# North Atlantic winter cyclones starve seabirds

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## Summary

Each winter the North Atlantic Ocean is the stage for numerous cyclones, the most severe ones leading to seabird mass-mortality events called 'winter wrecks' [1–3]. During those, thousands of emaciated seabird carcasses are washed ashore along European and North American coasts. Winter cyclones can therefore shape seabird population dynamics[4,5] by affecting survival rates as well as the body condition of surviving individuals and thus their future reproduction. However, most often the geographic origins of impacted seabirds and the causes of their deaths remain unclear[6]. We performed the first ocean-basin scale assessment of cyclone exposure in a seabird community, by coupling winter tracking data for ~1500 individuals of five key North Atlantic seabird species (*Alle alle, Fratercula arctica, Uria aalge, Uria lomvia* and *Rissa tridactyla*) and cyclone locations. We then explored the energetic consequences of different cyclonic conditions using a mechanistic bioenergetics model[7] and tested the hypothesis that cyclones dramatically increase seabird energy requirements. We demonstrated that cyclones of high-intensity impacted birds from all 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 broad-scale 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[8].

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

## Results

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

### *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[13] 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 category for each 250 km grid cell, we demonstrated that a limited number of localized low intensity cyclones (Class 1 and 2) occurred mainly in the Baffin Bay, the Gulf of Maine and the

Mediterranean Sea regions (see Data S1A). Class 3 cyclones were more numerous and widespread, particularly in October and November, and mainly occurred in the Baffin and Hudson bays, the Davis Strait, the Labrador Sea, east off Newfoundland, around Iceland and in the Barents Sea. Finally, Class 4 cyclones were observed in all winter months off west Iceland, the Norwegian coast and in the Barents Sea, whereas the Davis Strait and the Labrador Sea were only affected by Class 4 cyclones between December and February.

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

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

*Seabird energy requirements under cyclonic and non-cyclonic conditions*

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

To test the hypothesis that cyclones dramatically increase seabird energy requirements, we modeled species-specific, monthly energy requirements for each winter between 2000 and 2016 on a 1000km*1000km area off North Newfoundland (see Figure S1), using the mechanistic model Niche Mapper$^{TM}$ (Porter & Mitchell, 2006, see STAR Methods) under four intensities of cyclones and under non-cyclonic conditions (see STAR Methods). Following the protocol used by Grémillet and colleagues[21], we calculated how many days each of the five studied species could fast before dying, when exposed to Class 2, Class 3 and Class 4 cyclones in the studied area (see STAR Methods). Statistical analyses revealed several significant differences (Kruskal-Wallis, $p<0.05$) in seabird energy requirements (see Table 1) between the six categories of 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). In a very limited number of cases, cyclonic conditions led to increases (up to 36%) in seabird energy requirements in comparison with non-cyclonic conditions with cyclonic flight/diving activities (post hoc Dunn’s test, $p<0.05$). Surprisingly, we found that seabird energy requirements were generally similar or lower during cyclones, compared to non-cyclonic conditions (see Figure 3 and Data S1G-S1K). In particular, for little auks and black-legged kittiwakes, energy requirements were generally significantly lower during Class 2, 3 and 4 cyclones than during non-cyclonic conditions experienced with 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 specific cyclonic conditions) (see Table 1). Further, seabird energy requirements were not significantly different during Class 1 cyclones than for non-cyclonic conditions experienced with usual flight/diving activities (post hoc Dunn's test, $p<0.05$).

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

## 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.

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

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

What exactly prevents seabirds from feeding during cyclonic conditions remains unclear. One possibility is that cyclones may enhance water turbidity, decrease underwater light intensity, and perturb prey patches and vertical migration. Potentially disrupting water stratification, cyclones may modify prey aggregation and negatively impact seabird foraging efficiency[25]. Therefore, this ‘washing-machine effect’ could strongly affect seabirds feeding within the 50 upper meters of the water column, such as black-legged kittiwakes and little auks in our study. Further, cyclones and associated disturbances alter underwater soundscapes and thus constrain the detection of acoustic cues by seabirds, being from conspecifics, prey or predators[26,27]. Prey could also occur deeper in the water column during cyclones as already observed for some elasmobranchs or teleosts[28,29], but how this impacts pursuit-diving species such as puffins and guillemots, is not known. By continuing to dive during cyclones, deep divers such as guillemots and puffins potentially take the risk of using energy reserves in an attempt to track inaccessible prey. However, common and Brünnich's guillemots have been observed switching their diet during strong winds, from schooling fish to amphipods or smaller sandeels, potentially targeting prey that required less underwater searching[30,31]. Alternatively, cyclones may shift alcids away from their preferred prey patches and into unprofitable foraging habitats[32]. Overall, even if starvation may be the main driver of seabird winter wrecks, we cannot exclude others causes of mortality, such as drowning[6], or collision with reefs and rocky coastlines (Mark Baran, personal comm) or inland stranding[32].

*Potential limitations*

Despite these advances, we recommend caution in interpreting our results as they are based on reanalyzed environmental data and on thermodynamic modeling. Notably, measuring empirical data is nearly impossible during cyclones. This calls for the use of modeling approaches to characterize these climatic events and their energy consequences for seabirds, but also constrains model outputs. This lack of in-situ measurements influenced NicheMapper$^{TM}$ simulations in two main ways. First, the behavior of pelagic seabirds is hard to assess under cyclonic conditions, and the animal module mainly relies on the assumption that North Atlantic seabirds significantly reduce flying and/or diving during cyclones. On a worldwide scale, while many seabird species exhibit avoidance behavior seeking coastal shelter and/or reducing activity levels during high-intensity cyclones[33], others, such as great frigatebirds (*Fregata minor*) take advantage of cyclonic winds to save energy while gliding over thousands of kilometers[34]. Such extreme gliders, which occur in the tropics and Southern Ocean, are rarer in the North Atlantic, an area dominated by alcid species in terms of abundance[35]. 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[30], and therefore tend to prevent them from flying. Second, since direct measurements of environmental data during cyclones were lacking at the spatio-temporal scales needed for our analyses, we depicted cyclonic conditions in the microclimate module using a limited number of reconstructed data at a broad scale, potentially missing other relevant differences between non-cyclonic and cyclonic conditions. Finally, due to a lack of available information, we only modeled the effects of temperature, wind speed and reduced activity on heat loss and energy requirements during cyclones, omitting other variables such as wind gust speed, water velocity, wave height, as well as other conditions potentially affecting seabird thermoregulation and thus their energy requirements. For example, localized wind gusts, sea spray and high-speed precipitation could all reduce plumage insulation, thereby increasing seabird heat loss and energy requirements. Further, tall waves could require the birds to dive more frequently, increasing energy requirements. Thus, current predictions on seabird energy requirements during cyclones should be interpreted as likely conservative estimates. However, given the current lack of information, mechanistic models remain important tools to explore potential impacts, and to generate hypotheses that could be further investigated. Additional direct measurements could help to refine these modeling approaches and evaluate initial assumptions. For example, deploying electronic devices to study North Atlantic seabird 3D movements during cyclones is a key objective for future research, which will allow testing our assumption that these animals are less active under passing cyclones. Such deployments will also help infer additional energetic costs in 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$^{-1}$ under Class-4 cyclones[36]). Finally, future efforts will allow researchers to take into account inter- and intra-individual morphological, physiological and behavioral variability across winter in seabird energetic modeling, improving output accuracy.

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

### *Seabird storm exposure under climate change*

It is well-established that seabirds experience direct and indirect negative stressors from global warming [38]. Since the 1970s, the frequency and intensity of the strongest tropical cyclones in the North Atlantic have increased markedly[39]. 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[39]. Moreover, cyclone tracks will likely shift northwards under climate change[40], increasing the storminess of Western Europe[41] and of the high Arctic[42,43]. Since storm activity is positively correlated to the magnitude of seabird wrecks[44,45] and the

North Atlantic Ocean seabird community is also predicted to shift northwards, following its prey base[46], we infer that this community will become even more susceptible to mass mortality caused by winter wrecks. This might be particularly marked in areas such as the Bay of Biscay, the North Sea, the Norwegian and the Barents Seas. In this context, our study provides an essential conceptual and methodological framework to identify the vulnerability of specific populations to cyclone events at the scale of the North Atlantic Ocean.

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## Author Contributions

Conceived and designed the project: D.G., J.F, M.C. Software developers and data providers: W.P, P.M, J.F, H.S, B.M, P.F, S.D, H.H, V.S.B, B.M, T.A-N, I.S.B, O.C, S.C-D, J.D, F.D, N.D, K.E.E, A.E, M.G, Y.K, M.L, S.H.L, M.N, B.O, T.K.R, G.S, T.L.T, M.B, T.D, A.L.F, M.G.F, M.F, H.G.G, T.G, N.P.H, M.J, K.L.J, A.L.K, J.F.L, L.MT, M.M, F.R.M, W.M, A.M, A.P, D.G. Analyzed the data: M.C. Wrote the paper: M.C., D.G. All authors reviewed the manuscript.

## Declaration of interests

The authors declare no competing interests.

## 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.

**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.

## 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 Data S1G-S1K.

| | **Little auks** | | | **Black-legged kittiwakes** | | | **Atlantic puffins** | | | **Common guillemots** | | | **Brünnich's guillemots** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | df | p | $\chi^2$ | df | p | $\chi^2$ | df | p | $\chi^2$ | df | p | $\chi^2$ | 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 |

## STAR Methods

### *Resources Availability*

*Lead contact*

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Manon Clairbaux (clairbauxm@gmail.com).

*Materials availability*

This study did not generate new unique reagents.

*Data and code availability*

- Environmental variables, bird and cyclone location are publicly available online. 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.

### *Experimental Model and Subject details*

We focused on the winter distribution of five seabird species (little auk (*Alle alle),* Atlantic puffin *(Fratercula arctica),* common guillemot *(Uria aalge),* Brünnich's guillemot *(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[35] are also among the most severely hit by winter high-intensity cyclones[2,3]. Bird locations were obtained from Global Location Sensors (GLS) deployed and retrieved during the breeding season for 1532 individuals from 39 breeding colonies across the North Atlantic Ocean (see Figure S1 and Table S1). Birds were caught at the nest according to ethical approval from each country's appropriate organization.

### *Method details*

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

According to the National Hurricane Center, cyclones are defined as large-scale air masses that rotate around a center of low atmospheric pressure. Their locations were obtained from the 'Northern Hemisphere Cyclone Locations and Characteristics from NCEP/NCAR Reanalysis Data, Version 1' online dataset[47]. Locations were calculated using the updated Serreze (1997)[48] algorithm on daily Sea Level Pressure from the National Center for Environmental Prediction (NCEP) and National Center for Atmospheric Research (NCAR) Reanalysis data set in a 250 km grid. We focused on winter cyclones (October to February) in the North Atlantic and adjacent seas (100°W–100°E, 30°N–90°N) between 2000 and 2016. Using the Dvorak storm classification[13] 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.

*Winter distribution of seabirds*

Two locations per day were obtained through the recorded light levels by Global Location Sensors for each individual with an accuracy of +/- 200 km[49,50]. We focused on locations acquired during the winter period (October to February) and removed locations obtained during the two weeks on either side of the equinoxes[49] as well as spurious locations and those falling on land. For each species, we then calculated monthly utilization distributions (UD) for each individual using the BRB-MKDE software ([14], March 2018 version for location in decimal degrees with hmin=250 km) before averaging by seabird colony and species. To avoid that some individuals drive the UD of the colony, we performed a kernel stability analysis and for each month, we only considered individuals which had a sufficiently large number of locations to satisfy this stability criteria. To perform this stability analysis we calculated for each individual and for each month (n/4) UD, with n the total number of locations (after quality and equinoxes checks) for the individual and month considered: the first UD was calculated with 4 locations, the second 8, the third one 12, etc. until the total number of locations was included. Then, for each individual and for each month, we calculated the percentage of overlap between each UD and the UD obtained considering all the locations. Finally, for each species, we plot for each month the individual percentage of overlap against the number of locations included in the UD calculation and we visually determined the minimum number of locations needed to reach a high overlap 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:

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

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).

*Modeling seabird energy requirements under non-cyclonic and cyclonic conditions*

We used the mechanistic model Niche Mapper$^{TM}$ [7] to calculate energy requirements for each species under cyclonic and non-cyclonic conditions for each wintering month. Niche Mapper$^{TM}$ is based on a microclimate model and an animal module: the microclimate model calculates hourly environmental conditions for the near surroundings of the bird and the animal module uses the resulting outputs together with bird morphological, behavioral and physiological properties to estimate the metabolic rate needed by the bird to maintain its body temperature at a given time with a specific behavioral time budget. We focused on a 1000 km x 1000 km area off North Newfoundland (see Figure S1) where the five seabird species aggregate during winter. This area experienced numerous cyclones during the winter months between 2000 and 2016 (see Figure S3). For each of them, we extracted environmental characteristics (sea surface temperature, air temperature and relative humidity), before averaging the values obtained by intensity class for each winter month (see Figure S4) to parameterize the microclimate module of Niche Mapper$^{TM}$. For each cyclone, we extracted corresponding sea surface temperatures using the NOAA High Resolution SST dataset provided by the NOAA/OAR/ESRL PSL (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html#detail)[51]. The corresponding air temperature and relative humidity were extracted from the NCEP/NCAR Reanalysis dataset previously used to define cyclone locations (see above). We set the wind speed of each cyclone according to its intensity (5-13 $m.s^{-1}$ = Class 1; 13.1-17 $m.s^{-1}$= Class 2; 17.1-32.5 $m.s^{-1}$ = Class 3; > 32.6 $m.s^{-1}$ = Class 4) using the Dvorak classification[13]. We then averaged the values obtained by intensity class to calculate mean environmental characteristic of each class for each winter month between 2000 and 2016. Finally, for each year, non-cyclonic conditions were defined by calculating the daily mean characteristics of each month using the same environmental dataset after excluding cyclone days. Wind speeds were obtained from the NCEP/NCAR Reanalysis data set. All environmental data used were interpolated in a 250 km grid. Mean environmental conditions encountered during cyclonic and non-cyclonic events are presented in Figure S4.

Once we had parameterized the microclimate model of Niche Mapper$^{TM}$, we parameterized its animal module to obtain seabird daily energy requirements. As this module had already been parameterized to model energy expenditure in little auks, Brünnich’s guillemots and common guillemots[17,52], we re-used most Niche Mapper $^{TM}$ input values. Missing values and values required to parameterize Niche Mapper $^{TM}$ for black-legged kittiwakes and Atlantic puffins, were sourced from the literature (see Table S2) and obtained through dedicated measurements. Specifically, we set the proportion of time spent flying per day during winter under non-cyclonic conditions to 9%, 11.8%, 5.7% and 4.5% for little auks, black-legged kittiwakes, Atlantic puffins and guillemots, respectively[17,53–55]. Further, under those conditions, we considered that those species spent respectively, 24%, 18.8%, 16.9% and 16% of the day diving during winter[17,52,53,56]. Feather reflectivity was measured with a double beam spectrophotometer (CARY 5000 UV-VIS-NIR, Agilent, USA) with a deuterium-tungsten-mercury light source. We used an integrative sphere to measure spectral and diffuse reflectance with a 1 nm resolution across all wavelengths between 300 and 2500 nm. This range covers approximately 98% of the solar spectrum that reaches the Earth's surface. Reflectance spectra relative to a Spectralon white standard were then computed with the Cary WinUV software. For each species, measurements were made on one ventral and dorsal patch for six individuals. We then calculated the reflectivity of each sample following the methods of Medina et al.[57]. For each species, the results were averaged across patches. Other morphological properties such as body dimensions were measured on adult bird carcasses of five Atlantic puffins and four black-legged kittiwakes collected on Ré Island (France) during February 2014. All Niche Mapper input data are available in Table S2.

There is limited information about the behavior of seabirds under cyclonic conditions. Yet, we benefited from personal field observations performed by a wide range of North Atlantic seabird experts (e.g., most authors of this publication, as well as Dr. Kyle Elliott and Prof Sarah Wanless, see Table S3). Those led us to assume that the seabird species considered in our study react to winter cyclones by reducing their flight activity to zero when wind speeds exceed 15 $m.s^{-1}$ (corresponding to cyclones of Class 2, 3 and 4). In surface-feeding black-legged kittiwakes, we also assumed that conditions experienced, when wind speeds exceed this threshold, precluded them from diving and feeding. Further, for little auks diving in the upper 30 m of the water column[58], we assumed that birds are also severely impacted by those cyclonic conditions, as the water here is too perturbed for them to dive and prey on zooplankton. In contrast, deeper diving species such as puffins and guillemots, which can dive down to 75 and 250 m, respectively[59,60], may still manage to feed[31]. Therefore, seabirds were modeled as resting at the surface of water when they did not fly and/or dive. Moreover, flight and diving activities were assumed to remain unchanged under cyclone of Class 1 (for which wind speeds are below 13 $m.s^{-1}$, see above).

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

*Estimation of fasting endurance*

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

## ***Quantification and Statistical Analysis***

Monthly mean energy requirements per condition tested (Class 1 to 4 cyclones, non-cyclonic conditions with usual seabird flight/diving activities, non-cyclonic conditions with cyclonic seabird flight/diving activities) were compared for each species using a Kruskal-Wallis test (Table 1). When this test was significant ($p<0.05$), a posthoc Dunn's test was conducted (p values adjusted with the Benjamini-Hochberg method) to conclude on the difference between energy requirements experienced under cyclonic and non-cyclonic conditions (Data S1G-S1K).

**Excel file**

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

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

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

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

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

D) Average number of cyclones within the core use areas of black-legged kittiwake colonies (Alkefjellet (AL), Anda (AN), Bjørnøya (BJ), Cape Krutik (CK), Faroe Islands (FI), Franz Josef Land (FJL), Hornøya (HJ), Isfjorden (IS), Isle of May (IoM), Kara Gate (KG), Kippaku (KI), Kongsfjorden (KO), Langanes and Skjalfandi (LaS), Røst (RO), Runde and Alesund (RaA), Sklinna (SK)) between 2000 and 2016 in October (A), November (B), December (C), January

(D), February (E).

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

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

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

H) Average energy requirements for Atlantic puffins in the studied area off Newfoundland for each wintering month under cyclonic and non-cyclonic conditions between 2000 and 2016. Kruskal-Wallis tests revealed some differences between energy requirements experienced by Atlantic puffins under cyclonic and non-cyclonic conditions in October, December, January and February (see Table 1). A posthoc Dunn's test was conducted (p.values adjusted with the

Benjamini-Hochberg method) for those months and different letters indicates significant differences between the corresponding conditions in October (A), December (B), and February (C). The posthoc Dunn's test wasn't significant in January.

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

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

K) Average energy requirements for Brunnïch's guillemots in the studied area off Newfoundland for each wintering month under cyclonic and non-cyclonic conditions between 2000 and 2016. Kruskal-Wallis tests revealed some differences between energy requirements experienced by Brunnïch's guillemots under cyclonic and non-cyclonic conditions in January (see Table 1) but the posthoc Dunn's test wasn't significant.

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