

1 **Bycatch mitigation could prevent strong changes in the ecological**  
2 **strategies of seabird communities across the globe**

3  
4 Cerren Richards<sup>1</sup>, Robert S. C. Cooke<sup>2-4</sup>, Diana E. Bowler<sup>5-7</sup>, Kristina Boerder<sup>8</sup>, Amanda E.  
5 Bates<sup>1</sup>

6  
7 <sup>1</sup>Department of Ocean Sciences, Memorial University of Newfoundland, St. John's,  
8 Newfoundland, Canada

9 <sup>2</sup>Department of Biological and Environmental Sciences, University of Gothenburg, Box 463, SE-  
10 405 30, Göteborg, Sweden

11 <sup>3</sup>Gothenburg Global Biodiversity Centre, Box 461, SE-405 30, Göteborg, Sweden

12 <sup>4</sup>UK Centre for Ecology & Hydrology, Oxfordshire, OX10 8BB, United Kingdom

13 <sup>5</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz  
14 5e, 04103 Leipzig, Germany

15 <sup>6</sup>Friedrich Schiller University Jena, Institute of Biodiversity, Dornburger Str. 159, 07743 Jena,  
16 Germany

17 <sup>7</sup>Helmholtz-Center for Environmental Research - UFZ, Department Ecosystem Services,  
18 Permoserstraße 15, 04318 Leipzig, Germany

19 <sup>8</sup>Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

20

21

22

23 **Keywords:** bycatch; ecosystem functioning; fisheries; marine spatial planning;  
24 seabird; trait

25

26 **Corresponding Author:** Cerren Richards<sup>1</sup> ([cerrenrichards@gmail.com](mailto:cerrenrichards@gmail.com);  
27 [cerridwenr@mun.ca](mailto:cerridwenr@mun.ca))

## 28 **Abstract**

29 Fisheries bycatch, the incidental mortality of non-target species, is a major threat to seabirds  
30 worldwide. Mitigating bycatch is an important factor to reduce seabird population declines and  
31 consequent changes in ocean trophic dynamics and ecosystem functioning. However, it remains  
32 an open question how and where mitigating bycatch at a global scale may conserve seabird traits  
33 and the ecological strategies that traits represent. Here we combine a dataset of species' traits and  
34 distribution ranges for 341 seabirds with spatially resolved fishing effort data for gillnet,  
35 longline, trawl, and purse seine gears to: (1) understand spatial variation in seabird community  
36 traits; and (2) test whether mitigating fisheries bycatch may prevent shifts in traits of seabird  
37 communities and loss of ecological strategies. We find distinct spatial variation in the  
38 community weighted mean of five seabird traits (clutch size, body mass, generation length,  
39 foraging guild, and diet guild). Furthermore, our analysis suggests that successful bycatch  
40 mitigation could prevent strong shifts in the traits of seabird communities across the globe  
41 particularly in the North Atlantic and Southern Oceans. Specifically, changes in dominant  
42 foraging and diet guilds, and shifts towards communities with faster reproductive speeds (larger  
43 clutch sizes and shorter generation lengths) and smaller body masses could be avoided.  
44 Therefore, bycatch mitigation may have important indirect benefits for sustaining ecosystem  
45 functioning, as mediated by species traits. Incorporating species traits into management actions  
46 will provide valuable tools for marine spatial planning and when evaluating the success of  
47 conservation initiatives.

## 48 **1.0 Introduction**

49 Global fishing effort and capacity have more than doubled since 1950 (Rousseau et al., 2019)  
50 with direct and indirect ecological consequences for marine fauna (Komoroske and Lewison,  
51 2015; Lewison et al., 2004; Senko et al., 2014). Fisheries bycatch, the incidental mortality of  
52 non-target species, is a serious threat to seabirds, (Alverson et al., 1994; Lewison et al., 2004)  
53 driving population declines worldwide (Anderson et al., 2011; Croxall et al., 2012; Dias et al.,  
54 2019; Hedd et al., 2016). For instance, the populations of three South Georgian albatross species  
55 have plummeted by 40-60 % over 35 years due to bycatch (Pardo et al., 2017). Identifying areas  
56 of high overlap between fisheries and seabirds could therefore provide critical insights for  
57 marine spatial planning and opportunities to reduce fisheries bycatch. This in turn could prevent

58 the direct declines of seabird populations and indirect loss of ecosystem functions, such as  
59 nutrient transportation, provided by seabirds (Komoroske and Lewison, 2015).

60  
61 A trait-based approach offers a valuable tool set in which to evaluate conservation successes and  
62 highlight regions where conservation strategies will provide the greatest gains. Traits are  
63 attributes of organisms measured at the individual level (Gallagher et al., 2020; Violle et al.,  
64 2007), such as body mass and foraging guild. When traits relate to function, they can be used to  
65 infer species' contributions to ecosystem functioning (Gallagher et al., 2020). For example,  
66 seabirds are often top predators, consequently their diet and foraging strategy can relate to  
67 functions such as trophic regulation of populations and nutrient storage (Tavares et al., 2019).  
68 Thus, trait analyses may offer opportunities to highlight oceanic regions susceptible to the  
69 greatest loss of ecosystem functioning without bycatch mitigation measures.

70  
71 Simple, innovative, and inexpensive mitigation solutions have substantially reduced bycatch  
72 across gear types and species (Croxall, 2008). These solutions include gear modifications that  
73 increase net visibility and deter species with scaring lines, and management actions including  
74 time-area closures that prohibit fishing in an area or at specific times (Senko et al., 2014). For  
75 example, the introduction of bird-scaring lines in a South African trawl fishery reduced albatross  
76 death rates by up to 95% (Maree et al., 2014). However, it remains an open question how and  
77 where mitigating bycatch at a global scale may conserve seabird traits and the ecological  
78 strategies that traits represent (Gallagher et al., 2020).

79  
80 Here we combine a dataset of five traits across 341 seabird species with global seabird range  
81 maps and a spatially resolved fishing effort dataset for gillnet, longline, trawl, and purse seine  
82 gears to: (1) map and describe the spatial variation in community traits; and (2) test whether  
83 mitigating fisheries bycatch may prevent shifts in traits of seabird communities and loss of  
84 ecological strategies. Collectively, these objectives allow us to identify the oceanic regions  
85 potentially susceptible to the greatest loss of ecosystem functioning without bycatch mitigation  
86 measures.

## 87 **2.0 Methods**

### 88 **2.1 Spatial data**

89 To identify areas where fisheries and seabirds overlap, we first extracted distribution polygons  
90 for 341 seabirds from BirdLife International data zone (BirdLife International, 2017), available  
91 upon request from <http://datazone.birdlife.org/species/requestdis>. These spatial polygons  
92 represent the coarse distributions that species likely occupy, and are presently the best available  
93 data for the ranges of all seabirds. We subset the spatial data to only retain the extant, native,  
94 resident, breeding season and non-breeding season polygons. We created a 1° resolution global  
95 presence-absence matrix based on the seabird distribution polygons using the package ‘letsR’  
96 and function *lets.presab* (Vilela and Villalobos, 2015) for further analyses. All land was removed  
97 from the presence-absence matrix using the *wrld\_simpl* polygon from the package ‘maptools’  
98 (Bivand and Lewin-Koh, 2020) and function *lets.pamcrop* from the package ‘letsR’ (Vilela and  
99 Villalobos, 2015).

100

101 Second, we downloaded fine scale spatio-temporal fishing effort data from Global Fishing  
102 Watch ([globalfishingwatch.org](http://globalfishingwatch.org)). Global Fishing Watch analyses fishing activity data using the  
103 Automatic Identification System (AIS). While AIS is a safety device used onboard vessels to  
104 avoid collisions, it also transmits data about a vessel’s identity, type, location, speed and  
105 directions (Kroodsma et al., 2018). These data are processed using convolutional neural  
106 networks to characterise fishing vessel identity, gear types and periods of fishing activity with  
107 94–97% accuracy when compared with labelled data (Guet et al., 2019; Kroodsma et al., 2018).  
108 AIS is mandated on vessels larger than 300 gross tonnes travelling in international waters  
109 (International Maritime Organization) and is estimated to cover over 50% of nearshore and up to  
110 80% of high sea fishing effort (Sala et al., 2018). We extracted the daily fishing activity data for  
111 gillnets, longlines, trawls, and purse seines from Global Fishing Watch. These gear types were  
112 selected because they cause the greatest seabird bycatch mortalities worldwide (Dias et al.,  
113 2019). Fishing activity between 2015 and 2018 across the four gear types was aggregated per 1°  
114 global grid cell to produce a single fishing activity layer (Fig. 1).

115

116 To ensure consistency between the species' distribution and fishing activity layer, we re-  
117 projected all spatial data to a raster format with the same coordinate reference system (WGS84)  
118 and resolution ( $1^\circ \times 1^\circ$  global grid cells). To achieve this, we used the package 'raster' and  
119 function *rasterFromXYZ* (Hijmans, 2020).

120  
121 Finally, we built a second seabird raster representing the distributions where seabirds could  
122 become locally extinct due to bycatch. To achieve this, we removed all cells where the  
123 distributions of seabirds listed as threatened from bycatch by the International Union for  
124 Conservation of Nature (IUCN) threat classification scheme (n = 134 species, threats 5.4.3 &  
125 5.4.4 from IUCN (2012a)) overlapped with the fishing activity layer.

## 126 **2.2 Community Weighted Mean**

127 To map and describe the global distribution of seabird traits, we selected five traits (Table 1):  
128 *clutch size*, the number of eggs per clutch; *body mass*, the median mass in grams; *generation*  
129 *length*, the age at which a species produces offspring in years; *foraging guild*, the dominant  
130 foraging strategy of the species (diver, surface feeder, ground feeder, generalist); and *diet guild*,  
131 the dominant diet of the species (omnivore, invertebrate, vertebrate & scavenger). All traits were  
132 extracted from a recently compiled and imputed dataset of seabird traits (Richards et al., 2021).  
133 Next, we calculated the community weighted mean (CWM) for each  $1^\circ$  grid cell with the  
134 function *functcomp*, package 'FD' (Laliberté & Legendre, 2010; Laliberté et al., 2014).  
135 Community weighted means describes the typical characteristics within a set of species by  
136 combining information on species' traits and distributions (Duarte et al., 2017). For continuous  
137 data, CWM is the mean trait value of all species present in each  $1^\circ$  grid cell, and for categorical  
138 data, CWM is the most dominant class per trait within each  $1^\circ$  grid cell. We do not weight the  
139 CWM by species relative abundances because these data were not available.

## 140 **2.3 Trait shifts**

141 To quantify the extent mitigating fisheries bycatch could prevent shifts in seabird traits, we  
142 calculated the deviation between the observed CWM (i.e., all species) and CWM after the  
143 removal of bycatch-threatened seabirds from cells overlapping with fishing activities, for each  $1^\circ$   
144 grid cell. For continuous traits (clutch size, body mass, generation length), the percentage

145 deviation in CWM for each grid cell CWM ( $\text{Deviation}_{\text{Continuous}}$ ) was calculated with the following  
146 equation:

$$\text{Deviation}_{\text{Continuous}} = \left( \frac{\text{CWM}_{\text{Bycatch}} - \text{CWM}_{\text{Total}}}{\text{CWM}_{\text{Total}}} \right) \times 100$$

147

148 Where  $\text{CWM}_{\text{Bycatch}}$  is the community weighted mean after removing bycatch-threatened seabirds if  
149 the cell overlapped with fishing activities, and  $\text{CWM}_{\text{Total}}$  is the observed community weighted  
150 mean.

151

152 To quantify the shift in categorical traits, we calculated the proportion of each foraging (*diver*,  
153 *surface*, *ground*, *generalist*) and diet guild (*omnivore*, *invertebrate*, *vertebrate* & *scavenger*)  
154 category per grid cell as observed ( $\text{Proportion}_{\text{Total}}$ ), and again after the removal of bycatch-  
155 threatened species for cells overlapping with fishing activities ( $\text{Proportion}_{\text{Bycatch}}$ ). We then  
156 calculated the deviation between these values per grid cell ( $\text{Deviation}_{\text{Categorical}}$ ) with the following  
157 equation:

$$\text{Deviation}_{\text{Categorical}} = \text{Proportion}_{\text{Bycatch}} - \text{Proportion}_{\text{Total}}$$

158

159 To describe the spatial trends in trait shifts across latitude, we fitted either general additive  
160 models (GAM) using the package ‘mgcv’ and function *gam* (Wood, 2017), or additive quantile  
161 regression models using the package ‘qgam’ and function *qgam* (Fasiolo et al., 2017) depending  
162 on the most appropriate fit. For each trait, latitude was included as the predictor and  
163  $\text{Deviation}_{\text{Continuous}}$  or  $\text{Deviation}_{\text{Categorical}}$  as the response. All analyses were completed in R version 3.5.0  
164 (R Core Team, 2020).

## 165 **3.0 Results**

### 166 **3.1 Spatial variation in community traits**

167 We find large spatial variation in the community weighted mean (CWM) of clutch size, body  
168 mass, generation length, foraging guild and diet guild traits across the globe (Fig. 2). Species  
169 with the largest clutch sizes are distributed along coastlines, particularly in the Northern  
170 Hemisphere. In contrast, species with the smallest clutch sizes are highly pelagic and distributed

171 across all oceans. The CWM for body mass is more evenly distributed, with the heaviest species  
172 being located in the Southern Ocean. Species with small body masses are distributed between  
173 30°N and 30°S. Generation length is also evenly distributed globally. Species with the longest  
174 generation lengths are concentrated in the Southern Ocean, whilst the shortest generation lengths  
175 are along coastlines. For the foraging guild, surface foragers typically dominate most oceans  
176 below 50°N, whilst divers are the most dominant above 50°N and along the coast of Atlantic  
177 Central America and Oceania. Generalists are concentrated around the coasts of Europe  
178 (Mediterranean Sea, Black Sea, Baltic Sea, North Sea) and ground foragers dominate in the high  
179 Arctic. For the diet guild, vertebrate & scavenger consumers dominate the Southern and Pacific  
180 Oceans, while invertebrate consumers dominate the Atlantic and Indian Oceans. Omnivores are  
181 only dominant in the Caspian Sea.

### 182 **3.2 Preventing trait shifts**

183 Our results suggest that successful bycatch mitigation has the potential to prevent shifts in the  
184 traits of seabird communities across the globe (Figs. 2 & 3). Removal of bycatch threats could  
185 prevent an increase in clutch size above 50°S, and a decrease in clutch size below 50°S (Fig.  
186 3A). Furthermore, the global shift in CWM to species with shorter generation lengths and  
187 smaller body masses could be avoided (Figs. 3B-C). This trend is particularly prominent between  
188 30° and 70° in both hemispheres. Bycatch mitigation could further prevent shifts in diet guilds  
189 from a dominance of invertebrate consumers to vertebrate & scavenger consumers in the North  
190 Atlantic Ocean, and shifts to more omnivores around European waters (Figs. 2 & 3D-F). For  
191 foraging guild, shifts from a dominance of diving and surface foragers to generalist and ground  
192 foragers above 40°N could be prevented (Figs. 2 & 3G-J). Below 40°N, we find surface foragers  
193 may remain the dominant foraging guild without bycatch intervention (Fig. 2), but their  
194 proportion within the community could increase (Fig. 3G). The proportion of divers within the  
195 community may also increase slightly between 40°N and 50°S, but decrease below 50°S (Fig.  
196 3H). Generalist foragers could decrease below 40°N (Fig. 3I), and ground foragers may remain  
197 relatively stable (Fig. 3J).

## 198 **4.0 Discussion**

199 Here we find that mitigating bycatch could prevent large shifts in traits of seabird communities.  
200 Specifically, changes in dominant foraging and diet guilds, and shifts towards communities with  
201 faster reproductive speeds (larger clutch sizes and shorter generation lengths) and smaller body  
202 masses could be avoided. Therefore, bycatch mitigation may have important indirect benefits for  
203 sustaining ecosystem functioning, as mediated by species traits. For example, body mass is  
204 strongly linked to nutrient transport and storage because large individuals hold and disperse large  
205 nutrient quantities (Anderson et al., 2011; Doughty et al., 2016; Tavares et al., 2019).  
206 Consequently, preventing shifts to smaller body masses could protect important zoogeochemical  
207 cycles of major elements worldwide (Speakman, 2005; Wing et al., 2014; Graham et al., 2018;  
208 Schmitz et al., 2018; Tavares et al., 2019). Moreover, preventing shifts to species with faster  
209 reproductive speeds (decreased generation lengths and increased clutch size), such as gulls and  
210 tern, could have implications for nutrient storage and cycling, and food provisioning (Tavares et  
211 al., 2019). Additionally, the conservation of foraging strategy and diet guild traits may sustain  
212 trophic regulations and community structures, because, as top predators, seabirds influence  
213 marine food webs from the top down via direct and indirect pathways (Ripple et al., 2017).

214  
215 Few management actions have incorporated biological trait analyses for marine spatial planning  
216 and when evaluating the success of conservation initiatives (Miatta et al., 2021). Moreover, a  
217 number of studies highlight the importance of including biological communities and ecosystem  
218 functions into conservation policy because focusing on biodiversity metrics alone may exclude  
219 functionally and ecologically important locations (Bremner et al., 2006; Frid et al., 2008; Miatta  
220 et al., 2021; Rees et al., 2012). Thus, considering the traits of species assemblages in a  
221 quantitative framework offers valuable tools for advancing marine conservation outcomes  
222 (Miatta et al., 2021). While trait-based approaches do not directly quantify the ecosystem  
223 functions that seabirds deliver, here we show biological traits could provide new insights for  
224 assessing the success of bycatch mitigation simply because fishing non-randomly targets species  
225 with different traits (Richards et al., 2021; Zhou et al., 2019). Our findings identify the oceanic  
226 regions potentially the most susceptible to shifts in seabird ecological strategies and ecosystem  
227 changes without improved conservation measures. We find the North Atlantic Ocean may be  
228 particularly vulnerable to shifts in all five seabird traits, and the Southern Ocean may be at risk to



229 changes in reproductive speed and body mass traits without bycatch mitigation methods. These  
230 finding could be incorporated into management actions to inform marine protected area design  
231 with the intent to protect the ecosystem functions which seabirds provide.

232  
233 Our results further provide a basis to advise conservation interventions, such as actions that align  
234 with the IUCN Conservation Actions Classification Scheme (IUCN, 2012b), which presents a  
235 hierarchical structure of conservation actions presently needed for species. For instance, through  
236 *water protection* actions (IUCN Action 1), the locations of greatest ecological strategy shifts  
237 could help guide where to designate and prioritise Marine Protected Areas (MPAs), therefore  
238 reducing seabird conflict with fishing gears. Our findings could further inform *water*  
239 *management* actions (IUCN Action 2) through identifying areas which would benefit from  
240 bycatch mitigation methods, such as fishing gear modifications, and fisheries closures during  
241 sensitive times for seabirds. Future studies and management actions may consider assessing the  
242 response of trait and ecosystem function shifts to bycatch at the local scales in these regions. For  
243 example, large-scale closure of the eastern Canadian gillnet fishery saw a positive population  
244 response in a number of seabird species (Regular et al., 2013). This example could provide a  
245 valuable case study to quantify the response of conserving whole species assemblage for regional  
246 ecosystem functioning.

247  
248 We focus solely on fishing threats because bycatch is named the greatest threat to seabirds  
249 worldwide, however, seabirds face a diversity of threats throughout their life including invasive  
250 species, climate change, and pollution (Dias et al., 2019). Future studies may consider  
251 investigating how managing threats through space and time conserves seabird traits and  
252 ecosystem functions. For example, coupling extensive seabird tracking data with colony-specific  
253 trait information and regional threat patterns could provide a powerful and informative tool for  
254 local management. Finally, since our approach assumed the complete removal of species which  
255 are threatened from bycatch in areas overlapping with fishing activities, i.e. local extinction of  
256 these species, future studies may consider investigating how reduced population sizes and  
257 changes in proportions of species abundance caused by bycatch could influence community  
258 traits.

259

260 The Global Fishing Watch layers provides unprecedented understanding of the global fishing  
261 fleet and its spatiotemporal variations (Kroodsmas et al., 2018). Consequently, the dataset is an  
262 invaluable resource to advance our understanding of fisheries bycatch on seabirds and other  
263 marine organisms. For example, here through integrating these fine-scale fisheries data with  
264 seabird traits and distribution data, we provided a new perspective on the potential successes of  
265 bycatch mitigation for conserving species ecological strategies and opportunities to identify  
266 oceanic areas of conservation priorities. Similarly, recent research employed the Global Fishing  
267 Watch data and biologging data to detect albatross association and encounters with commercial  
268 fishing vessels in the North Pacific Ocean, thus further revealing the fishing dataset's value as a  
269 novel conservation and management tool (Orben et al., 2021). We encourage use of fine-scale  
270 spatial datasets to provide additional angles for seabird research, and to expand on the present  
271 study. For example, fishing activity and seabird distributions vary at different time scales, with  
272 distinct diurnal, seasonal, and annual patterns. Incorporating finer-scale data (e.g., biologging  
273 data) which encompasses these temporal signals is a direction for future studies that may provide  
274 further insights into the impacts of fishing on changes to seabird ecological strategies. Moreover,  
275 we focus on the combined distribution of gillnet, longline, trawl, and purse seine fishing activity  
276 on the overall shift in seabird traits. Additional research may consider quantifying the response  
277 of seabird ecological strategies to the spatiotemporal variations in individual gear types and  
278 intensities. Finally, the Global Fishing Watch data are fundamentally constrained by the  
279 limitations of AIS including incomplete satellite coverage in some regions, device tampering,  
280 and not all vessels carry an AIS transponder. Additionally, distributions of small-scale  
281 subsistence, and illegal, unreported, and unregulated (IUU) fishing activities were unavailable,  
282 and therefore not included in our study. However, as the AIS datasets are improved with time  
283 and fine-scale IUU fishing data become available, new patterns of seabird ecological strategy  
284 changes could be revealed.

285  
286 Overall, we use extinction simulations to infer how a trait-based approach has potential to  
287 provide a unique perspective on the success of bycatch mitigation across the global seabird  
288 species pool. Specifically, we find traits can be used to identify regions potentially at risk to  
289 shifts in the ecological strategies of the species which dominate, and the impact of these species  
290 on ecosystem functions without bycatch mitigation strategies. Management actions that

291 incorporate species' traits and fine-scale fisheries datasets as tools for marine spatial planning  
292 will add an important dimension when evaluating the success of conservation initiatives.

## 293 **Data Sharing and Accessibility**

294 Seabird traits were extracted from Richards et al. (2021), specifically  
295 <https://doi.org/10.5061/dryad.x69p8czhd>. Species distribution polygons are available upon  
296 request from <http://datazone.birdlife.org/species/requestdis>. Fishing effort data for 2015 and  
297 2016 are available for download, and data for 2017 and 2018 are available upon request from  
298 <https://globalfishingwatch.org/>. Please contact Cerren Richards ([cerrenrichards@gmail.com](mailto:cerrenrichards@gmail.com)) for  
299 access to R code.

## 300 **References**

- 301 Alverson, D.L., Freeberg, M.H., Pope, J.G., Murawski, S.A., 1994. A global assessment of  
302 fisheries bycatch and discards (No. 339). Rome.
- 303 Anderson, O.R.J., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O., Black, A.,  
304 2011. Global seabird bycatch in longline fisheries. *Endanger. Species Res.* 14, 91–106.  
305 <https://doi.org/10.3354/esr00347>
- 306 [dataset] BirdLife International and Handbook of the Birds of the World, 2017. Bird species  
307 distribution maps of the world. Version 2017.2.  
308 <http://datazone.birdlife.org/species/requestdis>
- 309 Bivand, R., Lewin-Koh, N., 2020. *maptools: Tools for Handling Spatial Objects*. R package  
310 version 1.0-1. <https://cran.r-project.org/package=maptools>
- 311 Bremner, J., Paramor, O.A.L., Frid, C.L.J., 2006. Developing a methodology for incorporating  
312 ecological structure and functioning into designation of Special Areas of Conservation  
313 (SAC) in the 0-12 nautical mile zone. School of Biological Sciences, University of  
314 Liverpool, Liverpool, UK.
- 315 Croxall, J.P., 2008. The role of science and advocacy in the conservation of Southern Ocean  
316 albatrosses at sea. *Bird Conserv. Int.* 18, 13–29.  
317 <https://doi.org/10.1017/S0959270908000300>
- 318 Croxall, J.P., Butchart, S.H.M., Lescelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor,  
319 P., 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird*

- 320 Conserv. Int. 22, 1–34. <https://doi.org/10.1017/S095>
- 321 Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O.,  
322 Lascelles, B., Borboroglu, P.G., Croxall, J.P., 2019. Threats to seabirds: A global  
323 assessment. *Biol. Conserv.* 237, 525–537. <https://doi.org/10.1016/j.biocon.2019.06.033>
- 324 Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning,  
325 J.B., Svenning, J.-C., 2016. Global nutrient transport in a world of giants. *Proc. Natl. Acad.*  
326 *Sci.* 113, 868–873. <https://doi.org/10.1073/pnas.1502549112>
- 327 Duarte, L., Debastiani, V., Carlucci, M., Diniz-Filho, J., 2017. Analyzing community-weighted  
328 trait means across environmental gradients: should phylogeny stay or should it go? *Ecology*  
329 99, 385–398. <https://doi.org/10.1111/ijlh.12426>
- 330 Fasiolo, M., Goude, Y., Nedellec, R., Wood, S., 2017. Fast calibrated additive quantile  
331 regression. *arxiv*. <https://doi.org/https://arxiv.org/abs/1707.03307>
- 332 Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological  
333 functioning into the designation and management of marine protected areas. *Hydrobiologia*  
334 606, 69–79. <https://doi.org/10.1007/s10750-008-9343-y>
- 335 Gallagher, R. V, Falster, D.S., Maitner, B.S., Salguero-gómez, R., Vandvik, V., Pearse, W.D.,  
336 Schneider, F.D., Kattge, J., Poelen, J.H., Madin, J.S., Ankenbrand, M.J., Penone, C., Feng,  
337 X., Adams, V.M., Alroy, J., Andrew, S.C., Balk, M.A., Bland, L.M., Boyle, B.L., Bravo-  
338 avila, C.H., Brennan, I., Carthey, A.J.R., Catullo, R., Cavazos, B.R., Conde, D.A., Ray,  
339 C.A., Rossetto, M., Sauquet, H., Sparrow, B., Spasojevic, M.J., Telford, R.J., Tobias, J.A.,  
340 Violle, C., Walls, R., Weiss, K.C.B., Westoby, M., Wright, I.J., Enquist, B.J., 2020. Open  
341 Science principles for accelerating trait-based science across the Tree of Life. *Nat. Ecol.*  
342 *Evol.* 4, 294–303. <https://doi.org/10.1038/s41559-020-1109-6>
- 343 Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., MacNeil, M.A., 2018. Seabirds  
344 enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559,  
345 250–253. <https://doi.org/10.1038/s41586-018-0202-3>
- 346 Guiet, J., Galbraith, E., Kroodsmas, D., Worm, B., 2019. Seasonal variability in global industrial  
347 fishing effort. *PLoS One* 14, 1–17. <https://doi.org/10.1371/journal.pone.0216819>
- 348 Hedd, A., Regular, P.M., Wilhelm, S.I., Rail, J.-F., Drolet, B., Fowler, M., Pekarik, C.,  
349 Robertson, G.J., 2016. Characterization of seabird bycatch in eastern Canadian waters,  
350 1998–2011, assessed from onboard fisheries observer data. *Aquat. Conserv. Mar. Freshw.*

- 351 Ecosyst. 26, 530–548. <https://doi.org/10.1002/aqc.2551>
- 352 Hijmans, R.J., 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-13.  
353 <https://CRAN.R-project.org/package=raster>
- 354 IUCN, 2012a. Threats Classification Scheme (Version 3.2).  
355 <https://www.iucnredlist.org/resources/threat-classification-scheme> (accessed 28 April  
356 2021).
- 357 IUCN, 2012b. Conservation Actions Classification Scheme (Version 2.0).  
358 <https://www.iucnredlist.org/resources/conservation-actions-classification-scheme> (accessed  
359 28 April 2021).
- 360 Komoroske, L.M., Lewison, R.L., 2015. Addressing fisheries bycatch in a changing world.  
361 *Front. Mar. Sci.* 2, 83. <https://doi.org/10.3389/fmars.2015.00083>
- 362 Kroodsma, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A.,  
363 Bergman, B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C., Worm, B.,  
364 2018. Tracking the global footprint of fisheries. *Science*. 359, 904–908.  
365 <https://doi.org/10.1126/science.aao5646>
- 366 Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity  
367 from multiple traits, *Ecology*. 91, 299-305. <https://doi.org/10.1890/08-2244.1>
- 368 Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple  
369 traits, and other tools for functional ecology. R package version 1.0-12.  
370 <https://rdrr.io/cran/FD/>
- 371 Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of  
372 fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19, 598–604.  
373 <https://doi.org/10.1016/j.tree.2004.09.004>
- 374 Maree, B.A., Wanless, R.M., Fairweather, T.P., Sullivan, B.J., Yates, O., 2014. Significant  
375 reductions in mortality of threatened seabirds in a South African trawl fishery. *Anim.*  
376 *Conserv.* 17, 520–529. <https://doi.org/10.1111/acv.12126>
- 377 Miatta, M., Bates, A.E., Snelgrove, P.V.R., 2021. Incorporating Biological Traits into  
378 Conservation Strategies. *Ann. Rev. Mar. Sci.* 13, 421–443. [https://doi.org/10.1146/annurev-  
379 marine-032320-094121](https://doi.org/10.1146/annurev-marine-032320-094121)
- 380 Orben, R.A., Adams, J., Hester, M., Shaffer, S.A., Suryan, R.M., Deguchi, T., Ozaki, K., Sato,  
381 F., Young, L.C., Clatterbuck, C., Conners, M.G., Kroodsma, D.A., Torres, L.G., 2021.

- 382 Across borders: External factors and prior behaviour influence North Pacific albatross  
383 associations with fishing vessels. *J. Appl. Ecol.* 00, 1–12. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2664.13849)  
384 2664.13849
- 385 Pardo, D., Forcada, J., Wood, A.G., Tuck, G.N., Ireland, L., Pradel, R., Croxall, J.P., Phillips,  
386 R.A., 2017. Additive effects of climate and fisheries drive ongoing declines in multiple  
387 albatross species. *Proc. Natl. Acad. Sci.* 114, E10829–E10837.  
388 <https://doi.org/10.1073/pnas.1618819114>
- 389 R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for  
390 Statistical Computing. <https://www.r-project.org/>
- 391 Rees, S.E., Austen, M.C., Attrill, M.J., Rodwell, L.D., 2012. Incorporating indirect ecosystem  
392 services into marine protected area planning and management. *Int. J. Biodivers. Sci.*  
393 *Ecosyst. Serv. Manag.* 8, 273–285. <https://doi.org/10.1080/21513732.2012.680500>
- 394 Regular, P., Montevecchi, W., Hedd, A., Robertson, G., Wilhelm, S., 2013. Canadian fishery  
395 closures provide a largescale test of the impact of gillnet bycatch on seabird populations.  
396 *Biol. Lett.* 9, 20130088. <https://doi.org/10.1098/rsbl.2013.0088>
- 397 Richards, C., Cooke, R.S.C., Bates, A.E., 2021. Biological traits of seabirds predict extinction  
398 risk and vulnerability to anthropogenic threats. *Glob. Ecol. Biogeogr.* 30, 973–986.  
399 <https://doi.org/10.1111/geb.13279>
- 400 Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2017.  
401 Extinction risk is most acute for the world’s largest and smallest vertebrates. *Proc. Natl.*  
402 *Acad. Sci.* 114, 10678–10683. <https://doi.org/10.1073/pnas.1702078114>
- 403 Rousseau, Y., Watson, R.A., Blanchard, J.L., Fulton, E.A., 2019. Evolution of global marine  
404 fishing fleets and the response of fished resources. *Proc. Natl. Acad. Sci.* 116, 12238–  
405 12243. <https://doi.org/10.1073/pnas.1820344116>
- 406 Sala, E., Mayorga, J., Costello, C., Kroodsma, D., Palomares, M.L.D., Pauly, D., Sumaila, U.R.,  
407 Zeller, D., 2018. The economics of fishing the high seas. *Sci. Adv.* 4, eaat2504.  
408 <https://doi.org/10.1126/sciadv.aat2504>
- 409 Schmitz, O., Wilmers, C., Leroux, S., Doughty, C., Atwood, T., Galetti, M., Davies, A., Goetz,  
410 S., 2018. Animals and the zoogeography of the carbon cycle. *Science.* 362, eaar3213.  
411 <https://doi.org/10.1126/science.aar3213>
- 412 Senko, J., White, E.R., Heppell, S.S., Gerber, L.R., 2014. Comparing bycatch mitigation

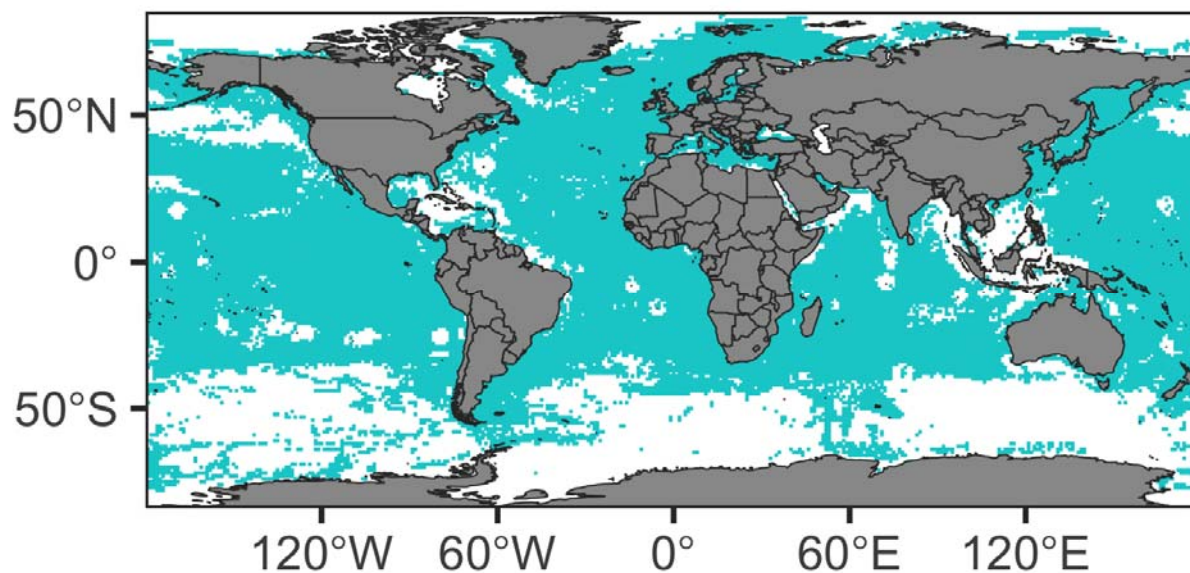
- 413 strategies for vulnerable marine megafauna. *Anim. Conserv.* 17, 5–18.  
414 <https://doi.org/10.1111/acv.12051>
- 415 Speakman, J.R., 2005. Body size, energy metabolism and lifespan. *J. Exp. Biol.* 208, 1717–1730.  
416 <https://doi.org/10.1242/jeb.01556>
- 417 Tavares, D.C., Moura, J.F., Acevedo-Trejos, E., Merico, A., 2019. Traits shared by marine  
418 megafauna and their relationships with ecosystem functions and services. *Front. Mar. Sci.* 6,  
419 262. <https://doi.org/10.3389/fmars.2019.00262>
- 420 Vilela, B., Villalobos, F., 2015. letsR: a new R package for data handling and analysis in  
421 macroecology. *Methods Ecol. Evol.* 6, 1229–1234. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.12401)  
422 [210X.12401](https://doi.org/10.1111/2041-210X.12401)
- 423 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let  
424 the concept of trait be functional! *Oikos* 116, 882–892. [https://doi.org/10.1111/j.2007.0030-](https://doi.org/10.1111/j.2007.0030-1299.15559.x)  
425 [1299.15559.x](https://doi.org/10.1111/j.2007.0030-1299.15559.x)
- 426 Wing, S., Jack, L., Shatova, O., Leichter, J., Barr, D., Frew, R., Gault-Ringold, M., 2014.  
427 Seabirds and marine mammals redistribute bioavailable iron in the Southern Ocean. *Mar.*  
428 *Ecol. Prog. Ser.* 510, 1–13.
- 429 Wood, S., 2017. *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman  
430 and Hall/CRC.
- 431 Zhou, C., Jiao, Y., Browder, J., 2019. Seabird bycatch vulnerability to pelagic longline fisheries:  
432 Ecological traits matter. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 1324–1335.  
433 <https://doi.org/10.1002/aqc.3066>
- 434
- 435

436 **Table 1.** Description of the traits used in the present study and their relation to ecosystem  
437 functioning. Table modified from (Richards et al., 2021).  
438

<b>Trait</b>	<b>Description</b>	<b>Ecosystem Function</b>
Clutch Size	Number of eggs per clutch	Nutrient storage
Body Mass	Log <sub>10</sub> (median body mass in grams)	Nutrient storage and transport
Generation Length	Log <sub>10</sub> (generation length in years)	Nutrient storage
Foraging Guild	The dominant foraging guild of the species <i>Diver; Surface; Ground; Generalist</i>	Nutrient storage; Trophic-dynamic regulations of populations
Diet Guild	The dominant diet of the species <i>Omnivore; Invertebrate; Vertebrate &amp; scavenger</i>	Nutrient storage; Trophic-dynamic regulations of populations

439

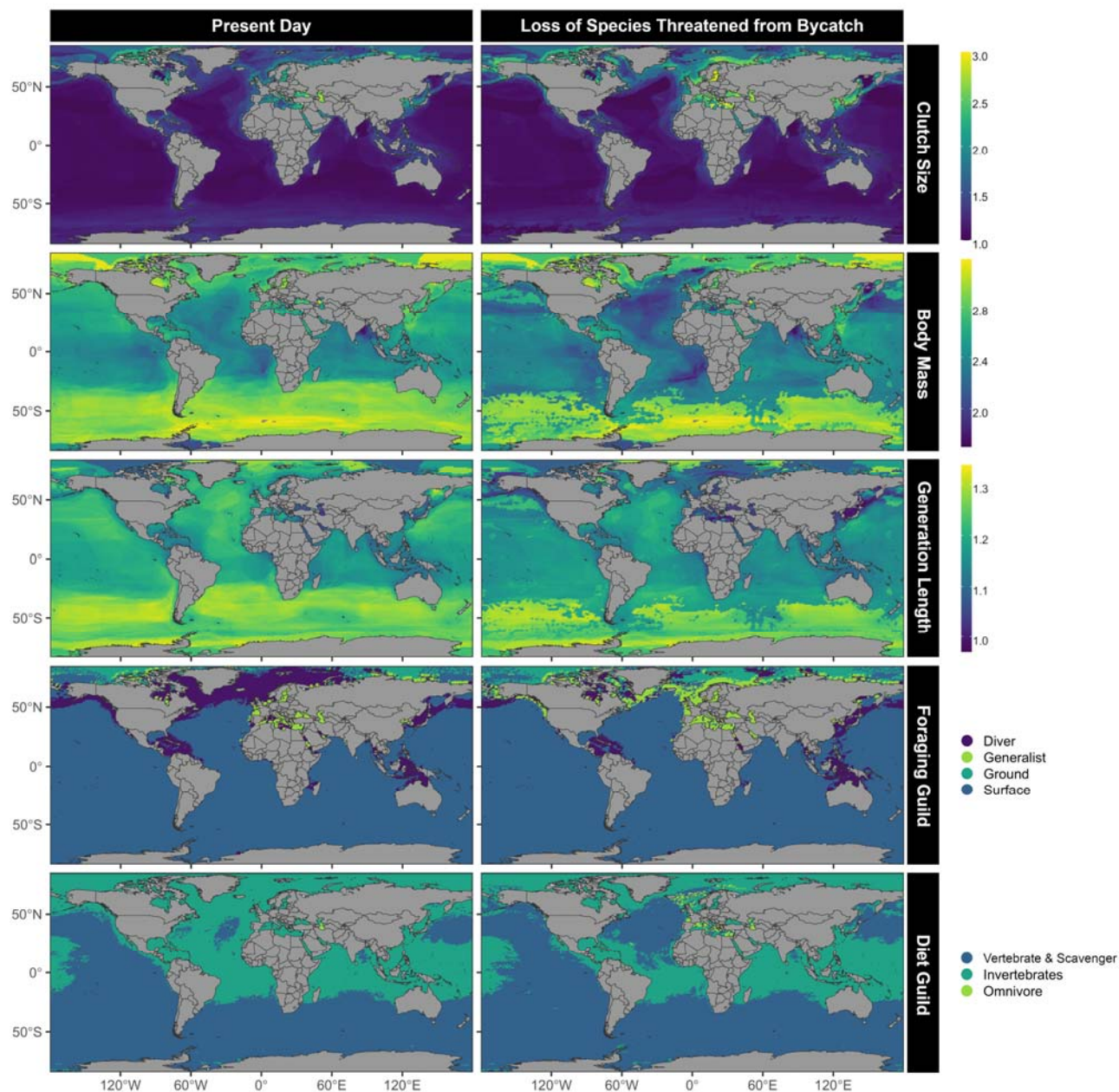




440

441 **Figure 1.** Combined distribution of fishing activity for gillnets, longlines, trawls, and purse  
442 seines identified from Automatic Identification System (AIS) by Global Fishing Watch between  
443 2015 and 2018. Fishing effort was grouped per 1° global grid cell.

444



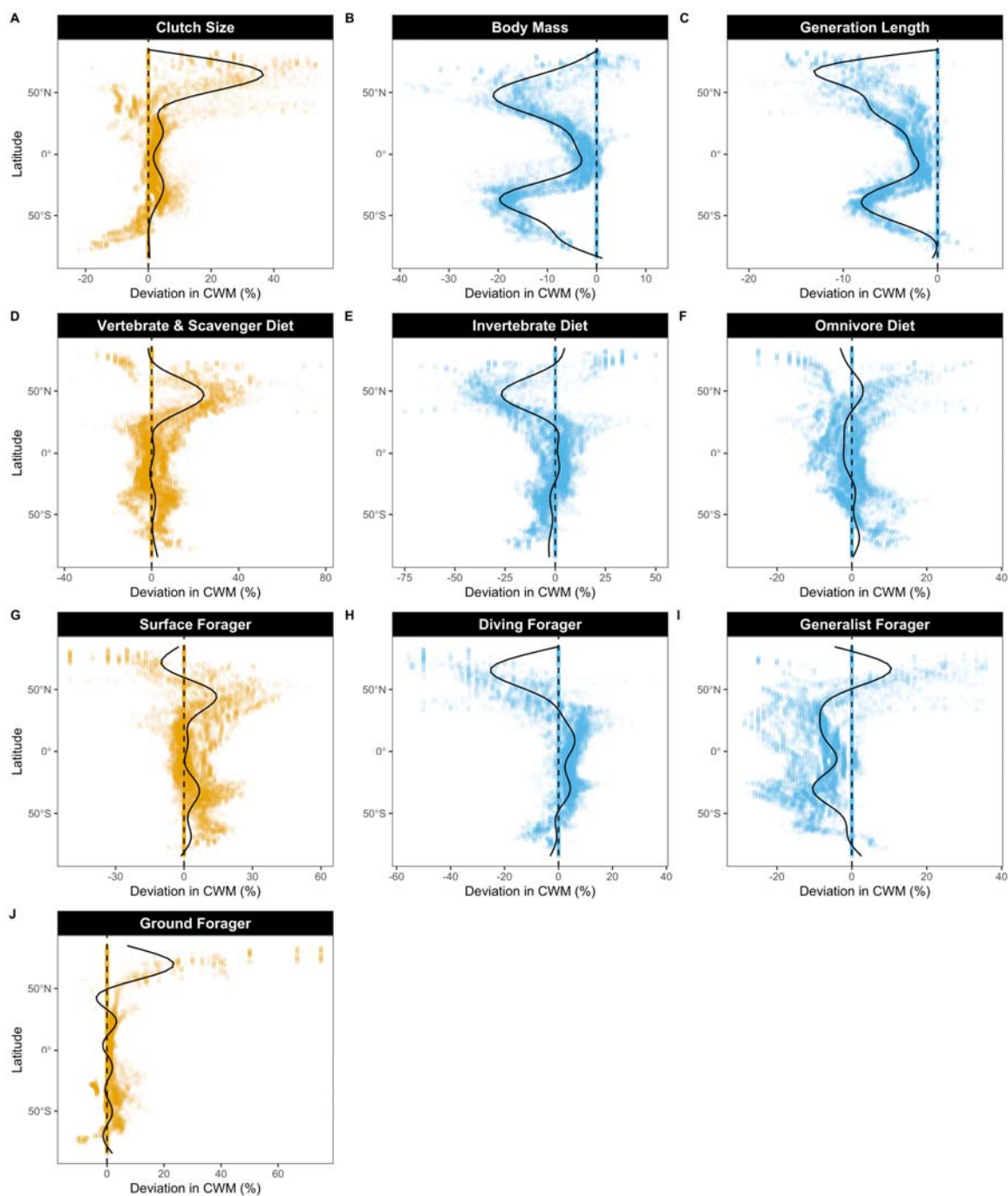
445  
446 **Figure 2.** Community weighted mean (CWM) of five traits based on the distributions of  
447 341 presently extant seabird species (left panels), and following the predicted local loss of 134  
448 species threatened from bycatch in areas where their distributions overlap with fishing activity  
449 (right panels). Therefore, the difference represents the shifts in traits that may be prevented  
450 through successfully mitigating seabird bycatch. For continuous data, CWM is the mean trait  
451 value of all species present in each 1° grid cell. For categorical data, CWM is the most dominant  
452 class per trait within each 1° grid cell. Body mass and generation length traits are log<sub>10</sub>

453 transformed, and truncated to the 0.1 - 99.9% range to aid visual clarity. Maps including all the  
454 data are in Appendix 1, Fig. S1.

455

456

457



458

459 **Figure 3.** Shift in community weighted mean (CWM) across latitude following removal of  
460 134 species threatened from bycatch in areas where their distributions overlap with fishing  
461 activity. Each data point represents the CWM within a 1° grid cell. Dashed zero line represents  
462 the CWM of the total species list (341 species). Solid black lines in A and D-J are fitted  
463 generalized additive models, and in B-C are additive quantile regression models describing the

464 spatial trends in trait shifts across latitude. Orange represents a significant overall positive shift  
465 from the model output, and blue a significant overall negative shift in the CWM following  
466 removal of species threatened from bycatch. Figures were truncated to the 0.1 - 99.9% range to  
467 remove extreme values. Figure which include all values are in Appendix 1, Fig. S2.