

# North Atlantic winter cyclones starve seabirds

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- 56 Summary

57 Each winter the North Atlantic Ocean is the stage for numerous cyclones, the most severe 58 ones leading to seabird mass-mortality events called 'winter wrecks' <sup>1-3</sup>. During those, 59 thousands of emaciated seabird carcasses are washed ashore along European and North American coasts. Winter cyclones can therefore shape seabird population dynamics<sup>4,5</sup> by 60 61 affecting survival rates as well as the body condition of surviving individuals and thus their 62 future reproduction. However, most often the geographic origins of impacted seabirds and the causes of their deaths remain unclear<sup>6</sup>. We performed the first ocean-basin scale assessment 63 64 of cyclone exposure in a seabird community, by coupling winter tracking data for ~1500 65 individuals of five key North Atlantic seabird species (Alle alle, Fratercula arctica, Uria 66 aalge, Uria lomvia and Rissa tridactyla) and cyclone locations. We then explored the 67 energetic consequences of different cyclonic conditions using a mechanistic bioenergetics model<sup>7</sup> and tested the hypothesis that cyclones dramatically increase seabird energy 68 69 requirements. We demonstrated that cyclones of high-intensity impacted birds from all 70 studied species and breeding colonies during winter, but especially those aggregating in the Labrador Sea, the Davis Strait, the surroundings of Iceland and the Barents Sea. Our broadscale analyses suggested that cyclonic conditions do not increase seabird energy requirements, implying that they die because of the unavailability of their prey and/or their inability to feed during cyclones. Our study provides essential information on seabird cyclone exposure in a context of marked cyclone regime changes due to global warming<sup>8</sup>.

76 Keywords: At-sea distribution, Cyclones, Energy expenditure, GLS tracking, Seabird
77 migration, Seascape ecology

78 Results

79 Cyclone-induced seabird mortality adds to other threats such as habitat loss, invasive 80 species or interactions with fisheries, contributing to the general downward trend of the global seabird community<sup>9</sup> and making them one of the most threatened bird groups<sup>10</sup>. It is therefore 81 82 essential to understand the causes of seabird mortality during cyclones, and to identify factors 83 contributing to contrasting spatio-temporal mortality patterns at the seabird-community level. 84 Multiple seabird species from different breeding colonies may inhabit different wintering areas<sup>11,12</sup>, and this may strongly affect the composition of seabird winter wrecks. In this 85 86 context, community-wide analyses are lacking due to the technical difficulties of studying 87 seabirds wintering far out at sea under harsh conditions.

88 Winter cyclone exposure of the North Atlantic seabird community

The North Atlantic Ocean and adjacent seas (100°W–100°E, 30°N–90°N, see Figure S1) is the stage for numerous winter cyclones (October to February) (see Figure S2), which are defined by the National Hurricane Center, as large-scale air masses that rotate around a center of low atmospheric pressure. Their locations between 2000 and 2016 were obtained from climatic reanalysis data (see STAR Methods). Using the Dvorak storm classification<sup>13</sup> we sorted them across their duration into one of the four classes of cyclone intensity defined (see STAR Methods). Calculating, for each month, the average number of cyclones of each

96 category for each 250 km grid cell, we demonstrated that a limited number of localized low 97 intensity cyclones (Class 1 and 2) occurred mainly in the Baffin Bay, the Gulf of Maine and 98 the Mediterranean Sea regions (see Data S1A). Class 3 cyclones were more numerous and 99 widespread, particularly in October and November, and mainly occurred in the Baffin and 100 Hudson bays, the Davis Strait, the Labrador Sea, east off Newfoundland, around Iceland and 101 in the Barents Sea. Finally, Class 4 cyclones were observed in all winter months off west 102 Iceland, the Norwegian coast and in the Barents Sea, whereas the Davis Strait and the 103 Labrador Sea were only affected by Class 4 cyclones between December and February.

104 Winter bird locations were obtained from Global Location Sensors (GLS) deployed and 105 retrieved during the breeding season on 1532 individuals from 39 breeding colonies across the 106 North Atlantic Ocean (see STAR Methods and Table S1). We approximated core use areas 107 for each colony and species during the winter months, calculating monthly utilization distributions (UD) with the BRB-MKDE software (<sup>14</sup>, see STAR Methods). To conclude on 108 109 seabird cyclone exposure, we overlapped cyclone locations with core wintering areas of 110 different seabird species and populations (see Figure 1, Data S1A-S1F), before calculating an 111 average cyclone exposure index (see Figure 2 and STAR Methods).

112 Low intensity cyclones (Class 1 and 2) showed limited overlap with the seabird community. 113 However, birds from all species and colonies were likely to encounter Class 3 and 4 cyclones 114 during winter, with substantial inter-annual variability in the mean number of such events 115 occurring within seabird core use areas (Figure 1 and Data S1B-S1F). Notably, seabirds from 116 Canadian, Greenlandic and Icelandic colonies were exposed to Class 3 and 4 cyclones in the 117 Davis Strait, the Labrador Sea and off Newfoundland, while Norwegian and Russian seabirds 118 were likely impacted by those occurring in the Barents Sea. In contrast, Class 3 cyclones were 119 fewer in the mid-west Atlantic Ocean and were more likely to spare seabirds wintering there 120 (see Data S1A). Due to major seabird aggregation and the marked presence of Class 3 and 4 121 cyclones, areas such as the Labrador Sea, the Davis Strait, the vicinity of Iceland and the122 Barents Sea are predicted as sources of major winter wrecks (Figure 2).

123

124 Seabird energy requirements under cyclonic and non-cyclonic conditions

125 Necropsies suggest that seabirds are lean after being exposed to high-intensity  $cvclones^{6,15}$  and that the resulting mortality can be aggravated by mercury contamination<sup>16</sup>. 126 127 Yet, we do not know whether they starve due to abnormally high-energy expenditure linked 128 to harsh climatic conditions<sup>17</sup>, because of reduced foraging profitability and energy inputs, or 129 because both these constraints synoptically affect their energy balance. Recent research has 130 shown that seabirds wintering in the North Atlantic Ocean track environmental gradients to 131 remain in an energetic steady state<sup>18–20</sup>, but how winter cyclones affect this delicate balance 132 remains mysterious.

133 To test the hypothesis that cyclones dramatically increase seabird energy requirements, we 134 modeled species-specific, monthly energy requirements for each winter between 2000 and 135 2016 on a 1000km\*1000km area off North Newfoundland (see Figure S1), using the mechanistic model Niche Mapper<sup>TM</sup> (Porter & Mitchell, 2006, see STAR Methods) under 136 137 four intensities of cyclones and under non-cyclonic conditions (see STAR Methods). Following the protocol used by Grémillet and colleagues<sup>21</sup>, we calculated how many days 138 139 each of the five studied species could fast before dving, when exposed to Class 2, Class 3 and 140 Class 4 cyclones in the studied area (see STAR Methods). Statistical analyses revealed several 141 significant differences (Kruskal-Wallis, p<0.05) in seabird energy requirements (see Table 1) 142 between the six categories of conditions tested (Class 1 to 4 cyclones, non-cyclonic conditions 143 with usual seabird flight/diving activities, non-cyclonic conditions with cyclonic seabird 144 flight/diving activities). In a very limited number of cases, cyclonic conditions led to 145 increases (up to 36%) in seabird energy requirements in comparison with non-cyclonic

146 conditions with cyclonic flight/diving activities (post hoc Dunn's test, p<0.05). Surprisingly, 147 we found that seabird energy requirements were generally similar or lower during cyclones, 148 compared to non-cyclonic conditions (see Figure 3 and Data S1G-S1K). In particular, for 149 little auks and black-legged kittiwakes, energy requirements were generally significantly 150 lower during Class 2, 3 and 4 cyclones than during non-cyclonic conditions experienced with 151 usual flight/diving activities (post hoc Dunn's test, p < 0.05). Those differences were not significant for deep divers (except for Atlantic puffins in October and December under 152 153 specific cyclonic conditions) (see Table 1). Further, seabird energy requirements were not 154 significantly different during Class 1 cyclones than for non-cyclonic conditions experienced 155 with usual flight/diving activities (post hoc Dunn's test, p < 0.05).

156 Energy requirements under Class 2, Class 3 and Class 4 cyclones were not significantly 157 different (see Data S1G-S1K) and these classes were therefore pooled when calculating 158 fasting endurance. Between October and December, average fasting endurance was 2.2 days 159 (+/- 0.1) for little auk and 6.5 days (+/- 2.5) for Atlantic puffins while black-legged 160 kittiwakes, Brünnich's guillemots and common guillemots could fast 8.4 days (+/- 0.5), 7.3 161 days (+/- 0.06) and 8.1 days (+/- 0.1), respectively. With winter's advance, these durations 162 dropped respectively to 1.6 days (+/- 0.1), 4.6 days (+/- 0.6), 6.4 days (+/- 0.5), 5.9 days (+/-163 0.6) and 6.3 days (+/- 0.7), between January and February.

#### 164 **Discussion**

We demonstrated that seabirds wintering in areas such as the Labrador Sea, the Davis Strait, the vicinity of Iceland and the Barents Sea, are particularly exposed to cyclones. Crucially, our broad-scale analyses led us to reject our hypothesis: climatic conditions experienced by seabirds during cyclones generally did not enhance their energy requirements. These results suggest that seabird mortality during winter high intensity cyclones is likely caused by starvation due to the unavailability of prey and/or their incapacity to feed.

#### 171 Mechanistic insights into storms impacts on seabirds

172 Our surprising conclusion regarding death causes in seabirds exposed to cyclones is in 173 agreement with a study conducted on greater flamingos (Phoenicopterus roseus) during cold spells in the Camargue, France<sup>22</sup>: Thousands of flamingos died, not because of hypothermia 174 175 but due to inaccessible food in frozen salt pans. Conversely, our results contrast with former 176 modeling work which pointed to weather-induced energetic bottlenecks in seabirds wintering in the North Atlantic Ocean<sup>17</sup>. Birds were predicted to experience markedly higher 177 178 thermoregulatory costs in December, because of lower air and water temperatures, and higher 179 wind speeds. Yet this previous study investigated seabird energetics at the scale of months, 180 whereas cyclones affect them at the scale of days. In this context, little auks appear as 181 particularly vulnerable to fasting induced by cyclones, because of low lipid reserves and high 182 mass-specific energy expenditure, likely explaining extensive and recurrent winter wrecks on North American coasts near their main wintering grounds<sup>23,24</sup>. Other species were predicted to 183 184 cope with relatively longer fasts, but remain vulnerable to prolonged cyclonic conditions 185 especially at the end of winter. Therefore, recurrent cyclones affecting a specific area/seabird 186 population are predicted as strong drivers of winter wrecks.

187 What exactly prevents seabirds from feeding during cyclonic conditions remains unclear. One 188 possibility is that cyclones may enhance water turbidity, decrease underwater light intensity, 189 and perturb prey patches and vertical migration. Potentially disrupting water stratification, 190 cyclones may modify prey aggregation and negatively impact seabird foraging efficiency $^{25}$ . 191 Therefore, this 'washing-machine effect' could strongly affect seabirds feeding within the 50 192 upper meters of the water column, such as black-legged kittiwakes and little auks in our 193 study. Further, cyclones and associated disturbances alter underwater soundscapes and thus 194 constrain the detection of acoustic cues by seabirds, being from conspecifics, prey or 195 predators<sup>26,27</sup>. Prey could also occur deeper in the water column during cyclones as already

observed for some elasmobranchs or teleosts<sup>28,29</sup>, but how this impacts pursuit-diving species 196 197 such as puffins and guillemots, is not known. By continuing to dive during cyclones, deep 198 divers such as guillemots and puffins potentially take the risk of using energy reserves in an 199 attempt to track inaccessible prey. However, common and Brünnich's guillemots have been 200 observed switching their diet during strong winds, from schooling fish to amphipods or 201 smaller sandeels, potentially targeting prey that required less underwater searching $^{30,31}$ . 202 Alternatively, cyclones may shift alcids away from their preferred prey patches and into 203 unprofitable foraging habitats<sup>32</sup>. Overall, even if starvation may be the main driver of seabird winter wrecks, we cannot exclude others causes of mortality, such as drowning<sup>6</sup>, or collision 204 with reefs and rocky coastlines (Mark Baran, personal comm) or inland stranding<sup>32</sup>. 205

#### 206 Potential limitations

207 Despite these advances, we recommend caution in interpreting our results as they are based 208 on reanalyzed environmental data and on thermodynamic modeling. Notably, measuring 209 empirical data is nearly impossible during cyclones. This calls for the use of modeling 210 approaches to characterize these climatic events and their energy consequences for seabirds, 211 but also constrains model outputs. This lack of in-situ measurements influenced NicheMapper<sup>TM</sup> simulations in two main ways. First, the behavior of pelagic seabirds is hard 212 213 to assess under cyclonic conditions, and the animal module mainly relies on the assumption 214 that North Atlantic seabirds significantly reduce flying and/or diving during cyclones. On a 215 worldwide scale, while many seabird species exhibit avoidance behavior seeking coastal 216 shelter and/or reducing activity levels during high-intensity cyclones<sup>33</sup>, others, such as great 217 frigatebirds (Fregata minor) take advantage of cyclonic winds to save energy while gliding over thousands of kilometers<sup>34</sup>. Such extreme gliders, which occur in the tropics and Southern 218 219 Ocean, are rarer in the North Atlantic, an area dominated by alcid species in terms of 220 abundance<sup>35</sup>. This seabird family, which is morphologically adapted to using its wings for

underwater propulsion, has high wing-loading, and very limited capacity to ride strong winds.
 Thus, cyclonic conditions dramatically increase flight costs in alcids<sup>30</sup>, and therefore tend to
 prevent them from flying.

224 Second, since direct measurements of environmental data during cyclones were lacking at the 225 spatio-temporal scales needed for our analyses, we depicted cyclonic conditions in the 226 microclimate module using a limited number of reconstructed data at a broad scale, 227 potentially missing other relevant differences between non-cyclonic and cyclonic conditions. 228 Finally, due to a lack of available information, we only modeled the effects of temperature, 229 wind speed and reduced activity on heat loss and energy requirements during cyclones, 230 omitting other variables such as wind gust speed, water velocity, wave height, as well as other 231 conditions potentially affecting seabird thermoregulation and thus their energy requirements. 232 For example, localized wind gusts, sea spray and high-speed precipitation could all reduce 233 plumage insulation, thereby increasing seabird heat loss and energy requirements. Further, tall 234 waves could require the birds to dive more frequently, increasing energy requirements. Thus, 235 current predictions on seabird energy requirements during cyclones should be interpreted as 236 likely conservative estimates. However, given the current lack of information, mechanistic 237 models remain important tools to explore potential impacts, and to generate hypotheses that 238 could be further investigated. Additional direct measurements could help to refine these 239 modeling approaches and evaluate initial assumptions. For example, deploying electronic 240 devices to study North Atlantic seabird 3D movements during cyclones is a key objective for 241 future research, which will allow testing our assumption that these animals are less active 242 under passing cyclones. Such deployments will also help infer additional energetic costs in 243 seabirds floating across rough seas, especially if they try to dive under each wave and/or to stay in the same area rather than drifting away with surface currents (up to 2.5 m.s<sup>-1</sup> under 244 245 Class-4 cyclones<sup>36</sup>). Finally, future efforts will allow researchers to take into account interand intra-individual morphological, physiological and behavioral variability across winter inseabird energetic modeling, improving output accuracy.

248 Despite these limitations, our study provides essential new knowledge, notably on the 249 vulnerability of wintering seabirds to high intensity cyclones in the Labrador Sea, off 250 Newfoundland, off southern Greenland, around Iceland, off the Norwegian coast and in the 251 Barents Sea. These results are supported by the numerous seabird winter wrecks observed across years on beaches close to those areas<sup>2,6,23,24,37</sup> (and Flemming Ravn Merkel personal 252 253 communication about Brünnich's guillemot wrecks in south Greenland). Yet, as GLS-tracking 254 is based on individuals who survived the non-breeding period, we cannot exclude the 255 possibility that wrecked individuals wintered in different locations with higher cyclone 256 exposure, even though seabirds are highly gregarious, also at sea. Further, the localization and 257 study of winter wrecks on beaches is impacted by oceanic currents carrying seabird carcasses, 258 and by the accessibility of these beaches to observers. This potentially leads to spatio-259 temporal mismatches between seabird wrecks as perceived by researchers and the general 260 public, and areas of major winter high intensity cyclone impacts on seabirds offshore. Such a 261 mismatch may explain why we found limited overlap between seabird winter distributions 262 and cyclones in the Eastern Atlantic, despite the fact that large winter wrecks have regularly 263 been recorded along the shores of Western Europe.

### 264 Seabird storm exposure under climate change

It is well-established that seabirds experience direct and indirect negative stressors from global warming <sup>38</sup>. Since the 1970s, the frequency and intensity of the strongest tropical cyclones in the North Atlantic have increased markedly<sup>39</sup>. Considering future North Atlantic cyclone regimes, there are still uncertainties but model outputs predict some common features: There will be fewer cyclones in the future, but the frequency of the strongest ones is predicted to increase with global warming<sup>39</sup>. Moreover, cyclone tracks will likely shift

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northwards under climate change<sup>40</sup>, increasing the storminess of Western Europe<sup>41</sup> and of the 271 high Arctic<sup>42,43</sup>. Since storm activity is positively correlated to the magnitude of seabird 272 wrecks<sup>44,45</sup> and the North Atlantic Ocean seabird community is also predicted to shift 273 northwards, following its prey base<sup>46</sup>, we infer that this community will become even more 274 275 susceptible to mass mortality caused by winter wrecks. This might be particularly marked in 276 areas such as the Bay of Biscay, the North Sea, the Norwegian and the Barents Seas. In this 277 context, our study provides an essential conceptual and methodological framework to identify 278 the vulnerability of specific populations to cyclone events at the scale of the North Atlantic 279 Ocean.

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#### **303** Author Contributions

- 304 Conceived and designed the project: D.G., J.F, M.C. Software developers and data providers:
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- 308 A.P, D.G. Analyzed the data: M.C. Wrote the paper: M.C., D.G. All authors reviewed the
- 309 manuscript.

#### **Declaration of interests**

311 The authors declare no competing interests.

#### 312 Figures

Figure 1: Average number of cyclones within the core use areas of common guillemot from different colonies between 2000 and 2016 in October. Colonies abbreviations: Bjørnøya (BJ), Cape Gorodetskiy (CG), Faroe Islands (FI), Grimsey (GR), Hjelmsøya (HJ), Hornøya (HO), Jan Mayen (JM), Langanes and Skjalfandi (LaS), Latrabjarg (LA), Sklinna (SK). Error bars correspond to standard deviations capturing the variation between years. Results for other species, colonies and months are provided in Data S1B-S1F.

**Figure 2: Mean cyclone exposure index across the North Atlantic Ocean during winter.** See STAR Methods for details on index calculation.

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Figure 3: Average energy requirements for little auks (A) and Atlantic puffins (B) in the studied area off Newfoundland for each wintering month under cyclonic and non-cyclonic conditions between 2000 and 2016. Error bars were halved for clarity reasons and correspond to standard deviations capturing between-year variation. Results for other species are presented in Data S1G-Data S1K.

#### 314 Tables

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

320 Data S1G-S1K.

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

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#### 322 STAR Methods

#### 323 Resources Availability

- 324 *Lead contact*
- 325 Further information and requests for resources and reagents should be directed to and will be
- 326 fulfilled by the lead contact, Manon Clairbaux (clairbauxm@gmail.com).
- 327 <u>Materials availability</u>
- 328 This study did not generate new unique reagents.
- 329 *Data and code availability*
- Environmental variables, bird and cyclone location are publicly available online.
- 331 Physiological, behavioral and morphological characteristic of the species studied are
- available in the Table S2.

- All original code has been deposited at (http://dx.doi.org/10.17632/rzszr9fpt4.1) and is
   publicly available as of the date of publication. DOIs are listed in the key resources
   table.
- Any additional information required to reanalyze the data reported in this paper is
  available from the lead contact upon request.
- 338

### 8 Experimental Model and Subject details

339 We focused on the winter distribution of five seabird species (little auk (Alle alle), 340 Atlantic puffin (Fratercula arctica), common guillemot (Uria aalge), Brünnich's guillemot 341 (Uria lomvia) and black-legged kittiwake (Rissa tridactyla)). These species, which account for ca. 75% of the total number of seabirds breeding along the North Atlantic Ocean<sup>35</sup> are also 342 343 among the most severely hit by winter high-intensity cyclones<sup>2,3</sup>. Bird locations were obtained 344 from Global Location Sensors (GLS) deployed and retrieved during the breeding season for 345 1532 individuals from 39 breeding colonies across the North Atlantic Ocean (see Figure S1 346 and Table S1). Birds were caught at the nest according to ethical approval from each 347 country's appropriate organization.

#### 348 Method details

#### 349 Locations and characteristics of North Atlantic cyclones during winter

350 According to the National Hurricane Center, cyclones are defined as large-scale air 351 masses that rotate around a center of low atmospheric pressure. Their locations were obtained 352 from the 'Northern Hemisphere Cyclone Locations and Characteristics from NCEP/NCAR 353 Reanalysis Data, Version 1' online dataset<sup>47</sup>. Locations were calculated using the updated Serreze (1997)<sup>48</sup> algorithm on daily Sea Level Pressure from the National Center for 354 355 Environmental Prediction (NCEP) and National Center for Atmospheric Research (NCAR) 356 Reanalysis data set in a 250 km grid. We focused on winter cyclones (October to February) in 357 the North Atlantic and adjacent seas (100°W-100°E, 30°N-90°N) between 2000 and 2016.

Using the Dvorak storm classification<sup>13</sup> on the cyclone central pressure we defined four classes of cyclone intensity (> 1009 hPa = Class 1; 1005-1009 hPa = Class 2; 987-1005 hPa = Class 3; < 987 hPa = Class 4) and classified each cyclone in the studied area across its duration. Finally, for each month, we calculated the average number of cyclones of each category that occurred between 2000 and 2016 for each 250 km grid cell.

#### 363 Winter distribution of seabirds

Two locations per day were obtained through the recorded light levels by Global 364 Location Sensors for each individual with an accuracy of +/- 200 km<sup>49,50</sup>. We focused on 365 366 locations acquired during the winter period (October to February) and removed locations obtained during the two weeks on either side of the equinoxes<sup>49</sup> as well as spurious locations 367 368 and those falling on land. For each species, we then calculated monthly utilization 369 distributions (UD) for each individual using the BRB-MKDE software (<sup>14</sup>, March 2018 370 version for location in decimal degrees with hmin=250 km) before averaging by seabird 371 colony and species. To avoid that some individuals drive the UD of the colony, we performed 372 a kernel stability analysis and for each month, we only considered individuals which had a 373 sufficiently large number of locations to satisfy this stability criteria. To perform this stability 374 analysis we calculated for each individual and for each month (n/4) UD, with n the total 375 number of locations (after quality and equinoxes checks) for the individual and month 376 considered: the first UD was calculated with 4 locations, the second 8, the third one 12, etc. 377 until the total number of locations was included. Then, for each individual and for each 378 month, we calculated the percentage of overlap between each UD and the UD obtained 379 considering all the locations. Finally, for each species, we plot for each month the individual 380 percentage of overlap against the number of locations included in the UD calculation and we 381 visually determined the minimum number of locations needed to reach a high overlap 382 percentage for the maximum of individuals. This threshold was set at 30 locations for little auks and black-legged kittiwakes and was set at 20 locations for Atlantic puffins, common
and Brunnïch's guillemots. Therefore individuals having less locations than the number
needed wasn't considered when averaging UD by colony and species.

We then used 25% utilization kernels to approximate areas of core use for each colony and species during the winter months (see Data S1A). For each month, we calculated the average number of cyclones of each category that occurred between 2000 and 2016 within each colony core use areas (Figure 1 and Data S1B-S1F). Finally, we interpolated each colony's UD on a 250 km grid before calculating, for each pixel, the following cyclone exposure index (CEI) for each wintering month:

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$$CEI(i,j) = NC(i,j) \times UDT(i,j)$$

where NC(i,j) is the average number of cyclones between 2000 and 2016 within the pixel *i* for the month *j* and UDT(i,j) is the sum, all species considered, of average UD of each colony for the pixel *i* and the month *j*. The monthly cyclone exposure indexes were then averaged to obtain a unique index for the wintering period (see Figure 2).

#### 397 Modeling seabird energy requirements under non-cyclonic and cyclonic conditions

398 We used the mechanistic model Niche Mapper<sup>TM 7</sup> to calculate energy requirements 399 for each species under cyclonic and non-cyclonic conditions for each wintering month. Niche 400 Mapper<sup>TM</sup> is based on a microclimate model and an animal module: the microclimate model 401 calculates hourly environmental conditions for the near surroundings of the bird and the 402 animal module uses the resulting outputs together with bird morphological, behavioral and 403 physiological properties to estimate the metabolic rate needed by the bird to maintain its body 404 temperature at a given time with a specific behavioral time budget. We focused on a 1000 km 405 x 1000 km area off North Newfoundland (see Figure S1) where the five seabird species 406 aggregate during winter. This area experienced numerous cyclones during the winter months 407 between 2000 and 2016 (see Figure S3). For each of them, we extracted environmental

408 characteristics (sea surface temperature, air temperature and relative humidity), before 409 averaging the values obtained by intensity class for each winter month (see Figure S4) to parameterize the microclimate module of Niche Mapper<sup>TM</sup>. For each cyclone, we extracted 410 411 corresponding sea surface temperatures using the NOAA High Resolution SST dataset 412 provided NOAA/OAR/ESRL PSL by the (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html#detail)<sup>51</sup>. 413 The 414 corresponding air temperature and relative humidity were extracted from the NCEP/NCAR 415 Reanalysis dataset previously used to define cyclone locations (see above). We set the wind speed of each cyclone according to its intensity  $(5-13 \text{ m.s}^{-1} = \text{Class 1}; 13.1-17 \text{ m.s}^{-1} = \text{Class 2};$ 416 17.1-32.5 m.s<sup>-1</sup> = Class 3; > 32.6 m.s<sup>-1</sup> = Class 4) using the Dvorak classification<sup>13</sup>. We then 417 418 averaged the values obtained by intensity class to calculate mean environmental characteristic 419 of each class for each winter month between 2000 and 2016. Finally, for each year, non-420 cyclonic conditions were defined by calculating the daily mean characteristics of each month 421 using the same environmental dataset after excluding cyclone days. Wind speeds were 422 obtained from the NCEP/NCAR Reanalysis data set. All environmental data used were 423 interpolated in a 250 km grid. Mean environmental conditions encountered during cyclonic 424 and non-cyclonic events are presented in Figure S4.

Once we had parameterized the microclimate model of Niche Mapper<sup>TM</sup>, we parameterized its 425 426 animal module to obtain seabird daily energy requirements. As this module had already been 427 parameterized to model energy expenditure in little auks, Brünnich's guillemots and common guillemots<sup>17,52</sup>, we re-used most Niche Mapper <sup>TM</sup> input values. Missing values and values 428 required to parameterize Niche Mapper<sup>TM</sup> for black-legged kittiwakes and Atlantic puffins, 429 430 were sourced from the literature (see Table S2) and obtained through dedicated 431 measurements. Specifically, we set the proportion of time spent flying per day during winter 432 under non-cyclonic conditions to 9%, 11.8%, 5.7% and 4.5% for little auks, black-legged

kittiwakes, Atlantic puffins and guillemots, respectively<sup>17,53–55</sup>. Further, under those 433 434 conditions, we considered that those species spent respectively, 24%, 18.8%, 16.9% and 16% of the day diving during winter<sup>17,52,53,56</sup>. Feather reflectivity was measured with a double beam 435 436 spectrophotometer (CARY 5000 UV-VIS-NIR, Agilent, USA) with a deuterium-tungsten-437 mercury light source. We used an integrative sphere to measure spectral and diffuse 438 reflectance with a 1 nm resolution across all wavelengths between 300 and 2500 nm. This 439 range covers approximately 98% of the solar spectrum that reaches the Earth's surface. 440 Reflectance spectra relative to a Spectralon white standard were then computed with the Cary 441 WinUV software. For each species, measurements were made on one ventral and dorsal patch 442 for six individuals. We then calculated the reflectivity of each sample following the methods of Medina et al.<sup>57</sup>. For each species, the results were averaged across patches. Other 443 444 morphological properties such as body dimensions were measured on adult bird carcasses of 445 five Atlantic puffins and four black-legged kittiwakes collected on Ré Island (France) during 446 February 2014. All Niche Mapper input data are available in Table S2.

447 There is limited information about the behavior of seabirds under cyclonic conditions. Yet, 448 we benefited from personal field observations performed by a wide range of North Atlantic 449 seabird experts (e.g., most authors of this publication, as well as Dr. Kyle Elliott and Prof 450 Sarah Wanless, see Table S3). Those led us to assume that the seabird species considered in 451 our study react to winter cyclones by reducing their flight activity to zero when wind speeds 452 exceed 15 m.s<sup>-1</sup> (corresponding to cyclones of Class 2, 3 and 4). In surface-feeding black-453 legged kittiwakes, we also assumed that conditions experienced, when wind speeds exceed 454 this threshold, precluded them from diving and feeding. Further, for little auks diving in the upper 30 m of the water column<sup>58</sup>, we assumed that birds are also severely impacted by those 455 456 cyclonic conditions, as the water here is too perturbed for them to dive and prey on 457 zooplankton. In contrast, deeper diving species such as puffins and guillemots, which can dive

458 down to 75 and 250 m, respectively<sup>59,60</sup>, may still manage to feed<sup>31</sup>. Therefore, seabirds were 459 modeled as resting at the surface of water when they did not fly and/or dive. Moreover, flight 460 and diving activities were assumed to remain unchanged under cyclone of Class 1 (for which 461 wind speeds are below 13 m.s<sup>-1</sup>, see above).

462 Using climatic, morphological and behavioral information as stated above, we modeled 463 species-specific, monthly energy requirements for each winter between 2000 and 2016, under 464 four intensities of cyclones and under non-cyclonic conditions. To disentangle the effects of 465 changes in behavior (decreased flight/diving activities) and of weather conditions on bird 466 energy requirements during cyclones, we also calculated those requirements for each species 467 under non-cyclonic conditions, setting behavioral parameters as those displayed during a 468 cyclone with wind speed > 15 m.s<sup>-1</sup>.

#### 469 *Estimation of fasting endurance*

470 Fasting endurance was calculated for each species under Class 2, Class 3 and Class 4 cyclonic 471 conditions in the studied area off Newfoundland for each winter months using the method described in<sup>21</sup>. In this particular context, we assumed that none of the species could feed 472 473 under cyclonic conditions even if deep divers continued diving. The energy requirement to be supplied was calculated previously using Niche Mapper<sup>TM</sup> (see above). The amount of energy 474 475 available was calculated as the masses of lipids and proteins that could be metabolized during 476 a prolonged fast (95% and 25%, respectively<sup>61</sup>), converted into energy (caloric equivalents 39.3 and  $18.0 \cdot kJ \cdot g^{-1}$ , respectively<sup>62</sup>). The body fat and protein contents of each species are 477 478 indicated in Table S2. Integrating daily body component losses through an iterative 479 procedure, we calculated the maximal duration of fasting that lipid and protein reserves could 480 sustain before one of them was used up. We assumed that lipids and proteins accounted for 75 481 and 25% of the energy expenditure until 3/4 of lipid reserves were used. They then accounted 482 for 63 and 37%, respectively<sup>61,63</sup>.

## 483 Quantification and Statistical Analysis

484	Monthly mean energy requirements per condition tested (Class 1 to 4 cyclones, non-cyclonic							
485	conditions with usual seabird flight/diving activities, non-cyclonic conditions with cyclonic							
486	seabird flight/diving activities) were compared for each species using a Kruskal-Wallis test							
487	(Table 1). When this test was significant (p<0.05), a posthoc Dunn's test was conducted (p							
488	values adjusted with the Benjamini-Hochberg method) to conclude on the difference between							
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490	S1K).							
491	Excel	file						
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Energy requirements in kJ.day-1