



# Demographic responses of North Atlantic seabirds to seasonal ocean warming

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Climate-driven ocean warming is profoundly reshaping marine ecosystems, with cascading effects on biodiversity and trophic interactions. For migratory marine predators such as seabirds, demographic responses to warming depend on when and where populations are exposed across the annual cycle. Therefore, integrating demographic monitoring and tracking data, across broad geographic and temporal scales, is essential, given the spatial and seasonal variability in ocean warming. Here, we integrated long-term demographic data, seasonal distributions, and sea surface temperatures (SSTs) for 26 populations of five seabird species breeding in the North–East Atlantic to assess the effects of SSTs on reproduction, survival, and population growth trajectories. Demographic responses varied widely among populations and seasons, but negative effects were most consistently associated with warming during the autumn period postbreeding, particularly in the Barents and East Greenland Seas. Winter warming also corresponded to reduced survival, while breeding-season SSTs showed fewer significant effects on reproductive rates. Populations with dual responses to warming in both the breeding and nonbreeding seasons had the lowest projected population growth rates under future SSTs given a high emissions scenario. These results demonstrate that population vulnerability reflects the interaction between seabirds' year-round distributions and regional ocean warming. This underlines the need to integrate year-round tracking and long-term monitoring to inform conservation strategies and marine spatial planning to ensure climate-resilient marine ecosystems.

climate change | seabirds | population dynamics | North–East Atlantic | marine ecosystems

Climate-driven biodiversity loss is one of the greatest challenges of our time. Increased knowledge of populations' responses to rising ocean temperatures (1), and thereby forecasting population viability, is key for the conservation of threatened marine species. Climate change is causing ocean surface waters to warm, with effects on the physical environment, such as acidification, intensified stratification, and sea ice melt (2), with knock-on biological effects, e.g., shifting biogeographic distributions, community changes, and local extinctions (3). Warmer oceans are causing far-reaching, bottom–up changes to marine food webs, from primary productivity to top predators (2). However, as a result of global ocean circulation patterns, there is strong spatial heterogeneity in regional ocean warming rates, where areas of most rapid warming have been referred to as “warming hotspots” (1, 4). Demographic studies of climate change effects tend to focus on a single species and/or population, yet it is only by comparing multiple populations with a range of breeding and nonbreeding habitats, that we can identify the wider, species-level consequences of ocean warming for highly mobile species. Hotspots of ocean warming can have severe consequences for marine communities, particularly when they coincide with important staging areas for migrants (5). Migratory populations spend the nonbreeding season away from their breeding areas and utilize multiple habitats during this period, which makes assessments of year-round climate change effects complex. In such cases, tracking data can determine important seasonal foraging areas to model correlations between ocean temperature anomalies in these habitats and demographic rates, and thereby determine how this might impact population trends (6). A species' life-history strategy (e.g., fast or slow pace of life) defines the demographic responses to shifting climate regimes where, for example, long-lived species have the potential for more complex multifaceted responses (e.g., ref. 7). Therefore, determining the population consequences of climate warming in seasonal habitats, and the underlying demographic rates affected (e.g., age-specific reproduction, survival, or movement), is crucial for informed conservation.

## Significance

Understanding how climate change affects the viability of migratory populations requires leveraging data of demography, movement, and environmental conditions across the annual cycle. Such integrative, multispecies datasets remain rare, particularly in marine ecosystems. We combined long-term tracking and demographic monitoring of 26 seabird populations, across five species, to quantify effects of seasonal sea surface temperatures (SSTs) on seabird population dynamics in the North–East Atlantic. Our results reveal that demographic responses are strongly shaped by when and where populations are exposed to ocean warming, with particularly negative effects during the postbreeding season. This study provides a large-scale, multiseason assessment of climate change impacts on long-distance migrants, offering critical insight for climate-resilient conservation and marine spatial planning.

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However, this requires extensive, long-term monitoring data, which is lacking for many highly mobile taxa.

Seabirds are considered ecological sentinels of marine ecosystems due to their position in the upper trophic levels (8). Evidence is accumulating that many seabird species are particularly vulnerable to the effects of climate change, manifested through bottom-up trophic interactions, as they rely on prey at lower trophic levels (9). As top predators in most marine ecosystems, seabirds have contributed substantially to existing knowledge of climate change effects on marine ecosystems (10). Around 25% of seabird species globally are listed as threatened due to persistent population declines (11, 12). In the North-East Atlantic, climate change is listed as the most important threat, followed by fisheries bycatch, shipping, and renewable energy (13). Through national and international monitoring programs, long-term demographic and year-round tracking data are available for several species of seabirds, making them ideal candidates for assessing the wider consequences of climate change on marine biodiversity and predicting the future viability of threatened populations (e.g., ref. 14). Seabirds are generally migratory but exhibit intra- and interspecific variability in migration routes and nonbreeding stopover areas (15). This results in differences in available food resources and in their exposure to ocean warming (16). Ocean warming hotspots are also under pressure from other human activities, like commercial fisheries and shipping, potentially compounding impacts on those species that are reliant upon them (4). Comparative studies of seabird populations and species, with different migratory strategies and population dynamics, can reveal the ubiquity and strength of climate change and its role in driving population trends through effects on demographic rates.

Seabirds' life-history strategies have evolved to favor longevity and high survival of mature adults (17) and reproductive rates of long-lived species are more responsive to short-term changes in environmental conditions. Therefore, bottom-up effects of climate change tend to be more directly observable on reproductive rates than on adult survival (18). However, reproduction is also driven by other factors, e.g., predation or disturbance at breeding colonies, which can mask more subtle, large-scale effects of progressive climate change (19). Climate effects outside of the breeding season, when individuals are less constrained to their breeding colony, can also be affected by other factors including fishery, shipping, human infrastructure, and extreme weather (19, 20). This necessitates studies of both survival and reproduction, in combination with year-round tracking, to determine the mechanisms by which climate change is driving seabird population dynamics and, thus, the magnitude of the threat this poses to natural populations.

Here, we identify the demographic pathways by which ocean warming may affect population trajectories, given seabird populations' distributions and demography. We do so by combining unique timeseries of year-round tracking data and demographic monitoring. Data were available from 26 populations of five species of seabirds in the North-East Atlantic: Atlantic puffin ("puffin," *Fratercula arctica*), black-legged kittiwake ("kittiwake," *Rissa tridactyla*), Brünnich's guillemot (*Uria lomvia*), common guillemot (*Uria aalge*), and little auk (*Alle alle*). These populations breed in mainland Norway, Svalbard and Jan Mayen, but in the nonbreeding season they are distributed throughout the North Atlantic (Fig. 1). We extracted annual sea surface temperatures (SSTs) from populations' breeding and nonbreeding distributions and modeled the effects of annual variation in SSTs on their reproduction and adult survival rates. There is substantial species- and population-level diversity in seasonal distributions among the study populations (Fig. 1) and, as a consequence,

in their seasonal exposure to ocean temperatures and ocean temperature anomalies (Fig. 2). Therefore, we could evaluate whether stronger SST–demography relationships were found in populations occupying regions that have undergone more rapid warming (i.e., stronger responses in "warming hotspots").

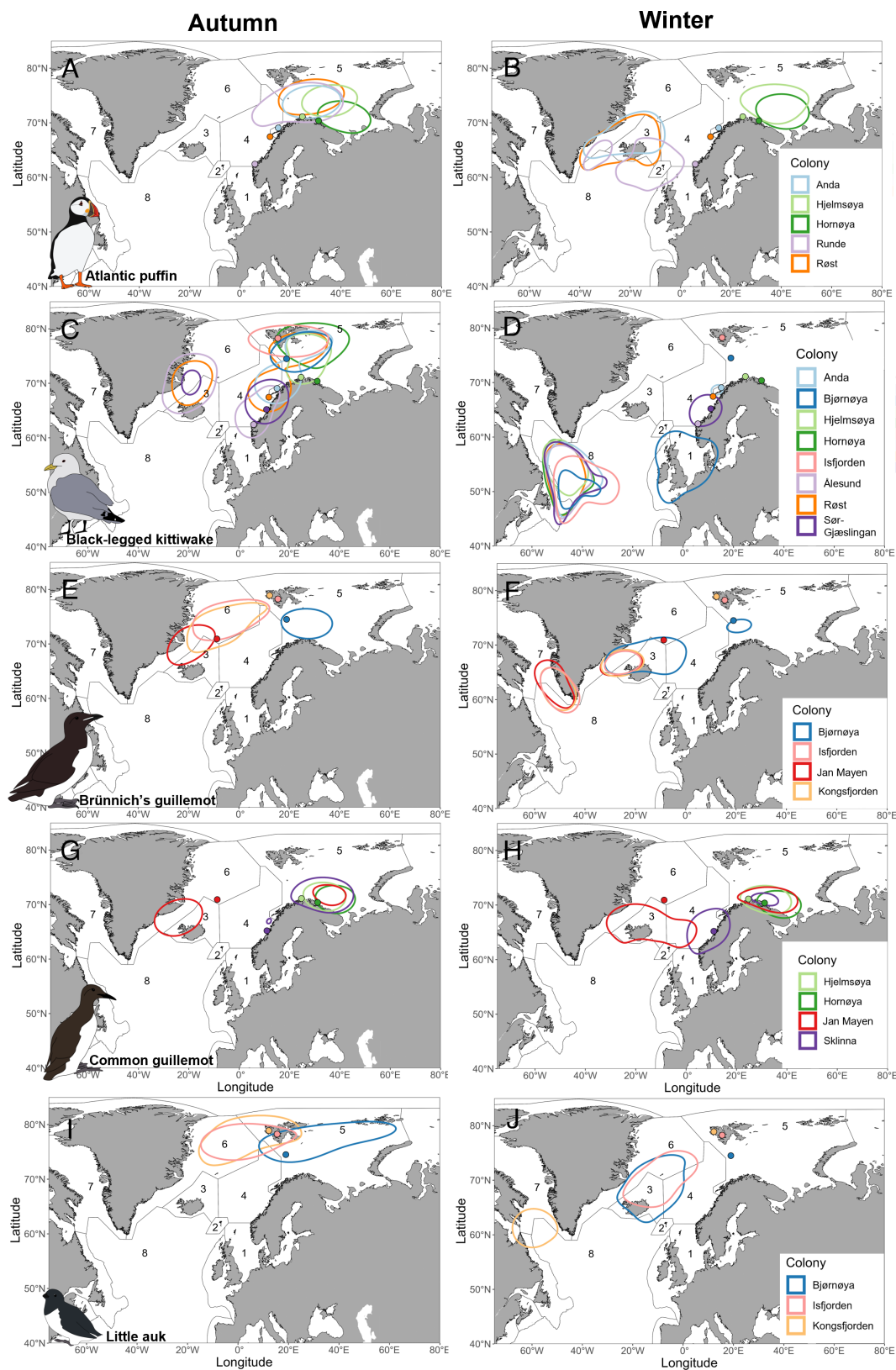
## Results

**Seasonal SST Anomalies and Seabird Distributions.** Substantial seasonal and regional variability in SST anomalies was observed between the study periods 1980–1984 and 2018–2022 (Fig. 2), which encompasses the period of demographic monitoring, across seabirds' nonbreeding foraging areas and breeding season distributions (Fig. 1). Winter and spring exhibited the most pronounced warming, particularly in the northern Barents Sea, East Greenland, and Canadian Eastern Arctic–West Greenland LMEs (Large Marine Ecosystems, Fig. 2). In contrast, summer SST anomalies were weaker, and some breeding colonies experienced cooling or no trends (Table 1). During autumn, warming was observed across most seabird distributions, with SST anomalies ranging from 1.22 to 1.81 °C. The Greenland Sea–East Greenland region had the highest anomalies in autumn, particularly in the foraging areas of Brünnich's guillemots and little auks (Table 1). The Barents Sea, hosting most study populations in autumn, also exhibited strong warming, but the highest SST anomalies were in winter and spring (Table 1).

The majority of the populations (20 out of 26) in this study also breed at colonies within the Barents Sea LME (21), which encompasses the areas of Lofoten and Vesterålen and therefore the breeding colonies at Spitsbergen, Bjørnøya, Jan Mayen, Hornøya, Hjelmsøya, Røst, and Anda. The remaining populations breed in the Norwegian Sea LME (Runde and Sklinna, Fig. 1). In autumn, most populations remain in, or migrate to, the Barents Sea, although several Brünnich's guillemot and little auk populations migrate to the Greenland Sea–East Greenland region. In winter, seabird distributions diverge: puffin populations overwinter around Iceland or remain in the Barents Sea; kittiwakes primarily occupy the Atlantic North region, south of Greenland; and common guillemots and little auks are distributed around Iceland and Greenland or remain in ocean areas close to their breeding colonies (Fig. 1).

**Temporal Trends in Demographic Rates.** Across the 26 study populations, temporal trends in both demographic rates revealed high interannual variability, and especially in their reproductive rates. Some populations showed declines in both survival and reproductive rates. At the species level, statistically significant declines in adult survival were found in kittiwakes ( $P < 0.001$ ), with a weaker, nonsignificant trend in puffins (*SI Appendix, section S7 and Table S6*). At the population level, significant declines in adult survival were detected in kittiwake colonies at Røst and Hjelmsøya (*SI Appendix, Fig. S4*).

Reproductive rates showed a similar pattern: A statistically significant species-level decline was again found only for kittiwakes, with a marginal tendency toward a decline in puffins (*SI Appendix, section S7 and Table S8*). For both species, this appears to be driven largely by local declines in the populations breeding at Hornøya in the southern Barents Sea (*SI Appendix, Fig. S3*). In contrast, little auks showed a weak but positive species-level trend ( $p = 0.057$ ), although none were statistically significant at the population level. Some populations had positive trends in reproductive rates, including puffins breeding at Sklinna, kittiwakes at Sør-Gjaeslingan (both located in the Norwegian Sea), and Brünnich's guillemots at Kongsfjorden (Svalbard) (*SI Appendix, Fig. S3*).

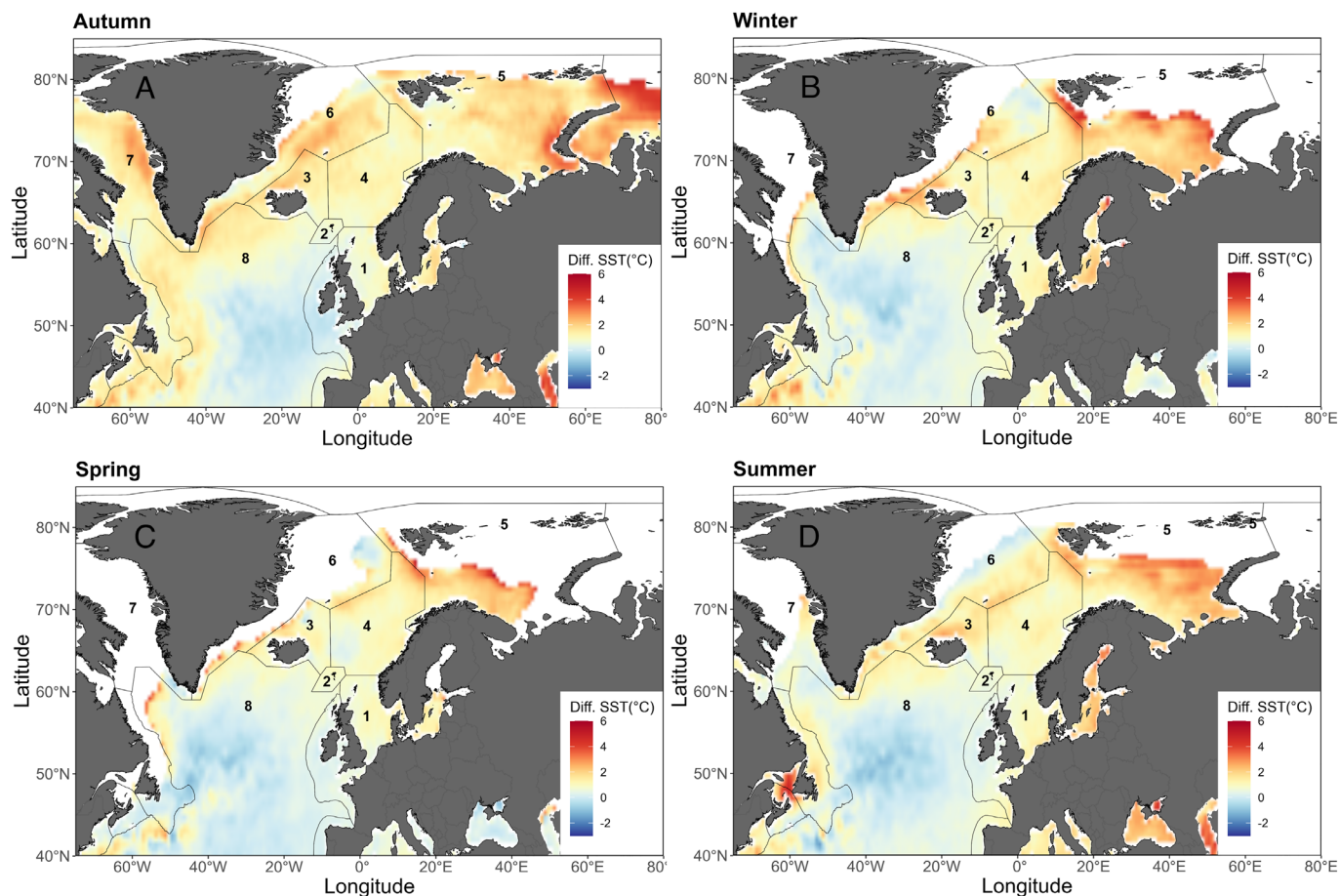


**Fig. 1.** Core distributions (50% kernel density contours) of seabird populations during autumn (August–September, *Left panel*) and winter (November–December, *Right panel*) for each species. (A and B) Atlantic puffin. (C and D) black-legged kittiwake. (E and F) Brünnich's guillemot. (G and H) common guillemot. (I and J) little auk. Colored lines represent 50% kernel contours for each population. During the breeding season, individuals remain close to the breeding colonies (colored points). Large marine ecosystems (LMEs) are indicated with gray ocean borders. Numbering refers to the names of the LMEs: 1) North Sea, 2) Faroe Plateau, 3) Iceland Shelf and Sea, 4) Norwegian Sea, 5) Barents Sea, 6) Greenland Sea–East Greenland, 7) Canadian Eastern Arctic–West Greenland and 8) the high seas area Atlantic North.

**Demographic Responses to Changes in SST.** SSTs were significantly associated with variation in both adult survival and reproductive rates across some of the study populations. We

identified four significant effects of variation in breeding season SST on reproductive rates and 22 significant effects of autumn or winter SST on survival rates. Of the four significant effects of





**Fig. 2.** Average sea surface temperature (SST) anomaly for (A) autumn (August–September), (B) winter (November–December), (C) spring (February–March), and (D) summer (May–June) from a baseline period (1980–1984 average) to a more recent period (2018–2022 average). LMUs are represented as black ocean borders. Numbering refers to the names of the LMUs: 1) North Sea, 2) Faroe Plateau, 3) Iceland Shelf and Sea, 4) Norwegian Sea, 5) Barents Sea, 6) Greenland Sea–East Greenland, 7) Canadian Eastern Arctic–West Greenland and 8) the high seas area Atlantic North. Ocean areas in white reflect those with sea ice, where anomalies could not be calculated.

breeding season SSTs on reproductive rates, three were negative (puffins breeding at Hornøya, kittiwakes at Røst, and Brünnich's guillemots at Bjørnøya) and one was positive (little auks at Isfjorden, Table 2). Of these 22 significant effects on survival, 17 were negative and five were positive, i.e., higher SSTs were associated with lower seabird survival rates in most cases. Models including autumn SSTs as a predictor were also generally a better fit than those with winter SSTs (*SI Appendix, section S6*).

Of the 24 populations for which nonbreeding season SST effects on survival were estimated, 15 populations exhibited a significant effect of either autumn or winter SST (Table 2). Of these, 14 populations were affected by variation in autumn SST and eight by winter SST. Of the 14 significant effects of autumn SST on survival, three were positive: for little auks breeding at Bjørnøya and Kongsfjorden, with autumn distributions in the Barents Sea and Greenland Sea–East Greenland, respectively, and kittiwakes breeding at Hjelmsøya distributed in the Barents Sea in autumn (Table 2, Fig. 1). Of the 11 negative effects of autumn SST, two of the affected populations were distributed in the Greenland Sea–East Greenland and nine in the Barents Sea in autumn (Table 1). Of the eight significant effects of winter SST on survival, two were positive and were found in little auks breeding at Kongsfjorden and located in the Canadian Eastern Arctic in winter, and kittiwakes breeding at Anda that are located in the Atlantic North area in winter. With the exception of kittiwakes, negative effects of winter SST (six) were found in populations of all species, and these populations were distributed in

the Iceland Shelf and Sea ( $n = 4$ ), Barents Sea region (1), and Canadian Eastern Arctic (1) LMUs in winter (Table 2). No statistically significant relationships were found between the magnitude of seasonal autumn or winter SST anomalies and their effects on survival ( $p_{\text{aut}} = 0.51$ ,  $p_{\text{win}} = 0.26$ ). Out of the 24 populations with reproductive data, the four significant effects were all on populations breeding at colonies in the Barents Sea region, where 20 out of these 24 populations were located.

There was a significant, negative relationship between the magnitude of breeding-season SST anomalies and the estimated effect of SST on reproductive rates ( $P < 0.05$ ), i.e., there were more negative SST effects on reproductive rates in breeding areas with stronger spring–summer warming.

**Population Projections Under Current and Future Ocean Temperatures.** Estimates of population growth rates under present-day SSTs indicated that most populations were in decline, with population growth rates below one in 13 out of 15 populations (Fig. 3). The lowest current growth rates were observed in Atlantic puffins at Hornøya and Runde, and Brünnich's guillemots at Bjørnøya. The only two populations with growth rates overlapping one under current SSTs were Brünnich's guillemots at Isfjorden and common guillemots at Jan Mayen, indicating potential stability in these colonies. Given forecasted SSTs under a high-emissions future (SSP5-8.5), population growth rates were projected to decline further in most populations—apart from little auks at Bjørnøya that increased to stable growth (Fig. 3). In contrast,

**Table 1. SST anomalies reflecting the change in SSTs for years 1980–1984 versus 2018–2022 in the Breeding season, Autumn, and Winter**

Population	Breeding	Autumn	Winter
<b>Atlantic puffin</b>			
Hjelsmøya	-0.31 <sup>[BS]</sup>	1.55 <sup>[BS]</sup>	3.07 <sup>[BS]</sup>
Hornøya	-0.33 <sup>[BS]</sup>	1.71 <sup>[BS]</sup>	2.21 <sup>[BS]</sup>
Anda	-0.03 <sup>[BS]</sup>	1.30 <sup>[BS]</sup>	2.54 <sup>[IS]</sup>
Røst	-0.11 <sup>[BS]</sup>	1.33 <sup>[BS]</sup>	2.13 <sup>[IS]</sup>
Skinna	-0.17 <sup>[NW]</sup>		
Runde	-0.32 <sup>[NW]</sup>	1.23 <sup>[BS]</sup>	1.05 <sup>[IS]</sup>
<b>Black-legged kittiwake</b>			
Isfjorden	-4.51 <sup>[BS]</sup>	1.33 <sup>[BS]</sup>	0.11 <sup>[AN]</sup>
Bjørnøya	-1.25 <sup>[BS]</sup>	1.30 <sup>[BS]</sup>	0.62 <sup>[NT]</sup>
Hjelsmøya	-0.31 <sup>[BS]</sup>	1.25 <sup>[BS]</sup>	0.15 <sup>[AN]</sup>
Hornøya	-0.33 <sup>[BS]</sup>	1.54 <sup>[BS]</sup>	0.19 <sup>[AN]</sup>
Anda	-0.04 <sup>[BS]</sup>	1.22 <sup>[BS]</sup>	0.15 <sup>[AN]</sup>
Røst	-0.11 <sup>[BS]</sup>	1.43 <sup>[BS]</sup>	0.22 <sup>[AN]</sup>
Sør-Gjæslingan	-0.27 <sup>[NW]</sup>	1.32 <sup>[NW]</sup>	0.31 <sup>[AN]</sup>
Ålesund	-0.32 <sup>[NW]</sup>	1.52 <sup>[NW]</sup>	0.19 <sup>[AN]</sup>
<b>Brünnich's guillemot</b>			
Isfjorden	-4.78 <sup>[BS]</sup>	1.79 <sup>[GS]</sup>	1.54 <sup>[CE]</sup>
Kongsfjorden	0.25 <sup>[BS]</sup>	1.77 <sup>[GS]</sup>	1.66 <sup>[CE]</sup>
Bjørnøya	-1.11 <sup>[BS]</sup>	1.25 <sup>[BS]</sup>	1.98 <sup>[IS]</sup>
Jan Mayen	-0.68 <sup>[BS]</sup>	1.81 <sup>[GS]</sup>	2.22 <sup>[CE]</sup>
<b>Common guillemot</b>			
Bjørnøya	-1.14 <sup>[BS]</sup>		
Hjelsmøya	-0.32 <sup>[BS]</sup>	1.36 <sup>[BS]</sup>	1.79 <sup>[BS]</sup>
Jan Mayen	-0.68 <sup>[BS]</sup>	1.44 <sup>[GS]</sup>	1.79 <sup>[IS]</sup>
Hornøya	-0.32 <sup>[BS]</sup>	1.46 <sup>[BS]</sup>	1.90 <sup>[NW]</sup>
Skinna		1.38 <sup>[BS]</sup>	1.39 <sup>[NW]</sup>
<b>Little auk</b>			
Isfjorden	-4.65 <sup>[BS]</sup>	1.59 <sup>[GS]</sup>	1.82 <sup>[IS]</sup>
Kongsfjorden		1.71 <sup>[GS]</sup>	2.25 <sup>[CE]</sup>
Bjørnøya	-1.22 <sup>[BS]</sup>	1.55 <sup>[BS]</sup>	2.06 <sup>[IS]</sup>

The fill color for SST anomalies ranges from red (strongest positive anomaly, warming) to blue (strongest negative anomaly, cooling). Populations are ordered according to the breeding colony latitude. Letters in brackets are abbreviations of the LME each population was distributed in during that season (Breeding, Autumn, or Winter); BS = Barents Sea region, NW = Norwegian Sea, NT = North Sea, IS = Iceland Shelf and Sea, AN = Atlantic North, GS = Greenland Sea–East Greenland, CE = Canadian Eastern Arctic–West Greenland.

all populations of puffins, kittiwakes, and both guillemot species had reduced growth rates, with some, such as puffins at Anda and common guillemots at Jan Mayen, showing large (>10%) growth reductions.

Discussion

**Seasonal Exposure to Ocean Warming.** This study demonstrates that the demographic consequences of ocean warming in North Atlantic seabirds are highly season- and region-specific and critically shaped by seabirds’ diverse distributions during their annual cycle. Regional variability in SST anomalies across the North Atlantic has been well documented (4). Although the most rapid warming was observed during winter in the Barents Sea and Greenland Sea–East of Greenland LMEs, the strongest demographic responses were associated with variation in autumn SSTs. This aligns with the period when seabirds from many of the breeding populations in this study concentrate in these ocean areas for postbreeding foraging and molt. Here, despite only moderate autumn SST anomalies relative to winter, survival rates were negatively affected in several of the study populations. This reflects a mismatch between warming intensity and associated survival responses. Among the 16 populations distributed in the Barents Sea in autumn, there were nine significant negative effects and two significant positive effects. A previous study of puffins breeding at Røst found a positive SST relationship, mediated through the availability of young herring, *Clupea harengus*, a key food item in the Barents Sea in autumn (22). The Barents Sea attracts many seabirds in autumn (15) due

to comparably abundant prey resources such as small pelagic fish and plankton during this period (23). Additionally, many seabirds undergo molt during this period, reducing mobility and increasing energy requirements (24). Both the Barents and Greenland Seas have experienced warming-driven shifts in zooplankton and pelagic fish distributions (25, 26). Thus, even moderate warming may be exacerbating foraging constraints or increase intra- and interspecific competition given the climate-driven changes in prey phenology and composition (27).

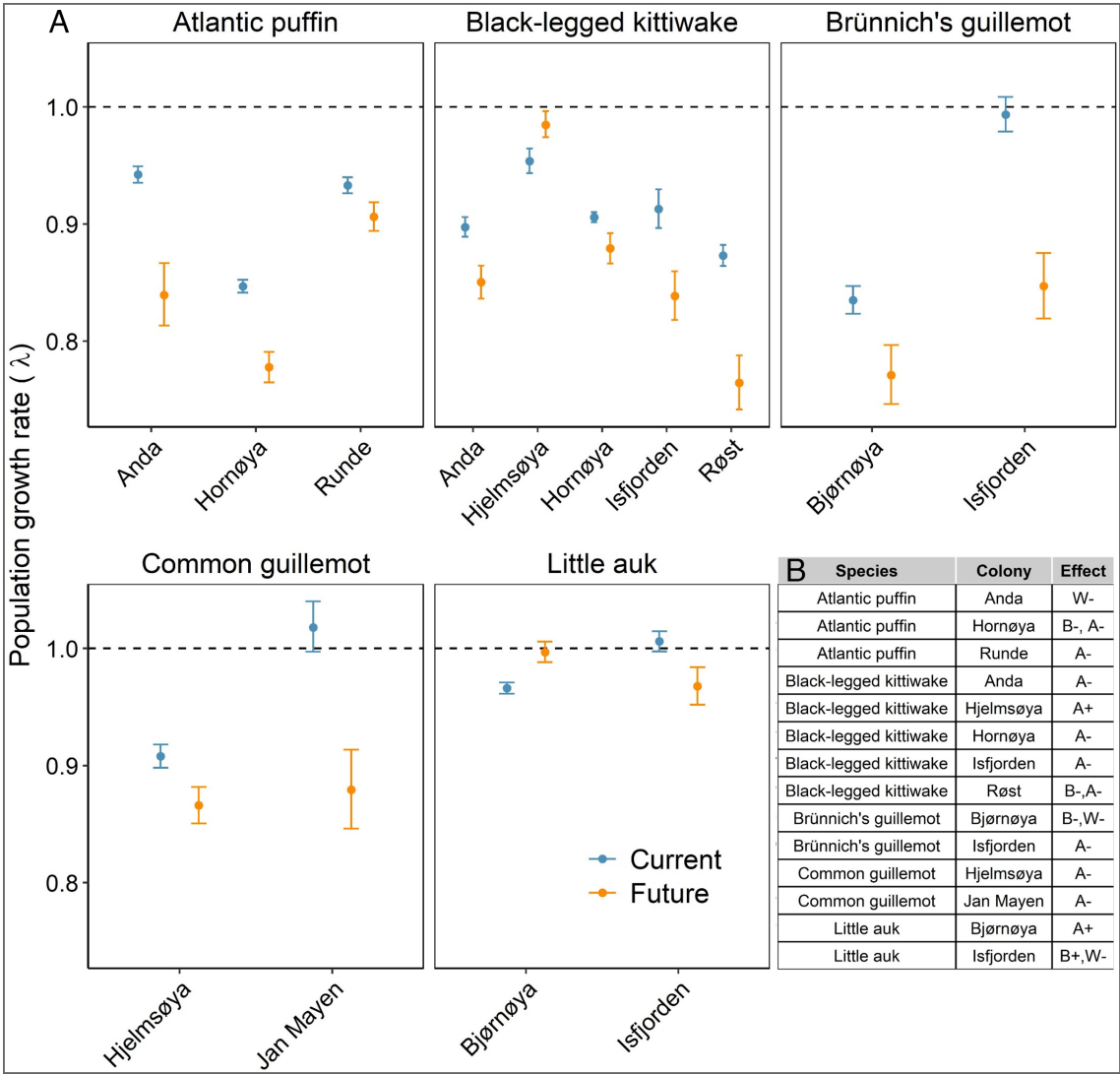
Advection of warmer, sub-Arctic water masses into polar regions (“borealization,” 28) has led to high warming rates in winter, with widespread consequences for marine Arctic communities, in, e.g., the Barents Sea (29) and Greenland Sea (30). However, demographic responses were more limited in winter, with the exception of, e.g., Atlantic puffins breeding at Anda and Brünnich’s guillemots at Bjørnøya. Populations wintering in more southerly ocean areas, such as the Atlantic North region that encompasses the NACES Marine Protected Area (31), showed no significant SST effects on survival. Similarly, no significant SST effects on demographic rates were found for populations distributed in the Norwegian Sea, which has also experienced slower warming rates.

**Demographic Responses to Ocean Warming.** The direction and magnitude of SST-related demographic responses varied markedly across species. For most piscivorous species, including puffins, both guillemots, and kittiwakes, warmer SSTs were generally associated with declines in survival or reproductive rates. These species depend on energy-rich forage fish during both the

**Table 2. Estimated effects of scaled SSTs on demographic rates**

Population	Reproduction ~ SST <sub>bre</sub>	Survival ~ SST <sub>aut</sub>	Survival ~ SST <sub>win</sub>
<b>Atlantic puffin</b>			
Hjelsmøya	0.22 ± 0.68	-0.34 ± 0.36	1.52 ± 1.93
Hornøya	-0.58 ± 0.41	-0.44 ± 0.11	-0.21 ± 0.13
Anda	-0.58 ± 0.53	-0.21 ± 0.20	-0.36 ± 0.21
Røst	-0.33 ± 0.58	-0.10 ± 0.12	-0.02 ± 0.10
Skinna	0.01 ± 0.49		
Runde	-0.04 ± 0.63	-0.23 ± 0.21	-0.10 ± 0.24
<b>Black-legged kittiwake</b>			
Isfjorden	-0.10 ± 0.51	-0.34 ± 0.26	-0.01 ± 0.23
Bjørnøya	-0.12 ± 0.14	-0.10 ± 0.17	0.01 ± 0.19
Hjelsmøya	0.10 ± 0.76	0.56 ± 0.36	0.40 ± 0.41
Hornøya	-0.17 ± 0.32	-0.12 ± 0.12	0.08 ± 0.12
Anda	-0.23 ± 0.28	-0.21 ± 0.17	0.18 ± 0.15
Røst	-0.39 ± 0.32	-0.36 ± 0.18	0.15 ± 0.16
Sør-Gjæslingan	-0.95 ± 1.59	-0.15 ± 0.34	-0.07 ± 0.33
Ålesund	-0.12 ± 0.30	0.10 ± 0.20	-0.15 ± 0.25
<b>Brünnich's guillemot</b>			
Isfjorden	-0.36 ± 0.43	-0.63 ± 0.44	-0.35 ± 0.23
Kongsfjorden	-0.32 ± 0.33	0.05 ± 0.35	0.00 ± 0.34
Bjørnøya	-0.31 ± 0.26	-0.24 ± 0.22	-0.53 ± 0.21
Jan Mayen	0.20 ± 0.44	-0.17 ± 0.41	-0.33 ± 0.42
<b>Common guillemot</b>			
Bjørnøya	-0.21 ± 0.21		
Hjelsmøya	0.11 ± 0.62	-0.41 ± 0.29	-0.05 ± 0.50
Jan Mayen	0.12 ± 0.42	-0.72 ± 0.58	-0.50 ± 0.49
Hornøya	0.14 ± 0.93	0.09 ± 0.32	0.18 ± 0.29
Skinna		-0.13 ± 0.22	-0.03 ± 0.29
<b>Little auk</b>			
Isfjorden	0.55 ± 0.38	0.05 ± 0.19	-0.23 ± 0.19
Kongsfjorden		0.19 ± 0.11	0.15 ± 0.14
Bjørnøya	-0.03 ± 0.27	0.11 ± 0.08	0.01 ± 0.08

We report the effect of breeding season SST (SST<sub>bre</sub>) on reproductive rates, autumn SST (SST<sub>aut</sub>) and winter SST (SST<sub>win</sub>) on survival rates. For effects that were statistically significant at the 0.05 level, the text is highlighted in bold and encircled in a black box. Coloring reflects the effect size, where color ranges from red (a more negative effect) to blue (a more positive effect). Effects are reported as means and half width CI (upper confidence limit – lower confidence limit/2).



**Fig. 3.** (A) Mean population growth rate (asymptotic  $\lambda$ ) and 95% CI, based on reproduction and survival rates predicted at the mean SST over the period 2015 to 2020 ("Current," blue) and predicted at SSTs over the future period 2035 to 2040 ("Future," orange), based on estimated linear relationships. Only populations which had significant effects of SST on either reproduction or survival were included. Pairs of values (current and future predicted  $\lambda$ ) are shown per colony (x-axis). (B) Table representing which of the seasonal SST effect pathways were included in each population projection. A "B" indicates that reproduction was predicted as a function of breeding season (SST<sub>Bre</sub>), an "A" if survival was predicted as a function of autumn SST (SST<sub>Aut</sub>) or a "W" if winter SST (SST<sub>Win</sub>) was included and the sign indicates if the effect was positive ("+" or negative ("-").

breeding and nonbreeding season and are potentially vulnerable to changes in prey availability or distributional shifts driven by ocean warming. In particular, among surface-feeding seabirds like kittiwakes (9, 32), where an abrupt increase in SSTs coincided with steep population declines in more than 500 kittiwake colonies (16). Species-level declines in both survival and reproduction were detected in our study and multiple kittiwake colonies showed significant associations between SSTs and demographic rates, supporting the evidence of widespread ocean warming-driven declines in kittiwake populations along the Norwegian coast (33). Several, single-population studies have demonstrated associations between SST and demographic rates in Norwegian-breeding puffin populations through bottom-up effects on the abundances and distributions of their prey (34, 35, 36). This bottom-up effect via prey quality was exemplified in puffins breeding at Røst, where higher SSTs were associated with poorer herring larvae quality, a key determinant of fledging success and adult survival (22, 36). Our results reinforce such findings: Where direct, negative effects of SSTs on demographic rates were found in several puffin populations: colonies Hornøya, Anda, and Runde. However, previous studies

have also included lags due to prey recruitment dynamics (e.g., ref. 34), reflecting delayed effects on prey recruitment, which were not considered here. For example, for puffins breeding at Hornøya colony, higher SSTs were associated with lower abundance of capelin, an important prey type in the breeding season (34). Furthermore, the projected population growth rates of several puffin populations under future SSTs were among the lowest in this study. Capelin, as well as young age classes of herring and cod, are also important for common guillemots in the Barents Sea (23), where a similar mechanism as described above for puffins may also explain the negative relationships between autumn and winter SSTs and the survival rates of common guillemots breeding at Hjelsmøya and Jan Mayen. Negative effects of warming SSTs were found on reproductive and survival rates of Brünnich's guillemots breeding at Bjørnøya, and on survival rates only for the Isfjorden breeding population. As Arctic breeders, Brünnich's guillemots rely on ice-associated prey such as 0-group polar cod (*Boreogadus saida*), which are considered vulnerable to warming as the sea ice retreats, and such Arctic species are being replaced by Atlantic species such as Atlantic cod (*Gadus morhua*) (37). In contrast, little auks showed



predominantly positive or no demographic responses to variation in SSTs. These responses may reflect dietary differences, as little auks primarily feed on zooplankton rather than fish (38). Although warming has shifted plankton community composition toward more Atlantic species (37), little auks may have greater potential to compensate through plasticity in foraging behavior (39). Additionally, little auks are smaller seabirds (higher surface:volume ratio) than the other study species and may benefit from alleviated energetic costs of thermoregulation under warming, given the cold polar temperatures (40).

**Implications for Population Viability.** Seabird populations exposed to negative effects of SST on both survival and reproduction were those with the poorest projected population growth rates. This pattern was most pronounced in some populations breeding in the Barents Sea, such as Atlantic puffins breeding at Hornøya and Brünnich's guillemots at Bjørnøya. Long-lived species like seabirds can buffer environmental variability by maintaining adult survival (18), but such buffering capacity is clearly exceeded when reproduction and survival both respond to environmental stress. While some plasticity, e.g., in behavior or phenology (41), or potentially genetic adaptation (42), may help to mitigate negative effects, it appears insufficient to compensate for rapid, persistent changes in marine ecosystems in several populations. Although positive survival and reproductive responses were evident in some populations, e.g., little auks. Nevertheless, forecasted SST conditions under high-emissions scenarios further reduced population growth in nearly all affected populations. This suggests that current environmental conditions are already sufficiently poor to drive long-term declines in many populations and that continued warming may exacerbate this trend. However, forecasts assume that the estimated linear relationships between SSTs and demographic rates hold in the future, which is likely oversimplistic given the multifaceted effects of ocean warming on marine ecosystems. Several assumptions were also made in the matrix models due to the lack of data on age at recruitment, immature survival, and breeding propensity (see Materials and Methods). Population dynamics were modeled as density independent although breeding population size can influence demographic rates through density-dependent mechanisms (43), despite limited evidence of this in Norwegian-breeding populations (33). While breeding population size may covary with SST, we were unable to include it in our models due to limited colony size data across all populations and years. However, correlation tests between annual variation in population sizes and breeding SSTs, where available, were not significant for any population (*SI Appendix, section S8*). Nevertheless, causal effects of SST should be interpreted with this caveat in mind, particularly in population viability analyses (44). Finally, while our analysis only considered direct by SST effects on demographic rates to reduce model complexity and avoid possible spurious correlations, lagged effects remain plausible and likely important (9).

**Toward Climate-Resilient Marine Conservation.** Some populations showed heightened vulnerability to ocean warming. This has implications for conservation actions and marine spatial planning, which should consider regions and periods coinciding with strong demographic sensitivity to ocean warming (45). For instance, the Barents Sea region in the postbreeding season, which supports large seabird aggregations during this time, and the Greenland Sea–East Greenland where several study populations were distributed in autumn. Also, integrating prey dynamics, fisheries effects, phenology, and dietary information in future studies will be essential to further mechanistic understanding. Ultimately, our findings emphasize that seabird demographic responses to climate change

are not uniform and marine conservation strategies should recognize this heterogeneity to promote adaptive responses at appropriate spatial and temporal scales. This will ensure the resilience of marine ecosystems to resist and recover future climate change.

## Materials and Methods

Capture-mark-resight (CMR) and reproduction data were used to estimate the annual survival and reproduction of breeding adults from 26 populations of five species monitored through the Norwegian national monitoring program SEAPOP ([www.seapop.no/en](http://www.seapop.no/en)) at breeding colonies on mainland Norway, Jan Mayen, Bjørnøya, and Svalbard (ranging from 62°N to 79°N). Time series length and sample sizes for each population are given in *SI Appendix, Table S1.1*, and colony sizes and locations are given in *SI Appendix, Table S1.2*.

**Demographic Data.** We modeled survival rates using individual CMR data. Each year, breeding adults were caught and marked at the breeding colonies with individually coded color rings or a unique color ring combination. Birds were either captured at the nest, with noose traps, or in mist nets. Visual resighting of ringed birds was conducted in subsequent years. Annual reproduction was recorded at the population level as the number of fledged chicks or the number of chicks alive at age 20 d per breeding pair or occupied nest, from a given sample of pairs or nests in each colony. Data were used to estimate annual reproductive rates as a measure of productivity. Although productivity was monitored differently among species and colonies, this was not considered an issue for analysis given the goal was not to compare absolute values of demographic rates but, rather, the effects of ocean warming on reproductive rates (*SI Appendix, Table S1*).

**Nonbreeding Distributions.** The core autumn and winter foraging areas of the populations were defined as the 50% kernel utilization distributions (UDs), which were derived from tracking data using light-level loggers (geolocator sensors) deployed between 2008 and 2020 (15). Data were processed according to Bråthen, Moe (46). Raw light-level data were first converted to geographic locations per bird per day, then filtered to remove locations over land, locations during the equinox periods (defined as 8th September–20th October and 20th February–3rd April), when day length is approximately the same at all locations on earth, and polar day/night periods, when there are no twilight events. To avoid gaps in tracks, missing locations were interpolated based on the Informed Random Movement Algorithm (IRMA), which takes into account complementary information on light levels, land masks, and saltwater immersion data to infer colony presence and longitude during the equinoxes. In this way, missing locations are replaced by plausible estimates (47). For map representation, kernel UD's were projected to latitude and longitude coordinates on the WGS84 reference ellipsoid. Sample sizes are reported in *SI Appendix, Tables S2 and S3*.

**Climate Data.** We used observations of SSTs and uncoupled simulations of future climate forcings derived from CMIP6 Shared Socioeconomic Pathways SSP5–8.5 simulations, from the third Hadley Centre Global Environment Model (HadGEM3–GC3.1–MM, 48). Observational SST records were available from 1850 to 2014 from in situ observations, supplemented with satellite observations to provide consistent gridded data. Any values below  $-2^{\circ}\text{C}$  were considered to be sea ice temperatures and were masked out. SSTs (2014 onward) were taken from the HighResSST-future experiment for HadGEM3–GC3.1–MM, which were part of the High-Resolution Model Intercomparison Project (HiResMIP), at a spatial resolution of approximately  $1^{\circ} \times 1^{\circ}$  latitude and longitude and at a monthly time scale. All HighResSST-future model experiments used the same SSTs derived by combining the warming obtained from a combination of CMIP5 RCP8.5 simulations with the variability derived from the historic 1950–2014 period (49). SSP5–8.5 represents the Shared Socioeconomic Pathways representing high greenhouse gas emissions, rapid economic growth, increased fossil fuel use, and limited climate policies.

To model effects of changes in SSTs on demographic rates, a monthly mean was extracted from the gridded SST data for each year 1980–2020 from the area representing the seasonal 50% UD's for each species and population (Fig. 1). Mean SSTs were calculated for two nonmigratory stop-over periods during the nonbreeding season: autumn (August–September) and winter (November–December) for each

study year. Mean annual SSTs were calculated for the breeding season (including prebreeding) which was defined as February–July for nonarctic colonies. Breeding season SSTs were limited to March–August for Bjørnøya and Jan Mayen and to May–August for Spitsbergen, to limit the presence of sea ice in the dataset. For the breeding season only, gridded SST data were aggregated to a weighted mean for each population, using a distance decay rule of the following form, which allocated more weight to locations close to the colony, following Searle, Butler (43), Carroll, Butler (50);

$$w \propto \exp(-\lambda d),$$

where  $d$  represents the distance by sea from the grid cell midpoint to the colony, and  $\lambda$  represents the decay rate. The decay rate  $\lambda$  for each species was the value where 95% of all weights would, in an area of sea without land, be allocated to locations within the published mean-max foraging range (black-legged kittiwake: 156.1 km, Brünnich's guillemot: 10.0 km, common guillemot: 73.2 km, Atlantic puffin: 137.1 km, little auk: 125.4 km). Foraging ranges were taken from (51), except for the little auk and Brünnich's guillemot, which were taken from (52). We then set the weights equal to zero for locations beyond the mean-max foraging range and rescaled so that the weights summed to one by dividing each weight by the sum of the weights across all grid cells.

For visual representation (Figs. 1 and 2), and to summarize the results according to management-relevant entities (see, e.g., ref. 21), ocean areas were divided into Large Marine Ecosystems (LMEs).

**Demographic Models.** The CMR analysis was based on a Cormack–Jolly–Seber (CJS) model framework. For each study population, apparent survival and resighting rates were estimated using MARK via the R package RMark (53). The goodness of fit (GOF) of this model to the data was assessed using UCARE (54). For all populations, there was support for trap dependence (dependence of resighting rates across years, Test 2.CT). We accounted for trap dependence with a one-year trap dependence structure to distinguish between individuals resighted the previous year and individuals that were not, where the additive effect  $td$  reflects the resighting rate of individuals resighted the previous year (55). For some capture histories, there was also evidence of transience (Test 3.SR) (SI Appendix, Table S4), which reflects the lower chance of reobserving individuals the first year after marking, compared to later years. For populations with a significant effect of transience, models were fitted with a first-year survival effect, allowing survival in the first age class to differ from subsequent years. For all populations, including time dependence in recapture rates improved the model fit, to control for differences in effort, disturbance and capture effects (56). The survival model was run as 1) constant, 2) with a temporal trend, 3) time-dependent (year as a fixed-effect), and with 4) autumn ( $SST_{aut}$ ) and 5) winter ( $SST_{win}$ ) SST as time-varying covariates. Covariate models were fitted separately due to relatively high temporal correlations between SST covariates. SST covariates were normalized (mean = 0, SD = 1) when included in the models. The proportion of variation explained by a given model,  $R^2$ , was calculated as [Model Deviance (SST model) – Deviance (intercept model)]/[Deviance (time-dependent model) – Deviance (intercept model)]. The model fit (Akaike's information criterion corrected for small sample sizes, AICc, and model weights) of models 1 to 5 are reported in SI Appendix, Table S5.

Reproduction was modeled assuming a binomial distribution, with the numerator (successes) corresponding to the number of offspring and the denominator (number of trials) defined as the number of sampled breeding pairs or nests, multiplied by modal brood size for each species. However, there are disparities in how reproduction was estimated (e.g., reproductive rates were based on the number of large chicks rather than fledged birds) among populations which would lead to an overestimation of reproduction and thus population growth rates. All species have a clutch size of one, except black-legged kittiwakes, which were assumed to have a modal clutch size of two, although this species infrequently has clutch sizes of one or three, we use an upper bound of two in line with previous studies (e.g., ref. 57). Models were fitted as quasi-binomial generalized linear models (GLMs), with the quasi-binomial error distribution used due to overdispersion. Models were fitted using "lme4" package version 1.1 to 27.1.

We fitted linear regression models to test our hypothesis that there was a statistical relationship between the strength of ocean warming (SST anomaly between 1980–1984 and 2018–2022) and the direction and strength of SST effects on survival or reproductive rates. Linear models were fitted with SST anomaly in each population's seasonal distribution as the predictor and SST effect coefficient

describing 1) the effect of  $SST_{bre}$  on reproductive rates or effects of 2)  $SST_{aut}$  and 3)  $SST_{win}$  on survival rates as the response. Only significant effects ( $p < 0.05$ ) of SST on demographic rates were included.

**Current and Future Population Growth Rates.** We predicted demographic rates under the mean value of SST for the years 2015–2020 ("Current") and for the years 2035–2040 ("Future"), based on the estimated linear relationships with SST and the global warming scenario SSP5–8.5. Reproduction was predicted as a function of SST when the SST slope coefficient was statistically significant ( $P < 0.05$ ) and for survival when the CI of the slope coefficient did not overlap zero, for each population. When SST effects on survival or reproduction were not statistically significant, that rate was estimated as the 2015–2020 mean for both Current and Future scenarios, as we did not have sufficient evidence supporting an effect of SST. As autumn SST and winter SST were correlated, the SST covariate from the survival model with the lowest AICc was used (SI Appendix, Table S5). Populations with only reproduction or survival data were not included in the matrix-based population projections.

We used a matrix population model (MPM) to calculate the asymptotic population growth rate ( $\lambda$ ) for the two scenarios (Current and Future) for each study population. We constructed an  $n \times n$  postbreeding matrix, where  $n$  is the age at first reproduction. We parameterized the MPMs with the following demographic rates: juvenile survival ( $\Phi_{ju}$ ), immature survival until age at first breeding ( $\Phi_{im}$ ), breeding adult survival ( $\Phi_{ad}$ ), and reproduction ( $F$ ). Age at first breeding was specified as three for little auks, four for black-legged kittiwakes, five for Atlantic puffins and Brünnich's guillemots and six for common guillemots (following 58). The following matrix is for little auks ( $3 \times 3$ ):

$$\begin{bmatrix} 0 & 0 & F\Phi_{ad}0.5 \\ \Phi_{ju} & 0 & 0 \\ 0 & \Phi_{im} & \Phi_{ad} \end{bmatrix}.$$

$\Phi_{ju}$  represents survival from fledging to first year and  $\Phi_{im}$  from age one to the age at first breeding. Estimates of immature survival and breeding propensity were lacking. We therefore assumed all adults bred every year, which is unlikely; however, many seabird studies have also made this assumption given the lack of data (59). We assumed first year, postfledging survival to be 75% that of adults and immature survival to be 87.5%, following an analysis of immature black-legged kittiwakes (60). This is further supported by other studies, which have found juvenile survival rates to be the lowest across all age classes, followed by immatures, with adults having the highest survival rates. However, this is a conservative estimate as immature survival tends to approach that of adults as individuals approach maturity (61). Matrices were created for 100,000 iterations, based on the modeled uncertainties in demographic rates, to give 100,000  $\lambda$ s for each population, from which a mean and 95% CI were calculated.

**Data, Materials, and Software Availability.** The data and code to run the analyses have been deposited in Zenodo (62).

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