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1 **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' ¹⁻³. During those,
59 thousands of emaciated seabird carcasses are washed ashore along European and North
60 American coasts. Winter cyclones can therefore shape seabird population dynamics^{4,5} by
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
63 causes of their deaths remain unclear⁶. We performed the first ocean-basin scale assessment
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
68 model⁷ and tested the hypothesis that cyclones dramatically increase seabird energy
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

71 Labrador Sea, the Davis Strait, the surroundings of Iceland and the Barents Sea. Our broad-
72 scale analyses suggested that cyclonic conditions do not increase seabird energy requirements,
73 implying that they die because of the unavailability of their prey and/or their inability to feed
74 during cyclones. Our study provides essential information on seabird cyclone exposure in a
75 context of marked cyclone regime changes due to global warming⁸.

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
81 seabird community⁹ and making them one of the most threatened bird groups¹⁰. It is therefore
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
85 areas^{11,12}, and this may strongly affect the composition of seabird winter wrecks. In this
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*

89 The North Atlantic Ocean and adjacent seas (100°W–100°E, 30°N–90°N, see Figure
90 S1) is the stage for numerous winter cyclones (October to February) (see Figure S2), which
91 are defined by the National Hurricane Center, as large-scale air masses that rotate around a
92 center of low atmospheric pressure. Their locations between 2000 and 2016 were obtained
93 from climatic reanalysis data (see STAR Methods). Using the Dvorak storm classification¹³
94 we sorted them across their duration into one of the four classes of cyclone intensity defined
95 (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
108 distributions (UD) with the BRB-MKDE software (¹⁴, see STAR Methods). To conclude on
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 the
122 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
126 cyclones^{6,15} and that the resulting mortality can be aggravated by mercury contamination¹⁶.
127 Yet, we do not know whether they starve due to abnormally high-energy expenditure linked
128 to harsh climatic conditions¹⁷, 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 state¹⁸⁻²⁰, 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
136 mechanistic model Niche MapperTM (Porter & Mitchell, 2006, see STAR Methods) under
137 four intensities of cyclones and under non-cyclonic conditions (see STAR Methods).
138 Following the protocol used by Grémillet and colleagues²¹, we calculated how many days
139 each of the five studied species could fast before dying, 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
152 significant for deep divers (except for Atlantic puffins in October and December under
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 (\pm
163 0.6) and 6.3 days (± 0.7), between January and February.

164 **Discussion**

165 We demonstrated that seabirds wintering in areas such as the Labrador Sea, the Davis
166 Strait, the vicinity of Iceland and the Barents Sea, are particularly exposed to cyclones.
167 Crucially, our broad-scale analyses led us to reject our hypothesis: climatic conditions
168 experienced by seabirds during cyclones generally did not enhance their energy requirements.
169 These results suggest that seabird mortality during winter high intensity cyclones is likely
170 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
174 spells in the Camargue, France²²: Thousands of flamingos died, not because of hypothermia
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
177 in the North Atlantic Ocean¹⁷. Birds were predicted to experience markedly higher
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
183 North American coasts near their main wintering grounds^{23,24}. Other species were predicted to
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 efficiency²⁵.
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^{26,27}. Prey could also occur deeper in the water column during cyclones as already

196 observed for some elasmobranchs or teleosts^{28,29}, but how this impacts pursuit-diving species
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 alcid away from their preferred prey patches and into
203 unprofitable foraging habitats³². Overall, even if starvation may be the main driver of seabird
204 winter wrecks, we cannot exclude others causes of mortality, such as drowning⁶, or collision
205 with reefs and rocky coastlines (Mark Baran, personal comm) or inland stranding³².

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
212 NicheMapperTM simulations in two main ways. First, the behavior of pelagic seabirds is hard
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 cyclones³³, others, such as great
217 frigatebirds (*Fregata minor*) take advantage of cyclonic winds to save energy while gliding
218 over thousands of kilometers³⁴. Such extreme gliders, which occur in the tropics and Southern
219 Ocean, are rarer in the North Atlantic, an area dominated by alcid species in terms of
220 abundance³⁵. This seabird family, which is morphologically adapted to using its wings for

221 underwater propulsion, has high wing-loading, and very limited capacity to ride strong winds.
222 Thus, cyclonic conditions dramatically increase flight costs in alcids³⁰, and therefore tend to
223 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
244 stay in the same area rather than drifting away with surface currents (up to 2.5 m.s⁻¹ under
245 Class-4 cyclones³⁶). Finally, future efforts will allow researchers to take into account inter-

246 and intra-individual morphological, physiological and behavioral variability across winter in
247 seabird 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
252 across years on beaches close to those areas^{2,6,23,24,37} (and Flemming Ravn Merkel personal
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*

265 It is well-established that seabirds experience direct and indirect negative stressors from
266 global warming³⁸. Since the 1970s, the frequency and intensity of the strongest tropical
267 cyclones in the North Atlantic have increased markedly³⁹. Considering future North Atlantic
268 cyclone regimes, there are still uncertainties but model outputs predict some common
269 features: There will be fewer cyclones in the future, but the frequency of the strongest ones is
270 predicted to increase with global warming³⁹. Moreover, cyclone tracks will likely shift

271 northwards under climate change⁴⁰, increasing the storminess of Western Europe⁴¹ and of the
272 high Arctic^{42,43}. Since storm activity is positively correlated to the magnitude of seabird
273 wrecks^{44,45} and the North Atlantic Ocean seabird community is also predicted to shift
274 northwards, following its prey base⁴⁶, we infer that this community will become even more
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**

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309 manuscript.

310 **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.

313

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**

315 **Table 1: Results of Kruskal-Wallis tests.** Comparisons were made between mean energy
 316 requirements per conditions tested (Class 1 to 4 cyclones, non-cyclonic conditions with usual seabird
 317 flight/diving activities, non-cyclonic conditions with cyclonic seabird flight/diving activities), for each
 318 species and each month. Statistical significant results ($p < 0.05$) are indicated in bold. χ^2 , Chi square;
 319 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		
	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p
October	48.6	5	<0.0001	50.4	5	<0.0001	12.5	5	0.029	21.2	5	<0.0001	6.98	5	0.223
November	48.8	5	<0.0001	44.5	5	<0.0001	10.1	5	0.072	8.70	5	0.122	9.98	5	0.076
December	38.6	5	<0.0001	36.9	5	<0.0001	26.7	5	<0.0001	7.28	5	0.201	10.16	5	0.071
January	26.1	5	<0.0001	25.8	5	<0.0001	12.9	5	0.024	12.2	5	0.032	14.4	5	0.013
February	14.0	5	0.016	11.5	5	0.042	17.9	5	0.003	9.99	5	0.076	10.8	5	0.055

321

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 *Materials availability*

328 This study did not generate new unique reagents.

329 *Data and code availability*

- 330 • Environmental variables, bird and cyclone location are publicly available online.
 331 Physiological, behavioral and morphological characteristic of the species studied are
 332 available in the Table S2.

- 333 • All original code has been deposited at (<http://dx.doi.org/10.17632/rzszzr9fpt4.1>) and is
334 publicly available as of the date of publication. DOIs are listed in the key resources
335 table.
- 336 • Any additional information required to reanalyze the data reported in this paper is
337 available from the lead contact upon request.

338 ***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
342 for ca. 75% of the total number of seabirds breeding along the North Atlantic Ocean³⁵ are also
343 among the most severely hit by winter high-intensity cyclones^{2,3}. 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 dataset⁴⁷. Locations were calculated using the updated
354 Serreze (1997)⁴⁸ algorithm on daily Sea Level Pressure from the National Center for
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.

358 Using the Dvorak storm classification¹³ on the cyclone central pressure we defined four
359 classes of cyclone intensity (> 1009 hPa = Class 1; 1005-1009 hPa = Class 2; 987-1005 hPa =
360 Class 3; < 987 hPa = Class 4) and classified each cyclone in the studied area across its
361 duration. Finally, for each month, we calculated the average number of cyclones of each
362 category that occurred between 2000 and 2016 for each 250 km grid cell.

363 *Winter distribution of seabirds*

364 Two locations per day were obtained through the recorded light levels by Global
365 Location Sensors for each individual with an accuracy of +/- 200 km^{49,50}. We focused on
366 locations acquired during the winter period (October to February) and removed locations
367 obtained during the two weeks on either side of the equinoxes⁴⁹ as well as spurious locations
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 (¹⁴, 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

383 auks and black-legged kittiwakes and was set at 20 locations for Atlantic puffins, common
384 and Brunnich's guillemots. Therefore individuals having less locations than the number
385 needed wasn't considered when averaging UD by colony and species.

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

$$392 \quad CEI(i, j) = NC(i, j) \times UDT(i, j)$$

393 where $NC(i, j)$ is the average number of cyclones between 2000 and 2016 within the pixel i for
394 the month j and $UDT(i, j)$ is the sum, all species considered, of average UD of each colony for
395 the pixel i and the month j . The monthly cyclone exposure indexes were then averaged to
396 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 MapperTM 7 to calculate energy requirements
399 for each species under cyclonic and non-cyclonic conditions for each wintering month. Niche
400 MapperTM 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
410 parameterize the microclimate module of Niche MapperTM. For each cyclone, we extracted
411 corresponding sea surface temperatures using the NOAA High Resolution SST dataset
412 provided by the NOAA/OAR/ESRL PSL
413 (<https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html#detail>)⁵¹. 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
416 speed of each cyclone according to its intensity (5-13 m.s⁻¹ = Class 1; 13.1-17 m.s⁻¹= Class 2;
417 17.1-32.5 m.s⁻¹ = Class 3; > 32.6 m.s⁻¹ = Class 4) using the Dvorak classification¹³. We then
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.

425 Once we had parameterized the microclimate model of Niche MapperTM, we parameterized its
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
428 guillemots^{17,52}, we re-used most Niche MapperTM input values. Missing values and values
429 required to parameterize Niche MapperTM for black-legged kittiwakes and Atlantic puffins,
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

433 kittiwakes, Atlantic puffins and guillemots, respectively^{17,53–55}. Further, under those
434 conditions, we considered that those species spent respectively, 24%, 18.8%, 16.9% and 16%
435 of the day diving during winter^{17,52,53,56}. Feather reflectivity was measured with a double beam
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
443 of Medina et al.⁵⁷. For each species, the results were averaged across patches. Other
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 $15 \text{ m}\cdot\text{s}^{-1}$ (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
455 upper 30 m of the water column⁵⁸, we assumed that birds are also severely impacted by those
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^{59,60}, may still manage to feed³¹. 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 $13 \text{ m}\cdot\text{s}^{-1}$, 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 $> 15 \text{ m}\cdot\text{s}^{-1}$.

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
472 described in²¹. In this particular context, we assumed that none of the species could feed
473 under cyclonic conditions even if deep divers continued diving. The energy requirement to be
474 supplied was calculated previously using Niche MapperTM (see above). The amount of energy
475 available was calculated as the masses of lipids and proteins that could be metabolized during
476 a prolonged fast (95% and 25%, respectively⁶¹), converted into energy (caloric equivalents
477 39.3 and $18.0 \cdot \text{kJ}\cdot\text{g}^{-1}$, respectively⁶²). The body fat and protein contents of each species are
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^{61,63}.

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
489 energy requirements experienced under cyclonic and non-cyclonic conditions (Data S1G-
490 S1K).

491 **Excel file**

492 **Data S1. Maps, overlap analysis and statistic results. Related to STAR Methods Figure**
493 **1, Figure 3 and Table 1.**

494 Error bars correspond to standard deviations capturing the variation between years.

495 A) Overlap between core use areas of little auks from the two studied colonies (Kap Hoegh in
496 blue and Qoororsuaq in green) and average number of Class-1 (A), Class-2 (B), Class-3 (C),
497 Class-4 (D) cyclones in October between 2000 and 2016. Graticules are set at 15° intervals
498 and the map is projected as NSIDC EASE (Equal-Area Scalable Earth) grid for the northern
499 hemisphere. Maps for other species, colonies and months are available upon request.

500 B) Average number of cyclones within the core use areas of little auk colonies between 2000
501 and 2016 in October (A), November (B), December (C), January (D), February (E).

502 C) Average number of cyclones within the core use areas of Atlantic puffin colonies (Flatey
503 (FL), Gull Island (GI), Machias Seal Island (MSI), Skellig Michael (SM), Skomer Island (SI),
504 Storholdi (ST)) between 2000 and 2016 in October (A), November (B), December (C),
505 January (D), February (E).

506 D) Average number of cyclones within the core use areas of black-legged kittiwake colonies
507 (Alkefjellet (AL), Anda (AN), Bjørnøya (BJ), Cape Krutik (CK), Faroe Islands (FI), Franz

508 Josef Land (FJL), Hornøya (HJ), Isfjorden (IS), Isle of May (IoM), Kara Gate (KG), Kippaku
509 (KI), Kongsfjorden (KO), Langes and Skjalfandi (LaS), Røst (RO), Runde and Alesund
510 (RaA), Sklinna (SK)) between 2000 and 2016 in October (A), November (B), December (C),
511 January (D), February (E).

512 E) Average number of cyclones within the core use areas of common guillemot colonies
513 (Bjørnøya (BJ), Cape Gorodetskiy (CG), Faroe Islands (FI), Grimsey (GR), Hjelmøya (HJ),
514 Hornøya (HO), Jan Mayen (JM), Langes and Skjalfandi (LaS), Latrabjarg (LA), Sklinna
515 (SK)) between 2000 and 2016 in October (A), November (B), December (C), January (D),
516 February (E).

517 F) Average number of cyclones within the core use areas of Brunnich's guillemot colonies
518 (Bjørnøya (BJ), Cape Gorodetskiy (CG), Coat Islands (CI), Digges Islands (DI), Gannet
519 Islands (GI), Hornøya (HO), Isfjorden (IS), Jan Mayen (JM), Kara Gate (KG), Kippaku (KI),
520 Langes and Skjalfandi (LaS), Latrabjarg (LA), Minarets (MI), Prince Leopold Island (PLI),
521 Ritenbenk (RI), Saunders (SA), Kitsissut Avaliit (KA)) between 2000 and 2016 in October
522 (A), November (B), December (C), January (D), February (E).

523 G) Average energy requirements for little auks in the studied area off Newfoundland for each
524 wintering month under cyclonic and non-cyclonic conditions between 2000 and 2016.
525 Kruskal-Wallis tests revealed some differences between energy requirements experienced by
526 little auks under cyclonic and non-cyclonic conditions for all wintering months (see Table 1).
527 A posthoc Dunn's test was conducted (p.values adjusted with the Benjamini-Hochberg
528 method) for each month and different letters indicates significant differences between the
529 corresponding conditions in October (A), November (B), December (C), January (D) and
530 February (E).

531 H) Average energy requirements for Atlantic puffins in the studied area off Newfoundland for

532 each wintering month under cyclonic and non-cyclonic conditions between 2000 and 2016.
533 Kruskal-Wallis tests revealed some differences between energy requirements experienced by
534 Atlantic puffins under cyclonic and non-cyclonic conditions in October, December, January
535 and February (see Table 1). A posthoc Dunn's test was conducted (p.values adjusted with the
536 Benjamini-Hochberg method) for those months and different letters indicates significant
537 differences between the corresponding conditions in October (A), December (B), and
538 February (C). The posthoc Dunn's test wasn't significant in January.

539 I) Average energy requirements for black-legged kittiwakes in the studied area off
540 Newfoundland for each wintering month under cyclonic and non-cyclonic conditions between
541 2000 and 2016. Kruskal-Wallis tests revealed some differences between energy requirements
542 experienced by black-legged kittiwakes under cyclonic and non-cyclonic conditions in
543 October, November, December, and January (see Table 1). A posthoc Dunn's test was
544 conducted (p.values adjusted with the Benjamini-Hochberg method) for those months and
545 different letters indicates significant differences between the corresponding conditions in
546 October (A), November (B), December (C) and January (D).

547 J) Average energy requirements for common guillemots in the studied area off Newfoundland
548 for each wintering month under cyclonic and non-cyclonic conditions between 2000 and
549 2016. Kruskal-Wallis tests revealed some differences between energy requirements
550 experienced by common guillemots under cyclonic and non-cyclonic conditions in October
551 and January (see Table 1). A posthoc Dunn's test was conducted (p.values adjusted with the
552 Benjamini-Hochberg method) for those months and different letters indicates significant
553 differences between the corresponding conditions in October (A). The posthoc Dunn's test
554 wasn't significant in January.

555 K) Average energy requirements for Brunnich's guillemots in the studied area off

556 Newfoundland for each wintering month under cyclonic and non-cyclonic conditions between
557 2000 and 2016. Kruskal-Wallis tests revealed some differences between energy requirements
558 experienced by Brunnich's guillemots under cyclonic and non-cyclonic conditions in January
559 (see Table 1) but the posthoc Dunn's test wasn't significant.

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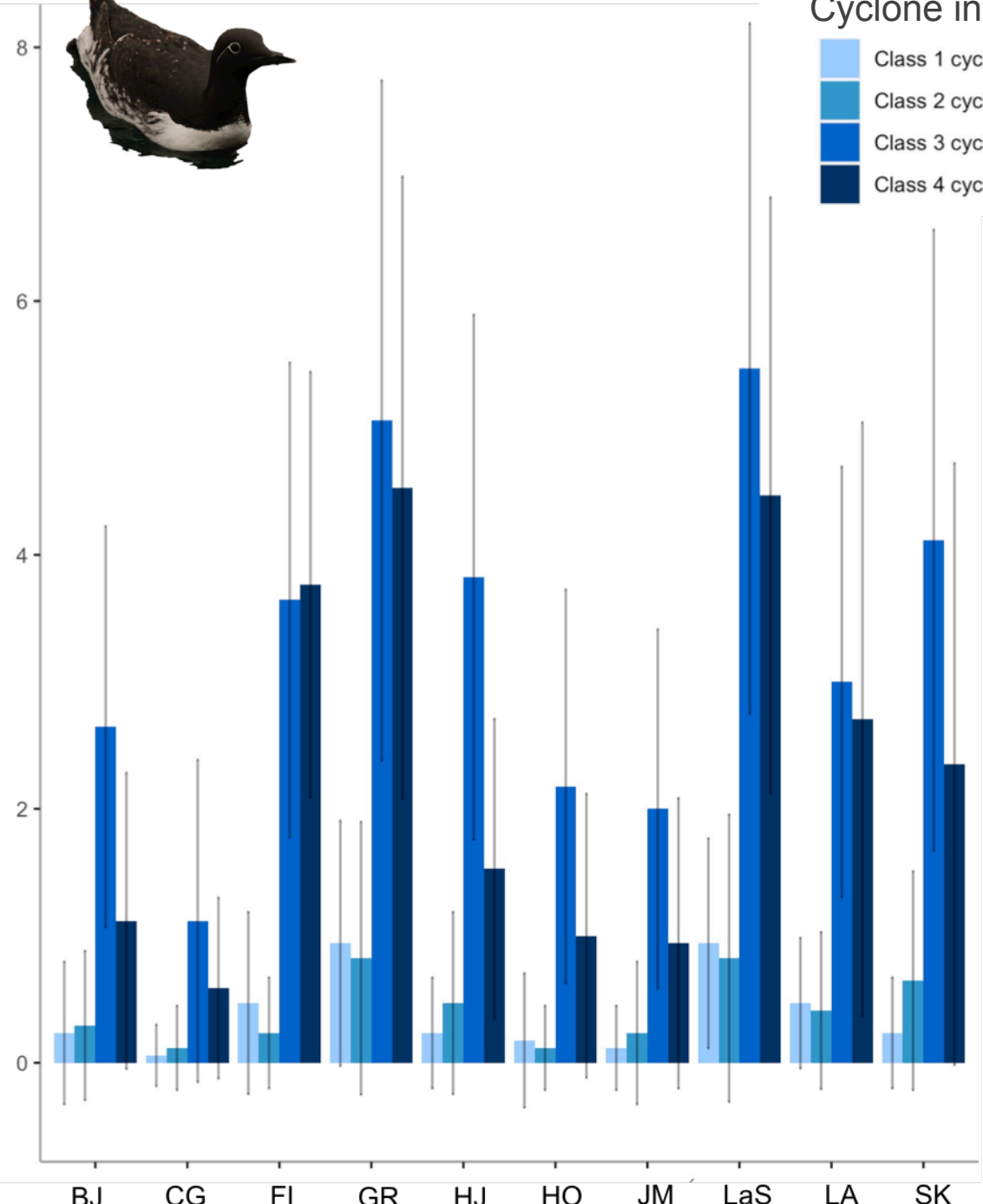
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Average number of cyclones within the core use areas between 2000 and 2016

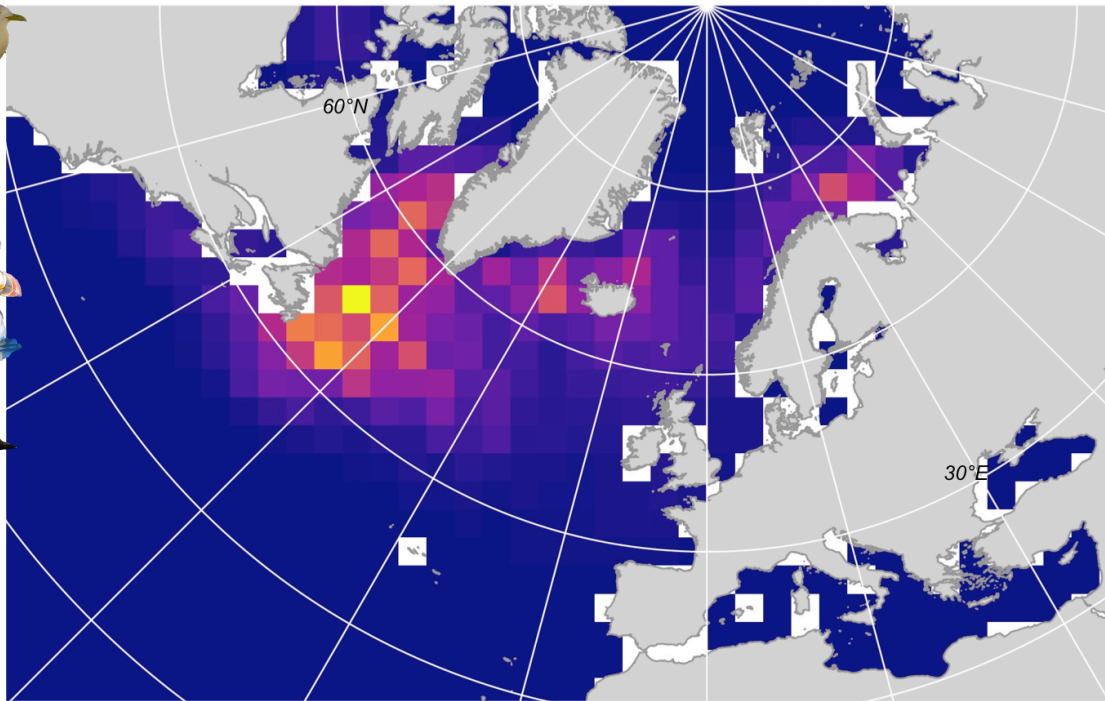


Cyclone intensity

- Class 1 cyclone
- Class 2 cyclone
- Class 3 cyclone
- Class 4 cyclone



Colonies



High

Low

