

**Seabird diversity hotspot linked to ocean productivity in the
Canary Current Large Marine Ecosystem**

Journal:	<i>Biology Letters</i>
Manuscript ID	RSBL-2016-0024.R3
Article Type:	Research
Date Submitted by the Author:	21-Jul-2016
Complete List of Authors:	Grecian, James; University of Glasgow, Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences Witt, Matthew; University of Exeter College of Life and Environmental Sciences Attrill, Martin; University of Plymouth, Bearhop, Stuart; University of Exeter, Cornwall Campus, Centre for Ecology and Conservation Becker, Peter; Institute of Avian Research, Population Ecology Egevang, Carsten Furness, Robert; Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow Godley, B; University of Exeter, Cornwall Campus, Centre for Ecology and Conservation Gonzalez-Solis, Jacob; University of Barcelona, Animal Biology Gremillet, David; CNRS, CEFE Kopp, Matthias Lescroel, Amelie; CEFE-CNRS, Ecologie Evolutive Matthiopoulos, Jason; University of Glasgow Patrick, Samantha; University of Liverpool, School of Environmental Sciences Peter, Hans-Ulrich Phillips, Richard; British Antarctic Survey, Biological Sciences Division Stenhouse, Iain Votier, Stephen; University of Exeter
Subject:	Ecology < BIOLOGY, Behaviour < BIOLOGY
Categories:	Conservation Biology
Keywords:	bio-logging, human impacts, marine protected areas, migration, upwelling, marine conservation

SCHOLARONE™
Manuscripts

For Review Only

1 **Seabird diversity hotspot linked to ocean productivity in the Canary**
2 **Current Large Marine Ecosystem**

3

4 W. James Grecian^{1*}, Matthew J. Witt², Martin J. Attrill³, Stuart Bearhop⁴, Peter H. Becker⁵,
5 Carsten Egevang⁶, Robert W. Furness¹, Brendan J. Godley⁴, Jacob González-Solís⁷, David
6 Grémillet^{8,9}, Matthias Kopp¹⁰, Amélie Lescroël⁸, Jason Matthiopoulos¹, Samantha C.
7 Patrick¹¹, Hans-Ulrich Peter¹⁰, Richard A. Phillips¹², Iain J. Stenhouse¹³ & Stephen C.
8 Votier^{2*}

9

10 ¹ Institute of Biodiversity, Animal Health & Comparative Medicine, University of Glasgow,
11 Glasgow, G12 8QQ, UK

12 ² Environment and Sustainability Institute, ⁴ Centre for Ecology and Conservation, University
13 of Exeter, Penryn, Cornwall, TR10 9EZ, UK

14 ³ Marine Institute, Plymouth University, Plymouth, Devon, PL4 8AA, UK

15 ⁵ Institut für Vogelforschung ‘Vogelwarte Helgoland’, An der Vogelwarte 21,
16 Wilhelmshaven, D-26386, Germany

17 ⁶ Greenland Institute of Natural Resources, Kivioq 2, 3900 Nuuk, Greenland

18 ⁷ Institut de Recerca de la Biodiversitat (IRBio) and Departament de Biologia Animal,
19 Universitat de Barcelona, Av. Diagonal 643, Barcelona, 08028, Spain

20 ⁸ CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry
21 Montpellier – EPHE, 1919 route de Mende, 34293 Cedex 05, Montpellier, France

22 ⁹ DST/NRF Centre of Excellence, Percy FitzPatrick Institute, University of Cape Town,
23 Rondebosch 7701, South Africa

24 ¹⁰ Institute of Ecology, Friedrich-Schiller University, 07743 Jena, Germany

25 ¹¹ School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, UK

26 ¹² British Antarctic Survey, Natural Environment Research Council, Cambridge, CB3 0ET,

27 UK

28 ¹³ Biodiversity Research Institute, 276 Canco Road, Portland, ME 04103, USA

29 * james.grecian@glasgow.ac.uk; s.c.votier@exeter.ac.uk

30

31 ORCID ID

32 W. James Grecian: 0000-0002-6428-719X

33 Matthew J. Witt: 0000-0002-9498-5378

34 Stuart Bearhop: 0000-0002-5864-0129

35 Brendan J. Godley: 0000-0003-3845-0034

36 Jacob González-Solís: 0000-0002-8691-9397

37 Iain J. Stenhouse: 0000-0003-3614-9862

38 Stephen C. Votier: 0000-0002-0976-016

39

40 **Abstract**

41 Upwelling regions are highly productive habitats targeted by wide-ranging marine predators
42 and industrial fisheries. In this study, we track the migratory movements of 8 seabird species
43 from across the Atlantic; quantify overlap with the Canary Current Large Marine Ecosystem
44 (CCLME); and determine the habitat characteristics that drive this association. Our results
45 indicate the CCLME is a biodiversity hotspot for migratory seabirds; all tracked species and
46 >70% of individuals used this upwelling region. Relative species richness peaked in areas
47 where sea surface temperature averaged between 15 and 20°C, and correlated positively with
48 chlorophyll *a*, revealing the optimum conditions driving bottom-up trophic effects for
49 seabirds. Marine vertebrates are not confined by international boundaries, making
50 conservation challenging. However, by linking diversity to ocean productivity, our research
51 reveals the significance of the CCLME for seabird populations from across the Atlantic,
52 making it a priority for conservation action.

53

54 **1. Introduction**

55 Upwelling regions are globally important marine biodiversity hotspots. The mixing of
56 nutrient-rich cool water with warm surface layers fuels primary production, driving bottom-
57 up cascades that also support large communities of upper trophic-level consumers [1]. As a
58 result, they are attractive foraging grounds targeted by a wide-range of marine animals
59 throughout the annual cycle [2]. These characteristics make upwelling regions strong
60 candidates for protection, but this is challenging as they often cross national boundaries,
61 occur in international waters, and protection may conflict with fisheries interests [3].

62
63 Marine environments are facing unprecedented levels of anthropogenic-driven pressure;
64 including climate change, pollution, and offshore development [4–6]. The foremost threat to
65 upwelling regions is biodiversity loss through overfishing; upwellings cover < 1% of the
66 world's ocean by area but provide ~20% of global catch [7]. Commercial capture fisheries
67 deplete stocks, remove top-predators through bycatch, and alter the trophic structure of
68 ecosystems [8,9]. The Canary Current Large Marine Ecosystem (CCLME) now incorporates
69 one of the most intensively fished areas on Earth [8,10], yet also supports large populations
70 of migratory marine vertebrates from breeding populations across the Atlantic [11–13].

71
72 Considering the increasing industrialisation of fisheries [10], the pervasive threat from
73 bycatch [14], and a paucity of quantitative information on habitat or space use, understanding
74 marine vertebrate distributions in the CCLME and beyond is a key conservation goal [15]. In
75 this study, we use miniaturised light loggers to reconstruct the non-breeding movements of
76 eight migratory seabird species from disparate regions of the Atlantic that have been
77 previously recorded in the CCLME [12]. Our aims are (i) to map the distribution of these
78 birds and identify areas of high diversity, (ii) to quantify the extent to which each species

79 utilises the CCLME, and (iii) to determine the oceanographic characteristics that drive this
80 association. We use our findings to assess the importance of the CCLME as a biodiversity
81 hotspot and discuss the potential conflict between fisheries and seabirds in this region.

82

83 **2. Methods**

84 We collated data on the non-breeding movements of eight seabird species; Cory's
85 shearwaters (*Calonectris borealis*); Scopoli's shearwaters (*C. diomedea*); lesser black-backed
86 gulls (*Larus fuscus*); northern gannets (*Morus bassanus*); great skuas (*Stercorarius skua*);
87 south polar skuas (*S. maccormicki*); common terns (*Sterna hirundo*); and Sabine's gulls
88 (*Xema sabini*). While these species have been recorded previously in the CCLME, the true
89 importance of this region for specific populations is unknown. Between 2000 and 2011, 123
90 birds were tracked using miniaturised light loggers from 12 breeding colonies from the north
91 (75°N) to the south (62°S) of the Atlantic (see Supplementary Materials). To quantify the
92 extent to which each species utilises the CCLME, we calculated the proportion of time each
93 individual spent in this region [16]. To identify areas of high species richness we constructed
94 spatial density maps by binning location data into 200 km diameter tessellated hexagons
95 spanning the Atlantic. We calculated relative richness by summing the number of species
96 occurring in each hexagon during the non-breeding period.

97

98 To characterise the marine environment we extracted winter seasonal climatology composites
99 (Dec-Mar, 2002-2010) of sea surface temperature (SST, °C) and chlorophyll *a* concentration
100 (CHL, mg m⁻³) from the MODIS instrument onboard the Aqua (EOS PM) satellite
101 (<http://oceancolor.gsfc.nasa.gov/>) and calculated mean SST and CHL values for each
102 hexagon. We also included a measure of null usage that incorporated both habitat availability

103 and sampling effort, as this was not uniform across species or colonies [17] (see
104 Supplementary Materials). These data are available via Dryad [18].

105

106 We examined correlations between the observed patterns in relative richness and these
107 covariates using generalised additive models fitted with the packages mgcv [19] and MuMIn
108 [20] in R version 3.1.0 [21]. We \log_{10} transformed CHL prior to use. We included SST, CHL,
109 and null usage as covariates in the global model with thin plate regression splines fitted with
110 a maximum of 10 knots; superfluous knots were penalised during model fitting. Variance
111 Inflation Factors revealed no collinearity between covariates ($VIF < 3$). We also included the
112 central X and Y coordinates of each hexagon as a spatial smooth term implemented with a
113 soap film boundary [22]. The soap film specifies the extent of the predicted surface,
114 preventing smoothing across boundary features such as the Iberian Peninsula. Variograms of
115 model residuals revealed no spatial autocorrelation in final models. Model selection was
116 based on Akaike's Information Criterion (AIC), with parameters excluded if their inclusion
117 did not improve the model by more than $2 \Delta AIC$ relative to the lowest AIC.

118

119 **3. Results**

120 The eight species tracked from 12 colonies over 10 years were widely distributed across the
121 Atlantic during the non-breeding period (figure 1). Highest relative richness was observed in
122 the CCLME, with other hotspots in the Bay of Biscay, Mid-Atlantic Ridge, Brazilian coast
123 and Benguela Current (figure 1). On average, $76.6\% \pm 28.1\%$ of individuals from each
124 species visited the CCLME, including all Scopoli's shearwaters, Sabine's gulls, south polar
125 skuas, and common terns, the majority of lesser black-backed gulls and northern gannets, but
126 only 25% of great skuas (table 1). The proportion of time each species spent in the CCLME
127 was highest for Scopoli's shearwaters (0.35 ± 0.28), northern gannets (0.26 ± 0.29), and

128 common terns (0.24 ± 0.22). There was a high degree of variation both within and among
129 species; individuals may use the CCLME for the entire non-breeding period, only as a staging
130 area, or not at all (table 1).

131

132 Relative richness correlated with SST and CHL; both terms were retained in the top ranked
133 model along with the soap film smooth term and measure of null usage (table 2). Model-
134 estimates indicated relative richness was highest in areas with sea surface temperatures
135 between 15 and 20°C, and there was a general positive correlation between relative richness
136 and CHL (figure 1).

137

138 **4. Discussion**

139 Here, we demonstrate that the CCLME is an area of high relative species richness for non-
140 breeding seabirds, and detail the environmental conditions that drive this association. More
141 than 70% of individuals from eight species, representing a range of functional groups, and
142 originating from breeding colonies across the Atlantic, visited this upwelling region. Relative
143 richness correlated with both sea surface temperature (SST) and chlorophyll *a* (CHL). By
144 tracking birds of known origin, our results illustrate the high connectivity between seabird
145 breeding populations across the Atlantic and the CCLME, emphasising the importance of this
146 upwelling region as a non-breeding destination and migratory stopover site.

147

148 This study represents the most comprehensive collation of tracking data for the CCLME to
149 date, but our measure of relative species richness is limited to those populations included in
150 the study. While many other species also visit this region [12], modern developments in
151 biologging are revealing a diversity of migration strategies [23], and highlighting other
152 important areas across the Atlantic. Our measure of relative species richness represents the

153 maximum across the study period, and is likely to vary over the annual cycle in response to
154 seasonal differences in environmental conditions. For example, southern hemisphere
155 migrants following the austral summer overlap only briefly with northern hemisphere
156 migrants in the CCLME (Supplementary table 1). While our study highlights the CCLME as
157 a hotspot for migratory seabirds, further work is required to understand the significance of
158 other areas across the Atlantic and beyond.

159

160 These findings provide evidence of the links between biodiversity and ocean productivity in
161 an eastern boundary upwelling region. Relative richness was highest between 15 and 20°C,
162 and correlated positively with CHL; corroborating previous work on the oceanographic
163 drivers of marine predator diversity in the California Current [2]. This suggests that primary
164 productivity in the CCLME has bottom-up effects that are highly relevant to apex predators.
165 The mechanisms by which animals may target these regions are currently unknown, but
166 frontal density in the CCLME is high and these visible indicators of productivity are known
167 to aggregate marine predators such as seabirds [11,24].

168

169 The CCLME attracts some of the highest global fishing effort [8,10], yet there is a paucity of
170 information on the interactions between seabirds and fisheries in this region [15]. Fisheries
171 impact seabirds in three ways; either competing directly for fish, providing food in the form
172 of discarded fish, or posing the threat of bycatch mortality [14,25,26]. More research into
173 fine-scale, species-specific fisheries interactions in the CCLME is required, especially given
174 recent evidence of direct take of seabirds in the region (Kees Camphuysen, pers. com.); the
175 substantial under-reporting of catch in this area by China's distant-water fleet [27]; and the
176 prevalence of Illegal, Unreported and Unregulated fisheries [28].

177

178 Integrating data across multiple species and years highlights the importance of the CCLME
179 as a seabird biodiversity hotspot. Furthermore, environmental conditions such as sea surface
180 temperature and productivity may offer insights into how their distributions could shift in
181 response to global climate change. As marine vertebrates forage across dynamic pelagic
182 systems and are not confined by international boundaries, effective conservation will require
183 multilateral cooperation. Nevertheless, while site fidelity to persistent upwelling regions such
184 as the CCLME could aid conservation, it is unlikely that both a large diversity of marine
185 vertebrates and intense fisheries exploitation can be sustained in this region in the long-term.

186

187 **Ethics statement** All animal research was conducted in accordance with relevant in country
188 protocols.

189 **Data accessibility** The species richness and environmental covariate data underlying this
190 study are archived in the Dryad Digital Repository at <http://dx.doi.org/10.5061/dryad.01sd0>.
191 Individual species data are archived by BirdLife International (www.seabirdtracking.org).

192 **Author contributions** WJG conceived the study, conducted the data analysis and drafted the
193 manuscript; SCV supervised the project; all authors provided data, contributed to article
194 drafts, approved the final version of this manuscript and agree to be held accountable for the
195 content.

196 **Competing interests** The authors declare no competing interests.

197 **Funding statement** Funding for this work was provided by the Peninsula Research Institute
198 for Marine Renewable Energy, EU INTERREG project CHARM III, NERC
199 (NE/G001014/1), MINECO CGL2013-42585-P, Defra's Darwin Initiative and Centre
200 National de la Recherche Scientifique.

201 **Acknowledgements** We thank all those who supported fieldwork logistics and granted
202 permission for work. Four anonymous reviewers provided comments that greatly improved
203 this manuscript.

204

205 **References**

- 206 1. Mann, K. H. & Lazier, J. R. N. 2005 *Dynamics of Marine Ecosystems*. Third Edit.
207 Malden, MA USA: Blackwell Publishing Ltd. (doi:10.1002/9781118687901)
- 208 2. Block, B. A. et al. 2011 Tracking apex marine predator movements in a dynamic
209 ocean. *Nature* **475**, 86–90. (doi:10.1038/nature10082)
- 210 3. Hyrenbach, K. D., Forney, K. A. & Dayton, P. K. 2000 Marine protected areas and
211 ocean basin management. *Aquat. Conserv. Freshw. Ecosyst.* **10**, 437–458.
- 212 4. Islam, M. S. & Tanaka, M. 2004 Impacts of pollution on coastal and marine
213 ecosystems including coastal and marine fisheries and approach for management: a
214 review and synthesis. *Mar. Pollut. Bull.* **48**, 624–649.
215 (doi:10.1016/j.marpolbul.2003.12.004)
- 216 5. Inger, R. et al. 2009 Marine renewable energy: potential benefits to biodiversity? An
217 urgent call for research. *J. Appl. Ecol.* **46**, 1145–1153. (doi:10.1111/j.1365-
218 2664.2009.01697.x)
- 219 6. Sydeman, W. J., Poloczanska, E., Reed, T. E. & Thompson, S. A. 2015 Climate
220 Change and marine vertebrates. *Science* **350**, 772–777. (doi:10.1126/science.aac9874)
- 221 7. Pauly, D. & Christensen, V. 1995 Primary production required to sustain global
222 fisheries. *Nature* **374**, 255–257.

- 223 8. Laurans, M., Gascuel, D., Chassot, E. & Thiam, D. 2004 Changes in the trophic
224 structure of fish demersal communities in West Africa in the three last decades. *Aquat.*
225 *Living Resour.* **17**, 163–173.
- 226 9. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres Jr., F. 1998 Fishing
227 Down Marine Food Webs. *Science* **279**, 860–863. (doi:10.1126/science.279.5352.860)
- 228 10. Worm, B. et al. 2009 Rebuilding Global Fisheries. *Science* **325**, 578–585.
229 (doi:10.1126/science.1173146)
- 230 11. Wynn, R. B. & Knefelkamp, B. 2004 Seabird distribution and oceanic upwelling off
231 northwest Africa. *Br. Birds* **97**, 323–335.
- 232 12. Camphuysen, K. C. J. & van der Meer, J. 2005 Wintering seabirds in West Africa:
233 foraging hotspots off Western Sahara and Mauritania driven by upwelling and
234 fisheries. *African J. Mar. Sci.* **27**, 427–437.
- 235 13. Eckert, S. A. 2006 High-use oceanic areas for Atlantic leatherback sea turtles
236 (*Dermochelys coriacea*) as identified using satellite telemetered location and dive
237 information. *Mar. Biol.* **149**, 1257–1267.
- 238 14. Lewison, R. L., Crowder, L. B., Read, A. J. & Freeman, S. A. 2004 Understanding
239 impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* **19**, 598–604.
240 (doi:10.1016/j.tree.2004.09.004)
- 241 15. Grémillet, D., Peron, C., Provost, P. & Lescroël, A. 2015 Adult and juvenile European
242 seabirds at risk from marine plundering off West Africa. *Biol. Conserv.* **182**, 143–147.
243 (doi:10.1016/j.biocon.2014.12.001)
- 244 16. Claus, S., De Hauwere, N., Vanhoorne, B., Souza Dias, F., Hernandez, F., Mees, J. &

- 245 (Flanders Marine Institute) 2015 MarineRegions.org. Accessed at
246 <http://www.marineregions.org> on 2015-06-23.
- 247 17. Matthiopoulos, J. 2003 The use of space by animal as a function of accessibility and
248 preference. *Ecol. Modell.* **159**, 239–268. (doi:10.1016/S0304-3800(02)00293-4)
- 249 18. Grecian, W. J. et al. In press. Data from: Seabird diversity hotspot linked to ocean
250 productivity in the Canary Current Large Marine Ecosystem.
- 251 19. Wood, S. N. 2006 *Generalized Additive Models: An Introduction with R*. Chapman and
252 Hall/CRC.
- 253 20. Bartoń, K. 2015 MuMIn: Multi-Model Inference. R package version 1.15.1.
- 254 21. R Core Team 2015 R: A language and environment for statistical computing. *R Found.*
255 *Stat. Comput.*
- 256 22. Wood, S. N., Bravington, M. V. & Hedley, S. L. 2008 Soap film smoothing. *J. R. Stat.*
257 *Soc. Ser. B Stat. Methodol.* **70**, 931–955. (doi:10.1111/j.1467-9868.2008.00665.x)
- 258 23. Costa, D. P., Breed, G. a. & Robinson, P. W. 2012 New Insights into Pelagic
259 Migrations: Implications for Ecology and Conservation. *Annu. Rev. Ecol. Evol. Syst.*
260 **43**, 73–96. (doi:10.1146/annurev-ecolsys-102710-145045)
- 261 24. Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W. & Votier, S. C.
262 2014 On the Front Line: frontal zones as priority at-sea conservation areas for mobile
263 marine vertebrates. *J. Appl. Ecol.* , 1575–1583. (doi:10.1111/1365-2664.12330)
- 264 25. Okes, N. C., Hockey, P. a. R., Pichegru, L., Lingen, C. D. Van Der, Crawford, R. J. M.
265 & Grémillet, D. 2009 Competition for shifting resources in the southern Benguela
266 upwelling: Seabirds versus purse-seine fisheries. *Biol. Conserv.* **142**, 2361–2368.

- 267 (doi:10.1016/j.biocon.2009.05.031)
- 268 26. Votier, S. C. et al. 2004 Changes in fisheries discard rates and seabird communities.
269 *Nature* **427**, 727–730.
- 270 27. Pauly, D. et al. 2014 China's distant-water fisheries in the 21st century. *Fish Fish.* **15**,
271 474–488. (doi:10.1111/faf.12032)
- 272 28. Agnew, D. J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J. R. &
273 Pitcher, T. J. 2009 Estimating the Worldwide Extent of Illegal Fishing. *PLoS One* **4**,
274 e4570.
- 275

276 **Table 1** Summary statistics for tracking by seabird species. Values represent mean \pm SD.

277

Species	N	% visiting CCLME	Winter period (days)	Number of locations	Locations in CCLME	Proportion in CCLME
Lesser black-backed gull	7	71.4	208.4 \pm 27.4	151.1 \pm 20.8	21.0 \pm 24.0	0.09 \pm 0.10
Northern gannet	34	58.8	93.6 \pm 13.4	89.6 \pm 15.4	25.7 \pm 29.8	0.26 \pm 0.29
Great skua	16	25	92	91.9 \pm 0.4	11.1 \pm 21.8	0.12 \pm 0.24
Cory's shearwater	19	57.9	133.9 \pm 29.9	131.5 \pm 27.4	13.8 \pm 23.2	0.10 \pm 0.18
Scopoli's shearwater	9	100	104.5 \pm 40.8	102.3 \pm 39.6	35.4 \pm 36.9	0.35 \pm 0.28
Sabine's gull	7	100	287.9 \pm 12.7	228.6 \pm 18.6	22.3 \pm 3.1	0.08 \pm 0.01
South polar skua	19	100	237.2 \pm 35.1	176.3 \pm 21.6	8.7 \pm 14.3	0.04 \pm 0.07
Common tern	12	100	254.3 \pm 67.0	181.3 \pm 64.0	62.8 \pm 51.8	0.24 \pm 0.22

278 For full methods and description of winter period see supplementary material

279

280

281 **Table 2** Model selection testing correlations between relative richness and sea surface
 282 temperature (SST) and chlorophyll *a* (CHL). The full model included a soap film smooth
 283 term (XY) and measure of habitat availability (null). Models shown are those within 6 Δ AIC
 284 of the best-supported model.

285

Rank	Parameters	df	AIC	Δ AIC
1	SST + CHL + XY + null	173	5573	0.00
2	SST + XY + null	175	5576	2.84
3	SST + CHL + XY	171	5578	4.47
4	SST + XY	173	5579	6.28

286 Adj R^2 of best-supported model = 0.60

287

288

289 **Figure 1** Links between (a) Relative richness of eight seabird species tracked from pan-
290 Atlantic colonies between 2000 and 2011; and (b) Sea surface temperature and (c)
291 Chlorophyll *a*. Dark line in (a) represents the boundary of the Canary Current Large Marine
292 Ecosystem; blue dots represent colonies of origin for tracked birds, indicated by arrows. Dark
293 lines in (b) and (c) represent model-estimated response; dashed lines 95% CI; light grey dots
294 indicate the distribution of data.

295

For Review Only

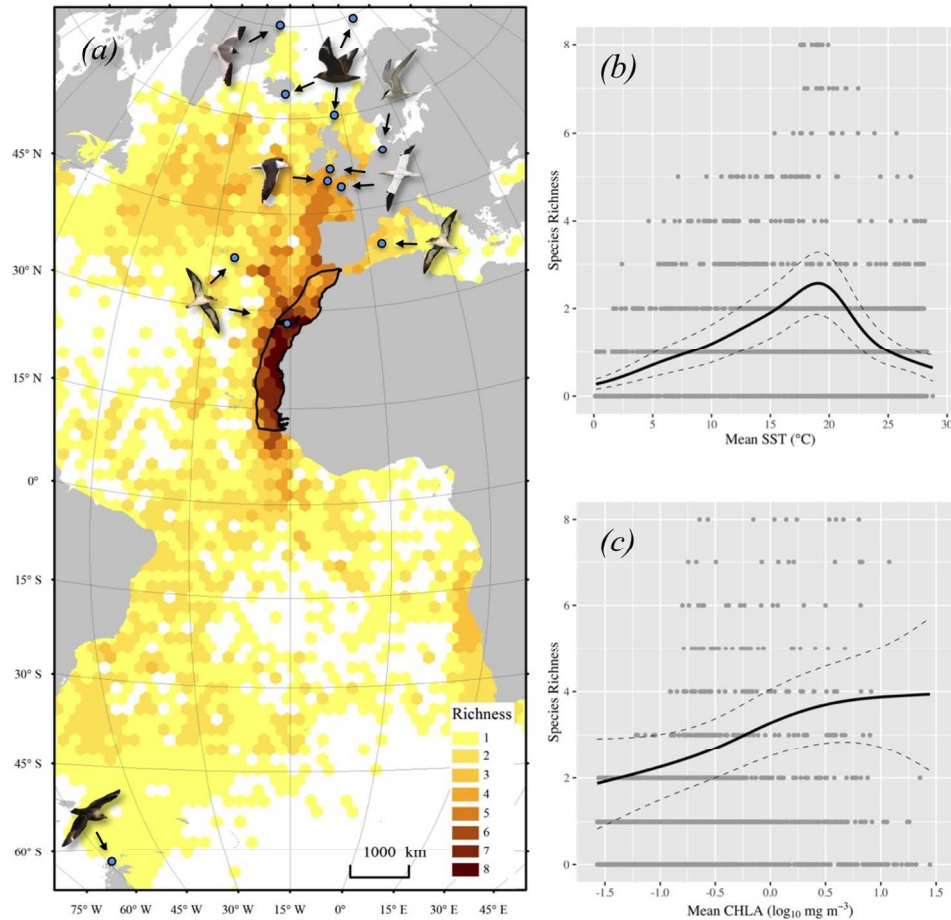


Figure 1 Links between (a) Relative richness of eight seabird species tracked from pan-Atlantic colonies between 2000 and 2011; and (b) Sea surface temperature and (c) Chlorophyll a. Dark line in (a) represents the boundary of the Canary Current Large Marine Ecosystem; blue dots represent colonies of origin for tracked birds, indicated by arrows. Dark lines in (b) and (c) represent model-estimated response; dashed lines 95% CI; light grey dots indicate the distribution of data.

figure 1

508x508mm (72 x 72 DPI)