



HAL
open science

Multispecies tracking reveals a major seabird hotspot in the North Atlantic

Tammy Davies, Ana P.B. Carneiro, Marguerite Tarzia, Ewan Wakefield, Janos Hennicke, Morten Frederiksen, Erpur Snær Hansen, Bruna Campos, Carolina Hazin, Ben Lascelles, et al.

► To cite this version:

Tammy Davies, Ana P.B. Carneiro, Marguerite Tarzia, Ewan Wakefield, Janos Hennicke, et al.. Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conservation Letters*, 2021, 14, pp.e12824. 10.1111/conl.12824 . hal-03331141

HAL Id: hal-03331141

<https://hal.science/hal-03331141v1>

Submitted on 17 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

LETTER

Multispecies tracking reveals a major seabird hotspot in the North Atlantic

Tammy E. Davies^{1,†}  | Ana P.B. Carneiro^{1,†} | Marguerite Tarzia¹ |
 Ewan Wakefield³ | Janos C. Hennicke⁴ | Morten Frederiksen⁵ |
 Erpur Snær Hansen⁶ | Bruna Campos^{2,7} | Carolina Hazin¹ | Ben Lascelles¹ |
 Tycho Anker-Nilssen⁸ | Hólmfríður Arnardóttir⁹ | Robert T. Barrett¹⁰ |
 Manuel Biscoito¹¹ | Loïc Bollache^{12,13} | Thierry Boulinier¹⁴ | Paulo Catry¹⁵ |
 Filipe R. Ceia¹⁶ | Olivier Chastel¹⁷ | Signe Christensen-Dalsgaard⁸ |
 Marta Cruz-Flores¹⁸  | Jóhannis Danielsen¹⁹ | Francis Daunt²⁰ | Euan Dunn²¹ |
 Carsten Egevang²² | Ana Isabel Fagundes²³ | Annette L. Fayet²⁴ | Jérôme Fort²⁵ |
 Robert W. Furness³ | Olivier Gilg^{12,13} | Jacob González-Solís¹⁸ |
 José Pedro Granadeiro²⁶ | David Grémillet^{17,42} | Tim Guilford²⁴ |
 Sveinn Are Hanssen⁸ | Michael P. Harris²⁰ | April Hedd²⁷ |
 Nicholas Per Huffeldt^{5,22}  | Mark Jessopp²⁸ | Yann Kolbeinsson²⁹ |
 Johannes Krietsch^{30,31} | Johannes Lang^{32,13} | Jannie Fries Linnebjerg⁵ |
 Svein-Håkon Lorentsen⁸ | Jeremy Madeiros³³ | Ellen Magnúsdóttir³⁴ |
 Mark L. Mallory³⁵ | Laura McFarlane Tranquilla³⁶ | Flemming R. Merkel^{5,22} |
 Teresa Militão¹⁸ | Børge Moe⁸ | William A. Montevecchi³⁷ |
 Virginia Morera-Pujol¹⁸ | Anders Mosbech⁵ | Verónica Neves³⁸ |
 Mark A. Newell²⁰ | Bergur Olsen¹⁹ | Vitor H. Paiva¹⁶ | Hans-Ulrich Peter³⁰ |
 Aevan Petersen³⁹ | Richard A. Phillips⁴⁰ | Iván Ramírez¹ | Jaime A. Ramos¹⁶ |
 Raül Ramos¹⁸ | Robert A. Ronconi⁴¹ | Peter G. Ryan⁴² | Niels Martin Schmidt⁵ |
 Ingvar A. Sigurðsson⁴³ | Benoît Sittler^{44,13} | Harald Steen⁴⁵ | Iain J. Stenhouse⁴⁶ |
 Hallvard Strøm⁴⁵ | Geir H. R. Systad⁸ | Paul Thompson⁴⁷ |
 Thorkell L. Thórarinnsson^{29,43} | Rob S.A. van Bemmelen⁴⁸ | Sarah Wanless²⁰ |
 Francis Zino⁴⁹ | Maria P. Dias^{1,15}

¹ BirdLife International, Cambridge, U.K.

² EuroNatur Foundation, Radolfzell, Germany

³ Institute of Biodiversity Animal Health and Comparative Medicine, University of Glasgow, Glasgow, U.K.

⁴ German Federal Agency for Nature Conservation, Putbus, Germany

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. Conservation Letters published by Wiley Periodicals LLC

- ⁵ Department of Bioscience, Aarhus University, Roskilde, Denmark
- ⁶ South Iceland Nature Research Centre, Vestmannaeyjar, Iceland
- ⁷ Stichting BirdLife Europe, Brussels, Belgium
- ⁸ Norwegian Institute for Nature Research, Trondheim, Norway
- ⁹ Fuglavernd / BirdLife in Iceland, Reykjavik, Iceland
- ¹⁰ Tromsø University Museum, Tromsø, Norway
- ¹¹ Funchal Natural History Museum, Funchal, Portugal
- ¹² UMR 6249 Chrono-environnement, Université de Bourgogne Franche-Comté, Besançon, France
- ¹³ Groupe de Recherche en Ecologie Arctique, Francheville, France
- ¹⁴ Centre d'Ecologie Fonctionnelle et Evolutive, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, Montpellier, France
- ¹⁵ MARE - Marine and Environmental Sciences Centre, ISPA - Instituto Universitário, Lisbon, Portugal
- ¹⁶ University of Coimbra, MARE-Marine and Environmental Sciences Centre, Dep. Life Sciences, Coimbra, Portugal
- ¹⁷ Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 CNRS-La Rochelle Université, Villiers-en-bois, France
- ¹⁸ Institut de Recerca de la Biodiversitat (IRBio) and Dept. de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Barcelona, Spain
- ¹⁹ Faroe Marine Research Institute, Tórshavn, Faroe Islands
- ²⁰ UK Centre for Ecology & Hydrology, Penicuik, U.K.
- ²¹ RSPB, Sandy, U.K.
- ²² Greenland Institute of Natural Resources, Nuuk, Greenland
- ²³ Portuguese Society for the Study of Birds (SPEA), Lisboa, Portugal
- ²⁴ University of Oxford, Oxford, U.K.
- ²⁵ Littoral, Environnement et Sociétés (LIENSs), UMR 7266 CNRS-La Rochelle Université, La Rochelle, France
- ²⁶ CESAM-Faculdade de Ciências da Universidade de Lisboa, Lisboa, Portugal
- ²⁷ Wildlife Research Division, Environment and Climate Change, Mount Pearl, NL, Canada
- ²⁸ School of Biological, Earth & Environmental Sciences, Environmental Research Institute, University College Cork, Ireland
- ²⁹ Northeast Iceland Nature Research Centre, Húsavík, Iceland
- ³⁰ Friedrich Schiller University, Institute of Ecology and Evolution, Jena, Germany
- ³¹ Max Planck Institute for Ornithology, Department of Behavioural Ecology and Evolutionary Genetics, Seewiesen, Germany
- ³² Justus-Liebig-University Giessen, Clinic for Birds, Reptiles, Amphibians and Fish, Working Group for Wildlife Research, Giessen, Germany
- ³³ Department of Environment and Natural Resources, Government of Bermuda, Paget, Bermuda
- ³⁴ Háskóli Íslands, University of Iceland, Reykjavik, Iceland
- ³⁵ Biology, Acadia University, Wolfville, NS, Canada
- ³⁶ Birds Canada, Sackville, NB, Canada
- ³⁷ Psychology Department, Memorial University of Newfoundland, St. John's, NL, Canada
- ³⁸ MARE - Marine and Environmental Sciences Centre, IMAR & Okeanos, Horta, Portugal
- ³⁹ Independent researcher, Reykjavik, Iceland
- ⁴⁰ British Antarctic Survey, Cambridge, U.K.
- ⁴¹ Canadian Wildlife Service, Environment and Climate Change Canada, Dartmouth, NS, Canada
- ⁴² FitzPatrick Institute of African Ornithology, Rondebosch, South Africa
- ⁴³ Icelandic Institute of Natural History, Garðabær, Iceland
- ⁴⁴ University of Freiburg, Freiburg, Germany
- ⁴⁵ Norwegian Polar Institute, Tromsø, Norway
- ⁴⁶ Biodiversity Research Institute, Portland, Maine, USA
- ⁴⁷ Lighthouse Field Station, School of Biological Sciences, University of Aberdeen, Cromarty, U.K.
- ⁴⁸ Bureau Waardenburg, Culemborg, The Netherlands
- ⁴⁹ Freira Conservation Project, Funchal, Portugal

Correspondence

Tammy E. Davies, BirdLife International,
David Attenborough Building, Pembroke
Street, Cambridge CB2 9QZ, UK.
Email: tammy.davies@birdlife.org,
tedavies23@gmail.com

†Joint authorship.

Abstract

The conservation of migratory marine species, including pelagic seabirds, is challenging because their movements span vast distances frequently beyond national jurisdictions. Here, we aim to identify important aggregations of seabirds in the North Atlantic to inform ongoing regional conservation efforts. Using tracking, phenology, and population data, we mapped the abundance and diversity of 21 seabird species. This revealed a major hotspot associated with a discrete area of the subpolar frontal zone, used annually by 2.9–5 million seabirds from ≥ 56 colonies in the Atlantic: the first time this magnitude of seabird concentrations has been documented in the high seas. The hotspot is temporally stable and amenable to site-based conservation and is under consideration as a marine protected area by the OSPAR Commission. Protection could help mitigate current and future threats facing species in the area. Overall, our approach provides an exemplar data-driven pathway for future conservation efforts on the high seas.

KEYWORDS

area beyond national jurisdiction, Atlantic, biologging, conservation, high seas, marine protected area, regional seas convention

1 | INTRODUCTION

Many seabird species are wide-ranging, traveling thousands of kilometers across jurisdictional and international waters, only returning to land to breed (Harrison et al., 2018). Such migratory species are increasingly exposed to the expanding cumulative human impacts in the oceans (Halpern et al., 2019). Consequently, seabirds are one of the most threatened groups of vertebrates, with almost half of all species (47%) experiencing population declines (Dias et al., 2019).

As higher predators, seabirds play key roles in marine ecosystems making their conservation critical (Grémillet et al., 2018). However, their high mobility makes this challenging, particularly because seabirds rely on multiple, often geographically distant ecosystems, all of which need some form of protection for successful conservation (Dunn et al., 2019). For highly pelagic species, this is further complicated by the lack of an effective governance mechanism for areas beyond national jurisdictions (De Santo et al., 2019), and often incomplete knowledge of their distribution throughout all life-history stages (Carneiro et al., 2020).

Identifying important areas at-sea has been facilitated through advances in biologging technology (Lascelles et al., 2016). Individual-based tracking, using animal-attached devices, is becoming an indispensable tool for guiding conservation efforts through the identification of areas of high species diversity and abundance (hereafter,

“hotspots”) that are critical for species survival (e.g., molting or foraging areas) (Hays et al., 2019). Recent animal tracking studies have demonstrated that many pelagic seabird species consistently occur at predictable times and places at the macroscale (Frederiksen et al., 2016), often in association with particular habitats or migratory corridors (Dias et al., 2013). This presents an opportunity for area-based conservation for migratory species, particularly because many oceanic hotspots (i.e., areas beyond continental shelves) are often associated with persistent features, such as major frontal and upwelling systems (Block et al., 2011).

The North Atlantic is a priority area for seabird conservation because over the last decade many species in this region have experienced pronounced population declines, including Atlantic Puffin (*Fratercula arctica*), Black-legged Kittiwake (*Rissa tridactyla*), Common Guillemot (*Uria aalge*), and Northern Fulmar (*Fulmarus glacialis*) (Dias et al., 2019). While colonies in the Northeast Atlantic are generally afforded good protection, their foraging areas remain poorly known and protected (Ramirez et al., 2017). Moreover, many seabird species in the North Atlantic, such as shearwaters and auks, are impacted by marine-based threats (e.g., bycatch, pollution, and overfishing; Dias et al., 2019), indicating an urgent need to identify and protect important marine areas to address the recent declines of threatened seabird species.

The Oslo-Paris-Convention on the protection of the North-East Atlantic (OSPAR) is one of two regional seas

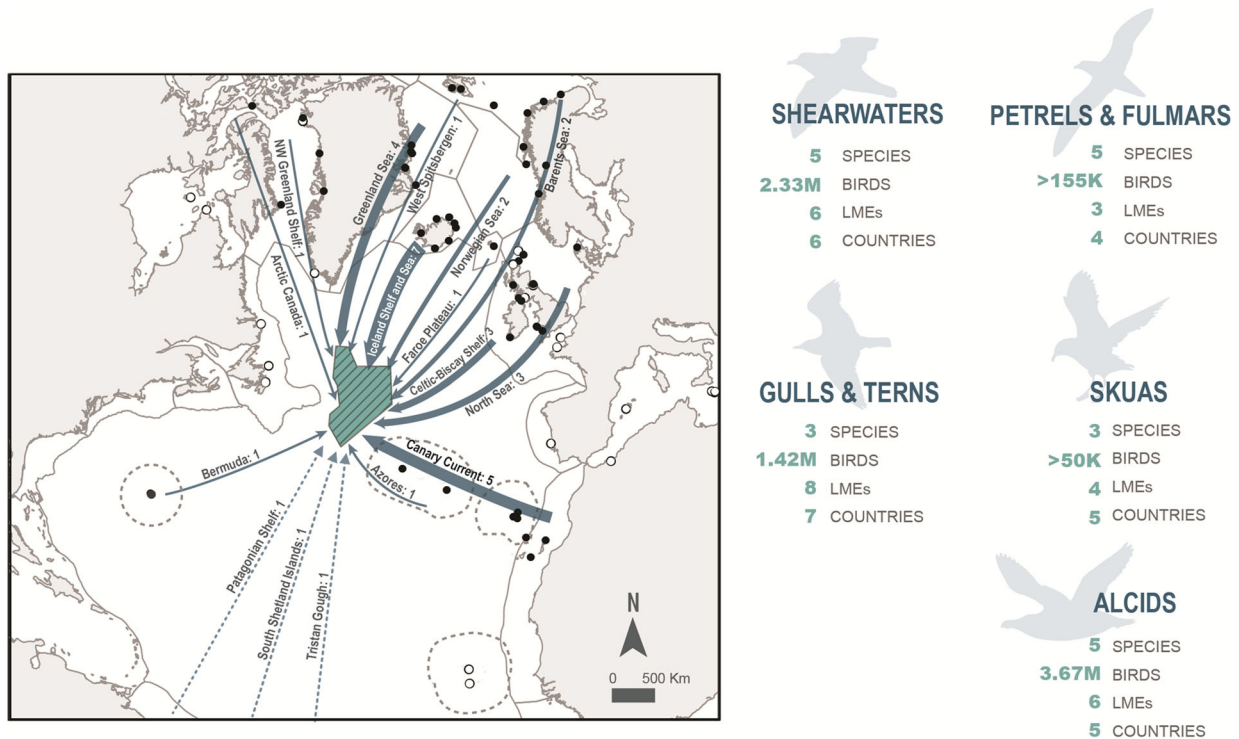


FIGURE 1 Location of identified hotspot in the middle of North Atlantic (green) and summary information of species groups at the site. Arrows indicate the LMEs the birds are traveling from to the site, labeled with LME name and number of species. Dashed arrows are from LMEs in the South Atlantic (not visible on the map). LMEs are shown by a solid gray line, with a dashed gray line for adapted LMEs (Azores, Bermuda, Cabo Verde, Madeira; the latter analyzed with the Canary Current LME). Colonies are shown in circles (black = data used in analysis, white = data considered but not included in final analysis). Figure prepared by Terra Communications

conventions (the other being the Commission for the Conservation of Antarctic Marine Living Resources) that have initiated actions within their remit in Areas Beyond National Jurisdiction (ABNJ), providing a unique opportunity for conservation action in ABNJ. OSPAR have established a number of marine protected areas (MPAs) in ABNJ and are working toward improving the ecological coherence of this network—including addressing an identified gap for seabirds, alongside achieving 10% protection of the OSPAR Maritime Area (Aichi Target 11) (Johnson et al., 2014; OSPAR, 2019). At-sea surveys (Bennison & Jessopp, 2015; Boertmann, 2011) and single species tracking studies (e.g., Dias et al., 2012; Egevang et al., 2010; Fayet et al., 2017) indicate that important seabird concentrations may occur around the Mid-Atlantic Ridge (MAR), and suggesting a community-level assessment of available tracking data is needed, and could help guide current policy and practice.

Here, we combine tracking, phenology, and population data on 21 Atlantic seabird species to quantify their distribution, density, and diversity in the ABNJ of OSPAR Region V. We reveal an important hotspot of unexpected extent and temporal stability. We suggest how our findings could guide conservation management, and provide

an exemplar for the use of multispecies tracking to identify sites suitable for protection in ABNJ.

2 | METHODS

2.1 | Study area

Our study area is defined as ABNJ within OSPAR Region V (www.ospar.org/convention/the-north-east-atlantic). This encompasses the deeper waters of the North Atlantic, between 35 and 62°N and from 10 to 42°W west of Iberia/France and west of the 200 m depth contour off the British Isles (Figure 1).

2.2 | Tracking data

We downloaded all available seabird tracking data that overlapped OSPAR Region V from the BirdLife Seabird Tracking Database (www.seabirdtracking.org) in 2016. These data comprised 2188 tracks of 23 species, from 105 colonies within 16 countries and 25 large marine ecosystems (LME), located in both the North and South Atlantic

(Figure S1). We excluded all tracks from colonies that had less than 2% overlap with the study area, unless other colonies in the same LME had higher overlap. The final analyses included 1524 tracked birds of 21 species, from 56 colonies, across 17 LMEs and 16 countries/jurisdictions (Table 1). Phenology and population data for each species and colony were obtained from the literature and verified by experts (Table S1, Figure S2). Following advice from the scientific community, and in line with other studies (e.g., Frederiksen et al., 2016; Frederiksen et al., 2012), colonies of the same species located in the same LME were combined and considered to represent unique populations. Our data were representative of the species distributions in the Atlantic (Table S2).

2.3 | Identification of marine Important Bird and Biodiversity Areas

We analyzed tracking data in combination with objective site selection criteria following the method developed to delineate marine Important Bird and Biodiversity Areas (IBAs) (Lascelles et al., 2016) and Key Biodiversity Areas (“track2kba” R package; Beal et al., 2020). This is a well-established, standardized approach to identify important hotspots for foraging seabirds based on kernel density analysis of tracking data, in combination with abundance estimates of the colonies of origin. The hotspots identified through this method are key sites for the persistence of species by regularly holding important numbers of a globally threatened species, or supporting > 1% of the global or biogeographic population (Lascelles et al., 2016). This method has been applied in all oceans, with many resultant sites informing conservation action (e.g., Hays et al., 2019; Waliczky et al., 2018). We checked tracked birds of nonthreatened species against the IBA criteria: 1% threshold (i.e., LME represents \geq 1% of the global [for species breeding outside Europe] or biogeographic population [EU number of individuals for European species]). Population sizes refer to the number of mature individuals.

We conducted all analyses in R, as detailed in the Supporting Methods. In brief, we first grouped tracking data by species, LME, and breeding stage (i.e., breeding, nonbreeding, migration, e.g., Black-legged Kittiwake, Iceland Shelf and Sea LME, nonbreeding; Figure S3). We followed the Lascelles et al. (2016) methodology for each group. We estimated the “core use area” of each bird in each group, defined by the 50% utilization distribution contour. We then calculated the proportion of core use areas occurring in each cell in a 0.2×0.2 degree grid (Lascelles et al., 2016). We then estimated the number of birds in each cell by multiplying the proportion of the tracked population in each

grid cell by the size of the LME population (Table S1) to generate one *density map/group*.

2.4 | Species richness and abundance hotspot identification

To identify areas that are important for multiple species at the same time of year, we aggregated the density maps in calendar seasons (Supporting Methods), defined as: Q1: January–March, Q2: April–June, Q3: July–September, and Q4: October–December. We weighted each *density map/group* by the average number of half months in each season spent in each breeding stage, based on the species’ phenology (Carneiro et al., 2020) to generate one *density map/species-LME-season*.

We combined all *density maps/species-LME-season* to produce: (1) *density maps/species-season*; (2) *density maps for all species combined/season*; and (3) *overall density map* (all species and seasons) (Figure S3). We also estimated species richness by binary coding presence/absence raster density maps and summing across species for each season. Finally, we combined the richness and density maps and used the 15% highest values to delimit the most important hotspot within the study area. We then excluded areas within extended shelf claims to facilitate the uptake of conservation measures (Ramirez et al., 2017), so the final area is located solely within ABNJ.

2.5 | Interannual consistency of area use

To assess the consistency in area use, we conducted additional analysis within groups with relatively large sample sizes (> 20 birds) in multiple years (Supporting Methods, Figure S4). We conducted an analysis of similarity (ANOSIM, a measure of relative within-group dissimilarity based on a bootstrap randomization; Oksanen et al., 2013) to test for differences in the distribution within and between-years using two metrics of distribution overlap (Bhattacharyya’s affinity and HR indexes; Fieberg & Kochanny, 2005).

3 | RESULTS

Our analysis revealed an extensive ($\sim 595,000$ km²) hotspot of seabird diversity and abundance near the western boundary of OSPAR Region V (Figure 1), extending from ~ 41 to 53° N and 32 to 42° W. The area is bounded in the north by the Charlie–Gibbs Fracture Zone, to the west by the Flemish Cap and the Grand Banks of Newfoundland,

TABLE 1 Summary of the final seabird tracking data used in the analyses

Species	IUCN status	No. colonies	No. birds	Tracking years (N)	Locations of colonies birds tracked from Large marine ecosystem	Country/jurisdiction
Cory's Shearwater, <i>Calonectris borealis</i>	LC	6	349	2002–2015 (14)	Azores Canary Current	Spain, Portugal
Manx Shearwater, <i>Puffinus puffinus</i>	LC	6	181	1999–2014 (11)	Celtic-Biscay Shelf Iceland Shelf and Sea	United Kingdom, Iceland
Audubon's Shearwater, <i>Puffinus lherminieri</i>	LC	2	23	2010–2014 (5)	Canary Current	Portugal
Great Shearwater, <i>Ardenna gravis</i>	LC	2	72	2006–2012 (6)	Tristan Gough*	Saint Helena, Ascension and Tristan da Cunha
Sooty Shearwater, <i>Ardenna grisea</i>	NT	1	18	2007–2009 (3)	Patagonian Shelf	Falkland Islands (Malvinas)
Northern Fulmar, <i>Fulmarus glacialis</i>	LC	1	72	2006–2013 (8)	North Sea	United Kingdom
Desertas Petrel, <i>Pterodroma deserta</i>	VU	1	39	2008–2013 (6)	Canary Current*	Portugal
Zino's Petrel, <i>Pterodroma madeira</i>	EN	1	12	2007–2010 (4)	Canary Current*	Portugal
Bermuda Petrel, <i>Pterodroma cahow</i>	EN	1	11	2009–2010 (2)	Bermuda*	Bermuda
Bulwer's Petrel, <i>Bulweria bulwerii</i>	LC	2	48	2009–2013 (5)	Canary Current	Portugal, Spain
Black-legged Kittiwake, <i>Rissa tridactyla</i>	VU	16	275	2007–2011 (5)	Barents Sea	Russian Federation, United Kingdom, Faroe Islands, Iceland, Denmark, Norway
					North Sea	
					Celtic-Biscay Shelf	
					Faroe Plateau	
					Iceland Shelf and Sea	
					Norwegian Sea	
					West Spitsbergen	
Sabine's Gull, <i>Xema sabini</i>	LC	1	8	2007–2008 (2)	Greenland Sea	Greenland
Arctic Tern, <i>Sterna paradisaea</i>	LC	1	9	2007–2008 (2)	Greenland Sea	Greenland
Great Skua, <i>Catharacta skua</i>	LC	1	11	2008–2009 (2)	Iceland Shelf and Sea	Iceland
South Polar Skua, <i>Catharacta macconnicki</i>	LC	1	32	2007–2010 (4)	South Shetland Islands	Antarctica
Long-tailed Jaeger, <i>Stercorarius longicaudus</i>	LC	6	42	2006–2015 (8)	Greenland Sea	Greenland, Norway, Sweden
Norwegian Sea + Barents Sea						

(Continues)

TABLE 1 (Continued)

Species	IUCN status	No. colonies	No. birds	Tracking years (N)	Locations of colonies birds tracked from Large marine ecosystem	Country/jurisdiction
Atlantic Puffin, <i>Fratrercula arctica</i>	VU	8	146	2007–2015 (9)	Celtic-Biscay Shelf Iceland Shelf and Sea North Sea	Ireland, Iceland, United Kingdom
Common Murre, <i>Uria aalge</i>	LC	3	20	2013–2014 (2)	Iceland Shelf and Sea	Iceland
Thick-billed Murre, <i>Uria lomvia</i>	LC	9	151	2007–2014 (7)	Arctic Canada NW Greenland Shelf	Canada, Greenland, Iceland
Razorbill, <i>Alca torda</i>	NT	3	20	2013–2015 (3)	Iceland Shelf and Sea	Iceland
Little Auk, <i>Alle alle</i>	LC	1	18	2010–2011 (2)	Greenland Sea	Greenland

Note: Tracking years show the overall year range, with the max number of years held per LME in brackets. * Species endemic to an LME. For further details on population (Table S1) and phenology (Figure S3).

to the east by the MAR and to the south by the Azores (Figure 1).

All 21 species used the identified hotspot, including five globally threatened species (endangered Bermuda Petrel [*Pterodroma cahow*], Zino's Petrel [*Pterodroma madeira*], and vulnerable Desertas Petrel [*Pterodroma deserta*], Black-legged Kittiwake and Atlantic Puffin; Table 1). We estimated that 2.9–5 million birds use the area throughout the year (Table 2) traveling from 56 colonies within 16 countries (Figure 1).

The highest abundance (ca. 4.4–5 million individuals) occurred during the boreal winter (October–March; Q4–Q1, Table 2). The highest number of species ($n = 21$) occurred in spring–summer (April–September), when ca. 2.9–3.3 million birds were present (Q2–Q3, Table 2). Consistency in area use was demonstrated for all nine species with multiyear data, with the ANOSIM index [R value] always lower than 0.12 (Supporting Methods, Figure S4).

The most abundant (2.3 million) species using the area was the Little Auk (*Alle alle*) during nonbreeding (January–March), followed by wintering Great Shearwater (*Ardenna gravis*; 1.8 million, July–September; Table 2), a migrant species breeding in Tristan da Cunha archipelago, South Atlantic. We found three species with more than 50% of their global population using the area as a winter or staging ground: South Polar Skua (*Catharacta maccormicki*; 64.8–68.4%, April–September), Long-tailed Jaeger (*Stercorarius longicaudus*; 63.3%, July–September), and Sooty Shearwater (*Ardenna grisea*; 61%, April–June; Figure 2). Almost 50% of the endangered Bermuda Petrel (45.8%) use the area during July–September.

Most seabirds used the area during their nonbreeding stage. This included three species of southern hemisphere breeders that winter in the area (Great Shearwater, Sooty Shearwater, and South Polar Skua), as well as Long-tailed Jaeger and Arctic Tern (*Sterna paradisaea*) that use the area as a staging ground for 1–4 weeks during their outward and return migrations. Seven species used the area throughout the year: Zino's Petrel, Great Skua (*Catharacta skua*; peak July–December), and the following species showing a peak in numbers October–March: Cory's Shearwater (*Calonectris borealis*), Northern Fulmar, Black-legged Kittiwake, Atlantic Puffin, and Thick-billed Murre (*Uria lomvia*). Four species also used the area while breeding (Manx Shearwater [*Puffinus puffinus*], Cory's Shearwater, Desertas Petrel, and Bulwer's Petrel [*Bulweria bulwerii*]).

4 | DISCUSSION

Our analysis revealed a major hotspot for foraging seabirds in the North Atlantic, used by 21 species totaling up to an

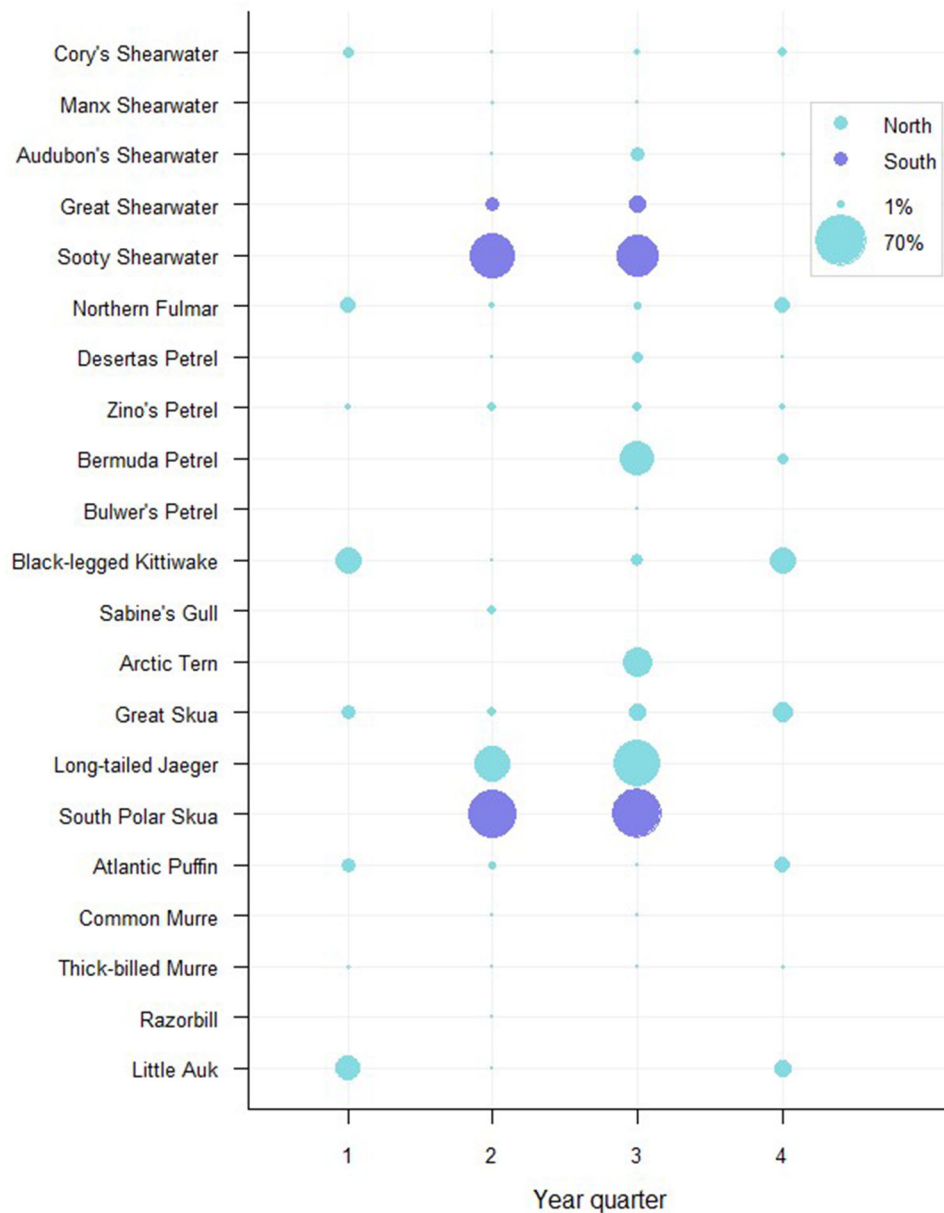


FIGURE 2 Percentage of biogeographic population of each species estimated to be using the hotspot for each year quarter. Colors indicate if the species breeds in the northern or southern hemisphere

estimated 5 million adults. At-sea surveys previously indicated that relative abundance peaked in this area, but this is the first time that a seabird aggregation of this absolute abundance has been robustly quantified anywhere in the high seas. The hotspot qualifies as an IBA and can be considered the most important oceanic foraging grounds for the community of seabirds in the OSPAR maritime high seas area and one of the most important concentrations of migratory seabirds in the Atlantic. Seabirds using this hotspot originated from a minimum of 56 colonies in 16 different countries. Many of these species traveled great distances to use the area, with some using it year-round, suggesting that food availability in the area is consistently

high. Boreal breeders, such as Arctic Terns, Long-tailed Jaegers, Sabine's Gulls, Manx Shearwaters, and Cory's Shearwaters, use the area as a staging area to fuel trans-equatorial migrations (Egevang et al., 2010; Guilford et al., 2009; Sittler et al., 2011), or to fuel the last migration leg to the breeding areas (Egevang et al., 2010; van Bemmelen et al., 2017) sometimes making detours of > 5000 km to do so (Dias et al., 2013). Southern Hemisphere breeders, such as South Polar Skuas, Sooty Shearwaters, and Great Shearwaters, migrate up to 13,000 km to spend some of the austral winter in the area (Hedd et al., 2012; Kopp et al., 2011).

Our analysis included tracking data from major colonies of each species in the Atlantic, including those that

represent more than 90% of the global or Atlantic population for many species (e.g., Cory's Shearwater, Sooty Shearwater, Great Shearwater; all gadfly petrels, genus *Pterodroma*). We only used tracks of adults, because relatively few juvenile and immature birds have so far been tracked, which can have an influence on the overall distribution of seabirds (Carneiro et al., 2020). Indeed, a recent study also found the area to be used by immature Cory's Shearwaters (Campioni et al., 2020). Thus, our estimates should be considered a minimum. Population estimates for each colony are subject to natural variation and recording error, and the number of birds using the area should ideally be updated regularly.

4.1 | Biodiversity hotspot

Recent studies have found additional seabird species use the area, including Leach's Storm-Petrel (*Oceanodroma leucorhoa*) (Pollet et al., 2019), Wilson's Storm-Petrel (*Oceanites oceanicus*), Great Black-backed Gull (*Larus marinus*), Arctic Jaeger (*Stercorarius parasiticus*), Pomarine Jaeger (*S. pomarinus*), and Northern Gannet (*Morus bassanus*) (Boertmann, 2011; Wakefield, 2018). Tracking studies also demonstrate that the area is used by many nonavian, wide-ranging species, including Blue Shark (*Prionace glauca*), Shortfin Mako Shark (*Isurus oxyrinchus*) (Queiroz et al., 2016), Basking Shark (*Cetorhinus maximus*) (Gore et al., 2008), Atlantic Bluefin Tuna (*Thunnus thynnus*) (Walli et al., 2009), Sei Whale (*Balaenoptera borealis*) (Prieto et al. 2014), and Leatherback Turtle (*Dermochelys coriacea*) (Fossette et al., 2014). At-sea surveys in the area have also found many cetacean species, including Blue Whale (*Balaenoptera musculus*), various beaked whales, Common and Spotted dolphins (Wakefield, 2018). Further work is needed to understand how these species use and interact in the area, and the role of oceanographic drivers in the region.

4.2 | Potential drivers of abundance and diversity

The hotspot is located in an area of complex oceanography, dominated by the North-Atlantic Current (NAC) and the associated Subpolar Frontal system (Belkin & Levitus 1996). These oceanographic drivers are both more intense and spatially stable due to bathymetric steering by the continental slope/Grand Banks to the West and Charlie-Gibbs Fracture Zone in the East (Rossby, 1996). The associated mesoscale turbulence creates high rates of primary production (Longhurst, 2010), and it is likely the combination of high primary production and spatiotemporal

predictability that allows the area to support large numbers of higher predators. Studies indicate that prey, such as zooplankton (e.g., calanoid copepods) and mesopelagic fish (e.g., myctophids; Fort et al., 2010; Hudson et al., 2014), are abundant in the area, with the availability to seabirds further enhanced through both mesoscale turbulence (McGillicuddy, 2016) and the diel vertical migration of mesopelagic prey (Dias et al., 2012). See Supporting Information—Oceanography.

4.3 | Conservation implications

Most seabirds used the multispecies hotspot during their nonbreeding stage—a period of their lifecycle that is currently poorly protected (Ramirez et al., 2017). Conditions during nonbreeding can directly affect subsequent breeding productivity via carryover effects (Fayet et al., 2017). This stage includes the mid-winter period, when adverse weather, food, and light conditions may account for the highest mortality of some Atlantic seabirds (Mesquita et al., 2015). Many of the studied seabird species use the hotspot while molting (Hedd et al., 2012; Wakefield, 2018). Molt is a critical time for seabirds because it is energetically demanding and can compromise flight efficiency, potentially increasing the susceptibility to natural and anthropogenic threats (Grissot et al., 2019).

We contend that the identified hotspot deserves year-round protection as an MPA, given the regular use by a large number of birds and spatiotemporal stability of the area (likely caused by stable physical drivers). Seventeen of the 21 species using the area are impacted by marine-based threats, including bycatch (65%), overfishing (29%), energy production and mining (18%), climate change (71%), pollution (including light pollution; 59%), and are undergoing population declines (Dias et al., 2019). Except for climate change, these threats can be reduced via area-based management (Game et al., 2009) and given that many breeding colonies are already protected, there is an urgent need for marine spatial protections. Although there is a debate about the utility of MPAs to protect migratory species (Game et al., 2009), there are an increasing number of studies showing their importance, particularly during spatially limited and vulnerable life-history stages (Péron et al., 2013; White et al., 2017; Young et al., 2015), and there have been demonstrated successes for seabirds when management measures have preserved their prey base (Croxall, 2008; Pichegru et al., 2010). MPAs can help reduce the likelihood of mortality, and even though the MPA may only represent a small portion of a seabirds' migratory range, they can serve a vital role in species conservation (Hooker et al., 2011; Péron et al., 2013). Given that many migratory species have limited protection at sea, even small

reductions in mortality rates can have decisive demographic benefits, especially for rare and endangered species (Caswell et al., 1999; Péron et al., 2013).

The identified hotspot is currently being discussed by the OSPAR Commission as the North Atlantic Current and Evlanov Seamount (NACES) MPA. Protection of this proposed MPA would address an identified gap in the OSPAR MPA network for seabirds (Johnson et al., 2014), and improve the coverage of nonbreeding areas more broadly (Game et al., 2009; Ramirez et al., 2017). Present threats to seabirds in the area are not fully understood: shipping lanes are predominantly in the southern part of the area (risk of disturbance, oil, and light pollution), some, limited long-line fishing occurs (bycatch risk), and recent oil exploration west of the hotspot (oil pollution and light pollution) (Impact Assessment Agency of Canada, 2020). Understanding the threats in the area, alongside the relevant contribution of other threats—both at breeding sites and across the rest of their migratory journeys—that are driving population declines should be evaluated. Understanding the relative contributions of different threats, both terrestrial and marine, that are driving population trends could help direct conservation priorities. However, it is also important to consider protection of remote areas before they become heavily exploited (McCauley et al., 2013) and to mitigate against future threats, particularly because impacts are increasing across the high seas (Halpern et al., 2019; O’Leary et al., 2020). MPAs are not a panacea for conserving marine biodiversity, and their capacity to reduce threats differs depending on their management and level of enforcement (Zupan et al., 2018). However, MPAs can contribute to biodiversity conservation where effectively managed, and the proposed NACES MPA should include measures to mitigate current and prevent future threats to seabirds. A research and monitoring plan should be adopted alongside the managed MPA, to understand more about the features supporting seabirds and other taxa, to monitor the effectiveness of the MPA, and to inform additional management measures if required. There are also increasing opportunities for monitoring remote areas using satellite and biologging technologies that could be explored (Harcourt et al., 2019; Sutherland et al., 2016). The current ABNJ MPAs under OSPAR are managed through a “Collective Arrangement” (NEAFC & OSPAR, 2015), and a collaborative approach to management would also be needed for this proposed MPA.

Overall, our analysis has demonstrated that multispecies tracking data can identify important sites in ABNJ that are suitable for protection. The ongoing work of the OSPAR Commission presents a unique opportunity for this study to inform policy and practice to benefit seabird conservation on the high seas. Once the new UN Treaty for the high seas has been adopted, replicating this approach for differ-

ent regions and taxa could provide a data-driven pathway for marine conservation in ABNJ.

ACKNOWLEDGMENTS

This work was supported by the Global Ocean Biodiversity Initiative (GOBI) with a grant from the International Climate Initiative (IKI). The German Federal Ministry for the Environment, Nature Conservation, and Nuclear Safety (BMU) supports GOBI on the basis of a decision adopted by the German Bundestag.

The authors thank David Boyle, Vegard Brathen, Kendrew Colhoun, Jan Esefeld, Arnþór Garðarsson, H. Grant Gilchrist, Matthias Kopp, Yuri Krasnov, Mandy Shailer, Deryk Shaw, and the SEATRACK project who facilitated access to part of the data used in this study. Funding sources for the data used in this study are listed in Supporting Information—Additional Acknowledgments.

AUTHORS’ CONTRIBUTIONS

Study conception: B.L., M.T., M.P.D., J.H., and B.C.; Methods workshop: M.T., A.P.B.C., M.P.D., B.C., C.H., J.H., H.A., J.D., E.D., M.F., J.P.G., T.G., E.S.H., B.M., V.H.P., Th.L.Th., and E.W.; Data collection/processing: T.A-N., R.T.B., M.B., L.B., T.B., P.C., F.R.C., O.C., S.C-D., M.C-F., J.D., F.D., M.P.D., C.E., A.I.F., A.L.F., J.F., M.F., R.W.F., O.G., J.G-S., J.P.G., D.G., T.G., E.S.H., S.A.H., M.P.H., A.H., N.P.H., M.J., Y.K., J.K., J.L., J.F.L., S-H.L., J.M., E.M., M.L.M., L.Mc.T., F.R.M., T.M., B.M., W.A.M., V.M-P., A.M., V.N., M.A.N., B.O., V.H.P., H-U.P., A.P., R.A.P., I.R., J.A.R., R.R., R.A.R., P.G.R., N.M.S., I.A.S., B.S., H.Ste., I.J.S., H.Str., G.H.R.S., P.T., Th.L.Th., R.S.A.Vb., S.W., and F.Z.; Data analysis; A.P.B.C. led the analysis, with support from M.P.D., T.E.D., M.T., and E.W.; Writing: T.E.D. led the writing of the manuscript with significant contributions from all coauthors. All authors reviewed and approved the final version for submission.

ETHICS STATEMENT

The authors adhered to all relevant laws, regulations, and protocols in conducting this research.


DATA ACCESSIBILITY STATEMENT


The data are deposited on BirdLife International’s Seabird Tracking Database <http://www.seabirdtracking.org/>

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Tammy E. Davies  <https://orcid.org/0000-0003-2535-1328>

Marta Cruz-Flores  <https://orcid.org/0000-0001-9905-4727>

Nicholas Per Huffeldt  <https://orcid.org/0000-0002-0154-2536>

REFERENCES

- Beal, M., Oppel, S., Handley, J. et al. (2020). BirdLifeInternational/track2kba. <http://doi.org/0.528/enodo.3823902>
- Belkin, I. M., Levitus, S. (1996). Temporal variability of the Subarctic Front near the Charlie-Gibbs Fracture Zone. *Journal of Geophysical Research: Oceans*, *101*(C12), 28317–28324. <https://doi.org/10.1029/96jc02794>.
- Bennison, A., & Jessopp, M. (2015). At-sea surveys confirm a North Atlantic biodiversity hotspot. *Bird Study*, *62*, 262–266.
- Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G., & Harrison, A.-L. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*, 86–90.
- Boertmann, D. (2011). Seabirds in the central North Atlantic, September 2006: Further evidence for an oceanic seabird aggregation area. *Marine Ornithology*, *39*, 183–188.
- Campioni, L., Dias, M. P., Granadeiro, J. P., & Catry, P. (2020). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *Journal of Animal Ecology*, *89*, 29–43.
- Carneiro, A. P. B., Pearmain, E. J., Oppel, S., Clay, T. A., Phillips, R. A., Bonnet-Lebrun, A.-S., Wanless, R. M., Abraham, E., Richard, Y., Rice, J., Handley, J., Davies, T. E., Dilley, B. J., Ryan, P. G., Small, C., Arata, J., Arnould, J. P. Y., Bell, E., Bugoni, L., Campioni, L., Catry, P., Clelland, J., Deppe, L., Elliott, G., Freeman, A., González-Solís, J., Granadeiro, J. P., Grémillet, D., Landers, T. J., Makhado, A., Nel, D., Nicholls, D. G., Rexer-Huber, K., Robertson, C. J. R., Sagar, P. M., Scofield, P., Stahl, J.-C., Stanworth, A., Stevens, K. L., Trathan, P. N., Thompson, D. R., Torres, L., Walker, K., Waugh, S. M., Weimerskirch, H., Dias, M. P. (2020). A framework for mapping the distribution of seabirds by integrating tracking, demography and phenology. *Journal of Applied Ecology*, *57*(3), 514–525. <https://doi.org/10.1111/1365-2664.13568>.
- Caswell, H., Fujiwara, M., & Brault, S. (1999). Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of Sciences*, *96*, 3308–3313.
- Croxall, J. P. (2008). The role of science and advocacy in the conservation of Southern Ocean albatrosses at sea. *Bird Conservation International*, *18*, S13–S29.
- De Santo, E. M., Asgeirsdottir, Á., Barros-Platiau, A., Biermann, F., Dryzek, J., Goncalves, L. R., Kim, R. E., Mendenhall, E., Mitchell, R., Nyman, E., Scobie, M., Sun, K., Tiller, R., Webster, D. G., & Young, O. (2019). Protecting biodiversity in areas beyond national jurisdiction: An earth system governance perspective. *Earth System Governance*, *2*, 100029. <https://doi.org/10.1016/j.esg.2019.100029>.
- Dias, M. P., Granadeiro, J. P., & Catry, P. (2012). Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. *Marine Ecology Progress Series*, *467*, 245–252.
- Dias, M. P., Granadeiro, J. P., & Catry, P. (2013). Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. *Animal Behaviour*, *86*, 359–364.
- Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. <https://doi.org/10.1016/j.biocon.2019.06.033>.
- Dunn, D. C., Harrison, A.-L., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E., Heywood, E., Kot, C. Y., Poulin, S., Whitten, M., Åkesson, S., Alberini, A., Appeltans, W., Arcos, J. M., Bailey, H., Ballance, L. T., Block, B., Blondin, H., Boustany, A. M., Brenner, J., Catry, P., Cejudo, D., Cleary, J., Corkeron, P., Costa, D. P., Coyne, M., Crespo, G. O., Davies, T. E., Dias, M. P., Douvère, F., Ferretti, F., Formia, A., Freestone, D., Friedlaender, A. S., Frisch-Nwakanma, H., Froján, C. B., Gjerde, K. M., Glowka, L., Godley, B. J., Gonzalez-Solis, J., Granadeiro, J. P., Gunn, V., Hashimoto, Y., Hawkes, L. M., Hays, G. C., Hazin, C., Jimenez, J., Johnson, D. E., Luschi, P., Maxwell, S. M., McClellan, C., Modest, M., Notarbartolo di Sciarra, G., Palacio, A. H., Palacios, D. M., Pauly, A., Rayner, M., Rees, A. F., Salazar, E. R., Secor, D., Sequeira, A. M. M., Spalding, M., Spina, F., Van Parijs, S., Wallace, B., Varo-Cruz, N., Virtue, M., Weimerskirch, H., Wilson, L., Woodward, B., & Halpin, P. N. (2019). The importance of migratory connectivity for global ocean policy. *Proceedings of the Royal Society B: Biological Sciences*, *286*, (1911), 20191472. <https://doi.org/10.1098/rspb.2019.1472>.
- Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., & Silk, J. R. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, *107*, 2078–2081.
- Fayet, A. L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K. E., Fifield, D., Fitzsimmons, M. G., Hansen, E. S., Harris, M. P., Jessopp, M., Kouwenberg, A.-L., Kress, S., Mowat, S., Perrins, C. M., Petersen, A., Petersen, I. K., Reiertsen, T. K., Robertson, G. J., Shannon, P., Sigurðsson, I. A., Shoji, A., Wanless, S., & Guilford, T. (2017). Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird. *Current Biology*, *27*, (24), 3871–3878.e3. <https://doi.org/10.1016/j.cub.2017.11.009>.
- Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management*, *69*, 1346–1359.
- Fort, J., Cherel, Y., Harding, A. M. A., Egevang, C., Steen, H., Kuntz, G., Porter, W. P., & Grémillet, D. (2010). The feeding ecology of little auks raises questions about winter zooplankton stocks in North Atlantic surface waters. *Biology Letters*, *6*, (5), 682–684. <https://doi.org/10.1098/rsbl.2010.0082>.
- Fossette, S., Witt, M. J., Miller, P., Nalovic, M. A., Albareda, D., Almeida, A. P., Broderick, A. C., Chacón-Chaverri, D., Coyne, M. S., Domingo, A., Eckert, S., Evans, D., Fallabrino, A., Ferraroli, S., Formia, A., Giffoni, B., Hays, G. C., Hughes, G., Kelle, L., Leslie, A., López-Mendilaharsu, M., Luschi, P., Prodocimi, L., Rodriguez-Heredia, S., Turny, A., Verhage, S., & Godley, B. J. (2014). Pan-Atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. *Proceedings of the Royal Society B: Biological Sciences*, *281*, (1780), 20133065. <https://doi.org/10.1098/rspb.2013.3065>.
- Frederiksen, M., Descamps, S., Erikstad, K. E., Gaston, A. J., Gilchrist, H. G., Grémillet, D., Johansen, K. L., Kolbeinsson, Y., Linnebjerg, J. F., Mallory, M. L., McFarlane Tranquilla, L. A., Merkel, F. R., Montevecchi, W. A., Mosbech, A., Reiertsen, T. K., Robertson, G. J., Steen, H., Strøm, H., & Thórarinnsson, T. L. (2016). Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: Conservation

- implications. *Biological Conservation*, 200, 26–35. <https://doi.org/10.1016/j.biocon.2016.05.011>.
- Frederiksen, M., Moe, B., Daunt, F., Phillips, R. A., Barrett, R. T., Bogdanova, M. I., Boulinier, T., Chardine, J. W., Chastel, O., Chivers, L. S., Christensen-Dalsgaard, S., Clément-Chastel, C., Colhoun, K., Freeman, R., Gaston, A. J., González-Solis, J., Goutte, A., Grémillet, D., Guilford, T., Jensen, G. H., Krasnov, Y., Lorentsen, S.-H., Mallory, M. L., Newell, M., Olsen, B., Shaw, D., Steen, H., Strøm, H., Systad, G. H., Thórarinnsson, T. L., & Anker-Nilssen, T. (2012). Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions*, 18, (6), 530–542. <https://doi.org/10.1111/j.1472-4642.2011.00864.x>.
- Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., Bustamante, R., Possingham, H. P., & Richardson, A. J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution*, 24, (7), 360–369. <https://doi.org/10.1016/j.tree.2009.01.011>.
- Gore, M. A., Rowat, D., Hall, J., Gell, F. R., & Ormond, R. F. (2008). Transatlantic migration and deep mid-ocean diving by basking shark. *Biology Letters*, 4, 395–398.
- Grémillet, D., Ponchon, A., Paleczny, M., Palomares, M.-L. D., Karpouzi, V., & Pauly, D. (2018). Persisting worldwide seabird-fishery competition despite seabird community decline. *Current Biology*, 28, 4009–4013. e4002.
- Grissot, A., Graham, I. M., Quinn, L., Bräthen, V. S., & Thompson, P. M. (2019). Breeding status influences timing but not duration of moult in the Northern Fulmar *Fulmarus glacialis*. *Ibis*, 162, 446–459.
- Guilford, T., Meade, J., Willis, J. et al. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: Insights from machine learning. *Proceedings of the Royal Society of London B: Biological Sciences*, 276, 1215–1223.
- Halpern, B. S., Frazier, M., Afflerbach, J., Lowndes, J. S., Micheli, F., O'Hara, C., Scarborough, C., & Selkoe, K. A. (2019). Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9, (1), <https://doi.org/10.1038/s41598-019-47201-9>.
- Harcourt, R., Sequeira, A. M. M., Zhang, X., Roquet, F., Komatsu, K., Heupel, M., McMahon, C., Whoriskey, F., Meekan, M., Carroll, G., Brodie, S., Simpfendorfer, C., Hindell, M., Jonsen, I., Costa, D. P., Block, B., Muelbert, M., Woodward, B., Weise, M., Aarestrup, K., Biuw, M., Boehme, L., Bograd, S. J., Cazau, D., Charassin, J.-B., Cooke, S. J., Cowley, P., de Bruyn, P. J. N., Jeanniard du Dot, T., Duarte, C., Eguíluz, V. M., Ferreira, L. C., Fernández-Gracia, J., Goetz, K., Goto, Y., Guinet, C., Hammill, M., Hays, G. C., Hazen, E. L., Hückstädt, L. A., Huveneers, C., Iverson, S., Jaaman, S. A., Kittiwattanawong, K., Kovacs, K. M., Lydersen, C., Moltmann, T., Naruoka, M., Phillips, L., Picard, B., Queiroz, N., Reverdin, G., Sato, K., Sims, D. W., Thorstad, E. B., Thums, M., Treasure, A. M., Trites, A. W., Williams, G. D., Yonehara, Y., & Fedak, M. A. (2019). Animal-Borne Telemetry: An Integral Component of the Ocean Observing Toolkit. *Frontiers in Marine Science*, 6, <https://doi.org/10.3389/fmars.2019.00326>.
- Harrison, A.-L., Costa, D. P., Winship, A. J., Benson, S. R., Bograd, S. J., Antolos, M., Carlisle, A. B., Dewar, H., Dutton, P. H., Jorgensen, S. J., Kohin, S., Mate, B. R., Robinson, P. W., Schaefer, K. M., Shaffer, S. A., Shillinger, G. L., Simmons, S. E., Weng, K. C., Gjerde, K. M., & Block, B. A. (2018). The political biogeography of migratory marine predators. *Nature Ecology & Evolution*, 2, (10), 1571–1578. <https://doi.org/10.1038/s41559-018-0646-8>.
- Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., Nico de Bruyn, P. J., Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., Halpin, P. N., Hamann, M., Hammerschlag, N., Harcourt, R., Harrison, A.-L., Hazen, E. L., Heupel, M. R., Hoyt, E., Humphries, N. E., Kot, C. Y., Lea, J. S. E., Marsh, H., Maxwell, S. M., McMahon, C. R., Notarbartolo di Sciarra, G., Palacios, D. M., Phillips, R. A., Righton, D., Schofield, G., Seminoff, J. A., Simpfendorfer, C. A., Sims, D. W., Takahashi, A., Tetley, M. J., Thums, M., Trathan, P. N., Villegas-Amtmann, S., Wells, R. S., Whiting, S. D., Wildermann, N. E., & Sequeira, A. M. M. (2019). Translating Marine Animal Tracking Data into Conservation Policy and Management. *Trends in Ecology & Evolution*, 34, (5), 459–473. <https://doi.org/10.1016/j.tree.2019.01.009>.
- Hedd, A., Montevecchi, W. A., Otle, H., Phillips, R. A., & Fifield, D. A. (2012). Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. *Marine Ecology Progress Series*, 449, 277–290.
- Hooker, S. K., Cañadas, A., Hyrenbach, K. D., Corrigan, C., Polovina, J. J., & Reeves, R. R. (2011). Making protected area networks effective for marine top predators. *Endangered Species Research*, 13, 203–218.
- Hudson, J. M., Steinberg, D. K., Sutton, T. T., Graves, J. E., & Latour, R. J. (2014). Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. *Deep Sea Research Part I: Oceanographic Research Papers*, 93, 104–116.
- Impact Assessment Agency of Canada. (2020). *Regional assessment of offshore oil and gas exploratory drilling east of Newfoundland and Labrador* (pp. 210). St. Johns, NL, Canada: Government of Canada.
- Johnson, D., Ardron, J., Billett, D. et al. (2014). When is a marine protected area network ecologically coherent? A case study from the North-east Atlantic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24, 44–58.
- Kopp, M., Peter, H., Mustafa, O., Lisovski, S., Ritz, M. S., Phillips, R. A., & Hahn, S. (2011). South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Marine Ecology Progress Series*, 435, 263–267. <https://doi.org/10.3354/meps09229>.
- Lascelles, B. G., Taylor, P. R., Miller, M. G. R., Dias, M. P., Opper, S., Torres, L., Hedd, A., Le Corre, M., Phillips, R. A., Shaffer, S. A., Weimerskirch, H., & Small, C. (2016). Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions*, 22, (4), 422–431. <https://doi.org/10.1111/ddi.12411>.
- Longhurst, A. R. (2010). *Ecological geography of the sea*. San Diego, CA: Academic Press.
- McCauley, D. J., Power, E. A., Bird, D. W., McInturff, A., Dunbar, R. B., Durham, W. H., Micheli, F., & Young, H. S. (2013). Conservation at the edges of the world. *Biological Conservation*, 165, 139–145. <https://doi.org/10.1016/j.biocon.2013.05.026>.
- McGillicuddy, D. J. (2016). Mechanisms of physical–biological–biogeochemical interaction at the oceanic mesoscale. *Annual Review of Marine Science*, 8, 125–159.
- Mesquita, M. D. S., Erikstad, K. E., Sandvik, H., Barrett, R. T., Reiertsen, T. K., Anker-Nilssen, T., Hodges, K. I., & Bader, J. (2015). There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in

- population growth rates of a long-lived seabird. *Frontiers in Ecology and Evolution*, 3, <https://doi.org/10.3389/fevo.2015.00043>.
- NEAFC & OSPAR. (2015). Information paper on the process of forming a cooperative mechanisms between NEAFC and OSPAR. UNEP Regional Seas Reports and Studies No 196, UNEP Regional Seas.
- O'Leary, B. C., Hoppit, G., Townley, A., Allen, H. L., McIntyre, C. J., & Roberts, C. M. (2020). Options for managing human threats to high seas biodiversity. *Ocean & Coastal Management*, 187, 105110.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Wagner, H. (2013). Package 'vegan'. Community ecology package, version 2, 1–295.
- OSPAR. (2019). 2018 Status report on the OSPAR network of marine protected areas (pp. 80). *Biodiversity and Ecosystems Series*. London: OSPAR.
- Péron, C., Grémillet, D., Prudor, A., Pettex, E., Saraux, C., Soriano-Redondo, A., Authier, M., & Fort, J. (2013). Importance of coastal Marine Protected Areas for the conservation of pelagic seabirds: The case of Vulnerable yelkouan shearwaters in the Mediterranean Sea. *Biological Conservation*, 168, 210–221. <https://doi.org/10.1016/j.biocon.2013.09.006>.
- Pichegru, L., Grémillet, D., Crawford, R., & Ryan, P. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biology Letters*, 6, 498–501.
- Pollet, I. L., Ronconi, R. A., Leonard, M. L., & Shutler, D. (2019). Migration routes and stopover areas of Leach's Storm Petrels *Oceanodroma leucorhoa*. *Marine Ornithology*, 47, 55–65.
- Prieto, R., Silva, M. A., Waring, G. T., Gonçalves, J. M. A. (2014). Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry. *Endangered Species Research*, 26(2), 103–113. <https://doi.org/10.3354/esr00630>.
- Queiroz, N., Humphries, N. E., Mucientes, G., Hammerschlag, N., Lima, F. P., Scales, K. L., Miller, P. I., Sousa, L. L., Seabra, R., & Sims, D. W. (2016). Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceedings of the National Academy of Sciences*, 113, (6), 1582–1587. <https://doi.org/10.1073/pnas.1510090113>.
- Ramirez, I., Tarzia, M., Dias, M. P., Burfield, I. J., Ramos, J. A., Garthe, S., & Paiva, V. H. (2017). How well is the EU protecting its seabirds? Progress in implementing the Birds Directive at sea. *Marine Policy*, 81, 179–184. <https://doi.org/10.1016/j.marpol.2017.03.034>.
- Rosby, T. (1996). The North Atlantic Current and surrounding waters: At the crossroads. *Reviews of Geophysics*, 34, 463–481.
- Sittler, B., Aebischer, A., & Gilg, O. (2011). Post-breeding migration of four long-tailed skuas (*Stercorarius longicaudus*) from North and East Greenland to West Africa. *Journal of Ornithology*, 152, 375–381.
- Sutherland, W. J., Broad, S., Caine, J., Clout, M., Dicks, L. V., Doran, H., Entwistle, A. C., Fleishman, E., Gibbons, D. W., Keim, B., LeAnstey, B., Lickorish, F. A., Markillie, P., Monk, K. A., Mortimer, D., Ockendon, N., Pearce-Higgins, J. W., Peck, L. S., Pretty, J., Rockström, J., Spalding, M. D., Tonneijck, F. H., Wintle, B. C., & Wright, K. E. (2016). A Horizon Scan of Global Conservation Issues for 2016. *Trends in Ecology & Evolution*, 31, (1), 44–53. <https://doi.org/10.1016/j.tree.2015.11.007>.
- van Bemmelen, R., Moe, B., Hanssen, S. A., Schmidt, N. M., Hansen, J., Lang, J., Sittler, B., Bollache, L., Tulp, I., Klaassen, R., & Gilg, O. (2017). Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua. *Marine Ecology Progress Series*, 578, 197–211. <https://doi.org/10.3354/meps12010>.
- Wakefield, E. D. (2018). *Transatlantic surveys of seabirds, cetaceans and turtles, July 2013 and July 2018*. Glasgow: University of Glasgow.
- Waliczky, Z., Fishpool, L. D. C., Butchart, S. H. M., Thomas, D., Heath, M. F., Hazin, C., Donald, P. F., Kowalska, A., Dias, M. P., & Allinson, T. S. M. (2018). Important Bird and Biodiversity Areas (IBAs): Their impact on conservation policy, advocacy and action. *Bird Conservation International*, 29(2), 199–215.
- Walli, A., Teo, S. L. H., Boustany, A., Farwell, C. J., Williams, T., Dewar, H., Prince, E., & Block, B. A. (2009). Seasonal Movements, Aggregations and Diving Behavior of Atlantic Bluefin Tuna (*Thunnus thynnus*) Revealed with Archival Tags. *PLoS ONE*, 4, (7), e6151 <https://doi.org/10.1371/journal.pone.0006151>.
- White, T. D., Carlisle, A. B., Kroodsma, D. A., Block, B. A., Casagrandi, R., De Leo, G. A., Gatto, M., Micheli, F., & McCauley, D. J. (2017). Assessing the effectiveness of a large marine protected area for reef shark conservation. *Biological Conservation*, 207, 64–71. <https://doi.org/10.1016/j.biocon.2017.01.009>.
- Young, H. S., Maxwell, S. M., Connors, M. G., & Shaffer, S. A. (2015). Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. *Biological Conservation*, 181, 226–235.
- Zupan, M., Bulleri, F., Evans, J., Frascchetti, S., Guidetti, P., Garcia-Rubies, A., Sostres, M., Asnaghi, V., Caro, A., Deudero, S., Goñi, R., Guarneri, G., Guilhaumon, F., Kersting, D., Kokkali, A., Kruschel, C., Macic, V., Mangialajo, L., Mallol, S., Macpherson, E., Panucci, A., Radolovic, M., Ramdani, M., Schembri, P. J., Terlizzi, A., Villa, E., & Claudet, J. (2018). How good is your marine protected area at curbing threats?. *Biological Conservation*, 221, 237–245. <https://doi.org/10.1016/j.biocon.2018.03.013>.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Tammy E. Davies, Ana P.B. Carneiro, Marguerite Tarzia, et al. Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conservation Letters*. 2021;14:e12824. <https://doi.org/10.1111/conl.12824>