 3 and Supplemental materials VIII. Statistical analyses revealed several significant differences (Kruskal-Wallis, $p < 0.05$) in seabird energy requirements (see Table 1) between the six categories of conditions tested (Class 1 to 4 cyclones, non-cyclonic conditions with usual seabird flight/diving activities, non-cyclonic conditions with cyclonic seabird flight/diving activities). In particular, energy requirements under non-cyclonic conditions with usual flight/diving activities were higher than those induced by non-cyclonic conditions with cyclonic behavior (post hoc Dunn's test, $p < 0.05$) for little auks and black-legged kittiwakes. Conversely, this difference was not significant for the other species except for Atlantic puffins in October and December (post hoc Dunn's test, $p < 0.05$). As these birds fly very little during winter (see Supplementary materials VI), it suggested that stop flying makes little difference on their energy requirements.

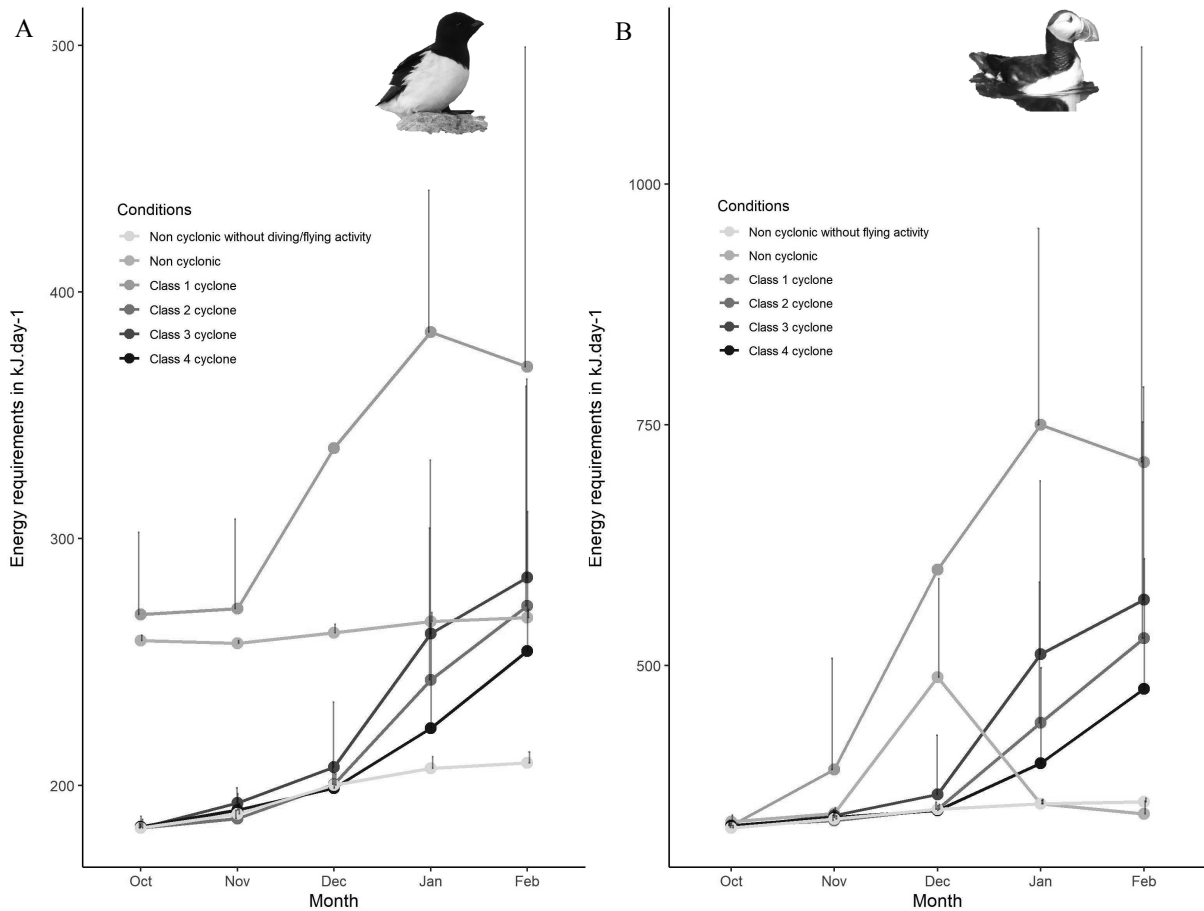


Figure 3. Average energy requirements for little auks (**A**) and Atlantic puffins (**B**) in the studied area off Newfoundland for each wintering month under cyclonic and non-cyclonic conditions between 2000 and 2016. Error bars were halved for clarity reasons and correspond to standard deviations capturing between-year variation. Results for other species are presented in Supplemental materials VIII.

In a very limited number of cases, cyclonic conditions led to increases (up to 36%) in seabird energy requirements in comparison with non-cyclonic conditions with cyclonic flight/diving activities (post hoc Dunn's test, $p < 0.05$). Moreover, for little auks and black-legged kittiwakes (except in February) and Atlantic puffins in October and December, energy requirements were significantly lower during specific cyclonic conditions than during non-cyclonic conditions experienced with usual flight/diving activities (post hoc Dunn's test, $p < 0.05$). Finally, for little auks and black-legged kittiwakes, energy requirements were significantly higher during Class 1 cyclones than for other cyclones classes (except in February) (post hoc Dunn's test, $p < 0.05$). Those differences were not significant for deep divers (except for Atlantic puffins, see above) (see Table 1).

	Little auks			Black-legged kittiwakes			Atlantic puffins			Common guillemots			Brünnich's guillemots		
	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p
October	48.6	5	<0.0001	50.4	5	<0.0001	12.5	5	0.029	21.2	5	<0.0001	6.98	5	0.223
November	48.8	5	<0.0001	44.5	5	<0.0001	10.1	5	0.072	8.70	5	0.122	9.98	5	0.076
December	38.6	5	<0.0001	36.9	5	<0.0001	26.7	5	<0.0001	7.28	5	0.201	10.16	5	0.071
January	26.1	5	<0.0001	25.8	5	<0.0001	12.9	5	0.024	12.2	5	0.032	14.4	5	0.013
February	14.0	5	0.016	11.5	5	0.042	17.9	5	0.003	9.99	5	0.076	10.8	5	0.055

Table 1. Results of Kruskal-Wallis tests comparing mean energy requirements per conditions tested (Class 1 to 4 cyclones, non-cyclonic conditions with usual seabird flight/diving activities, non-cyclonic conditions with cyclonic seabird flight/diving activities), for each species and each month. Statistical significant results ($p < 0.05$) are indicated in bold. χ^2 , Chi square; df., degrees of freedom; p, p.value. Outputs of the corresponding Dunn post hoc test are presented in Supplemental materials VIII.

Discussion

To our knowledge, our study is the first to map storm exposure and to evaluate storm impacts on seabird energetics. Thereby, we demonstrate that areas where wintering seabirds aggregate, such as the Labrador Sea, the Davis Strait, off Iceland and the Barents Sea, are particularly exposed to cyclones. They impacted birds from all studied species and breeding colonies, but seabirds wintering in the southern part of our study area, and in the mid-Atlantic Ocean, were less affected than others. Crucially, our broad-scale analyses resulted in rejection of our hypothesis: climatic conditions experienced by seabirds during storms seemed to have little or no impact on their energy requirements. By reducing their flight/diving activities during storm events, little auks and black-legged kittiwakes may be able to reduce their energy requirement to a level below that attained under non-cyclonic conditions. We therefore conclude that seabird mortality during winter storms is likely caused by starvation due to the unavailability of prey and/or their incapacity to feed. By continuing to dive during storms, deep divers take the risk of using energy reserves in an attempt to track inaccessible prey.

1. Potential limitations

Despite these advances, we recommend caution in interpreting our results for two principle reasons. First, the behaviour of pelagic seabirds is hard to assess under storm conditions, and our assumption that North Atlantic seabirds significantly reduce flying and diving (for little auk and black-legged kittiwakes) during cyclones is based on a limited number of observations and expert opinion. However, such knowledge was drawn from our very large team of authors, potentially corresponding to the best source of information currently available on North Atlantic seabird behaviour during storms. On a worldwide scale, while many seabird species seek coastal shelter and/or reduce activity levels during storms (Wilkinson, Satgé, Lamb, & Jodice, 2019), others, such as great frigatebirds (*Fregata minor*) take advantage of cyclonic winds to save energy while gliding over thousands of kilometers (Weimerskirch, Bishop, Jeanniard-du-Dot, Prudor, & Sachs, 2016). Such extreme gliders, which occur in the tropics and Southern Ocean, are rarer in the North Atlantic, an area dominated by alcid species in terms of abundance (Barrett et al., 2006). This seabird family, which is morphologically adapted to using its wings for underwater propulsion, has high wing-loading, hence very limited capacity to ride strong winds. Thus, cyclonic conditions dramatically increase flight costs in alcids (Elliott et al., 2014), and therefore tend to prevent them from flying. Nevertheless, deploying electronic devices to study North Atlantic seabirds' 3D movements during cyclones is a key objective for future research, which will allow testing our assumption that these animals are less active under passing cyclones.

Second, since direct measurements of environmental data during cyclones were lacking at the spatio-temporal scales needed for our analyses, we depicted cyclonic conditions using a limited number of reconstructed data at a broad scale, potentially missing other relevant differences between non-cyclonic and cyclonic conditions (for example related to temperature, precipitation or humidity (see methods)). Finally, due to a lack of available information, we also omitted other variables such as wind gust speed, water velocity, wave height, as well as other conditions potentially affecting seabird thermoregulation, and thus their energy requirements.

Despite these limitations, our study provides essential new knowledge, notably on the vulnerability of wintering seabirds to storms in the Labrador Sea, off Newfoundland, off southern Greenland, off the Norwegian coast and in the Barents Sea. These results are supported by the numerous seabird winter wrecks observed across years on beaches close to those areas (Camphuysen et al., 1999; Lucas, Horn, & Freedman, 2012; McFarlane Tranquilla et al., 2010; Morley et al., 2016; Stenhouse & Montevecchi, 1996) and Flemming Ravn Merkel personal communication about Brünnich's guillemot wrecks in south Greenland). Yet, retrieving only individuals who survived the non-breeding period, we cannot exclude the possibility that wrecked individuals wintered in different locations where the exposure to cyclones could be higher.

Further, the localization and study of winter wrecks on beaches is impacted by oceanic currents carrying seabird carcasses, and by the accessibility of these beaches to observers (i.e., a seabird wreck on a Greenlandic beach hundreds of km away from the nearest town will likely never be detected, unlike a wreck on Long Island, New York, U.S.A). This potentially leads to spatio-temporal mismatches between seabird wrecks as perceived by researchers and the general public and areas of major winter storm impacts on seabirds offshore. Such a mismatch may explain why we found limited overlap between seabird winter distributions and cyclones in the Eastern Atlantic, despite the fact that large winter wrecks have regularly been recorded along the shores of Western Europe.

2. Mechanistic insights into storms impacts on seabirds

Through modeling of seabird winter energetics, we concluded that storms generally did not increase seabird energy expenditure. We therefore infer that a seabirds incapacity to maintain sufficient energy inputs due to their inability to feed and the unavailability of prey are the main causes of winter wrecks. This surprising conclusion is in agreement with a study conducted on greater flamingos (*Phoenicopterus roseus*) during cold spells in the Camargue (Deville et al., 2014): thousands of flamingos died, not because of hypothermia but due to inaccessible food in frozen salt pans. Conversely, our results contrast with former modeling work which pointed to weather-induced energetic bottlenecks in seabirds wintering in the North Atlantic Ocean (Jérôme Fort et al., 2009). Birds were predicted to experience markedly higher thermoregulatory costs in December, because of lower air and water temperatures, and higher wind speeds. Yet this previous study investigated seabird energetics at the scale of months, whereas cyclones affect them at the scale of days, although we acknowledge that recurrence of storms during winter in the same area could lead to a gradual diminishment of seabird body reserves, finally leading to their death.

What exactly prevents seabirds from feeding during cyclonic conditions remains unclear. One possibility is that cyclones may enhance water turbidity, decrease underwater light intensity, and perturb prey patches and vertical migration. Potentially disrupting water stratification, cyclones may modify prey aggregation and negatively impact seabird foraging efficiency (Meyer et al., 2020). Therefore, the ‘washing-machine effect’ could strongly affect seabirds feeding within the fifty upper meters of the water column, such as black-legged kittiwakes and little auks in our study. Prey could occur deeper in the water column during cyclones as already observed for some elasmobranchs or teleosts (Patterson, Watterson, Shipp, & Cowan, 2001; Udyawer, Chin, Knip, Simpfendorfer, & Heupel, 2013), but how this impacts pursuit-diving species such as puffins and guillemots, is not known. Alternatively, cyclones may shift alcid away from their preferred prey patches and into unprofitable foraging habitats.

Overall, even if starvation may be the main driver of seabird winter wrecks, we cannot exclude others causes of mortality, such as drowning (Morley et al., 2016), physical impact with reefs and rocky coastlines (Mark Baran, personal comm) or inland stranding.

3. Seabird storm exposure under climate change

It is well-established that seabird experience direct and indirect negative stressors from global warming (Sydeman, Poloczanska, Reed, & Thompson, 2015) and those threats have to be addressed along with other anthropogenic stressors, such as habitat loss, predation by invasive species, competition with fisheries, and pollution (Dias et al., 2019). Since the 1970s, the frequency and intensity of the strongest tropical cyclones in the North Atlantic have increased markedly (IPCC, 2014). Considering future North Atlantic storm regimes, there are still some uncertainties but model outputs predict some common features: There will be fewer cyclones in the future, but the frequency of the strongest storm events is predicted to increase with global warming (IPCC, 2014). Moreover, storm tracks will likely shift northward under climate change (Tamarin-Brodsky & Kaspi, 2017), increasing the storminess of Western Europe (Wolf et al., 2020) and of the high Arctic (Akperov et al., 2019; Benestad, Parding, Isaksen, & Mezghani, 2016). Since the North Atlantic Ocean seabird community is also predicted to shift northwards, following its prey base (Beaugrand et al., 2019), we infer that this community will become even more susceptible to mass mortality caused by winter wrecks. This might be particularly marked in areas such as the Bay of Biscay, the North Sea, the Norwegian and the Barents Seas. In this context, our study provides an essential conceptual and methodological framework to identify the vulnerability of specific seabird populations to cyclone events at the scale of the North Atlantic Ocean.

Supplementary materials:

Available at: <https://osf.io/upt94>

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CONCLUSION

Using an energyscape approach, this thesis work explored climate change impacts on seabirds migrating and wintering in the North Atlantic Ocean. To the best of our knowledge, this is the first study addressing this issue by focusing on species distributions at the community level across an ocean basin, using energy expenditure as a universal currency for migrating animals. More precisely, this study investigated current drivers of seabird distributions, in order to assess climate change impacts and to predict future suitable wintering ground for the seabird community. Further, this work explored the potentiality of new migratory strategies induced by climate change, leading to an overturn of current migratory pathways. Finally, it assessed storm exposure of the North Atlantic seabird community, and modeled its energy requirements during storms. This led to the first regional map of current seabird community exposure to winter storms across the region, and helped rate future seabird vulnerability to extreme weather events in the context of climate change. Hereafter, we summarize and discuss this work, before suggesting perspectives for future investigations.

I. Main findings

1. Current distribution of the seabird community and storm exposure

Using tracking data for >1500 individuals from 39 breeding colonies, we identified the current wintering grounds of the seabird community in the North Atlantic Ocean. Our results show that seabirds aggregate during the non-breeding period in distinct hotspots (*sensu* Fort, Beaugrand, Grémillet, & Phillips, 2012) off Newfoundland, in the mid-Atlantic, off south Greenland and Iceland, in the North and the Barents Seas (see Chapter IV). With respect to the North Atlantic Ocean seabird community, our results confirmed the great importance of those areas (Afonso et al., 2020; Barrett et al., 2006; Bennison, Jessopp, Bennison, & Jessopp, 2015; Boertmann et al., 2004; Gabrielsen, 2009; Harris, Daunt, Newell, Phillips, & Wanless, 2010) for wintering seabirds.

Determining the wintering distributions of the seabird community is essential to assess its exposure and vulnerability to natural and anthropogenic threats, such as gas and oil exploration (Fort et al., 2013), oiling (Lieske, Mcfarlane, Ronconi, & Abbott, 2019), competition with fisheries or bycatch (Grémillet et al., 2018), and therefore to plan efficient spatial conservation measures. In this thesis, we showed that birds from all species and colonies studied are vulnerable to cyclones of high-intensity (Chapter IV), in particular along the Canadian coasts (in the Davis Strait, the Labrador Sea and off-Newfoundland), off Iceland and south west Greenland as well as in the Barents Sea. Conversely, birds wintering in the mid-Atlantic Ocean seemed less impacted by storm events. These results are coherent with the numerous seabird winter wrecks observed across years on specific beaches close to those areas (Camphuysen et al., 1999), even if oceanic currents and accessibility of beaches may bias the retrieval of seabird carcasses.

Finally, locating the different species across the non-breeding period allowed us to sample their ecological niche and statistically link surrounding environmental characteristics with their presence (Chapter II and III). We assessed the pertinence of resulting models through presence data (tracking and direct observations), concluding that their overall predictive quality is sufficiently good to determine the drivers of seabird at-sea distributions and to perform future projection.

2. Drivers of the seabird distribution and impacts of climate change

Predicting the impacts of climate change on seabird winter distribution is crucial, as inter-breeding ecology affects seabird demography and population biogeography, with consequences for the structure and functioning of ecosystems (Bauer & Hoyer, 2014). To this aim, we attempted to identify current main drivers of the seabird winter distribution for the five considered species, to then perform future projections. We thereby considered that the link established between environmental conditions and species presence holds across space and time. Previous studies mainly focused on abiotic factors, and concluded that sea surface temperature (Fort et al., 2012), bathymetry (Amélineau et al., 2016) or sea-ice concentration (Laidre, Heide-Jørgensen, Nyeland, Mosbech, & Boertmann, 2008) are key parameters driving seabird distributions at different spatial and temporal scales. Conversely, biotic factors are particularly difficult to assess (but see Amélineau et al., 2018), especially at global scales, and scientists usually used proxies to investigate their influence on seabird location choices, potentially leading to misinterpretations (Grémillet et al., 2008).

In this thesis work, whenever possible, we used mechanistic links between environmental conditions and seabird distributions by calculating energetic requirement as well as modeling abundance and concentration of prey (see Chapter II). When this was not possible, we shortlisted physical environmental variables in agreement with results from previous studies, to investigate little auk habitat selection (see Chapter III). We concluded that winter seabird habitat choices generally resulted from a trade-off between energy requirements and prey availability, and was predicted to be strongly explained by the former (see Chapter II). 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. Among environmental variables, air temperature was the main driver of little auk marine distributions, whereas distance from the coast was the main driver of their nesting distributions during the breeding season (see Chapter III).

According to the climatic models considered in this thesis, air and sea surface temperatures are predicted to increase, seabird energetic expenditure is supposed to decrease (see Figure 14) and seabird prey to shift northwards with global warming (see Chapter II), in agreement with previous studies (Beaugrand et al., 2019). However, the magnitude of such modifications and their effects on seabird distribution will depend on the climatic scenarios considered. Our results show that global

warming will result in northward seabird distribution shifts of varying magnitude, depending on the species and considered time period (Chapter II and III). Latitudinal shifts in response to climate change have been predicted and observed for many marine organisms, including top predators (Cristofari et al., 2018). More specifically, we predicted that seabird wintering hotspots might change, with areas such as Newfoundland, the Gulf of St Lawrence, and southern Greenland becoming increasingly attractive during winter because of diminishing seabird energy requirements. In some cases, southern parts of species' ranges are supposed to become unsuitable, decreasing the size of selected habitat for the species considered when the northern limits cannot expand northwards (see Figure 14 and Chapter II and III). As storm tracks are also predicted to shift northwards, mass mortality events will probably increase in the North Sea, the Norwegian and the Barents Seas (see Chapter IV). Crucially, meeting Paris Agreement Objectives will limit habitat range shifts of the North Atlantic Ocean seabird community in 21st century. In response to global warming, seabirds will potentially winter closer to the pole, diminishing their migratory distance and changing their migratory behavior. Therefore, new migratory strategies may arise in this context.

3. Climate change and new migratory strategies

Marine organisms including seabirds are predicted to shift northwards with global warming, modifying migratory distances. Global changes may even result in species/populations switching from a migratory to a resident strategy, and *vice versa* (Pulido & Berthold, 2010). Arctic sea-ice is currently an ecological barrier for migratory birds, however, the Arctic warms twice faster than the rest of the world and the central part of the Arctic Ocean is supposed to become completely sea ice free each summer before the mid-21st- century (Pörtner et al., 2019).

The melt of this migratory barrier will create favorable conditions for transarctic exchanges, as previously observed in the past (Vermeij & Roopnarine, 2008) and will induce warmer winter conditions. According to the capacities and behavior of Arctic birds, we identified 24 breeding birds species which may shift from a migratory strategy to high-Arctic year round residency (see Chapter III). We also identified 29 seabird species which could be involved in a transarctic migration in the future from the North Atlantic Ocean to the North Pacific Ocean or *vice versa* (see Chapter III).

Those new migratory strategies have to be in adequacy with suitable breeding and wintering habitats to evolve. Therefore, we propose a methodological framework using little auk as an example, to assess the adequacy of those new migratory strategies, and to calculate related levels of energetic expenditure. Through species distribution modelling, we conclude that suitable breeding and wintering habitats for little auks are currently circumpolar and that future suitability will be in adequacy with future high-arctic residency and trans-arctic migration (see Chapter III). Surprisingly, our results indicate that transarctic little auk migration, from the North Atlantic towards the North Pacific, may only be half as costly, energetically, than high-arctic residency or migration in the North Atlantic.

Circumpolar habitats suitability has been previously predicted for several seabirds species (Huettmann, Artukhin, Gilg, & Humphries, 2011) and recent studies showed that seabirds are already able to cross the Arctic Basin (Burnham et al., 2020) such as fishes (Wisz et al., 2015) and marine mammals (McKeon et al., 2016), validating our approach. Finally, high-arctic residency is also already observed, with seabirds foraging during the polar night at high latitude (Ostaszewska, Balazy, Berge, & Johnsen, 2017). However, this strategy seems to be particularly costly energetically (Fort, Steen, et al., 2013) and Chapter III), meaning that the species concerned are highly dependent on the availability and accessibility of the prey. This constraint might nonetheless be levied through enhanced high latitude prey abundance, promoted by global warming.

4. Energetic impacts of storm events

Storms are responsible for mass-mortality events during which thousands of emaciated seabird carcasses are washed ashore (see for example Morley et al., 2016), but what actually kills them during such extreme events remains unknown. Calculating the energetic expenditures of seabirds during winter storms, we tested the hypothesis that those extreme weather events dramatically increase seabird energy requirements, leading to their death. Surprisingly, we concluded that storms have little or no impact on seabird energy requirements. We therefore conclude that seabirds which die during winter storms probably starve due to the unavailability of their prey and/or their incapacity to feed. Our result is in agreement with a study conducted on greater flamingos (*Phoenicopterus roseus*) during cold spells in the Camargue (Deville et al., 2014): Thousands of flamingos did not die because of hypothermia but due to inaccessible food in frozen salt pans. However, recurrence of storms during winter in the same area could lead to a progressive diminishment of seabird reserves and body conditions, finally leading them to their death. What exactly prevents seabirds from feeding during cyclones remains unclear. One may speculate that cyclones may enhance water turbidity, decrease underwater light intensity, and perturb prey patches and their vertical migration. Prey could dive deeper in the water column during cyclones as already observed for some elasmobranchs or teleost (Patterson, Watterson, Shipp, & Cowan, 2001; Udyawer, Chin, Knip, Simpfendorfer, & Heupel, 2013), but how far this could affect pursuit-diving species such as puffins and guillemots, is still mysterious.

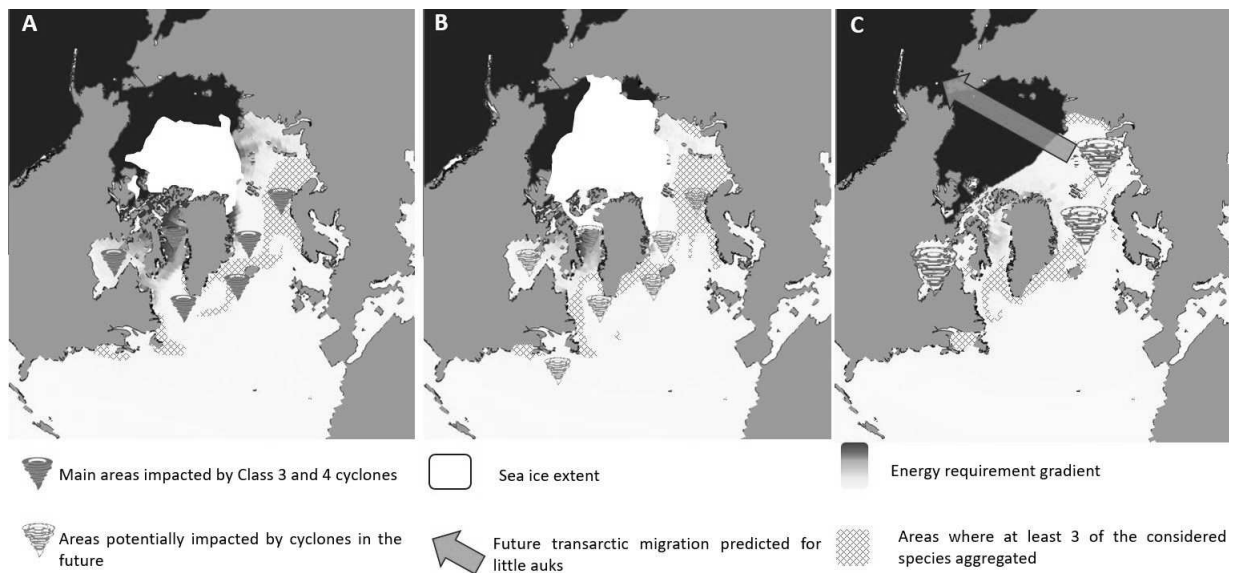


Figure 14. Modelled seabird aggregation, energy requirement (from yellowish: low to red: high) and cyclone exposure in October, (A) currently (B) in 2100 under the RCP2.6 scenario and (C) in 2100 under the RCP8.5 scenario where cyclones are predicted to be stronger and more frequent at high latitudes.

II. Studies limitations

During this thesis work, the different data and methods used allowed us to study the current and future winter distribution of the North Atlantic Ocean seabird community, investigating the drivers of this distribution, evaluating seabird vulnerability to storm events and concluding on climate change impacts. However, the methodology used has some limitations that have to be discussed and taken into account when interpreting our results, before suggesting some improvements.

1. Current and future seabird winter ecology

Conducting our studies, we made a series of assumptions regarding the behaviors, the diets and the capabilities of the seabird species. For example, we extrapolated their winter diets using information obtained for birds from a subsample of all colonies, regardless of local variability. Moreover, as storm conditions limit direct observations, we inferred the behavior of seabirds experiencing such events through a limited number of observations and/or direct observations during e.g. winter expeditions. We hope that such future investigations will lead to further detailing seabird migratory biology, notably behavioral patterns under non-cyclonic and cyclonic conditions, as well as investigating more accurately seabird diets and the energetic cost of their activities displayed in winter. Further, future studies will be crucial to better understand, whether and how, seabirds detect storms in order to investigate their ability to avoid them (see Weimerskirch & Prudor, 2019).

Moreover, by exploring climate change impacts on seabird distributions, we assumed that the statistical links built between their current occurrences and biotic/abiotic factors considered across our

studies (energyscape, prey field, sea-ice cover, sea surface temperature etc.) will hold across time. However, seabirds are likely to change their diets and behaviors (Vihtakari et al., 2018) to deal with shifts in marine ecosystems caused by global warming, through plasticity and/or microevolution (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, Divoky, & Friesen, 2019). Such plasticity is however constrained by the magnitude of environmental shifts (Radchuk et al., 2019) and reduced climate change will more likely keep them within the limits of seabird plastic responses. Nevertheless, there is also strong evidence that migratory birds do adjust their migratory ecology following global change (Visser et al., 2009).

Finally, our modeling work of future seabird migratory behavior and winter distribution did not take into account predation, competition, fidelity to wintering/breeding sites, the role of experience, learning and imitation within migratory behavior as well as migratory legacies of studied populations (Newton, 2010) beyond current biotic and abiotic forcing factors shaping seabird migration and winter distribution.

2. Seabird locations and environmental data

Opportunistic observations or tracking data from GLS are valuable to locate seabirds at-sea during the non-breeding period, but we face some biases and limitations using these resources. First, direct observations are rarely linked with additional information such as sex, age or breeding status, which could potentially influence winter migration, distribution (Bogdanova et al., 2011; Jarjour, Frei, & Elliott, 2017) and exposure/sensitivity to climate change (Jenouvrier et al., 2018). Further, opportunistic occurrence data may suffer from misidentification, and could be biased towards places with easier human access, potentially misrepresenting the species' observed niche (Guillera-Arroita et al., 2015). However, in this thesis, those limitations were taken into account when analyzing the corresponding data through dedicated statistical methods (see Chapter III). Additionally, our studies conducted with GLS data did not suffer from GLS inaccuracy due to the large scale considered, but further refinements needed to explore spatial patterns that only arise at finer scales would require more accurate devices. Further, GLS are usually deployed on few reachable breeders supposed to represent the colony: Those individuals are often close from each other for practical reasons, potentially biasing our study toward bold and maybe related individuals. As the effects of personality or kinship are not yet investigated for the species considered, it is difficult to assess impacts of this bias on our conclusions.

Moreover, investigating the drivers of seabird distribution in the North Atlantic Ocean, we used available environmental variables at this large spatial scale: Empiric measurements were not available and rebuilt or modeled variables were preferably used. We then faced space and temporal resolution constraints as well as limitations in the number of variables available for the climatic model needed.

However, as we focused on the ocean basin scale, with a low seabird location accuracy, we considered that the spatial resolution of available environmental data was sufficiently accurate to depict general patterns. Finally, we assumed that errors linked to each of those modeled variables were spatially homogeneously distributed: As we compared relative habitat suitability, this approach nonetheless limited their impacts on our conclusions. Nevertheless, future remote sensing and climatic modeling advances will certainly increase the temporal and spatial accuracy of environmental data, allowing further investigations at finer spatio-temporal scales.

3. Energetic requirements calculations

Using Niche MapperTM, we proposed a framework to assess the impact of climate change on seabirds using an energetics approach. Despite its great advantages (accuracy and possibility to model energetic expenditure at large temporal and spatial scales, etc. (Fort et al., 2011)) Niche MapperTM build on a large number of variables describing the physiology, morphology and behavior of the species considered. Even though such variables might be available through museum specimens, or from the literature, it might be difficult to obtain them for some species and account for inter-population differences, especially out of the breeding season, precluding the general use of this modeling approach.

Further, such models outputs are dependent on the resolution and quality of inputs data. In our case, we parameterized Niche MapperTM with rebuilt or modeled environmental data as well as with metabolic and behavioral data obtained from a limited number of studies, sometimes conducted in captivity or during the breeding season (see Supplemental materials XIII of Chapter II). Nevertheless, the energetic requirements obtained during this thesis work using Niche MapperTM seemed in agreement with other studies conducted on the species considered through others measurements (see for example Dunn et al., 2020). Further investigations will nonetheless improve input data, by focusing on winter behavior and conducting energetics measurements in free-living birds.

Finally, we conducted our energetics calculations by parameterizing Niche MapperTM with average values for physiological, morphological and behavioral variables, modeling an “average” individual of the species considered: In the future such calculations could be made for several individuals with different phenotypes to explore the impacts of inter-individual variability on energyscapes and on the drivers of winter distribution.

4. Modeling seabird distribution

Habitat Suitability Models used to describe seabird distributions are subjected to specific assumptions and limitations: We assumed that the seabird species considered are (i) at equilibrium with their environment and that (ii) we fully depicted the realized niche for those species. Indeed, despite the phenotypic plasticity observed for our species of interest (Grémillet et al., 2012), their sensitivity to environmental changes (Amélineau et al., 2019) allowed us to assume a steady state

between their distribution and their environment. Further, using opportunistic locations and GLS data from a limited number of individuals, colonies and year could lead to truncating the realized niche of the species considered. However, we presumed this bias to be limited, through the large amount and extent of the GLS data included in our analysis (see Chapter II). Additionally, after overlaying opportunistic occurrence data with existing ornithological atlas (del Hoyo, Elliott, & Sargatal, 1996) we visually inspected the data coverage and limited potential geographical and climatic biases impacts by using adapted statistical analyses (see Chapter III). Finally, due to a lack of data, we did not consider individual fitness at each little auk observation site when modeling their current breeding range (see Chapter III). Then, we probably included occurrence data from “sink areas”, where populations cannot maintain without constant immigration (Pulliam, 2000), potentially leading to a misrepresentation of the little auks’ fundamental niche during the breeding period. However, as we modeled processes at large spatial scales, this issue may have had limited effects on our results (Guisan et al., 2017).

To depict efficiently the realized niche of one species, it is also crucial to select the relevant environmental variables considered in the HSM. We selected those variables using the existing literature, including when possible biotic and mechanistic variables (see Chapter II). As those variables were modeled and combined in HSM, the propagated error is particularly difficult to track but such variables are better correlated with mechanisms underlying species range patterns (Kearney & Porter, 2009). Nevertheless, methods taking into account errors combined from different environmental variables in HSM are needed. In our case, predictions result from model stacking, but analyses yielded high predictive power and accuracy, providing support to our approach (see Chapter II and III). However, some mismatch between our predictions and observed distributions could arise (see Chapter III for example): This could be explain by the lack of some important biotic and abiotic variables in our HSM, such as microhabitats, day length, distance from colonies, or abundance of some ignored prey. Further, environmental variables could impact seabird distributions through lag effects (Wakefield, Phillips, & Matthiopoulos, 2009), which have to be investigated (but see Chapter III). Yet, a compromise has to be found between models accuracy and their complexity, linked with the number of variables considered. Moreover, in certain cases, direct observations of seabird locations are limited in remote areas, making difficult the assessment of such discrepancies.

Overall, and despite these limitations, our HSM outputs are in general adequacy with observed species locations and models were assessed as having a high predictive power. Assuming that the statistical links between species distributions and environmental data will still hold in the future, we projected future seabird distributions under different climatic scenarios. This hypothesis does not consider the constraints (climate change velocity, physical barrier etc.) which could preclude or limit species to track climate change (Burrows et al., 2014).

III. Perspectives

1. Others drivers of seabird migration

Studying the environmental predictors of the winter distribution of seabirds we have not taken into account a number of factors that seem to influence their migration strategies and choice of wintering areas. For example, we have focused only on breeding adults without distinction of social status, sex or reproductive success. Studies have shown for some species spatial segregation of sexes during wintering (Phillips, McGill, Dawson, & Bearhop, 2011) while Bogdanova and colleagues (2011) have demonstrated the impact of reproductive success on the wintering area.

Similarly, body condition is directly related to the amount of reserve stored by birds and therefore, to their ability to migrate, conditioning the accessibility of certain areas. Further age, experience and social interactions can also condition the migration journey (Newton, 2010). Climate change may affect differently certain areas and/or certain individuals in relation to their own characteristics, and such differences as their consequences on seabirds populations need to be assessed.

Finally, some seabird species are faithful to their breeding or wintering sites and numerous studies have shown that orientation as well as distance travelled during migration are genetically controlled (Newton, 2010). However, migratory shifts linked to climate change are already observed (Visser et al., 2009) despite these mechanisms. For example, more and more birds are opting for resident strategies at high latitudes. This strategy made possible by global warming may have been counter-selected in the past, thus eliminating individuals with resident genomes. Due to the softening of these conditions, these individuals tend to survive and reproduce, contributing to the establishment and maintenance of this strategy. Phenotypic plasticity phenomena are also to be expected but detangle processes (evolution or plasticity) underlying potential migratory shifts needs long-term individual monitoring (Teplitsky & Charmantier, 2019).

Therefore, distinguishing evolution and plasticity within migratory strategies in the context of climate change remains to be explored, but seems particularly important to better understand flexibility and then vulnerability of different species.

2. Climate change impacts across seabird life cycles

During this thesis we focused on the impact of climate change during the non-breeding period, and more particularly on the migratory and wintering phases, leaving aside molting period(s), potential periods of reproductive dispersal and commuting phases between breeding and inter-breeding areas.

The dispersal of immature and adults to new breeding sites is intended to redistribute individuals to good quality habitats in order to maximize reproductive success (Clobert, Danchin, Dhondt, & Nichols, 2001). The mechanisms associated with this dispersal and the prospecting for new habitats are complex; the ability of a species to disperse is a key adaptive mechanism in a changing environment, which could be based on the assessment of environmental quality through cues such as reproductive success of congeners (Doligez, Danchin, & Clobert, 2002). It seems essential to understand how climate change and its pace will impact these indices and therefore the ability to disperse.

Further, the molting period is particularly constraining for seabirds: Flightless, they are more vulnerable to environmental constraints such as extreme events that they cannot avoid. In addition, migration corridors and staging sites can be impacted by climatic conditions or shifting prey distributions. Climate change, by modifying both, may change the accessibility of certain wintering areas and/or change the costs associated with migration: all of these aspects clearly deserve further investigations.

Finally, knowing the distribution of birds in relation to individual (see above) and environmental characteristics for the whole life cycle will allow to identify all the effects of climate change on the spatial and temporal distribution of birds and these consequences on population dynamics (Weimerskirch et al., 2014).

3. Towards fully mechanistic models

Our studies (see Chapter II and III) are based on HSM, which are correlative models linking seabird locations and environmental characteristics. Widely used, those models are not particularly demanding in terms of knowledge regarding underlying processes of species distributions. However, those models do not specifically quantify the relationship between environmental variables and species distributions: Indeed, the given response could be a direct causal relationship, an indirect effect or a direct response linked to another collinear variable omitted in the model (Mac Nally, 2000).

Conversely, mechanistic models are main tools in the field of biophysical ecology that translate interactions of organismal functional traits with their environment into key fitness components. They model the effects of such interactions for key states such as body temperature, energy and water balances, allowing a better understanding of mechanisms limiting the distribution and abundance of organisms (Kearney & Porter, 2009). Further, as organisms can only live where their energy and mass

balances are positive, such models allow a description of the fundamental niche. Therefore, mechanistic models are more and more used to describe animal distributions, in particular for ectotherms (see for example Bartelt, Klaver, & Porter, 2010; Fitzpatrick et al., 2019; Kearney & Porter, 2004).

Therefore, by modelling energyscapes, Niche Mapper™ allows estimating the amount of resources (such as prey or water) needed by an organism, to then compare it with the quantity of resources available, to finally conclude on environmental suitability. For example, Kearney and colleagues (2008) used Niche Mapper™ to model the current and future distribution of an invasive species in Australia, the cane toad (*Bufo marinus*), assessing thermal constraints on the locomotor potential of the adult and the availability of water for the tadpole. In our case, energyscape calculations at the scale of a seabird community could easily be converted in a quantity of fish and zooplankton needed to sustain it. Comparing such outputs with available resources would be particularly interesting, to better describe ecosystems structure and functioning, as well as assess and limit fisheries pressures.

However, modelling absolute fish abundances actually present at a global scale is currently nearly impossible (DVEM provide relative fish abundance from 1950), limiting the use of Niche Mapper™ in itself to predict environmental suitability for seabirds. In the expectance of further improvements in fish abundance modelling, we included outputs from Niche Mapper™ in correlative HSM, arguing that energyscapes are proximal layers taking into account physiological mechanisms underlying seabird distributions. Such an approach, coupling mechanistic and correlative models have been previously used successfully (Mathewson et al., 2017; Meineri et al., 2015) even if submitted to HSM inherent limitations (see above).

4. Conservation implications

Seabirds are subjected to many anthropogenic threats (Dias et al., 2019) impacting negatively their populations worldwide. Modeling current and future seabirds hotspots in the North Atlantic Ocean, we provided information and methods needed (i) to identify important seabird areas during winter, (ii) to determine areas of conflicts between the seabird community and human-induced activities as well as (iii) to establish and manage marine protected areas (MPAs).

Indeed, better understanding where and why individuals and populations are vulnerable will allow building effective conservative measures. Anthropogenic threats are often cumulative across space and time (Halpern et al., 2008) and as migratory species, seabirds are subjected to numerous hazards across different regions during their life cycle. Therefore, macroecological studies and ambitious international collaborations have to be conducted to rebuild seabird populations by protecting crucial habitats (wintering, stop-over, molting, breeding and foraging sites) in marine and terrestrial ecosystems. MPAs have been created in North Atlantic (see Figure 15) and even if most of them are in coastal areas, they are an effective mean to protect seabirds and entire ecosystems for which they

function as ecological indicators and umbrella species (Handley et al., 2020; Pichegru, Grémillet, Crawford, & Ryan, 2010), notably by reducing overfishing and risk of bycatch. Although diminishing impacts of such threats increase seabird capacity to adjust to global warming, MPAs benefits will be negatively impacted by climate change (Bruno et al., 2018). Additionally, our work emphasizes that marine spatial planning involving protected areas will have to be adaptive, with protected areas adjusted according to species range shifts under the impact of global changes (Hindell et al., 2020). Furthermore, marine ecosystem protection has to balance exploitation and conservation, facing to geopolitical and economic interests when restricting resource exploitation (Hilborn et al., 2004).

In this context, the Arctic Ocean is coveted and already under substantial geopolitical pressure, due to its strategic location, its richness in yet unexploited geological and biological resources (Arruda, 2015; Stokke, 2017; Van Pelt, Huntington, Romanenko, & Mueter, 2017). With global warming it is likely that the high Arctic will be the last bastion for many organisms, including seabirds, as these species will be tracking climate change towards northern latitudes. It is therefore essential to study polar ecosystem functioning and structure to determine and protect irreplaceable habitats. Seabirds, as highly-mobile boundary objects (Lescroël et al., 2016) sentinels and indicators of marine ecosystems, will certainly be privileged studies' models and we believe that the methodological approaches developed in this thesis will be highly relevant.

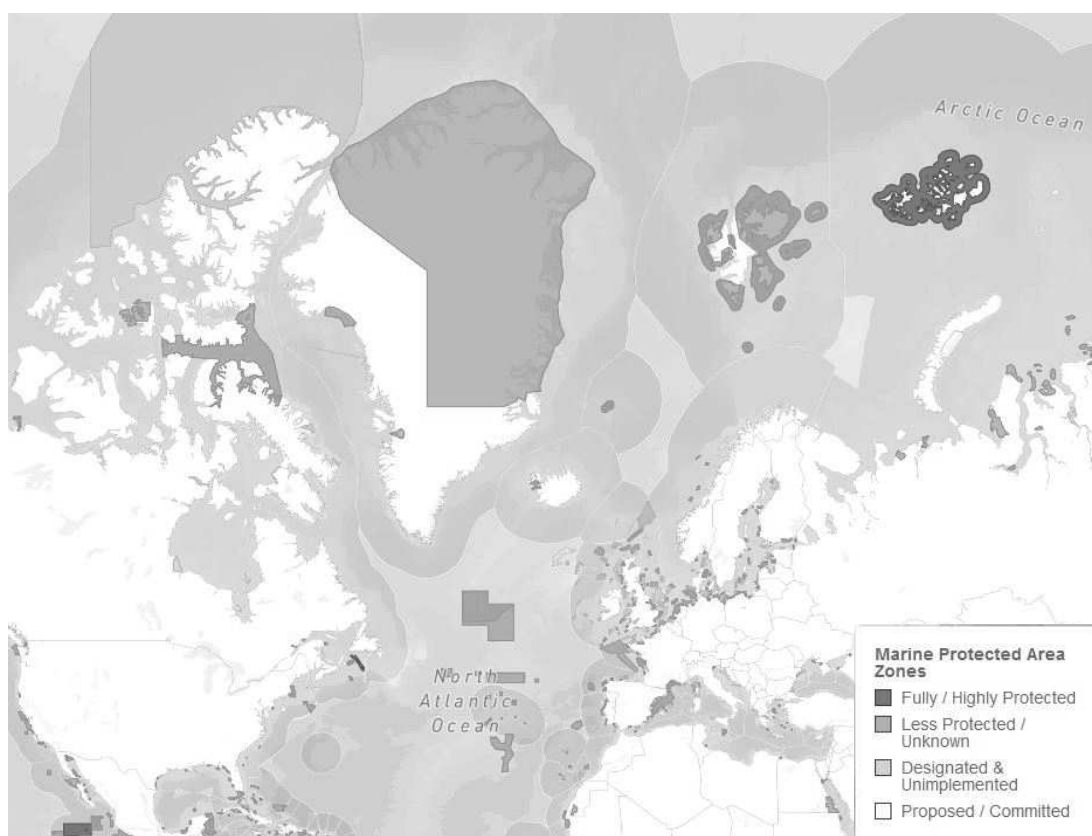


Figure 15. Map of the North Atlantic Marine Protected Areas Zones. Source: Marine Protection Atlas made by the Marine Conservation Institute

5. A framework to study animal and human movements

HSM are increasingly used to model future distributions of organisms in connection with growing concerns about the impacts of current and future climate change. By showing an example of how these models can be coupled with efficient bio-energetic mechanistic models we hope to open the door to new studies. Those will improve knowledge on the drivers of the distribution of particularly endangered species in order to protect them now, but also in the future, and facilitate conservation measures such as species translocation (Draper & Marques, 2019). Moreover, by demonstrating the interest of the energyscape concept, we hope to see its applications extended to other animals and migration types.

The marine world hides many cryptic animals with rare sightings and unknown behavior, diet, physiology and habitat. It therefore seems difficult to use Niche MapperTM on these kind of organisms but we argue that experiments conducted in aquariums on better-known or closely related species could be a promising start to parametrize Niche MapperTM. This will reveal the energyscapes of these animals, to identify favorable locations in terms of temperature or resources, allowing a considerable gain in the study and protection of such cryptic species.

Further, we focused on the horizontal migration of seabirds but many marine species migrate within the water column. Therefore it could be very interesting to model a vertical energyscape according to depth and vertical variation of water temperature. By extrapolating the result obtained, we could build three-dimensional energyscapes (according to longitude, latitude and depth) for these organisms and thus evaluate the impacts of climate change on their potential latitudinal and vertical distribution shifts.

Finally, past climate changes such as glaciation phenomena have shaped the distribution but also the migration of organism (Pérez-Tris, Bensch, Carbonell, Helbig, & Telleria, 2004; Svenning, Normand, & Kageyama, 2008; Zink & Gardner, 2017). HSM have been already used to model the past distributions of organisms; incorporating the concept of energyscape will allow a better understanding of the strategies displayed in the selection of refuges during glaciation or during the colonization of new areas after the deglaciation. For example, studying the link between the migratory routes of humans during the past in relation to their energyscape may provide a better understanding of the expansion of human societies and gene flows resulting from them.

Even if this energyscape approach seems applicable to our ancestors, it seems more challenging to use nowadays to characterize migratory flows. Yet, even if taking into account the social aspects or the contribution of technologies in the description of the ecological niche of contemporary humans seems difficult, many climatic refugees are indeed expected in the near future. Those will notably follow the rise of sea level, and using HSM could be interesting to relocate these people in adequate and safe places from an environmental point of view.

FRENCH SUMMARY

Introduction

I. Importance des périodes de migration et d'hivernage dans le cycle de vie des oiseaux

La migration animale désigne généralement un aller-retour régulier entre deux endroits distincts, rythmé de façon journalière, saisonnière ou annuelle, en réponse à des variations temporelles ou géographiques de la disponibilité en ressources (Dingle & Drake, 2007). Les voyages qui en résultent impliquent souvent des milliers d'organismes, façonnant la biogéographie des communautés à l'échelle locale, régionale ou mondiale (Somveille, 2016). En outre, le long de leur parcours, les animaux migrateurs modifient les interactions trophiques et jouent un rôle important dans le transfert de nutriments, de graines et d'agents pathogènes à travers des zones très éloignées les unes des autres, modifiant ainsi la structure et les fonctions des écosystèmes (Bauer & Hoye, 2014).

En raison de leur capacité de vol, les oiseaux sont les organismes les plus pré-adaptés à la migration sur de longues distances (jusqu'à 30 000 km pour la sterne arctique (*Sterna paradisaea*) (Egevang et al., 2010)). Leur migration correspond généralement à un mouvement régulier entre les zones de reproduction et d'hivernage (Newton, 2010) qu'ils effectuent chaque année pour maximiser leur valeur sélective, en étant présents dans leur zone de reproduction pendant le pic d'abondance des ressources et absents en période de disette (Somveille et al., 2015). Comme la période de reproduction des oiseaux est généralement limitée dans le temps par la disponibilité des ressources, la période de non-reproduction représente la plus grande partie du cycle annuel.

Les populations d'oiseaux migrateurs déclinent actuellement à un rythme plus élevé que celui des oiseaux sédentaires (Robbins, Sauer, Greenberg et Droege, 1989 ; Sanderson, Donald, Pain, Burfield et Bommel, 2006). Contrairement à leurs homologues résidents, les oiseaux migrateurs doivent faire face à des contraintes environnementales aussi bien sur leurs lieux de reproduction et d'hivernage que pendant leurs voyages ou bien lors des périodes passées sur les sites de mue et de repos, augmentant ainsi le nombre de menaces potentielles (Runge et al., 2015).

La majeure partie de la mortalité des oiseaux migrateurs a lieu pendant la période de non-reproduction (voir par exemple Harris & Wanless, 1996). Il est donc crucial d'identifier les différentes menaces qui surviennent pendant cette période et de comprendre leurs effets pour protéger les oiseaux migrateurs, en particulier lorsqu'un nombre limité de couloirs de migration, haltes et sites d'hivernage regroupent de nombreuses populations. Les oiseaux migrateurs sont ainsi particulièrement sensibles à la perte d'habitats (Bairlein, 2016), aux infrastructures anthropiques (Loss, Will, & Marra, 2015), à la pression de chasse (Jiguet et al., 2019), aux événements climatiques extrêmes (Newton, 2007) et aux impacts du réchauffement climatique (Robinson et al., 2009) qui les affectent simultanément ou à différentes

échelles spatio-temporelles tout au long de leur cycle de vie, pouvant entraîner des effets cumulés délétères.

II. Le changement climatique, une menace supplémentaire pour les organismes vivants

Depuis 1850 et la révolution industrielle, les températures ont augmenté à un rythme alarmant. Selon le Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC), la température moyenne à la surface du globe était de $0,87 \pm 0,12$ °C plus élevée entre 2006 et 2015 que pour la période 1850-1900 (Masson-Delmotte et al., 2018). L'océan s'est également réchauffé depuis 1970, et depuis 1993, il est probable que son taux de réchauffement ait plus que doublé (Pörtner et al., 2019). Avec l'augmentation des émissions de CO₂ et l'absorption océanique qui s'ensuit, l'océan s'est acidifié, appauvri en oxygène et le niveau de la mer a augmenté pour la période 2006-2015 à un taux sans précédent de $3,6 \text{ mm.an}^{-1}$ (Pörtner et al., 2019), principalement en raison de la fonte des calottes glaciaires du Groenland et de l'Antarctique (Pörtner et al., 2019). La banquise arctique est également plus mince et plus jeune, et son volume a diminué pour tous les mois de l'année entre 1979 et 2018, avec une réduction maximale de $12,8 \pm 2,3$ % par décennie en septembre (Pörtner et al., 2019). Enfin, la fréquence des vagues de chaleur et des fortes précipitations a augmenté dans certaines régions et l'activité des cyclones tropicaux a augmenté en Atlantique Nord depuis 1970 (GIEC, 2014).

Actuellement, le budget radiatif de notre planète est positif, en lien avec l'augmentation des concentrations atmosphériques de CO₂ depuis 1750, entraînant un réchauffement de la surface de la Terre (GIEC, 2014). En effet, les émissions anthropiques de gaz et d'aérosols ont augmenté depuis la période préindustrielle en raison de la croissance économique et démographique pour atteindre les niveaux les plus élevés jamais enregistré entre 2000 et 2010, (GIEC, 2014). Les effets des activités humaines ont ainsi été détectés dans la plupart des changements climatiques décrits précédemment, tels que le réchauffement des océans, la réduction de la concentration en neige et en glace et l'élévation du niveau de la mer à l'échelle mondiale (GIEC, 2014). Les impacts anthropiques sur le climat font partie des modifications drastiques de la biosphère causées par l'Homme (Diaz et al., 2019) depuis la révolution industrielle de 1850. Une nouvelle ère géologique a été proposée, "l'Anthropocène".

La recherche sur le climat progresse, permettant une meilleure compréhension des systèmes climatiques terrestres, et les modèles sont de plus en plus à même de représenter avec précision les phénomènes climatiques en cours. Les prévisions futures sont actuellement basées sur des scénarios de concentration représentatives (RCP) qui correspondent à quatre scénarios différents d'utilisations des terres et des émissions de gaz à effet de serre/de polluants atmosphériques au cours du 21^e siècle (GIEC, 2014). À court terme, la température moyenne à la surface du globe devrait augmenter (entre 0,3° et 0,7°C par rapport à 1986-2005) (GIEC, 2014) et il est également prédit que les océans se réchaufferont selon ces quatre scénarios (Pörtner et al., 2019). De plus, l'acidification des océans

devrait persister d'ici 2100, même si une légère amélioration est probable à partir de 2050, selon le scénario le plus optimiste (Pörtner et al., 2019). En outre, le niveau moyen mondial de la mer devrait continuer à augmenter à un rythme qui pourrait atteindre 15 mm.an^{-1} en 2100 selon le scénario le plus pessimiste (Pörtner et al., 2019). Enfin, les glaciers devraient perdre $18 \pm 7\%$ ou $36 \pm 8,5\%$ de leur masse entre 2015 et 2100 pour les scénarios les plus extrêmes (Pörtner et al., 2019). Tous les scénarios prévoient la fonte de la banquise arctique, mais le scénario le plus pessimiste est particulièrement alarmant en prévoyant sa fonte totale à la fin de chaque été d'ici 2050.

Les changements climatiques observés et à venir précédemment énumérés ont été décrits à l'échelle mondiale, masquant une grande hétérogénéité entre les régions du monde (GIEC, 2014). Par exemple, l'Atlantique Nord s'est davantage réchauffé que les autres océans entre 1971 et 2010 (Stocker et al., 2013). L'océan Atlantique est, après l'océan Pacifique, le deuxième plus grand océan de notre planète, et il joue un rôle clé dans la circulation océanique et la régulation climatique mondiale (Ottersen, Stenseth et Hurrell, 2004). Il est intensivement exploité par l'homme (Pauly & Maclean, 2003) et le réchauffement climatique n'est qu'une des nombreuses menaces anthropiques qui pèsent sur ses écosystèmes et sur chaque compartiment des chaînes alimentaires qu'il abrite (Halpern et al., 2008).

Les changements climatiques pourraient notamment avoir un impact sur les organismes via des modifications physiologiques et phénologiques, des changements dans leur abondance et leur distribution, entraînant ainsi des changements dans la structure des communautés (Hughes, 2000). Les impacts des changements climatiques sur les organismes sont donc à la fois directs et/ou indirects (par exemple par le biais des interactions prédateurs-proies (Ottersen et al., 2004)) et la vulnérabilité des espèces dépend de leur capacité d'adaptation, de leur sensibilité et du degré d'exposition aux effets du réchauffement climatique (Beaugrand, 2015). Les organismes sont interdépendants au sein des réseaux alimentaires auxquels ils appartiennent : l'abondance des producteurs primaires influence les niveaux supérieurs de la chaîne trophique (contrôle ascendant) et les prédateurs supérieurs agissent sur l'abondance des organismes inférieurs du réseau trophique (contrôle descendant). En outre, les fluctuations des organismes appartenant aux niveaux intermédiaires de la chaîne alimentaire affectent à la fois les niveaux supérieurs et inférieurs par le biais du contrôle dit « en taille de guêpe » (Cury et al., 2000), en particulier lorsque peu d'espèces composent ces niveaux intermédiaires. Par conséquent, les effets des changements climatiques sur un niveau trophique ont des répercussions dans l'ensemble de la chaîne alimentaire.

En réponse aux changements climatiques, les espèces peuvent suivre les conditions favorables dans le temps (changement de leur phénologie, (Parmesan, 2007), mais aussi dans l'espace en déplaçant leur aire de répartition vers des latitudes plus élevées ou des eaux plus profondes (Perry, Low, Ellis, & Reynolds, 2005). En raison d'un environnement physique moins contraignant et d'une gamme d'optimum thermique plus mince, les espèces marines sont davantage capables de suivre le réchauffement climatique que leurs homologues terrestres (Lenoir et al., 2020). La sensibilité aux

changements climatiques varie néanmoins en fonction des espèces, induisant des réponses différentes et créant parfois des décalages spatio-temporels entre les proies et leurs prédateurs (Burthe et al., 2012), modifiant la structure et le fonctionnement de communautés entières (Beaugrand et al., 2019). Enfin, les espèces peuvent également s'adapter aux changements climatiques grâce à leur plasticité comportementale et/ou physiologique ou encore grâce à la microévolution, mais pour analyser et comprendre les mécanismes et rôles de ces processus, des études rigoureuses basées sur des suivis individuels à long-terme sont nécessaires (Teplitsky & Charmantier, 2019).

L'Atlantique Nord fournit d'importants services écosystémiques et une meilleure compréhension des effets des changements climatiques sur ses écosystèmes et organismes représente un objectif scientifique majeur. Les prédateurs supérieurs sont des espèces clés qui intègrent l'état des chaînes trophiques sous-jacentes (Hammerschlag et al., 2019). Parmi ces prédateurs, les oiseaux marins sont particulièrement mobiles et bien étudiés, ce qui en fait des sujets d'étude idéaux pour comprendre les impacts des changements climatiques sur les espèces migratrices marines (Lescroël et al., 2016).

III. Les oiseaux marins au sein d'écosystèmes en mutation

Les oiseaux marins sont des prédateurs supérieurs charismatiques vivant dans tous les océans du monde et classés en 369 espèces (BirdLife International). Ils dépendent principalement des ressources marines pour se nourrir et passent donc 90 % de leur vie en mer, ne venant à terre que pour se reproduire et élever leurs petits (Schreiber & Burger, 2002). Pendant la période de reproduction, les déplacements des oiseaux marins sont limités autour des colonies afin de nourrir régulièrement les poussins : les oiseaux de mer sont alors qualifiés de "central place foragers" (Orians & Pearson, 1979).

Par le biais de ces trajets entre terre et mer, les oiseaux marins sont des ingénieurs de leur écosystème qui fournissent des nutriments marins aux alentours de leur colonie, modifiant ainsi considérablement la flore et la faune (González-Bergonzoni et al., 2017). Les ressources marines utilisées par les oiseaux marins sont situées dans des zones où les conditions océanographiques améliorent la productivité primaire et concentrent les proies (Boertmann, Lyngs, Merkel et Mosbech, 2004 ; Grecian et al., 2016 ; Stirling, 1995). En Atlantique Nord, les oiseaux marins dépendent principalement d'un nombre limité d'espèces (Ciannelli et al., 2005), et les changements dans l'abondance de ces proies ont un impact significatif sur les populations d'oiseaux marins (voir par exemple Reiertsen et al., 2014). Ainsi, ces derniers sont souvent utilisés comme sentinelles écologiques de l'état des écosystèmes marins (Durant et al., 2009), notamment pour évaluer les effets de la pêche sur les stocks de poissons (voir par exemple Barrett, 2002).

De plus, les oiseaux marins sont parmi les plus menacés de tous les oiseaux (Dias et al., 2019) et leur statut de migrateurs les rend particulièrement vulnérables. Ils sont particulièrement vulnérables face aux espèces envahissantes (Jones et al., 2016), aux captures accidentelles par les engins de pêche

(Lewison et al., 2014 ; Žydelis, Small, & French, 2013), à la surpêche de leurs proies (Grémillet et al., 2018) et aux effets directs et indirects des changements climatiques.

La plupart des études traitant des impacts des changements climatiques sur les oiseaux marins se concentrent sur les processus démographiques (Descamps et al., 2017) ou sur la saison de reproduction (Frederiksen, Anker-Nilssen, Beaugrand, & Wanless, 2013). Cependant, avec la miniaturisation des appareils électroniques, la période de non-reproduction a reçu de plus en plus d'attention au cours de la dernière décennie (Fort, Moe, et al., 2013 ; Frederiksen et al., 2012). Les scientifiques manquent néanmoins de connaissances sur les impacts du réchauffement climatique sur les oiseaux marins pendant cette période. Ces informations et cette compréhension sont pourtant essentielles car les conditions rencontrées pendant cette période peuvent fortement influencer la dynamique des populations d'oiseaux marins (Alves et al., 2013).

En ce sens, Grémillet et Boulinier (2009) ont souligné que l'identification des déterminants de la répartition des oiseaux marins en hiver est une priorité de recherche, tout comme la prévision des impacts futurs des changements climatiques sur leur dynamique spatiale. L'étude de plusieurs populations d'une même espèce est alors importante pour dépeindre pleinement la niche écologique de l'espèce considérée, mais aussi pour mieux comprendre le fonctionnement de la méta-population en dehors de la saison de reproduction et enfin, pour avoir une vue d'ensemble des impacts du réchauffement climatique.

IV. Paysage énergétique et étude de la migration animale

En écologie du déplacement, la théorie de l'approvisionnement optimum suggère que les organismes ont tendance à minimiser leur dépense énergétique lors de leurs recherches de nourriture, et à maximiser leur gain énergétique (Stephens, Brown, & Ydenberg, 2007). Par conséquent, les coûts liés au transport dans un paysage particulier peuvent expliquer pourquoi et comment les animaux se répartissent.

Récemment, Shepard (2013), Wilson (2012) et leurs collaborateurs ont défini les "paysages énergétiques" comme la variation des coûts de transport en fonction des caractéristiques de l'environnement, telles que la végétation, l'inclinaison, la vitesse ou la direction des courants océaniques. Cette approche permet notamment de comprendre comment l'hétérogénéité de l'environnement façonne les stratégies comportementales. Dans ce contexte, Amélineau et ses collaborateurs (2018) ont élargi le concept de paysage énergétique, et l'ont défini comme les variations du bilan énergétique d'un organisme dans l'espace en fonction des conditions environnementales, fournissant un cadre pour comparer le caractère favorable de différents endroits et un outil mécaniste pour étudier la distribution des animaux. Le potentiel de cette approche a été récemment démontré pour une espèce d'oiseaux marins (Amélineau et al., 2018), fournissant un cadre

conceptuel et méthodologique qui peut maintenant être étendu au niveau communautaire dans tout le bassin de l'Atlantique Nord.

V. Objectifs de la thèse

L'objectif général de ce travail de thèse est d'étudier les impacts du changement climatique sur la communauté d'oiseaux marins hivernant en Atlantique Nord, en se concentrant sur leur distribution et en utilisant une approche énergétique.

Plus précisément, les objectifs sont les suivants :

- Identifier les points chauds d'hivernage actuels de la communauté d'oiseaux marins de l'Atlantique Nord et déterminer leurs déterminants environnementaux à l'échelle du bassin océanique (chapitre II).
- Déterminer et prévoir les impacts des changements climatiques de l'Atlantique Nord sur la distribution des oiseaux marins, puis évaluer le potentiel de nouvelles stratégies de migration et d'hivernage induites par ces impacts (chapitres II et III).
- Déterminer l'exposition actuelle des oiseaux marins de l'Atlantique Nord aux tempêtes hivernales, afin de mieux comprendre leur vulnérabilité future à de tels événements (chapitre IV).

Après une brève description des méthodes utilisées (Chapitre I), cette thèse contient trois chapitres principaux correspondant à des articles publiés ou soumis. Les résultats obtenus au cours de cette thèse sont discutés en conclusion, ouvrant de nouvelles perspectives pour des travaux futurs.

Chapitre I: Méthodes

I. Espèces étudiées

La communauté d'oiseaux marins de l'Atlantique Nord est principalement représentée par cinq espèces, souvent touchées par les tempêtes hivernales (Camphuysen et al., 1999 ; Morley et al., 2016) et représentant 75 % du nombre total d'oiseaux marins se reproduisant en Atlantique Nord (Barrett et al., 2006) : le mergule nain (*Alle alle*), le macareux moine (*Fratercula arctica*), le guillemot de Troil (*Uria aalge*), le guillemot de Brunnich (*Uria lomvia*) et la mouette tridactyle (*Rissa tridactyla*). Comme ces espèces ont des régimes et des comportements alimentaires différents, nous émettons l'hypothèse que les changements climatiques les affectent différemment. Les chapitres II et IV se sont concentrés sur toutes ces espèces, tandis que le chapitre III s'est intéressé à déterminer quelles espèces d'oiseaux arctiques verraient leurs stratégies migratoires impactées par la fonte de la banquise, avant d'utiliser le mergule nain plus en détail.

II. Localisation des oiseaux marins pendant leurs migrations et hivernages

Localiser les oiseaux marins est la première étape dans l'étude des impacts du réchauffement climatique sur leur distribution hivernale. Cependant, les oiseaux marins hivernent généralement loin des côtes et/ou sont inatteignables pendant la majeure partie de l'année, limitant fortement l'acquisition des données nécessaires pour mieux comprendre leur écologie hivernale.

Certaines espèces migrant près des côtes sont observées et/ou chassées légalement, fournissant des informations sur leurs voies migratoires et leur régime alimentaire hivernal (Karnovsky et al., 2008). De plus, la localisation de nombreuses espèces peut être enregistrée lors de sorties en bateau et être fournie en ligne au sein de base de données en libre accès (voir le site web du GBIF par exemple). Toutefois, ces données peuvent être l'objet de mauvaises identifications et être biaisées vers des zones plus accessibles (Guillera-Arroita et al., 2015), en particulier en hiver lorsque les conditions de glace peuvent contraindre la navigation.

L'étude des déplacements des oiseaux marins a donc largement bénéficié des avancées technologiques. Par exemple, le suivi d'oiseaux de petite taille tout au long de l'année a été rendu possible au début des années 90 grâce à des enregistreurs particulièrement légers (moins de 2g) appelés GLS (Global Location Sensors) inventés par Rory P. Wilson et Roger Hill (Grémillet, 2015). Ces appareils enregistrent l'heure et le niveau de lumière ambiante correspondant, et fournissent 2 localisations par jour en utilisant la durée du jour comme approximation de la latitude et l'heure de midi pour la longitude (Hill, 1994 ; Wilson, Ducamp, Rees, Culik, & Niekamp, 1992). Les GLS sont relativement légers, bon marché et faciles à utiliser, mais les oiseaux équipés doivent être recapturés pour pouvoir télécharger les données stockées. De plus, les GLS ont une faible précision (186 km +/- 114 km, Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004) qui dépend fortement de la météo, du

comportement de l'animal, de son habitat et de la période de l'année (Lisovski et al., 2012). Enfin, les oiseaux ne peuvent pas être localisés avec les GLS en période d'équinoxe, lorsque les durées du jour et de la nuit sont égales (Hill, 1994 mais voir Merkel et al., 2016). Les données GLS utilisées dans ce travail de thèse ont été obtenues grâce à un déploiement massif de GLS rendu possible par un important effort de collaboration internationale, permettant de suivre plus de 1500 individus des cinq espèces étudiées, provenant de 39 colonies.

III. Modélisation des distributions actuelles et futures des oiseaux marins

Une fois les oiseaux marins localisés, il est important d'identifier les déterminants actuels de leur distribution afin de mieux comprendre leur écologie, d'évaluer les effets des conditions environnementales et de prévoir les impacts futurs du réchauffement climatique.

Pour occuper un site et y maintenir des populations, les espèces doivent atteindre ce site, et les conditions biotiques et abiotiques qui y règnent doivent être adaptées aux besoins de l'espèce (Lortie et al., 2004 ; Pulliam, 2000 ; Soberón, 2007). Les conditions abiotiques pour lesquelles les besoins physiologiques de l'espèce sont satisfaits correspondent à sa "niche fondamentale" (sensu Hutchinson, 1957) tandis que la distribution observée d'une espèce correspond à sa "niche réalisée", c'est-à-dire sa niche fondamentale limitée par les interactions biotiques et les limites de sa dispersion (Soberón, 2007). Quantifier cette niche réalisée permet d'identifier les déterminants de la répartition des espèces et d'évaluer l'adéquation d'une zone avec leurs besoins. Cette niche pourra, sous certaines hypothèses, être projetée dans le temps et dans l'espace (Elith & Leathwick, 2009) pour évaluer la distribution future des organismes étudiés.

Les modèles de distribution d'espèces (SDM) ont été développés dans ce but au cours des décennies précédentes et ont été largement utilisés pour prédire les impacts des changements climatiques sur la répartition des espèces, mais aussi en biogéographie, en écologie de la conservation et en gestion des espèces envahissantes (Guisan et al., 2013). Les SDM sont des modèles corrélatifs, qui relient mathématiquement la présence des espèces aux conditions environnementales rencontrées (Elith & Leathwick, 2009) avant d'être extrapolés pour prédire la distribution des espèces dans de nouvelles conditions.

Habituellement, les SDM se basent sur des variables, climatiques ou physiques, considérées comme pertinentes en tant que prédicteurs de la répartition des espèces. Certains SDM incluent des processus biotiques mais ces variables sont souvent difficiles à obtenir à l'échelle nécessaire, et les scientifiques utilisent généralement des variables de substitution pour étudier leur influence sur les choix des espèces en terme d'habitat. Les variables empiriques fournissant des informations sur l'abondance et la distribution des poissons et du zooplancton à l'échelle mondiale sont particulièrement rares et doivent la plupart du temps être modélisées avant d'être intégrées dans les SDM de leurs prédateurs. Dans ce travail de thèse, nous avons considéré la concentration en zooplancton obtenue via des modèles

climatiques. Les abondances actuelles et futures des poissons ont été obtenues grâce au modèle d'enveloppe bioclimatique dynamique (DBEM, Cheung et al., 2009). En effet, la combinaison des SDM avec des modèles de dispersion, de population et/ou mécanistes permet une meilleure représentation des processus écologiques au sein des modèles corrélatifs (voir par exemple Meineri, Deville, Grémillet, Gautier-Clerc, & Béchet, 2015). Dans cette optique, nous avons donc intégré l'approche mécaniste de calcul des paysages énergétiques dans la modélisation de la distribution des oiseaux marins.

IV. Un modèle bio-mécaniste : Niche MapperTM

Le calcul des besoins énergétiques des oiseaux marins dans l'espace en fonction des conditions environnementales (energyscape, Amélineau et al., 2018) est un outil puissant pour expliquer de façon mécaniste leur répartition et comparer le caractère favorable de l'environnement dans l'espace et dans le temps. Plusieurs méthodes existent pour mesurer ou calculer la dépense énergétique des animaux sauvage mais l'inaccessibilité des oiseaux marins en période de non-reproduction rend la plupart d'entre elles inadaptées et la modélisation semble alors particulièrement avantageuse. Malgré les connaissances limitées disponibles sur l'écologie hivernale des oiseaux marins, une telle modélisation a été menée avec succès sur plusieurs espèces (Amélineau et al., 2018 ; Fort et al., 2009 ; 2013), en utilisant le modèle mécaniste, Niche MapperTM.

Cet algorithme contient deux sous-modules : un modèle de microclimat, qui fournit des données environnementales (température de la surface de la mer, température de l'air, vitesse du vent, couverture nuageuse et humidité relative) pour l'environnement proche de l'animal, et un module animal, qui utilise les sorties du modèle de microclimat, ainsi que les caractéristiques morphologiques, comportementales et physiologiques de l'animal (voir chapitre II, Supplément XIII pour la liste des variables considérées). Ces variables sont utilisées pour estimer l'énergie nécessaire au maintien de la température corporelle de l'animal à un moment donné avec le comportement considéré.

Chapitre II: Atteindre les objectifs de l'accord de Paris pour limiter les changements de répartition hivernale des oiseaux marins en Atlantique Nord

Nous avons étudié les conséquences de l'accord de Paris visant à limiter le réchauffement climatique à 2°C, sur la distribution hivernale future de la communauté d'oiseaux marins de l'Atlantique Nord. Nous avons localisé et quantifié les habitats hivernaux actuels et futurs de cinq espèces d'oiseaux marins de l'Atlantique Nord (*Alle alle*, *Fratercula arctica*, *Uria aalge*, *Uria lomvia* et *Rissa tridactyla*) en utilisant des données de suivi de ~1500 individus, grâce à des fonctions de sélection de ressource basées sur une modélisation mécaniste des besoins énergétiques des oiseaux et un modèle d'enveloppe bioclimatique dynamique pour leurs proies. Nos résultats suggèrent une modification des distributions hivernales actuelles en lien avec les changements climatiques, en particulier lorsque le réchauffement global dépassera 2°C, modifiant ainsi les zones d'agrégation d'hivernage des oiseaux marins de l'Atlantique Nord. Nos conclusions suggèrent que la limitation du réchauffement climatique à moins de 2°C au-dessus des niveaux préindustriels limitera les changements dans la localisation et la taille des habitats favorables à l'hivernage des oiseaux marins de l'Atlantique Nord au 21^{ème} siècle.

Chapitre III: Le changement climatique pourrait bouleverser la migration des oiseaux. Vols transarctiques et sédentarité à hautes latitudes dans un Arctique libre de glace.

Les modèles climatiques prévoient la fonte totale de la banquise arctique à la fin de chaque été d'ici 2050, rendant l'océan Arctique totalement libre de glace à cette période de l'année. La suppression de cette barrière entre l'Atlantique et le Pacifique modifiera un large éventail de processus écologiques, dont la migration des oiseaux. Nous avons identifié 29 espèces d'oiseaux marins se reproduisant en Arctique qui pourraient effectuer une migration transarctique de l'Atlantique vers le Pacifique Nord (ou *vice versa*). Nous avons également identifié 24 espèces d'oiseaux marins arctiques qui pourraient passer d'une stratégie migratoire à une stratégie sédentaire à hautes latitudes. Pour illustrer les conséquences biogéographiques de ces changements migratoires drastiques, nous avons réalisé une étude approfondie sur le mergule nain (*Alle alle*), l'oiseau marin le plus nombreux de l'Arctique. En couplant les modèles de distribution de l'espèce et les modèles climatiques, nous avons évalué l'adéquation des futures zones d'hivernage et de reproduction avec une migration transarctique et une sédentarisation annuelle à hautes latitudes. De plus, nous avons utilisé un modèle bioénergétique mécaniste (Niche MapperTM), pour comparer les coûts énergétiques de la migration actuelle des mergules nains en Atlantique Nord avec ceux induits par les stratégies transarctique et

sédentaire. De façon surprenante, nos résultats indiquent que la migration transarctique des mergules nains, de l'Atlantique vers le Pacifique Nord, pourrait être deux fois moins coûteuse, sur le plan énergétique, que le sédentarisme ou la migration vers les zones d'hivernage actuelles. Notre étude illustre comment le réchauffement climatique peut modifier radicalement la biogéographie des espèces migratrices, et fournit un cadre méthodologique général reliant énergie migratoire et écologie spatiale.

Chapitre IV: Les tempêtes hivernales de l'Atlantique Nord affament les oiseaux marins

Chaque hiver, l'Atlantique Nord est le théâtre de tempêtes spectaculaires, dont certaines sont responsables d'échouages massifs d'oiseaux marins. Des milliers d'oiseaux marins émaciés, morts ou mourants, sont alors rejetés sur les côtes européennes et nord-américaines, mais leur origine géographique et les causes de leur mort restent floues. En couplant les données de suivi hivernal pour ~1500 individus de cinq espèces clés d'Atlantique Nord (*Alle alle*, *Fratercula arctica*, *Uria aalge*, *Uria lomvia* et *Rissa tridactyla*) avec la localisation des cyclones obtenue à partir des données climatiques, nous avons déterminé les zones de forte exposition aux cyclones pour la communauté d'oiseaux marins à l'échelle du bassin océanique. Nous avons ensuite exploré les conséquences énergétiques de l'exposition des oiseaux marins aux tempêtes en utilisant un modèle bioénergétique mécaniste (Niche MapperTM) pour différentes intensités de cyclones. Notre étude indique que les oiseaux marins qui hivernent au large de l'Islande et du sud du Groenland, dans la mer du Labrador ou dans la mer de Barents peuvent subir des cyclones de forte intensité. Les résultats de notre modèle suggèrent que les conditions cycloniques n'augmentent pas les besoins énergétiques des oiseaux marins. Ceci implique que l'indisponibilité des proies et/ou de l'incapacité à se nourrir pendant les cyclones causeraient leur mort. Notre étude fournit des informations essentielles sur l'exposition des oiseaux marins aux cyclones, dans un contexte de changements marqués du régime des tempêtes en lien avec le réchauffement climatique.

Conclusion

En utilisant une approche énergétique, ce travail de thèse s'est interrogé sur les impacts des changements climatiques sur les oiseaux marins hivernant en Atlantique Nord. À notre connaissance, c'est la première étude qui aborde cette question en se concentrant sur la répartition des espèces au niveau communautaire et à l'échelle d'un bassin océanique en utilisant la dépense énergétique comme principale variable explicative.

I. Résultats principaux

Nos résultats montrent que les oiseaux marins se regroupent pendant la période de non-reproduction au large de Terre-Neuve, au milieu de l'Atlantique, au large du sud du Groenland et de l'Islande, en mer du Nord et dans la mer de Barents (voir chapitre IV). Nous avons montré que les oiseaux de toutes les espèces et colonies étudiées sont vulnérables aux cyclones de forte intensité (chapitre IV), en particulier le long des côtes canadiennes (dans le détroit de Davis, la mer du Labrador et au large de Terre-Neuve), au large de l'Islande et du sud-ouest du Groenland ainsi que dans la mer de Barents. Inversement, les oiseaux hivernant au milieu de l'océan Atlantique semblent moins touchés par les tempêtes.

Nous avons également conclu que les choix d'habitat des oiseaux marins en hiver résultaient d'un compromis entre la dépense énergétique et la disponibilité des proies (voir chapitre II). Parmi les variables environnementales, la température de l'air était le principal déterminant de la répartition des mergules nains en mer, tandis que la distance à la côte était la variable principalement impliquée dans le choix de l'emplacement des sites de nidification pendant la saison de reproduction (voir chapitre III).

Selon les modèles climatiques considérés dans cette thèse, il est prédit que les températures de l'air et de la mer augmentent, que la dépense énergétique des oiseaux marins diminue et que leurs proies se déplacent vers le nord avec le réchauffement climatique (voir chapitre II), en accord avec les études précédentes (Beaugrand et al., 2019). Nous avons prédit que les zones d'agrégation hivernales des oiseaux marins pourraient changer avec le réchauffement climatique, avec des zones telles que Terre-Neuve, le golfe du Saint-Laurent et le sud du Groenland devenant de plus en plus attrayantes pendant l'hiver en raison de la diminution de la dépense énergétique des oiseaux marins dans ces zones. Dans certains cas, les parties méridionales des aires de répartition des espèces considérées sont censées devenir inadaptées, réduisant la taille des habitats favorables pour ces espèces (voir les chapitres II et III). Comme les trajectoires des tempêtes doivent également se déplacer vers le nord, les événements de mortalité massive augmenteront probablement en mer du Nord, en mer de Norvège et en mer de Barents (voir chapitre IV). Il est donc essentiel d'atteindre les objectifs de l'accord de Paris pour limiter les changements d'habitats de la communauté d'oiseaux marins de l'Atlantique Nord au 21e

siècle. Enfin, en réponse au réchauffement climatique, les oiseaux marins vont potentiellement hiverner plus près du pôle, diminuant ainsi leur distance de migration et modifiant leur comportement migratoire.

En fonction des capacités et du comportement des oiseaux arctiques, nous avons identifié 24 espèces d'oiseaux marins qui pourraient passer d'une stratégie migratoire à une sédentarisation annuelle dans le Haut-Arctique (voir chapitre III). Nous avons également identifié 29 espèces d'oiseaux marins qui pourraient être impliquées dans une future migration transarctique de l'Atlantique Nord vers le Pacifique Nord ou *vice versa* (voir chapitre III). De façon surprenante, nos résultats indiquent que la migration transarctique des mergules nains, de l'Atlantique Nord vers le Pacifique Nord, pourrait être deux fois moins coûteuse sur le plan énergétique, que la sédentarisation ou la migration habituelle en Atlantique Nord.

Enfin, nous avons conclu que les tempêtes ont peu ou pas d'impact sur les besoins énergétiques des oiseaux marins. Les oiseaux marins qui meurent pendant les tempêtes hivernales meurent donc probablement de faim en raison de l'indisponibilité de leurs proies et/ou de leur incapacité à se nourrir. On ne sait pas exactement ce qui empêche les oiseaux marins de se nourrir pendant les cyclones mais on peut supposer que les cyclones augmentent la turbidité de l'eau, diminuent l'intensité de la luminosité sous-marine et perturbent les proies et leur migration verticale.

II. Limites

En menant notre étude, nous avons fait une série d'hypothèses concernant les comportements, les régimes alimentaires et les capacités écophysologiques des espèces considérées. Nous espérons que des études futures permettront d'approfondir les connaissances de ces thématiques, notamment celles des comportements en conditions cycloniques. De plus, nous avons supposé que les liens statistiques établis entre la présence actuelle des oiseaux marins et les facteurs biotiques/abiotiques pris en compte dans nos études (paysage énergétique, champ de proies, température de surface, etc) resteraient inchangés dans le futur. Cependant, les oiseaux marins sont susceptibles de modifier leur régime alimentaire et leur comportement (Vihtakari et al., 2018) pour faire face aux changements des écosystèmes marins causés par le réchauffement climatique, par le biais de plasticité phénotypique et/ou de microévolution (Teplitsky & Charmantier, 2019). Enfin, notre travail n'a pas pris en compte la fidélité aux sites d'hivernage et de reproduction, le rôle de l'expérience, de l'apprentissage et de l'imitation dans le comportement migratoire (Newton, 2010) au-delà des facteurs biotiques et abiotiques actuels qui façonnent la migration et la distribution hivernale des oiseaux marins.

Les observations opportunistes ou les données de suivi par GLS sont précieuses pour localiser les oiseaux marins pendant la période de non-reproduction, mais nous nous sommes confrontés à certains biais et limites dans l'utilisation de ces ressources. Premièrement, les occurrences sont rarement liées à des informations supplémentaires telles que le sexe, l'âge ou le statut reproducteur, qui pourraient

potentiellement influencer la migration, la distribution hivernale (Bogdanova et al., 2011 ; Jarjour, Frei, & Elliott, 2017) et l'exposition/sensibilité au changement climatique (Jenouvrier et al., 2018).

En utilisant Niche MapperTM, nous avons proposé un cadre pour évaluer l'impact du changement climatique sur les oiseaux marins en utilisant une approche énergétique. Malgré ses avantages (précision et possibilité de modéliser la dépense énergétique à de grandes échelles temporelles et spatiales, notamment (Fort et al., 2011)). Niche MapperTM s'appuie sur un grand nombre de variables décrivant la physiologie, la morphologie et le comportement des espèces considérées. Même si ces variables sont disponibles via des spécimens de musée ou dans la littérature, il peut être difficile de les obtenir pour certaines espèces, surtout en dehors de la saison de reproduction, limitant l'utilisation de cette approche de modélisation. De plus, les résultats de ces modèles dépendent de la résolution et de la qualité des données utilisées. Dans notre cas, nous avons paramétré Niche MapperTM avec des données environnementales reconstruites ou modélisées ainsi qu'avec des données métaboliques et comportementales obtenues à partir d'un nombre limité d'études, parfois menées en captivité ou pendant la saison de reproduction (voir Matériels complémentaires XIII du chapitre II). Néanmoins, les besoins énergétiques obtenus au cours de ce travail de thèse semblent en accord avec les résultats d'autres études (voir par exemple Dunn et al., 2020).

Les modèles de distribution d'habitats utilisés pour décrire la répartition des oiseaux marins sont soumis à des hypothèses et des limites spécifiques : Nous avons supposé que les espèces d'oiseaux marins considérées sont (i) en équilibre avec leur environnement et que (ii) nous avons pleinement échantillonné la niche réalisée de ces espèces. Pour représenter efficacement la niche réalisée d'une espèce, il est crucial de sélectionner les variables environnementales pertinentes. Nous avons sélectionné ces variables en utilisant la littérature existante, y compris, si possible, des variables biotiques et mécanistes (voir chapitre II). Comme ces variables ont été modélisées et combinées, l'erreur est particulièrement difficile à évaluer au sein des différents modèles. Dans notre cas, l'empilement des modèles conduit à un modèle unique avec un pouvoir prédictif et une précision élevés, ce qui soutient notre approche (voir les chapitres II et III). Toutefois, un certain décalage existe entre nos prévisions et certaines des distributions observées (voir le chapitre III par exemple). Cela pourrait s'expliquer par l'absence de certaines variables biotiques et abiotiques importantes dans notre SDM.

III. Perspectives futures

Au cours de cette thèse, nous nous sommes concentrés sur l'impact du changement climatique pendant la période de non-reproduction, et plus particulièrement sur les phases de migration et d'hivernage, en laissant de côté la (les) période(s) de mue, les périodes potentielles de dispersion des reproducteurs et les trajets en eux-mêmes. Les mécanismes associés à la dispersion et à la prospection de nouveaux habitats sont complexes et la capacité d'une espèce à se disperser est un mécanisme adaptatif clé dans un environnement changeant basé sur des indices tels que le succès de reproduction des congénères (Doligez, Danchin, & Clobert, 2002). Il semble essentiel de comprendre comment le changement climatique et son rythme auront un impact sur ces indices et donc sur la capacité des individus à disperser. De plus, la période de mue est particulièrement contraignante pour les oiseaux marins. Incapables de voler, ils sont plus vulnérables aux contraintes environnementales telles que les événements extrêmes qu'ils ne peuvent éviter. Enfin, les couloirs de migration et les sites de repos peuvent être affectés par les conditions climatiques ou la distribution changeante des proies. Le changement climatique, en modifiant ces deux éléments, peut modifier l'accessibilité de certaines zones d'hivernage et/ou changer les coûts associés à la migration : tous ces aspects méritent donc d'être étudiés plus avant.

Nos études (voir les chapitres II et III) sont basées sur des SDM, qui sont des modèles corrélatifs reliant la localisation des oiseaux marins et les caractéristiques environnementales. Largement utilisés, ces modèles ne sont pas particulièrement exigeants en termes de connaissances sur les processus sous-jacents à la distribution des espèces. Cependant, ces modèles ne quantifient pas spécifiquement la relation entre les variables environnementales et les distributions des espèces : en effet, la réponse donnée pourrait être une relation causale directe, un effet indirect ou une réponse directe liée à une autre variable colinéaire omise dans le modèle (Mac Nally, 2000). Inversement, les modèles mécanistes traduisent les interactions des traits fonctionnels des organismes avec leur environnement en composantes clés tels que la température corporelle, ou les bilans énergétiques et hydriques, permettant une meilleure compréhension des mécanismes limitant la distribution et l'abondance des organismes (Kearney & Porter, 2009). Ainsi, en modélisant les paysages énergétiques, Niche MapperTM permet d'estimer la quantité de ressources (telles que les proies ou l'eau) dont un organisme a besoin, pour ensuite la comparer avec la quantité de ressources disponibles, pour finalement conclure à l'adéquation de l'environnement pour l'espèce considérée. Dans notre cas, les calculs de paysages énergétiques menés à l'échelle de la communauté d'oiseaux marins pourraient facilement être convertis en une quantité de poissons et de zooplancton nécessaire à sa subsistance. Il serait particulièrement intéressant de comparer ces résultats avec les ressources disponibles, afin de mieux décrire la structure et le fonctionnement des écosystèmes, ainsi que d'évaluer et de limiter les pressions exercées par la pêche.

Les oiseaux marins sont soumis à de nombreuses menaces anthropiques (Dias et al., 2019) qui ont un impact négatif sur leurs populations dans le monde entier. En modélisant les zones d'agrégation actuels et futurs des oiseaux marins en Atlantique Nord, nous avons fourni les informations et les méthodes nécessaires (i) pour identifier les zones importantes pour les oiseaux marins pendant l'hiver, (ii) pour déterminer les zones de conflits entre la communauté d'oiseaux marins et les activités anthropiques ainsi que (iii) pour établir et gérer les zones marines protégées (ZMP). En outre, nos travaux soulignent que la planification de l'espace marin impliquant des zones protégées devra être adaptative, en s'ajustant aux changements d'aires de répartition des espèces sous l'impact des changements globaux (Hindell et al., 2020).

Dans ce contexte, l'océan Arctique est convoité et déjà soumis à une pression géopolitique importante, en raison de sa situation stratégique, de sa richesse en ressources géologiques et biologiques encore inexploitées (Arruda, 2015 ; Stokke, 2017 ; Van Pelt, Huntington, Romanenko, & Mueter, 2017). Avec le réchauffement climatique, il est probable que le Haut-Arctique soit le dernier bastion pour de nombreux organismes, y compris les oiseaux marins, car ces espèces suivront le réchauffement climatique en allant vers les hautes latitudes. Il est donc essentiel d'étudier le fonctionnement et la structure des écosystèmes polaires afin de déterminer et de protéger des habitats qui pourraient être irremplaçables. Les oiseaux marins, en tant que passeurs de frontières hautement mobiles (Lescroël et al., 2016), sentinelles et indicateurs des écosystèmes marins, seront certainement des modèles d'études privilégiés, et nous pensons que les approches méthodologiques développées dans cette thèse seront particulièrement pertinentes dans ce contexte.

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APPENDIX

High dive costs in a small seabird disrupt the dynamic body acceleration – energy expenditure relationship

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Abstract

Energy is a fundamental currency in ecology but is difficult to measure in wild animals. Recently, accelerometry has been widely used to measure energy expenditure over both short and long timescales, and the method has been validated in running and flying animals. However, relationships between dynamic body acceleration and energy expenditure are likely much weaker in breath-hold divers due to high non-locomotory costs and non-linear energy expenditure during dives ('Halsey's hypothesis'). Here, we synoptically recorded daily energy expenditure (DEE) and dynamic body acceleration in a wing-propelled breath-hold diver, the dovekie (*Alle alle*), in order to test this hypothesis and estimate the activity-specific costs of flying and diving in this small seabird. DEE for chick-rearing dovekies was 621 ± 103 kJ/d in 2017 and 590 kJ/day ± 133 kJ/d in 2018. Despite recording much lower dynamic body acceleration and wingbeat frequencies for diving than for flying, both behaviours were found to have similarly high energetic costs (~ 8 - 9 x BMR). As expected, we found that overall dynamic body acceleration was a weak predictor of DEE in dovekies. Yet, importantly, we show that accelerometry data can be used to accurately predict little auk DEE using time-energy budget analyses. Additionally, the method allowed us to measure wingbeat frequencies in dovekies and, in turn, assess wingbeat allometry across flying ($\text{mass}^{-0.21}$) and diving ($\text{mass}^{-0.27}$) Alcids. Time spent flying and time spent diving were inversely correlated in little auks, supporting the notion that foraging dynamics are being driven by the increase in prey availability with distance from the colony (or Ashmole's Halo). In conclusion, accelerometers are an effective tool to estimate activity-specific costs, fine-scale behavioural differences among individuals, and DEE in dovekies. This information is essential to parametrize models forecasting the effects of global change on dovekie energy balance and survival.

Introduction

Energy is an important currency in animal ecology, influencing behavioural decisions, timing of reproduction and, ultimately, mortality (Alves et al. 2013; Shepard et al. 2013). Nonetheless, animal ecologists have developed only a handful of methods for measuring energy costs in the wild, all having strengths and weaknesses (Fort et al. 2011). For example, the doubly labelled water method provides only a single accurate, time-averaged value (Speakman 1997). Heart-rate methods provide values at fine temporal scales, but often involve surgery and can be influenced by cardiovascular adjustments that do not affect energy expenditure (Butler et al. 2004; Green et al. 2011). In the past 15 years, accelerometry has become a popular tool for measuring energy expenditure in wild animals (Wilson et al. 2006; Elliott 2016). Widely used in smartphones to quantify energy expenditure in humans, accelerometry was first validated in the lab on running animals (Halsey et al. 2011b). Because the dynamic component of body acceleration should be a robust index of mechanical power output for a known body mass, accelerometers can, in theory, provide an index of nearly instantaneous energy expenditure, provided that mechanical power is a constant proportion of total energy costs. Indeed, studies on several animal taxa have shown the effectiveness of accelerometers as tools for accurately estimating activity-specific energetic costs (Lear et al. 2017; Elliott et al. 2013a; Halsey et al. 2011b; Murchie et al. 2011). Although observation-based time-budgets have provided rough estimates of activity costs, accelerometers are capable of recording activity in greater detail and do not require constant visual contact by observers (Wilson et al. 2006; Halsey et al. 2011b). Furthermore, the continued miniaturization of technology means biologists are able to equip smaller and smaller organisms with accelerometers.

Breath-hold divers provide special challenges when attempting to measure energy expenditure via accelerometry (Halsey et al. 2011a; Grémillet et al. 2018). Small endotherms diving into cold water are likely to have high thermoregulatory costs unassociated with mechanical costs (Gabrielsen et al. 1991; Lovvorn and Jones 1991). Furthermore, dive costs increase non-linearly with dive duration as individuals suppress heart rate and body temperature to reduce costs (Niizuma et al. 2006; Meir et al. 2008; Elliott et al. 2013b). Thus, although dynamic body acceleration accurately predicts energy expenditure in flying and running animals (Wilson et al. 2006; Halsey et al. 2011b; Bishop et al. 2015), relationships in diving marine mammals are weak (Jeanniard-du-Dot et al. 2016, 2017; Rosen et al. 2017). Nonetheless, three studies on diving, flying seabirds have shown that accelerometers predict costs remarkably well in the wild (Elliott et al. 2013a,b; Stothart et al. 2016; Hicks et al. 2016). However, those studies were on relatively large, deep-diving species where thermoregulatory and dive costs may be straightforward to model. For instance, in one species, the fit was better when dive costs were modeled to decrease exponentially with dive duration (Elliott et al. 2013b). Small seabirds are likely to be especially difficult to model due to the variable mechanical costs associated with buoyancy (Gabrielsen et al. 1991; Lovvorn and Jones 1991; Lovvorn et al. 2004).

Dovekies (*Alle alle*) are Arctic-breeding seabirds in the family Alcidae. Their abundance makes them key components of many Arctic ecosystems, both as ecosystem engineers and as prey for terrestrial and avian predators (Burnham and Burnham 2005; González-Bergonzoni et al. 2017). As one of the smallest marine endotherms (only the *Aethia* auklets and *Pelecanoides* diving-petrels are slightly smaller), dovekies are also an important species from an energetic standpoint, and though their metabolism has been studied in the past, the energetic costs of flying and diving remain unknown (Gabrielsen et al. 1991; Harding et al. 2009; Welcker et al. 2009b). Dovekies are diving seabirds that feed on a variety of zooplankton, including fish larvae, euphausiids and their primary prey, copepods (Fort et al. 2010). Given that their preferred prey, *Calanus glacialis*, *Calanus finmarchicus* and *Calanus hyperboreus* are shifting northward beyond the dovekie range due to climate change, dovekies will likely have to switch to a less nutritious species or increase foraging effort, both of which may increase daily energy expenditure (Beaugrand et al. 2009; Grémillet et al. 2012; Kwasniewski et al. 2010; Amélineau et al. 2016). So far, dovekies have shown a remarkable resilience to the shift, but their ability to buffer its effects seems to be reaching its limit (Harding et al. 2009; Grémillet et al. 2012; Amélineau et al. 2019). The ability of alcids to increase energy expenditure is limited by an energetic trade-off between locomotion in the air and locomotion underwater (Elliott et al. 2013b). Broad wings on a relatively small body allow efficient flying, while relatively short powerful wings make for efficient diving (Elliott et al. 2013b). As such, a species with high wing loading would be expected to have high flight costs, but low dive costs. However, increasing body mass does not only increase flight costs, but has also been shown to increase dive costs in some species (Elliott et al. 2008; Elliott et al. 2013b). Buoyancy is another important contributor to the cost of diving in seabirds, particularly during shallow dives where buoyancy has a stronger effect on energy expenditure than drag (Lovvorn and Jones 1991). Dovekies, which generally dive to a depth of around 10 metres (Harding et al. 2009), likely have high costs associated with buoyancy.

Stroke frequency (or wingbeat frequency in birds) is closely related to locomotory energy expenditure in animals that swim and fly because it coincides directly with the power generated by the contraction of muscle fibers (Pennycuik 2008). Stroke frequency for swimming and flying specialists varies with $\text{mass}^{-1/3}$ across a wide range of animal taxa from small birds to large whales (Sato et al. 2007; Berg et al. 2019). However, Alcids at any given mass were consistently found to have lower than expected wingbeat frequencies (WBF) during dives and higher than expected WBF during flight because of the trade-offs between locomotion in air and water (Sato et al. 2007). Some models of wingbeat allometry across species have predicted a scaling exponent of closer to $-1/6$ (Lee et al. 2008; Pennycuik 2008), which is similar to the allometric exponent derived for Alcids during flight in a previous study (i.e. -0.22 ; Elliott et al. 2004). This exponent is predicted to approach $-1/2$ when wing morphology and size are held constant, as would be the case for a single individual of varying mass over time (Pennycuik 2008). Inter- and intra-individual studies have estimated scaling exponents between $-1/3$ and $-1/2$ (e.g.

Pennycuick et al. 1996; Schmidt-Wellenburg et al. 2007). Combined with energy expenditure data for free-roaming dovekies, measures of WBF during diving and flight could help explain estimated activity costs relative to other Alcids.

Developing a detailed understanding of the energetic costs of behaviours allows for better modeling of overall energy requirements in seabirds and facilitates accurate forecasting of the coping abilities of species faced with long-term environmental change (Fort et al. 2009; Elliott et al. 2013b; Amélineau et al. 2018). While biomechanical models exist to predict these costs in birds, true costs are often quite variable due to ecological and physiological differences among species that cannot be effectively accounted for by these models alone (Pennycuick 1989; Elliott et al. 2013b). Alcids, which have evolved to use their wings for both diving and flight, are particularly at risk of being misrepresented by models that assume efficient locomotion in water and air but fail to effectively account for the trade-offs between motion in both media (Sato et al. 2007). For example, flight costs in thick billed murre (*Uria lomvia*) were found to be 33% higher than those predicted by biomechanical models relying on morphological measurements (Elliott et al. 2013b). Cases such as this emphasize the need for species-specific models when addressing the metabolic ecology of wing-propelled diving seabirds like the dovekie.

There exists natural variation in the foraging strategies employed by dovekies, with some colonies having mean trip durations of twice as long as others (Brown et al. 2012). Trip duration does not only vary among populations, but also among individuals who must feed themselves and their chick (Welcker et al. 2009a; Brown et al. 2012). As has been observed in other Alcids, food may be depleted in waters near the colony ('Storer-Ashmole's halo'), and so, when feeding themselves, the increased costs of flying farther away from the colony may be outweighed by the benefits of feeding in richer distant prey patches (Elliott et al. 2009; Gaston et al. 2007). Though distance from the colony can have important effects on where seabirds choose to feed, other factors such as bathymetry and sea ice cover can be more important drivers of foraging behaviour in some seabirds, including dovekies (Amélineau et al. 2016; Elliott et al. 2009).

The goal of the present study is to estimate the energetic costs of flying and diving in dovekies using both time-averaged energy expenditure, obtained using the doubly labeled water (DLW) method, and individual activity profiles derived from acceleration data. We hypothesized that dynamic body acceleration would correlate only weakly with daily energy expenditure because of the variable non-mechanical costs associated with swimming in breath-hold diving species (Halsey's hypothesis). We also expected dive costs to be high relative to other auks due to high buoyancy and thermoregulatory costs for small, shallow-diving dovekies. Furthermore, we expected that birds that spent more time doing energetically expensive behaviours would consequently have higher daily energy expenditures. Based on allometric relationships in other taxa (Sato et al. 2007; Berg et al. 2019), we hypothesized that the wing-beat frequency of dovekies would differ from predicted values for similarly sized diving

or flying specialists with a scaling of $\text{mass}^{-1/3}$ across Alcidae. We also hypothesized that dovexies that foraged further away from the colony would spend less energy searching for prey underwater because of better foraging conditions with increasing distance from the colony. As such, we predicted that dovexies that spent more time flying would spend less time diving because of the improved resource patches in distant areas.

Methods

1. Study Area & Data Collection

Dovexies were studied at Ukaleqarteq, East Greenland (70° 43' N, 21° 33' W) during the 2017 and 2018 breeding seasons. 89 individuals (35 in 2017 and 54 in 2018) were captured using a variety of methods including noose carpets and lassos. Each dovexie was injected intraperitoneally with 0.3 mL (2017) or 0.45 mL (2018) of doubly-labelled water (the dosage was increased in 2018 to extend the recapture window; Speakman 1997). Of those birds, we taped small triaxial accelerometers (Axy4, Technosmart, Italy; 3.4g including tubing and tape) to the breast feathers of 60 birds to record their activity. Recaptures began approximately 20 hours after the birds were released.

2. Energy Expenditure

To estimate the average energy expenditure of each of our birds, we used the doubly labeled water (DLW) method (Speakman 1997; Welcker et al. 2009b). This method estimates carbon-dioxide production using the differential decline of heavy isotopes of hydrogen and oxygen in the body. The two-sample approach involves taking a blood sample at the beginning and at the end of a measurement period, while the single-sample approach involves taking only a final sample and interpolating the initial enrichments of ^{18}O and deuterium. We used the single-sample method for all our accelerometer-equipped birds to reduce handling time (handling time: ~10-15 minutes). The increased handling time associated with the two-sample approach is known to alter behaviour, and therefore energy expenditure, in other seabirds (Schultner et al., 2010). As such, the two-sample approach was reserved for the birds not being equipped with accelerometers and whose initial isotope enrichments could be used to interpolate the initial enrichments of the single-sample birds using body mass ($R^2 = 0.68-0.74$ between isotopes and mass depending on year; see data appendix).

Immediately following capture, all birds were weighed and then injected intraperitoneally with 0.3 (2017) or 0.45 (2018) mL of DLW (65% H_2O^{18} ; 35% D_2O). The single-sample birds were equipped with an accelerometer attached ventrally with tape, marked with dye, and then released. Following the DLW injection, we placed the two-sample birds in an opaque breathable bag and left them in the shade for one hour to allow the DLW to equilibrate with the body water. After the hour had elapsed, an initial blood sample was taken from each bird's brachial vein, following which, the birds were marked with dye and released. Birds were recaptured for a final weighing and blood sample between roughly

15 and 50 hours after having been initially released. The isotopic enrichments of blood samples were measured using an isotopic water analyzer (Los Gatos, San Jose, USA). We calculated the amount of carbon dioxide produced by individuals over the course of each deployment (See Speakman 1997 for details on calculations and supporting theory). To estimate energy expenditure, we converted these values into kilojoules using a conversion coefficient previously deemed appropriate for this species (27.97 J/mL of CO₂; Welcker et al. 2009b).

3. Accelerometry & Activity Costs

Raw acceleration data in the surge, heave and sway axes were recorded at a sampling rate of 50 Hz and used to calculate wingbeat frequency (WBF) and pitch (i.e. body angle) in R using code adapted from Patterson et al.'s work on thick-billed murres (2019). Plotted densities of WBF were used to select a threshold that could identify periods of flapping-flight in each deployment. As we did not have a pressure sensor, individual dives were identified automatically using a set of custom functions that used predictable changes in pitch and WBF to define the starts and ends of dives (available in Appendix). These diving periods were also identified visually in a subset of deployments in order to verify the validity of the automatic classifications and were found to be in close agreement (Cohen's kappa coefficient = 0.82 ± 0.08, n=10). As such, only automatically defined dives were used in all further analyses.

To estimate the energetic costs of flying and diving in dovekeys, we conducted a multiple regression analysis with daily energy expenditure (DEE) as the response variable and activity-specific time budgets (represented as proportions of total time) as explanatory variables. Three activity categories were selected for analysis: flying, diving and other (resting, walking, etc).

$$DEE = a(\%Time_{fly}) + b(\%Time_{dive}) + c(\%Time_{other})$$

The intercept was forced through zero to account for the fact that no energy is expended when no time has elapsed. The output of the multiple regression analysis was then used to estimate the relative contribution of flying and diving to the overall energy requirements of dovekeys. Other model variants were also tested against our basic model and the best was selected using Akaike's Information Criterion (AIC) which penalizes unnecessarily complex models. The first variant split the "other" behavioural category into "resting on land" and "unknown", while the second replaced time spent diving with an exponential cost function for each dive. All statistical analyses were conducted in R (R Core Team 2018).

Another multiple regression analysis was conducted using activity-specific overall dynamic body acceleration (ODBA) as an explanatory variable. ODBA represents the summed acceleration in all three axes minus that associated with gravity and body position. It can be a good predictor of activity-specific energetic costs in some alcid species (Elliott et al. 2013a); however, time's effect on summed ODBA can sometimes misrepresent and inflate its importance (Halsey 2017). As such, time averaged ODBA was used for the present analysis instead of summed ODBA.

$$DEE = a(\text{ODBA}_{\text{fly}}/\text{day}) + b(\text{ODBA}_{\text{dive}}/\text{day}) + c(\text{ODBA}_{\text{other}}/\text{day})$$

4. Time Budget Comparison

As well as estimating activity costs, we tested whether dovekeys that spent more time flying would spend less time diving. We compared the proportions of time spent doing either behaviour and checked for a significant Pearson correlation. All periods of flight were included in our analysis even though not all flight is related to foraging, as we could not accurately differentiate between foraging flight and flight used for other purposes (e.g. predator avoidance). Furthermore, our methods assume that time spent flying is a useful proxy for distance from the colony. This time-distance relationship has been supported by the findings of previous studies on the foraging behaviour of dovekeys, as well as other related Alcids (Cairns et al. 1987; Welcker et al. 2009a).

5. Allometry of Wingbeat Frequency

WBF density plots were used to identify the dominant WBF exhibited by individuals during locomotion in the air and underwater. We then tested for an intra-specific linear relationship between $\log_{10}(\text{WBF})$ and $\log_{10}(\text{mass})$ in dovekeys while flying and diving. We continued to plot the mean value observed across all sampled individuals with literature values for other vertebrates (Sato et al. 2007), as well as for Alcids specifically (Elliott et al. 2004). If a species was represented in both studies, we chose the value provided in Sato's paper which relied on accelerometer derived estimates instead of video analysis.

Results

Average daily energy expenditure (DEE) for dovebies in 2017 and 2018 was 621 ± 103 kJ/d and 590 ± 133 kJ/d, respectively (Table 1). Since the dovebies studied in 2017 make up the majority of individuals for which there is paired energy expenditure and activity data ($n=10$ in 2017 vs $n=3$ in 2018), we compared data separately for 2017 alone and pooled 2017 and 2018. Mass (2017 and 2018 data pooled GLM, with % time flying and % time diving as covariates: $t_9 = 6.32$; $P = 0.0001$) was a significant predictor of DEE. We consequently calculated subsequent analyses on mass-specific DEE (DEE was linearly related to body mass with an intercept whose confidence intervals included zero). With the intercept set to zero, our multiple regression analysis showed that percent time flying (2017 and 2018: 0.086 ± 0.010 kJ/g/d, $t_{10} = 8.49$, $P < 0.0001$; 2017 only: 0.096 ± 0.009 kJ/g/d, $t_7 = 10.67$, $P < 0.0001$), percent time diving (2017 and 2018: 0.099 ± 0.012 kJ/g/d, $t_{10} = 8.30$, $P < 0.0001$; 2017 only: 0.088 ± 0.011 kJ/g/d, $t_7 = 8.09$, $P < 0.0001$) and percent time in other activities (2017 and 2018: 0.012 ± 0.004 kJ/g/d, $t_{10} = 2.78$, $P = 0.02$; 2017 only: 0.013 ± 0.004 kJ/g/d, $t_7 = 3.56$, $P = 0.01$) were significant predictors of mass-specific DEE (Fig. 1a). Separating ‘other activities’ into resting on land ($t_9 = 1.56$, $P = 0.15$) and ‘unknown’ ($t_9 = 1.37$, $P = 0.21$) did not improve the model, nor did replacing time spent diving with an exponential cost function for each dive. Daily energy expenditure increased with average dynamic body acceleration in 2017 ($p < 0.001$; Fig. 1b). However, the relationship differed in 2018, when birds had lower daily energy expenditure despite higher average dynamic body acceleration ($p = 0.01$). Models using summed ODBA rather than total time in each activity did not improve the model (2017: $\Delta AIC = 8.92$; 2017 and 2018: $\Delta AIC = 10.36$). As predicted, time spent flying and diving were negatively correlated ($p < 0.01$, $R^2 = 0.37$, $n = 20$; Fig. 2). WBF varied significantly with mass across individuals during flight ($WBF = 94.914[\text{mass}]^{-0.416}$, $p < 0.05$, $R^2 = 0.35$; Fig. 3a), but not diving (Fig. 3b). Combining our mean WBF for dovebies with published values for other species of Alcid yielded an allometric scaling exponent of -0.21 ± 0.052 for flight ($p < 0.01$, $R^2 = 0.73$, $n = 8$), and -0.27 ± 0.033 for diving ($p < 0.01$, $R^2 = 0.96$, $n = 5$).

Table 1. Summary of daily energy expenditures (DEE) for nesting dovebies studied in Ukaleqarteq, East Greenland (70° 43' N, 21° 33 W) in 2017 and 2018.

Year	Bird	Protocol	Mass ^a (kg)	Deployment		
				Duration (hours)	KJ day ⁻¹	KJ day ⁻¹ g ⁻¹
2017	1	1-sample	158	20.8	602.6	3.83
2017	2	1-sample	165	35.2	720.3	4.37
2017	3	1-sample	153	22.6	621.1	4.07
2017	4	1-sample	167	23.1	608.3	3.64
2017	5	1-sample	149	27.2	659.2	4.44
2017	6	1-sample	141	21.6	565.1	4.01
2017	7	1-sample	150	21.1	656.1	4.39
2017	8	1-sample	147	19.0	555.1	3.79
2017	9	1-sample	149	35.7	757.4	5.10
2017	10	1-sample	162	26.6	710.7	4.40
2017	11	2-sample	148	21.0	379.0	2.56
2017	Mean		153	24.9	621.4	4.05
2018	12	1-sample	148	31.6	577.4	3.93
2018	13	1-sample ^b	135	27.2	655.7	4.65
2018	14	1-sample	148	35.5	475.0	3.19
2018	15	1-sample	153	20.3	644.5	4.19
2018	16	2-sample	154	52.6	538.4	3.46
2018	17	2-sample	140	30.5	512.4	3.56
2018	18	2-sample	159	31.5	567.5	3.64
2018	19	2-sample	159	30.3	542.1	3.33
2018	20	2-sample	149	19.7	560.7	3.64
2018	21	2-sample	145	49.5	579.6	3.86
2018	22	2-sample	153	23.1	992.2	6.44
2018	23	2-sample	152	35.4	460.4	3.05
2018	24	2-sample	132	43.8	565.8	4.29
2018	Mean		148	33.1	590.1	3.90

^aThe value reported here represents the average of initial mass and post-deployment mass.

^bAccelerometer stopped recording during deployment.

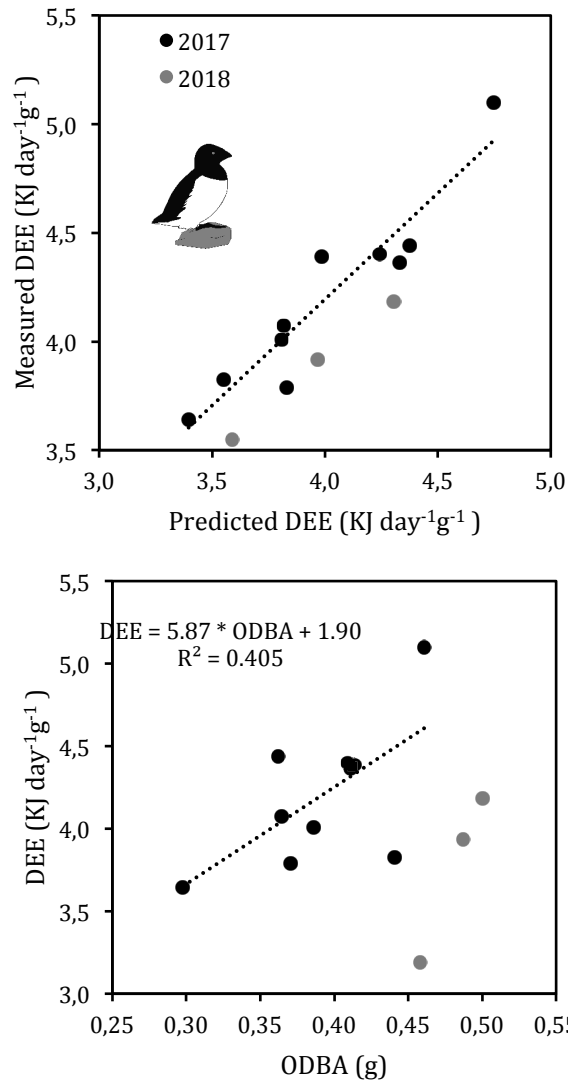


Figure 1. (A) Time-budget predicted daily energy expenditure relative to measured daily energy expenditure and (B) Daily energy expenditure relative to overall dynamic body acceleration (ODBA). The dotted trendline in both panels was derived using data from 2017 only.

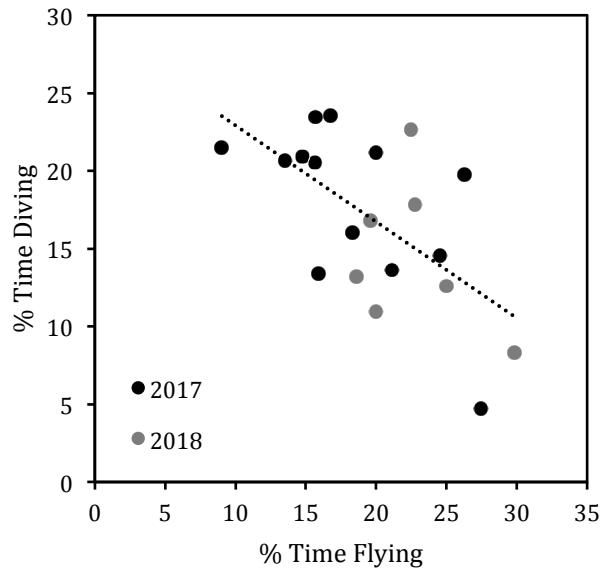


Figure 2. The proportion of time spent flying and diving in dovekeys. There is a significant negative correlation between the two (combined data for 2017 and 2018: $p < 0.01$, $R^2 = 0.37$, $n=20$). The dotted trendline encompasses data from both 2017 and 2018.

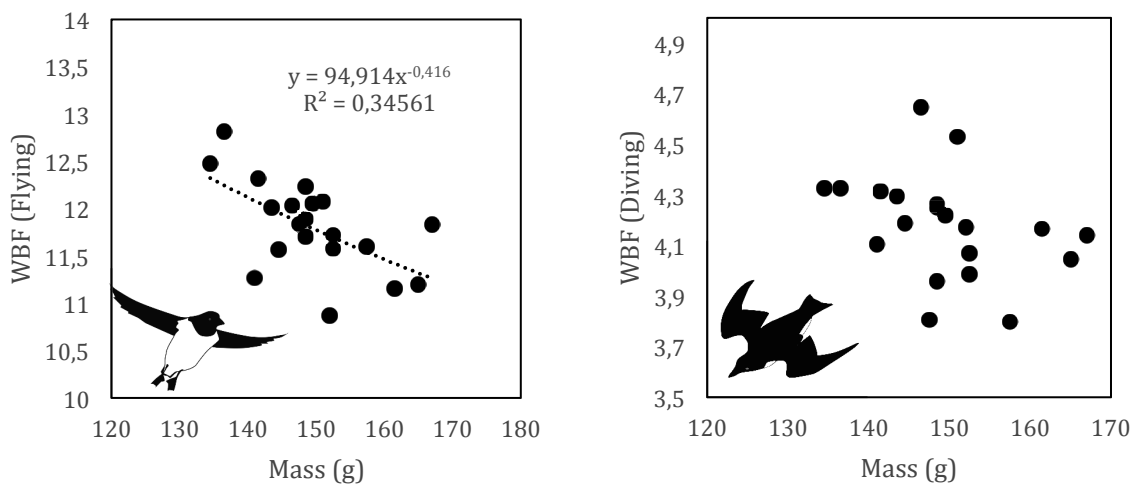


Figure 3. Dominant wingbeat frequencies plotted against mass for (A) flying and (B) diving dovekeys.

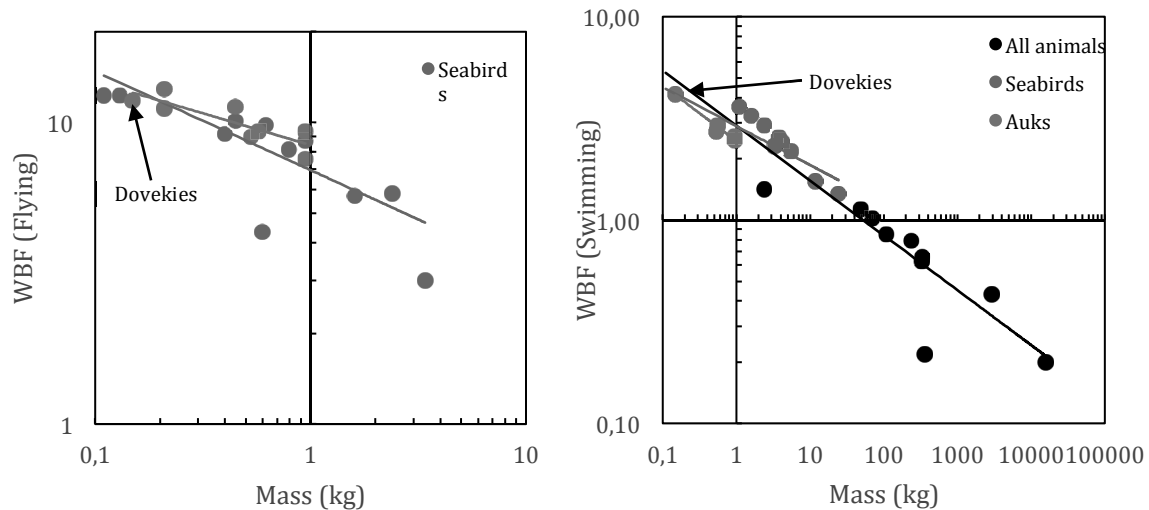


Figure 4. Mean wingbeat frequencies plotted against mass for (A) flying and (B) diving animals. Trendlines are inclusive of all data from each of their subcategories (i.e. the “All animals” trendline was derived from all points including those for the “Seabirds” and “Auks” categories. The “Seabirds” trendline is also inclusive of the “Auks” datapoints.).

Discussion

As expected, dive costs were relatively high for dovekies as shallow-diving, small endotherms swimming in cold water (8-9 times BMR). Furthermore, average ODBA correlated with DEE, but only weakly ($R^2 = 0.41$, compared with 0.72-0.85 in other studies; Elliott et al. 2013b; Stothart et al. 2016; Hicks et al. 2016). Moreover, ODBA did not improve on time budget models, demonstrating that the correlation between average ODBA and DEE was merely driven by those individuals that are more active (i.e. fly and dive more) having higher DEE. Thus, we support Halsey’s hypothesis (Halsey et al. 2011a) that ODBA is a weak predictor of DEE in breath-hold divers. Also as predicted, time budgets for flight and diving were negatively correlated, indicating a trade-off between these two energetically costly behaviours.

1. Daily Energy Expenditure

Despite rapid environmental change in the Arctic, DEE estimates for nesting dovekies in 2017 and 2018 were comparable to previous estimates going back almost 30 years (~600-760 kJ/day; Gabrielsen et al. 1991; Harding et al. 2009; Welcker et al. 2009b). Thermoregulatory energy savings resulting from warming temperatures may be offsetting losses associated with changing foraging dynamics and allowing dovekies to buffer the effects of climate change in East Greenland (Grémillet et al. 2012). However, as prey dynamics continue to shift with increasing temperatures, dovekies may soon face increased energetic demands that exceed their capacity to buffer, eventually leading to decreases in fitness (Kidawa et al. 2015; Amélineau et al. 2019). As such, it is essential that we continue to monitor the behaviour, energetics and breeding success of these abundant Arctic seabirds.

2. Activity Costs

Until now, only rough estimates of the energetic costs of flying and diving existed for dovekies and these were based on time-budgets obtained through field observations or biomechanical modeling (i.e. the Pennycuick model; Pennycuick 1989). Prior to the availability of fine scale movement data made possible through the use of accelerometers, diving and flying were estimated in dovekies to cost between 4.8 X and 11.6 X BMR (Gabrielsen et al. 1991; Fort et al. 2009). Both our estimated flight and dive costs fell within that range. Our model estimated flight costs to be approximately 8.8 X BMR in 2017 and 7.8 X BMR when using pooled data for 2017 and 2018. Similarly, dive costs varied between 8.0 X BMR (2017) and 9.0 X BMR (2017 and 2018). These activity costs can be used to inform our current understanding of the long-term health of dovekie populations globally by improving existing models (e.g. Clairbaux et al. 2019).

The flight costs derived in this study support the idea that high wing-loading in dovekies is resulting in high energetic costs during flapping-flight. For instance, these estimates are almost double that of the similarly sized sooty tern (*Sterna fuscata*), which has a much lower wing-loading than the dovekie (Flint and Nagy 1984). Even so, when compared to the flight costs of the largest auk species, the thick-billed murre (*Uria lomvia*, 31 BMR; Elliott et al. 2013b), dovekies have relatively low flight costs. Moreover, thick-billed murre have roughly three times higher wing-loading than dovekies, implying higher flight costs. The effect of mass has been widely studied and, though a level of variability exists, flight costs tend to increase with mass both inter- and intraspecifically in birds (Videler 2006). This pattern is obvious when comparing the flight costs of one of the smallest alcids (the dovekie) with the largest (the thick-billed murre) but may also be present among individual dovekies of varying mass, though this is beyond the scope of the present study.

As predicted, dovekies had relatively high dive costs. Though these small seabirds have short dive-adapted wings, they are still longer (relative to body size) than in other auk species like the thick-billed murre whose relative dive costs are approximately half those observed in dovekies (Elliott et al. 2013b). Longer wings increase hydrodynamic drag when moving through the water and this translates to increases in the energetic requirements of diving (Elliott et al. 2007). On average, dovekies also exhibit much shorter and shallower dives than thick-billed murre and this likely means that they face much higher costs linked to buoyancy when diving (Elliott et al. 2007; Harding et al. 2009; Lovvorn et al. 2004). Buoyancy is predicted to decline exponentially with depth and so shallow divers must spend more time and energy overcoming it (Lovvorn et al. 2004; Wilson et al. 1992). Dovekies have been recorded making up to 240 individual dives per day at an average depth of 10m, and so, the cost of buoyancy is likely a large contributor to the particularly high dive costs observed in these birds. Thermoregulatory costs are also likely much higher in diving dovekies than in thick-billed murre because of their relatively large surface area to volume ratio (Gabrielsen et al. 1991; Gardner et al. 2011).

The morphological characteristics of a species are not the only factors that can influence activity costs. Environmental conditions can also have significant effects on the energetic costs associated with specific behaviours and could explain some of the variation observed in our models. For example, a study undertaken on two species of seabird found that flight costs increased with increasing head winds (Elliott et al. 2014). As such, differences in the wind regimes experienced by the dovekies deployed in 2017 and 2018 could have led to differences in the relative energetic costs associated with flight in each cohort. Similarly, interannual differences in sea surface temperature could have affected the dive costs incurred by dovekies in both sampling years. For example, sea surface temperatures were higher in 2018 (low ice year) than 2017 (a high ice year), consistent with measured costs in 2018 being lower than expected from activity alone (Fig. 1). Conditions at sea could also have contributed to the weak correlation obtained between ODBA and DEE in this study. More specifically, increased wave action in 2018 could have inflated ODBA values for that year independently of activity, resulting in lower ODBA-specific DEEs (Fig. 1b).

3. Time-Budget Comparison

Birds that spent more time flying spent less time diving and vice versa ($R^2=0.37$, $n=20$; Figure 2). According to central place foraging theory, dovekies would be expected to prioritize their net energy gain and forage at a distance from the colony where travel costs are outweighed by the rewards offered by the prey patch (Elliott et al. 2009; Gaston et al. 2007). If we assume time spent flying is a reasonable proxy for distance from the colony and time spent diving for prey availability (Gaston et al. 2007; Monaghan et al. 1994; Welcker et al. 2009a), Ashmole's halo could explain the observed negative correlation between the two behaviours. However, sea ice cover may also be contributing to this pattern. Dovekies spend more time underwater and less time flying in years with higher levels of sea ice (Amélineau et al. 2019). We observed a similar pattern when comparing the time budgets of birds sampled in 2017 (a high ice year) and 2018 (a low ice year). Birds in 2017 spent less time flying and more time diving on average than in 2018 (Fig. 2), but the difference was only significant for flight ($p<0.05$, $n= 13$ [2017] and 7 [2018]).

4. Allometry of Wingbeat Frequency

The dominant WBF during flight varied across individual dovekies with $\text{Mass}^{-0.42}$, higher than the predicted inter- and intra-specific exponent of between $-1/6$ and $-1/3$, but lower than the $-1/2$ exponent predicted for intra-individual WBF allometry in birds (Pennycuik 2008; Berg et al. 2019). Inter-individual variation in wingspan and wing area may be relatively small across dovekies, leading to an allometric scaling exponent that approaches $-1/2$. This could be the case if mass differences are resulting from varying fat reserves instead of overall changes in body size (Pennycuik 2008). While nesting dovekies may benefit from large fat reserves, they also likely incur higher activity costs associated with increased WBF during flight (Taylor 1994). However, the high degree of variation

surrounding the relationship between body mass and WBF in flying dovekies and the lack of a significant relationship for diving dovekies suggests that other factors are at play here as well.

We combined the mean WBF of flying and diving dovekies with literature data for other Alcids to assess the inter-specific allometry of WBF in this family with the inclusion of one of its smallest members. As expected, WBF decreased with mass in both swimming and flying Alcids (Fig. 4). Despite having a lower mass-specific stroke frequencies than other swimming vertebrate taxa, the scaling exponent (-0.27) obtained for diving Alcids was nearly identical to that observed across birds, fish, reptiles and mammals in a previous study (-0.29, Sato et al. 2007; Figure 4b). This supports the idea that a morphological trade-off between efficient locomotion in air and water affects the intercept and not the slope of WBF allometry in diving Alcids (Sato et al. 2007). We obtained a similar — albeit slightly lower — scaling exponent of -0.21 for Alcids in flight. The difference could be due to high wing-loading in large Alcids, such as the thick-billed murre, leading to higher than expected mass-specific WBF during flight (Elliott et al. 2013b), but could also be an artifact of the small number of species included in our analysis (the 95% confidence intervals for both scaling exponents included each other). Finally, dovekies fit well on the Alcid wingbeat frequency regression, implying that their unusually high dive costs are not being driven by mechanical costs alone.

5. Conclusion

The use of accelerometers has greatly enhanced our ability to study the fine-scale behaviour and energetics of wildlife. However, our results add to the growing body of literature suggesting dynamic body acceleration alone is not an effective predictor of daily energy expenditure in many breath-hold divers (Halsey et al. 2011a). Nevertheless, acceleration derived time-budgets were effective at providing estimates of energy expenditure in dovekies and revealed that dive costs are quite high and variable in this species. Since the DLW method is challenging to perform in dovekies, accelerometers can be used to study their energetics going forward. To date, dovekies have demonstrated remarkable resilience to climate change. Continued monitoring of dovekie energetics over time and across their geographic distribution will allow for a more comprehensive understanding of activity costs in these birds, which in turn can help us predict and mitigate the impact of climate change.

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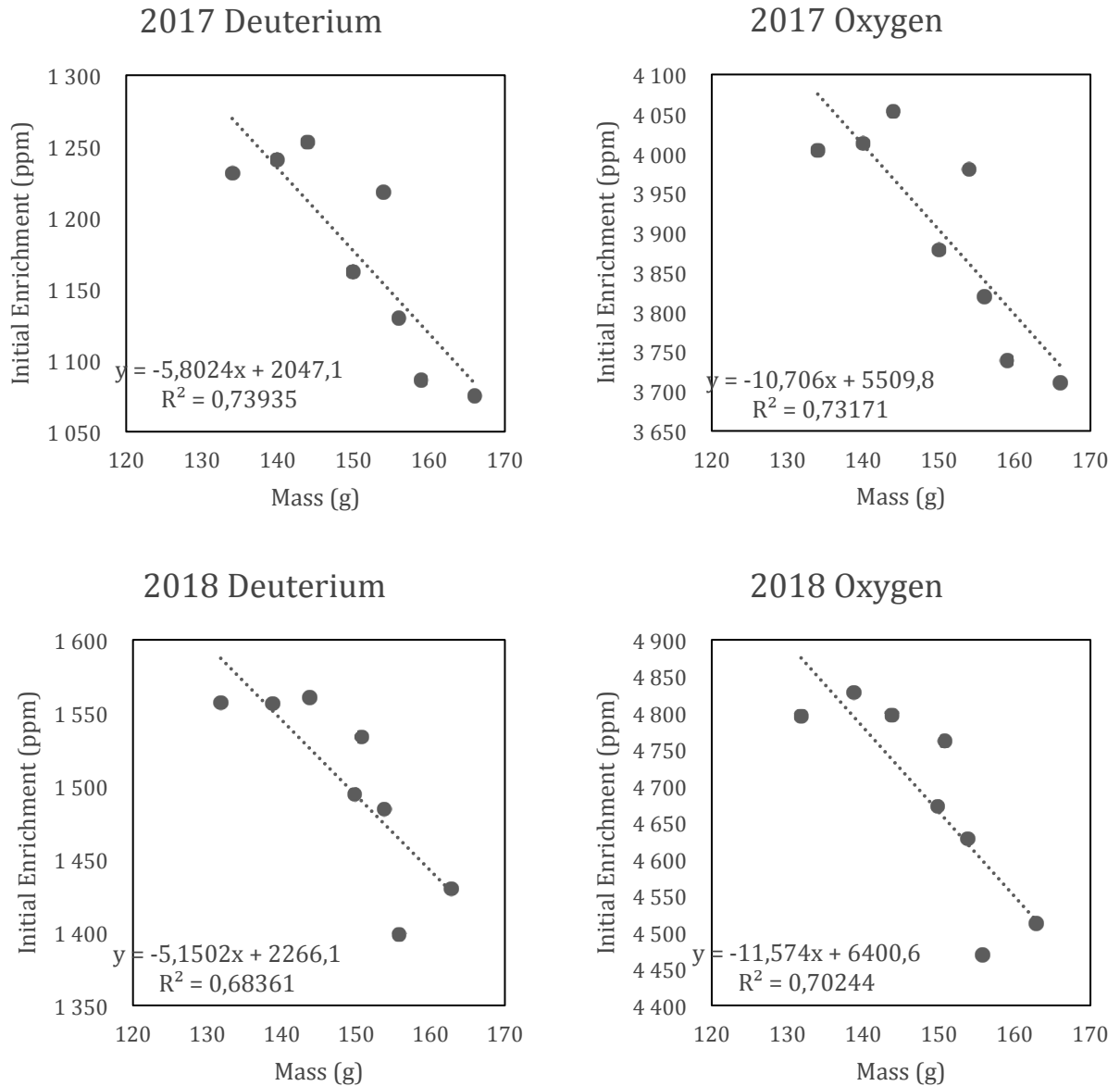
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Supplementary materials

1. Supplementary Figures



Supplementary figure 1. Initial enrichments of deuterium and 18 oxygen as a function of body mass for all two-sample birds injected with DLW. Initial blood samples were taken one hour post-injection.

2. Automatic Dive Classification R-Code

```

#Functions
diveDefinition <- function(accdata, diveIDX, maxDive, frequency, minWBF, maxWBF, changePitch,
meanPitch) {
  theDives <- rep(NA, nrow(accdata))
  for (dive in 1:length(diveIDX)) {
    #dive <- dive + 1
    diveStart <- diveStarts[dive]
    diveEnd <- diveStart + (maxDive * frequency)
    myDive <- accdata[accdata$FID %in% diveStart:diveEnd,]
    myDive$Angle[which(myDive$Angle == "Unknown" & myDive$WBF > minWBF &
myDive$WBF < maxWBF)] <- "Stroke"
    myDive$Angle[which(myDive$Angle == "Unknown" & abs(myDive$dPitch) > changePitch)] <-
"Pitchy"
    myDive$Angle <- filterClass(myDive$Angle, 2)
    downTime <- length(myDive$Angle[myDive$Session == myDive$Session[1]])

    if (is.na(myDive$AccDive[1]) & max(myDive$dPitch > 0)) {

      k <- downTime
      while ((myDive$Angle[k] == "Down") & (k < (maxDive - 1))) k <- k + 1
      while ((mean(myDive$dPitch[1:k]) < meanPitch) & (k < (maxDive - 1))) k <- k + 1
      while (!(myDive$Angle[k] %in% c("Unknown", "Flying")) & (k < (maxDive - 1))) k <- k + 1

      diveEnd <- k
      diveEnd <- myDive$FID[diveEnd]
      theDives[accdata$FID %in% diveStart:diveEnd] <- dive

      plotdat <- melt(myDive[,c("FID", "pitch", "dPitch", "WBF", "WBF3", "Angle")], id =
c("FID", "Angle"))
      names(plotdat) <- c("Time", "Angle", "Data", "Value")
      head(plotdat)

      ggplot(plotdat, aes(Time, Value)) +
        geom_hline(yintercept = 0, col = "red") +
        geom_line() +
        geom_point(aes(col = Angle)) +
        facet_grid(Data ~ ., scales = "free_y") +
        geom_vline(xintercept = diveEnd, linetype = 3)

    }
  }
  return(theDives)
}

filterClass <- function(rawClassification, mintime) {
  output <- rawClassification
  for (i in 2:(length(output) - mintime)) {
    temp <- output[i:(i + (mintime - 1))]
    temp <- ifelse(temp == "Diving", "Swimming", temp)
    tt <- which(names(table(temp)) == temp[1])
    if (table(temp)[tt] != mintime) output[i] <- output[i - 1]
  }
  output
}

```

```

}

getSessions <- function(behaviour, maxSession) {
  output <- 1
  j <- 1
  k <- 0
  for (i in 2:length(behaviour)) {
    j <- ifelse(behaviour[i] == behaviour[i - 1], j, j + 1)
    k <- ifelse(behaviour[i] == behaviour[i - 1], k + 1, 0)
    if (k >= maxSession) {
      j <- j + 1
      k <- 0
    }
    output[i] <- j
  }
  output
}

#####
library(caret)
library(zoo)
library(ggplot2)
library(doBy)
library(reshape2)

options(scipen = 4)
setwd("File location")
fileNames <- list.files()
fileNames

# Create thresholds for dive classification, you might want to try tweaking these to improve the
classification
downPitch <- -45
upPitch <- 45
flight <- 10
startminWBF <- 1
startmaxWBF <- 6
maxTime <- 120
freq <- 50
pitchChange <- 10
pitchMean <- -20

#####
myData <- read.csv(file.choose(), header = T)
myData$time <- as.POSIXct(strptime(as.character(myData$time), "%Y-%m-%d %H:%M:%OS"))

head(myData)

# Calculate some new statistics for the classification: change in pitch, mean pitch, mean WBF
myData$dPitch <- c(NA, myData$pitch[2:nrow(myData)] - myData$pitch[1:(nrow(myData) - 1)])
myData$Pitch3 <- rollapply(myData$pitch, 3, sum, fill = NA, align = "right")
myData$WBF3 <- rollapply(myData$WBF, 3, mean, fill = NA, align = "left")

# Calculate angles
myData$Angle <- "Unknown"

```

```

myData$Angle[myData$Pitch3 < downPitch] <- "Down"
myData$Pitch3 <- rollapply(myData$pitch, 3, sum, fill = NA, align = "left")
myData$Angle[myData$Pitch3 > upPitch] <- "Up"
myData$Angle[myData$WBF > flight] <- "Flying"
table(myData$Angle)

# make groups of data where bird is going up, down, or flying
myData$Angle <- filterClass(myData$Angle, 2)
myData$Session <- getSessions(myData$Angle, Inf)

# Find the starts of dives where birds are going down and stroking
myData$DiveStarts <- "Unknown"
myData$DiveStarts[which(myData$Angle == "Down" & myData$WBF > startminWBF &
myData$WBF < startmaxWBF)] <- "Diving"

# Make a list of these dive starts
myData$DiveStarts <- filterClass(myData$DiveStarts, 2)
myData$DiveStartID <- getSessions(myData$DiveStarts, Inf)
diveStarts <- summaryBy(FID~ DiveStartID, myData[myData$DiveStarts == "Diving"],
FUN = head, n = 1, keep.names = T)[,2]

# Run the dive classification
myData$AccDive <- NA
myData$AccDive <- diveDefinition(accddata = myData,
diveIDX = diveStarts,
maxDive = maxTime,
frequency = freq,
minWBF = startminWBF,
maxWBF = startmaxWBF,
changePitch = pitchChange,
meanPitch = pitchMean)
accDives <- ifelse(is.na(myData$AccDive), "Unknown", "Diving")
myData$Behaviour <- "Unknown"
myData$Behaviour[!is.na(myData$AccDive)] <- "Diving"
myData$Behaviour[myData$Behaviour == "Unknown" & myData$WBF > 10] <- "Flying"
table(accDives)

```


Paysages énergétiques des oiseaux marins hivernant en Atlantique Nord dans le contexte des changements climatiques

Les oiseaux marins sont particulièrement vulnérables aux effets directs et indirects du changement climatique, cependant on sait peu de choses sur ces impacts en dehors de la période de reproduction. Ce manque de connaissances est problématique car les conditions rencontrées pendant la migration et l'hivernage déterminent fortement les dynamiques populationnelles des oiseaux marins. Il est donc essentiel de comprendre les effets du climat sur leurs distributions hivernales et leurs itinéraires de migration. Lier distribution des organismes et facteurs environnementaux est une tâche primordiale bénéficiant du concept de paysages énergétiques (défini comme la variation des besoins énergétiques d'un organisme dans l'espace en fonction de l'environnement) qui a récemment permis de fournir une explication mécaniste à la distribution de nombreux animaux. Dans ce contexte, nous avons déterminé les habitats hivernaux actuels et futurs de cinq espèces représentant 75% de la communauté d'oiseaux marins en Atlantique Nord. Pour cela, nous avons suivi électroniquement les mouvements de plus de 1500 individus afin d'identifier leurs habitats préférentiels par le biais de fonctions de sélection de ressources basées sur la modélisation de leurs dépenses énergétiques et de la disponibilité de leurs proies. Les données de suivi électroniques ont également été recoupées avec les emplacements des cyclones afin de cartographier les zones d'exposition pour la communauté d'oiseaux marins à l'échelle de l'Atlantique Nord. De plus, nous avons exploré les conséquences énergétiques de l'exposition des oiseaux marins aux tempêtes en utilisant un modèle bioénergétique mécaniste. Enfin, nous avons examiné l'impact de la fonte totale de la banquise estivale à partir de 2050 sur la migration des oiseaux de l'Arctique. Nos analyses prévoient un déplacement vers le nord des zones préférentielles d'hivernage des oiseaux marins en Atlantique Nord, surtout si le réchauffement climatique mondial dépasse 2°C. Nos résultats suggèrent que les conditions cycloniques n'augmentent pas les besoins énergétiques des oiseaux marins, ce qui implique que l'indisponibilité des proies et/ou l'incapacité à se nourrir pendant les cyclones causent leur mort. Enfin, la fonte de la banquise au pôle nord pourrait permettre à 29 espèces d'oiseaux arctiques de bientôt effectuer de nouvelles migrations transarctiques entre l'Atlantique et le Pacifique. Nous estimons également que 26 autres espèces actuellement migratrices pourraient rester en Arctique toute l'année. Ce travail illustre comment les changements climatiques pourraient modifier radicalement la biogéographie des espèces migratrices et fournit une boîte à outils méthodologique permettant d'évaluer et de prévoir ces modifications en mariant écologie du mouvement et physiologie énergétique.

Energetic landscapes of North Atlantic wintering seabirds in a climate change context

Seabirds are particularly vulnerable to the direct and indirect effects of climate change, however little is known about those impacts outside of the breeding season. This lack of knowledge is problematic because the conditions encountered during migration and wintering strongly shape seabird population dynamics. It is therefore essential to understand the effects of climate on their winter distribution and migration routes. Linking the distribution of organisms to environmental factors is therefore a primary task benefiting from the concept of energyscapes (defined as the variation of an organism's energy requirements across space according to environmental conditions) which has recently provided a mechanistic explanation for the distribution of many animals. In this context, we have predicted the current and future winter habitats of five species representing 75% of the seabird community in the North Atlantic. To this aim, we monitored the movements of more than 1500 individuals to identify the birds' preferred habitats through resource selection functions based on the modeling of their energy expenditure and prey availability. Electronic tracking data were also overlaid with cyclone locations to map areas of high exposure for the seabird community across the North Atlantic. In addition, we explored the energetic consequences of seabird exposure to storms using a mechanistic bioenergetic model. Finally, we examined the impact of total summer sea ice melt from 2050 on Arctic bird migration. Our analyses predict a northward shift in the preferred wintering areas of the North Atlantic seabird community, especially if global warming exceeds 2°C. Our results suggest that cyclonic conditions do not increase the energy requirements of seabirds, implying that they die from the unavailability of prey and/or inability to feed during cyclones. Finally, the melting sea ice at the North Pole may soon allow 29 species of Arctic birds to make new trans-Arctic migrations between the Atlantic and the Pacific. We also estimate that an additional 26 currently migratory species could remain in the Arctic year-round. This work illustrates how climate change could radically alter the biogeography of migratory species and we provide a methodological toolbox to assess and predict these changes by combining movement ecology and energetic physiology.