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ARTICLE

Climate Ecology

An ice-obligate seabird responds to a multi-decadal decline in Arctic sea ice

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Abstract

The Arctic has experienced greatly decreased sea ice and increased ocean temperatures in recent decades but there is a paucity of biological time-series data allowing assessment of resulting temporal variation in the region's marine ecosystems. Seabirds, as highly mobile and highly visible, upper trophic-level predators, can be valuable monitors of modifications in marine ecosystems, especially for regions lacking commercial fisheries or regular oceanographic sampling. Since 1975, we have studied annually an Arctic Alaskan colony of Mandt's black guillemot (*Cepphus grylle mandtii*), an ice-obligate diving seabird, specializing on Arctic cod (*Boreogadus saida*), the primary forage fish of the ice-associated cryopelagic ecosystem. Using multi-state capture–mark–recapture models, matrix population models, and perturbation analysis, we quantified the environmental and demographic drivers of population change from 1980 to 2019 for the individually marked population. The colony increased rapidly, from <20 to >200 breeding pairs from 1975 to 1990 in response to increased availability of nesting cavities, before experiencing intermittent declines to <50 pairs in 2021. Immigration and apparent survival were the primary demographic parameters affecting population growth with sea ice extent in late summer and fall the primary environmental driver. The initial growth occurred during a period of primarily negative winter Arctic Oscillations (WAO) and extensive summer sea ice. The decline began when an extremely positive WAO in 1989/1990 initiated changes in atmospheric and oceanographic circulation causing major reductions in summer sea ice throughout the region. The three-decade decline in the population saw plateaus or minor growth with increasing frequency of negative WAOs and increasing declines following two previously identified “tipping points” in sea ice loss. Breeding success at the study colony declined with decreased availability of Arctic cod due to sea ice loss and increasing sea surface temperature and is presumed to have occurred at the source colonies for immigrants where similar oceanographic changes were occurring. Quasi-extinction of the colony (reduction to <25 pairs) is predicted within the next two decades. The sensitivity of Mandt's black guillemot to multi-decadal changes in the

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Arctic's cryopelagic ecosystem makes it an excellent sentinel species for the region with its recent collapse having dire implications for the Arctic Ocean's constituent species.

KEYWORDS

Arctic Oscillation, breeding, capture–recapture, *Cephus grylle mandtii*, climate change, demography, immigration, long-term study, Mandt's black guillemot, matrix population models, population dynamics, population growth rate, survival

INTRODUCTION

The disappearance of Arctic sea ice due to climate change is one of the largest losses of habitat on the planet from increasing atmospheric temperatures, with a 50% reduction, a loss of >3.5 million km², in sea ice extent in September since 1980 (<https://climate.nasa.gov/vital-signs/arctic-sea-ice/>). The most immediate and negative biological effects of this habitat loss would be expected to be on the unique sympagic (ice-associated) ecosystem associated with Arctic sea ice, composed of species with life histories and distributions shaped by the long-term temporal and spatial patterns of the ice (Wassmann 2011, Macias-Fauria and Post 2018). This cryopelagic ecosystem consists of specialized microalgae, adapted to a low-light, sub-zero environment growing in and attached to sea ice (Kohlbach et al. 2016), that support an under-ice fauna of zooplankton (Lonne and Gulliksen 1991) preyed on by Arctic cod (*Boreogadus saida*) (Kohlbach et al. 2017). Arctic cod is a lipid-rich forage fish occupying both pelagic and demersal habitats and historically provided more than 70% of the energy transfer to piscivorous fish, seabirds and marine mammals in some regions of the Arctic (Geoffroy et al. 2023).

Increasing ice melt has reduced the spatial and temporal distribution of the Arctic's cryopelagic ecosystem while also causing a concurrent reduction in habitat quality, as thicker multi-year ice has been replaced by thinner first-year ice (Maslanik et al. 2007, Maslanik et al. 2011, Stroeve and Notz 2018). Ice age and thickness affects the abundance and diversity of the under-ice biota (David et al. 2016, Ehrlich et al. 2020, Hop et al. 2020, Hop et al. 2021) as multi-year ice allows establishment of a relatively constant sympagic community, as opposed to annual reestablishment under first-year ice (Ehrlich et al. 2020). Arctic cod are more abundant in areas with older thicker ice (Geoffroy et al. 2023), due to both the increased prey availability and the deeper and more irregular ice subsurface facilitating avoidance of predators (Gradinger and Bluhm 2004). Due to both the remoteness of the region and the logistical constraints of sampling the sea ice environment, there has been a lack of

biological time-series data allowing assessment of the effects of the recent ice reductions on the Arctic's cryopelagic ecosystem.

We report here on the multi-decadal variation of a population of one cryopelagic indicator species, the Mandt's black guillemot (*Cephus grylle mandtii*; hereafter MBG), a diving upper-trophic level marine predator, and one of the few Arctic ice-obligate seabirds. Its population and demographic processes have been monitored at the study colony on Cooper Island, Alaska, annually since 1975. Seabirds, as mobile, upper-trophic level predators, are sensitive to spatial and temporal variation in prey availability and ultimately to variation in their food webs (Sydeman et al., 2015). Their relative accessibility compared to most marine organisms make them excellent monitors of ecosystem status (Furness & Camphuysen, 1997; Weimerskirch et al., 2003). Acquisition of longitudinal datasets on seabirds is facilitated by their conspicuousness and breeding in colonies occupied annually (Velarde et al., 2019). Changes in seabird population size, breeding success, and distribution can be among the first indicators of fluctuations in a marine ecosystem (Barbraud et al., 2018; Crawford et al., 2019; Piatt et al., 2007; Velarde et al., 2015). Documenting their variations is especially important for marine waters that are poorly sampled scientifically, or have no commercial fishery (Hazen et al., 2019), as with the Southern Ocean, in which an ecosystem monitoring program based on upper-level predators was devised (Croxall & Nicol, 2004).

MBG frequent sea ice throughout their annual cycle, typically breeding at colonies in close proximity to the marginal ice zone (MIZ) where sea ice concentration (SIC) varies between 15% and 80% (Strong & Rigor, 2013). The MIZ is occupied by nonbreeding MBG in summer and all age classes during the nonbreeding season (Divoky et al., 2016). The species' preferred prey in the Western Arctic is Arctic cod (*Boreogadus saida*), a lipid-rich forage fish associated with Arctic sea ice that historically supplied approximately 90% of the energy transfer to seabirds and marine mammals in High Arctic marine food webs (Welch et al., 1993). The importance of the cryopelagic ecosystem to MBG is exhibited by the

sensitivity of MBG's breeding success and chick growth and survival to Arctic cod availability (Divoky et al., 2015), a high dependence on productivity from ice algae (Budge et al., 2008), an increased diving effort in response to a decline and absence of sea ice and Arctic cod (Divoky et al., 2021), and the dependence of nonbreeders on the MIZ in summer (Divoky, 1987) and all birds during the nonbreeding season (Divoky et al., 2016). Unlike most Arctic seabirds, MBG is nonmigratory, having only facultative post-breeding movements in response to sea ice formation in the Chukchi and Bering seas (Divoky et al., 2016). These characteristics potentially make the MBG an excellent indicator of temporal alternations in the middle trophic level portion of the sea-ice Arctic ecosystem (Hazen et al., 2019).

Here, we examine the population dynamics and demographic processes of an MBG population in the western Beaufort Sea in response to atmospheric, oceanic, and cryospheric changes over a 47-year period. Our effort involves the modeling analysis of capture–recapture and population census data. The population has demonstrated a sensitivity to cryospheric changes since its establishment in the 1960s, when atmospheric warming reduced snow cover facilitating colonization by increasing the annual period birds had access to ground-level nest cavities, and by advancing breeding phenology in response to earlier snowmelt (Cox et al., 2017). Our dataset, initiated before the period before the onset of rapid environmental change in the Arctic in the late 20th century (Landrum & Holland, 2020), possesses annual observations conducted over nearly half a century.

Our objectives were to: (1) determine the large-scale atmospheric and oceanographic features affecting or correlated with the population's growth; (2) estimate the importance of five key demographic parameters to population change: survival, breeding probability, breeding success, probability to fledge two chicks, immigration rate, while accounting for age and breeding status; (3) assess the degree of correlation of the above demographic factors with annual climatic, oceanographic, and cryospheric factors and species interactions; (4) estimate the relative contribution of demographic parameters and environmental factors to variation in population growth rates during periods of colony increase and decrease; and (5) predict the future trajectory of the colony in terms of quasi-extinction.

Given the strong dependence of MBG on the cryopelagic ecosystem, we hypothesized that sea ice variables and the factors affecting their annual variation would be major drivers of population dynamics and demographic parameters. We also hypothesized that immigration would be an important factor in variation of colony growth given the extremely rapid initial increase

following provision of nest sites in the 1970s and 1980s, that could not be due to local productivity and indicated high breeding productivity at the source colonies of immigrants and a “floating population” (Penteriani et al., 2011) limited in recruitment by nest site availability (Divoky et al., 2015).

MATERIALS AND METHODS

Study species

MBG is the High Arctic subspecies of the black guillemot, which is found in the North Atlantic and Arctic oceans (Butler et al., 2020). It is one of the few Arctic ice-obligate seabirds, apparently due to their being restricted to an unglaciated part of the Arctic Ocean during the Last Glacial Maximum (Kidd & Friesen, 1998). It breeds in the Arctic Basin from the Canadian Beaufort Sea west to Spitsbergen (Storer, 1952) in close proximity to sea ice, and utilizes the MIZ in both the Bering Sea (Divoky et al., 2016) and Atlantic (Mosbech & Johnson, 1999; Renaud & Bradstreet, 1980) during the winter.

Cephus guillemots are cavity-nesting, primarily piscivorous wing-propelled divers whose life history traits differ from those of more pelagic and more highly colonial seabird species in several ways. They utilize the littoral zone during breeding typically feeding on demersal prey, which provides a more accessible and spatially predictable prey base (Litzow et al., 2004), than the pelagic prey of most seabirds (Weimerskirch, 2007). Feeding in relatively close proximity to the nest allows them to have a 2-egg clutch, unlike the typical single egg clutch of highly pelagic seabirds, especially petrels and albatross. Parents provision nestlings with a single fish per foraging trip, with a temporally reliable prey base within the <13 km foraging range required for successful breeding. Reliance on nearshore prey has resulted in black guillemots limited to shallow dives of short duration, with dives typically <30 m (Divoky et al., 2021; Shoji et al., 2015) restricting their ability to exploit prey deeper in the water column. They are semicolonial when breeding, frequently nesting as single pairs but with colonies occasionally limited by nest-site availability (Ainley et al., 1990; Petersen, 1981; Preston, 1968), which can result in a high percentage (50%–60%) of nonbreeders at some colonies (Ewins, 1985). Colony size for the genus may also be limited by density-dependent effects of prey availability in the extremely limited foraging range for a seabird (Cairns, 1987; Shoji et al., 2015).

The birds breeding on Cooper Island winter in the MIZ of the Bering Sea (Divoky et al., 2016) and make a directed migration over the sea ice in April to the

predictable lead system occurring west of Point Barrow. There they undergo a partial molt into breeding plumage in April and early May. Occupation of the study colony begins in early to mid-June, and is dependent on timing of snowmelt with the first eggs in the colony laid approximately two weeks after snow melt (Cox et al., 2017), indicating ovulation occurs with access to a nest cavity. Hatching occurs an average of 28 days after the typical 2-egg clutch is complete. Nestlings are provisioned by both parents for approximately 35 days with young becoming independent upon fledging. During the breeding season, nonbreeding birds occupying the MIZ in the Chukchi Sea are assumed to be primarily prebreeders <3 years and estimated to number 70,000 in the 1970s (Divoky, 1987). After breeding ends in late August or early September, birds depart the colony and move north to sea ice-associated waters, and undergo a molt of all body and flight feathers, rendering them flightless for as much as five weeks (Ewins, 1988). In late October and early November, there is a facultative migration south through the Chukchi Sea with the fall advance of the MIZ, typically entering the Bering Sea in December and remaining in the Bering MIZ until they fly north in April.

Study area and colony

Study area

The present investigation involves the MBG population that nests on Cooper Island, in the coastal Beaufort Sea, 30 km east of Point Barrow, Alaska (Figure 1). More detail is provided below, but in summary, the Western Arctic metapopulation of MBG occupies the Beaufort, Chukchi and East Siberian seas from approximately April to November moving south through the Chukchi Sea into the subarctic Bering Sea in response to sea ice formation north of the Bering Strait (Divoky et al., 2016). The three seas occupied in summer all have extensive shelf areas and complete ice cover for approximately 6–7 months annually, with major ice retreat occurring from June to late September. Ice advancement occurs in October and November, with the timing and extent of both having recent major annual variation. During the course of our study there were major changes in the region's marine environment driven by large-scale atmospheric and oceanographic processes, described below.

Oceanographic setting

Pacific Water entering the Arctic Basin through the Bering Strait has a major effect on the physical and biological

oceanography of the region (Woodgate et al., 2015), introducing warmer temperatures ($>5^{\circ}\text{C}$), nutrients, and Pacific-Bering zooplankton (Ashjian et al., 2021). This causes the Chukchi Sea to be more subarctic in nature with a longer period of open water annually and higher biological productivity and diversity than the adjacent Beaufort and East Siberian seas, where SST is typically $<5^{\circ}\text{C}$. Importantly, the area directly adjacent to our study population in the extreme western Beaufort Sea has its physical and biological oceanography affected by the advection of Pacific Water past Point Barrow, making the region more productive than neighboring waters. The flow of Pacific Water through Barrow Canyon, which straddles the boundary between the Chukchi and Beaufort seas, creates a nutrient-rich upwelling that increases local productivity (Beaird et al., 2020; Citta et al., 2015; Forster et al., 2020; Pisareva et al., 2019) east of Point Barrow and north of Cooper Island. Additionally, the convergence of the eastward-flowing Pacific Water with a westward-flowing current in the Beaufort creates episodic concentrations of zooplankton north of our study colony that are an important food source for bowhead whales (*Balaena mysticetus*) (Okkonen et al., 2011) and migrating seabirds (Divoky, 1984). The Bering Sea wintering area occupied by the study species from December to April, when the adjacent Arctic Ocean is heavily ice-covered, differs from the Arctic breeding area in being a subarctic sea, with higher marine productivity and diversity.

During our study, the seas occupied by MBG during summer have experienced major loss of sea ice, for example, September extent reduced by an average of 84%, from 1979 to 2018 (Stroeve & Notz, 2018). While decreases in September ice extent for the entire Arctic Ocean have had a linear relationship with cumulative anthropogenic CO_2 emissions (Notz & Stroeve, 2016), reductions in the Western Arctic have been highly episodic due to the effects of temporal variation in atmospheric and oceanographic circulation. Chief among these is the winter (November–April) Arctic Oscillation (WAO), an index of atmospheric circulation over the Arctic, which alternates between two distinct modes and describes variation in the pressure patterns over the Arctic and lower latitudes. In the WAO's negative (cold) phase, higher pressure in the Arctic maintains cold air in the region and winds and ice exhibit an anticyclonic movement maintaining older and thicker ice in the region. In the positive (warm) WAO phase, higher pressure at mid-latitudes brings warmer air northward with winds in the Arctic in a cyclonic mode that transports ice out of the area through Fram Strait. Ultimately this leads to a negative correlation in summer ice extent with the WAO of the previous winter (Rigor & Wallace, 2004; Williams et al., 2016).

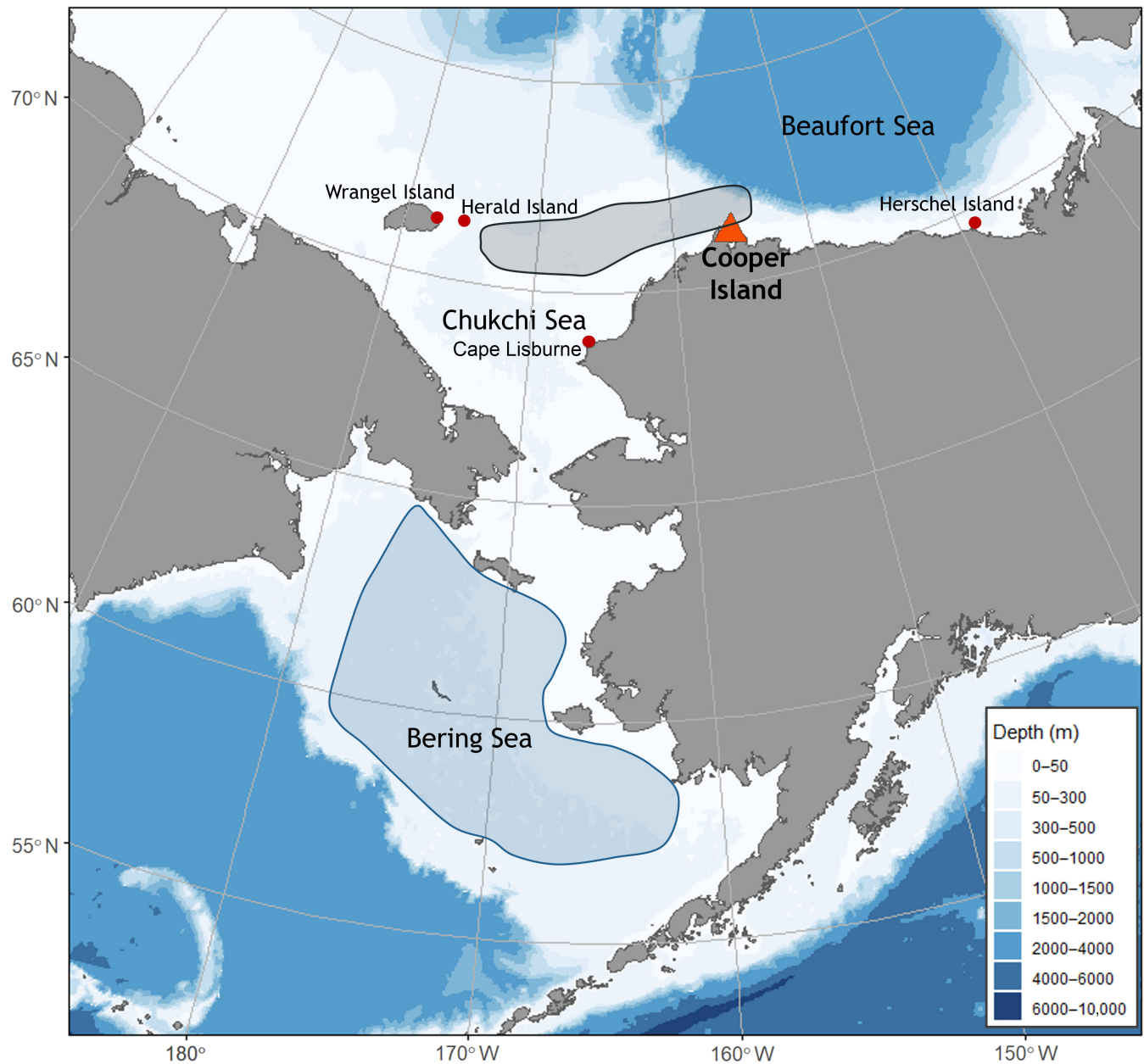


FIGURE 1 Western Arctic showing the location of the Cooper Island study colony, the presumed source colonies on Herald and Wrangel Islands and the two colonies also monitored, Cape Lisburne and Herschel Island. Delimited gray area shows location of summering (July–August) location of nonbreeding birds and fall (September–November) location of breeders. Delimited light blue area shows Bering Sea wintering (December–April) area.

The initial period of our study, 1975–1989, and the preceding decades, were dominated by years with negative WAOs (Appendix S1: Figure S1), that maintained cold air temperatures and high concentrations of multi-year ice in the region. That period ended abruptly with an extremely positive AO index during the winter of 1989/1990 (Thompson & Wallace, 1998) with the resulting decreased sea level pressure and subsequent wind anomalies modifying the size and direction of the Beaufort Gyre. That caused increased advection of multi-year ice out of the

region (Babb et al., 2023; Rigor et al., 2002; Rigor & Wallace, 2004). This ice loss and associated increases in SST began a feedback loop of “Arctic amplification” leading to further reductions in summer sea ice (Williams et al., 2016), particularly reducing the extent of multi-year ice and ice thickness (Overland & Wang, 2010; Stroeve & Notz, 2018). This in turn resulted in increased atmospheric temperatures (Schaefer et al., 2005) and more extensive ice melt in summer. The 1989/1990 extremely high WAO was hypothesized as a climatic “tipping point” since

subsequent ice loss and thinning was driven by the warming associated with the resulting ice-albedo feedback (Lindsay & Zhang, 2005) and not driven by earlier forcing factors. Additionally, since 1989/1990, the WAO has averaged approximately one SD above the 1950–1988 average (Morison et al., 2021). Ensuing decreases in the WAO did not result in increased sea ice (Stroeve et al., 2005) or cooler temperatures indicating a decreasing influence of the WAO on sea ice extent (Maslanik et al., 2007; Ogi et al., 2016) for the remainder of our study.

In addition to the changes caused by the 1989/1990 WAO regime shift reducing sea ice, waters overlying the Chukchi continental shelf began to warm in the early 1990s. While these waters showed a significant century-long increase from 1922 to 2018 of 1.4°C ($0.14 \pm 0.07^{\circ}\text{C}/\text{decade}$), the warming rate tripled to $0.43 \pm 0.35^{\circ}\text{C}/\text{decade}$ from 1990 to 2018 (Danielson et al., 2020). This latter change was due, in part, to increases in the amount and temperature of Pacific Water entering the Chukchi Sea, $0.27 \pm 0.23^{\circ}\text{C}/\text{decade}$ from 1991 to 2015 (Woodgate, 2018). The SST increase, thus, was not just from increased solar radiance on seawater due to the decreases in sea ice. The 1990 demarcation was also when sea ice thickness throughout the Arctic Ocean began a major and ongoing decline (Kwok, 2018; Li & Yin, 2020). Another identified tipping point for sea ice in the Arctic (Livina & Lenton, 2013), including the Beaufort Sea (Moore et al., 2022), occurred in 2007 when September extent for the entire Arctic Ocean reached an unprecedented low, primarily due to preceding multi-decadal thinning and decrease in extent in the Western Arctic (Lindsay et al., 2009; Overland et al., 2012) and an anonymously high export of multi-year ice coupled with low replenishment (Babb et al., 2023; Kwok, 2008; Sumata et al., 2023). Subsequent years saw reduced summer sea ice extent and thickness, and increased atmospheric temperature anomalies, compared to previous decades, driven, in part, by a persistent change in early summer Arctic wind patterns (Livina & Lenton, 2013; Mahoney et al., 2019). Additionally, in 2007 the annual mean transport and temperature of flow through the Bering Strait had record highs (Woodgate et al., 2010).

Unlike the major decadal declines in MBG's sea ice habitat in Arctic waters from April to December (breeding/molting season), sea ice extent in the subarctic Bering Sea wintering area was relatively stable during most of our study period, even increasing slightly from 1979 to 2012, despite much variation, for example, March maximum extent ranged from 307,000 to 790,000 km^2 (Wendler et al., 2013). However, in 2017 a change in atmospheric conditions occurred with increased southerly winds reducing Bering Sea ice extent to a record low

(Stabeno & Bell, 2019). This was considered to be the beginning of a long-term regime shift with increasing frequency of warm events predicted to continue for at least the next decade (Ballinger & Overland, 2022). The Bering Sea Cold Pool, bottom water $<2^{\circ}\text{C}$ formed by the formation of sea ice, facilitates the movement of Arctic cod from the Chukchi to the Bering Sea shelf with Cold Pool location and size dependent on the extent of winter sea ice in the Bering Sea (Clement Kinney et al., 2022; De Robertis et al., 2017). Decreased sea ice in the Bering would reduce both the MBG's sea ice habitat and their preferred prey.

The physical oceanography changes reviewed above have resulted in the transformation of the Chukchi Sea marine ecosystem with range retractions and decreased abundance of Arctic species and range expansions and increased abundance of subarctic species (Gall et al., 2017; Huntington et al., 2020). While the biological effects of the 1989/1990 WAO shift have been documented for species and ecosystems in the North Pacific and Bering Sea (Beamish et al., 1999; Benson & Trites, 2002; Hare & Mantua, 2000) the effects in the Arctic and the impact of the other identified environmental tipping points in 2007 and 2017 on Arctic species are less known due, in large part, to a lack of time series data including the period of the transition. The above extreme decreases in the sea ice habitat and subsequent increases in SST could be expected to cause major reductions in the abundance and availability of Arctic cod, the MBG prime prey species, throughout the MBG range in the Western Arctic (Baker, 2021). Lacking any long-term time series of Arctic cod prevalence anywhere in the Arctic, it remains for MBG, as an indicator species, to quantify its relative status.

Study colony

Cooper Island ($71^{\circ}20' \text{ N}$, $155^{\circ}41' \text{ W}$) (Figure 1) is a low ($<2 \text{ m}$ above sea level [asl]) sand and gravel barrier island lacking the rock cliff and talus habitat that typically provides nesting cavities to *Cephus* guillemots. It is in the middle of 1600 km of shoreline lacking natural cavities and consisting of low eroding tundra bluffs with nearshore depositional barrier islands. All nests in the study colony are in ground-level manmade structures, providing investigators access to breeding adults and all nest contents (Divoky, 1998; Divoky et al., 2015). Their location at ground level makes the phenology of the colony more sensitive to snow cover than cliff or talus colonies as snow blocking nest entrances restricts the birds' access for approximately nine months per year.

The colony was discovered in 1972 when 10 pairs were found nesting in boxes and other wood debris left

by the US Navy in the late 1950s (Divoky et al., 1974). Subsequently, from 1975 to 1984, 200 nest sites were created using additional material left by the Navy. After polar bear (*Ursus maritimus*) disturbance to nest sites increased in the early 21st century due to decreases in sea ice (Wilson et al., 2017), all nest sites were replaced with modified plastic Nanuk Cases (Plasticase, Montreal).

Field methodology

Since 1975, the majority of breeding adults and all fledging chicks have been banded for individual identification. Adult birds were captured either by hand or with a net while exiting the nest or with mats of monofilament snares placed adjacent to nests or at a communal roosting site. Birds were placed in a cloth bag within 30 s after capture and held <5 min while being banded and measured. Adults were given a numbered USGS metal band and a unique combination of three color bands to allow identification with binoculars. Nestlings were given a USGS band and single cohort year identifier. From 1975 to 2019, 4045 fledglings were banded and 729 later captured as adults and given a unique color-band combination. These individuals provide age-specific demographic information of breeding parameters. Age is defined as the number of calendar years since fledging. Of the 2140 adults banded, 1411 were unbanded at capture and are primarily immigrants, the exception being returning unbanded native birds fledging before 1975. Their contribution would be small given the size of the colony before our study and limited to the initial years of the study.

On average, 18% of banded adults attending the colony each year were nonbreeders but contributed a substantial portion, up to 44% in 1986, because recruitment was limited by nest-site availability (Figure 2). The nonbreeding component of the colony was comprised of: (1) floaters, defined as mature individuals, prevented from breeding due to lack of a nest site or mate; (2) paired individuals that occupied a nest site where eggs were not laid; and (3) immatures, defined as individuals younger than breeding age (3 years).

Breeding birds or nonbreeders occupying nest sites are much easier to capture than floaters, and the age of capture and the percentage of a returning cohort captured are dependent on recruitment opportunities available and banding effort when a cohort reaches breeding age.

To provide data on annual survival, all banded birds occupying or adjacent to nest sites or attending communal roosting areas were identified during daily censuses of the colony before and during the incubation period, when attendance and activity outside nest sites were highest. Resighting of banded birds was also done opportunistically

during daily nest checks during the nestling period. The total number of nonbreeders, both banded and unbanded, was obtained through regular censusing during the breeding season. Our methodology assumes no loss of a metal band as no bird was seen with only color bands and no metal band. Individuals losing color plastic bands were recaptured and rebanded. Breeding parameters were obtained from daily checks of all active nests during clutch initiation, incubation, and the nestling period.

Demographic and population modeling

We conducted data analyses in four steps. First, because the study was initiated in 1975, prior to satellite monitoring of environmental variables, we described and examined the trajectory of colony size and the effect of available environmental factors from 1975 to 2021. Second, we modeled and estimated demographic parameters using multi-state capture–recapture models for 1980–2019. Third, we built a matrix population model based on estimated demographic parameters to model population growth rate for 1980–2019, performed a Life Table Response Experiment (LTRE) to determine the contribution of each demographic parameter to variation of population growth, and estimated quasi-extinction probabilities (Caswell, 2001). Fourth, we tested for relationships between environmental covariates and demographic parameters for the years 1980–2019, and based on significant relationships, used our matrix population model to determine the contribution of each environmental covariate to variation of population growth.

Trajectory of colony size

We examined variation in population growth rate in response to the WAO (average of monthly values December–March) and climatological and oceanographic “tipping points” documented for the period of our study and described above. Observed population growth rate was calculated as $\lambda_{\text{obs}} = (N_t/N_0)^{1/T}$, where N_0 is the number of breeding pairs at the time when the first count was made, N_t the number at the end of the same period, and T the number of years elapsed between 0 and t (Caughley, 1977). We determined the relationship of λ_{obs} with the previous WAO and also examined the effect of WAO phase during four identified periods of growth (1975–1990, 1991–1998, 1999–2006, 2007–2021). For the latter, we treated the WAO as a binary factor (positive or negative), as done elsewhere (Pilfold et al., 2015), comparing the percentage of years with a negative phase with λ_{obs} during the period. We also examined the effect of identified

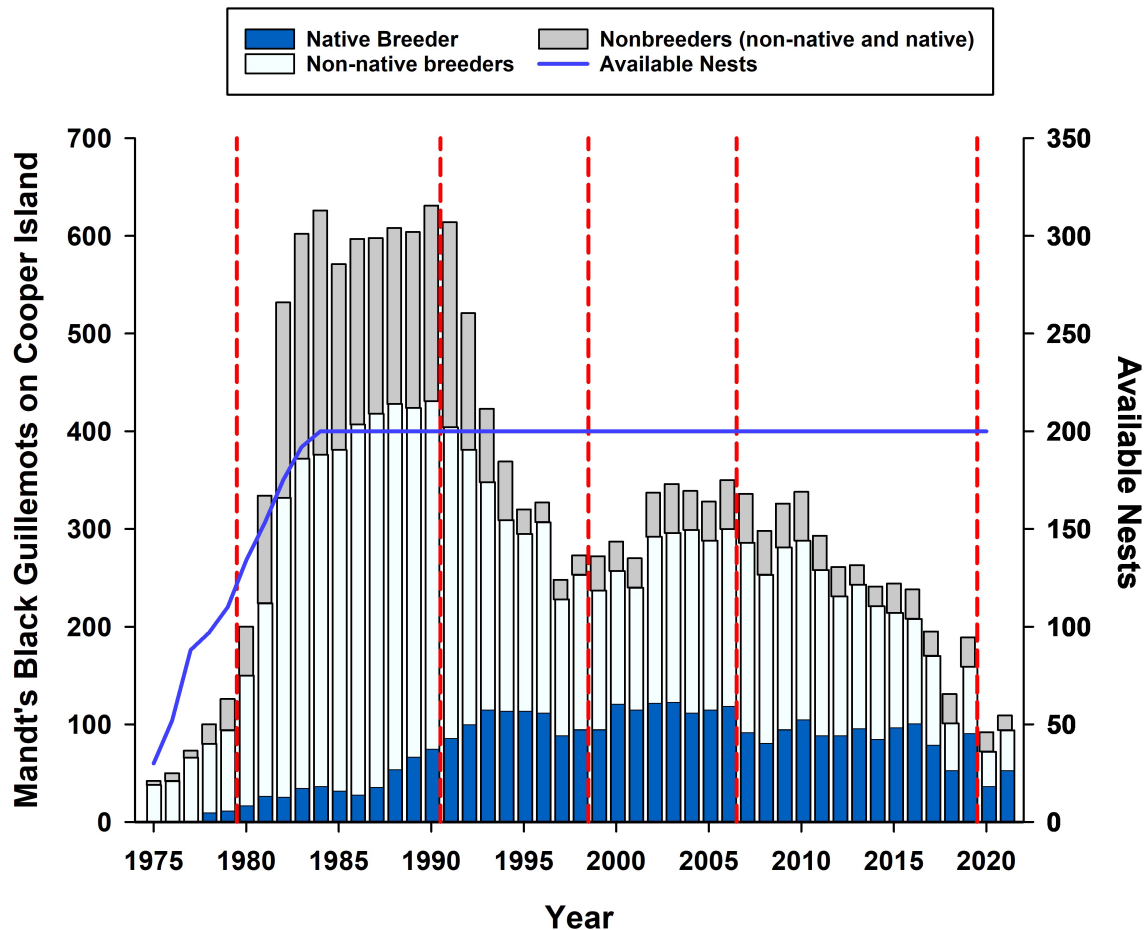


FIGURE 2 Mandt's black guillemot population (bars) and number of available nest sites (blue line) on Cooper Island 1975–2021. Native birds are individuals banded on Cooper Island as fledglings with all fledglings banded since 1975. Non-native birds are individuals captured and banded as adults. Dashed red lines indicate the four periods (1980–1990, 1990–1998, 1998–2006, 2006–2019) used in population modeling. Breeding pairs exceeded nest sites when multiple pairs bred in a single site and all nest sites were occupied (1986–1990).

oceanographic and cryospheric tipping points in the region's sea ice occurring in 1990, 2007, and 2016 as described above.

Modeling demographic parameters

The capture histories of MBG were used in a multi-state capture–recapture model (Brownie et al., 1993; Lebreton et al., 2009) to estimate demographic parameters. Except for initial banding of nestlings and their recapture as adults for color banding for individual identification, and initial capture of unbanded adults (immigrants) all subsequent “captures” refer to observations. The capture history of each individual was summarized by considering 40 occasions of capture (1980–2019), one occasion corresponding to one breeding season. We initially sought to develop a model that best fit our capture–recapture data by considering the effect of intrinsic factors known to affect the demographic parameters of long-lived birds:

previous breeding state and age (Pardo et al., 2014). Those parameters are linked because the probability of leaving inexperienced nonbreeder state (recruiting into the breeding population) increases with age, and all known-age individuals are local birds banded as nestlings on Cooper Island. We thus began performing model selection considering only the 4045 individuals banded as chicks to determine how to consider the effect of age and previous breeding state on demographic parameters.

Based on field observations, an individual was assigned to one of five states for a given breeding season:

1. inexperienced nonbreeder—an individual that had not previously bred and was not breeding;
2. adult nonbreeder—an individual that had previously bred and was not breeding;
3. failed breeder—an individual occupying a nest where eggs were laid but fledging did not occur;
4. breeder fledging one chick—an individual that fledged one chick; or

5. breeder fledging two chicks—an individual that fledged two chicks.

Adults could have any of the last four states, while individuals banded as chicks were considered inexperienced nonbreeders during their year of fledging and before recapture as a returning adult. We estimated the following demographic parameters:

1. apparent survival probability (ϕ)—probability of an individual surviving between year t and $t + 1$ given it was alive in year t . As no observation of banded birds were performed elsewhere, annual survival was considered as apparent since mortality and permanent emigration could not be separated;
2. breeding probability (β)—probability of an individual occupying a nest with at least one egg in year $t + 1$ given that it survived between year t and $t + 1$;
3. success probability (γ)—probability of an individual fledging as least one chick in year $t + 1$ given that it survived between year t and $t + 1$ and reproduced in year $t + 1$;
4. probability of fledging two chicks (δ)—probability of an individual fledging two chicks in year $t + 1$ given that it survived between year t and $t + 1$, reproduced in year $t + 1$ and was successful in year $t + 1$.

Inexperienced nonbreeders that never occupied a nest where egg laying occurred remained in the same state. Individuals that had previously bred but did not occupy a nest where eggs were laid in the current year, were considered experienced nonbreeders for that year. Details of the transition matrices are presented in Appendix S1: Table S3.

We constructed an initial model considering only the effect of every previous breeding state for every demographic parameter, and an effect of both time (in years) and previous state for detection. Effect of time was only considered additively for detection to keep a reasonable computation time and to allow estimation of all parameters. We then performed model selection in this order: detection (p), survival (ϕ), breeding probability (β), success probability (γ), probability to fledge two chicks (δ). We always kept the best model of previous model selection before modeling a new demographic parameter. Model selection was performed using the Akaike information criterion (AIC) (Burnham & Anderson, 2002), and started by aggregating the effect of state in five different classes and determining which aggregation would most decrease the AIC of the model: (1) every state differentiated, (2) inexperienced nonbreeders versus experienced birds, (3) nonbreeders versus breeders, (4) inexperienced nonbreeders versus adult nonbreeders

versus breeders, and (5) inexperienced nonbreeders versus adult nonbreeders versus failed breeders versus successful breeders. Age was then added in interaction with state in the best model, considering every age from 0 to 28 years (the longest-lived individual in our dataset being 28 years old, one year less than the longevity record for this species; Fransson et al., 2017). If adding age did not improve the AIC, model selection stopped at that point and only the effect of previous state was considered. If not, the highest age classes were progressively aggregated, one year by one year, until the difference between the AIC of the current model and the lowest AIC was higher than 4. Then, the highest age classes were aggregated according to the model with the lowest AIC, and we proceeded with the same method as for the lowest age classes. Once age classes for oldest and youngest individuals were defined, we tested a model aggregating all of the intermediate ages to see if it improved the AIC of the model. Finally, the model with the lowest AIC was kept as the best model, and model selection continued until all of the demographic parameters were considered. The complete list of tested models is presented in Appendix S1: Table S4.

Once the best fit was found for every parameter, interactions between previous state and age not present in the dataset (and, thus, considered as unidentifiable parameters) were removed from the model. Since the minimum age of first breeding is three, breeding probability, success probability and the probability to fledge two chicks for breeders of age two or less and for adult nonbreeders of age three or less were fixed to 0.

The age of individuals captured as unbanded adults, which were exclusively immigrants for the years included in this model, was unknown, and including these individuals in the model would require some assumptions. Breeding dispersal, a previously breeding bird breeding at another colony, is rare for *Cephus* species and other alcids (Divoky & Horton, 1995), and individuals banded as adults (immigrants) were considered as inexperienced nonbreeders until their first observed nesting attempt. We considered three possibilities for the age of individuals banded as adults: (1) most were in the oldest age class for each demographic parameter; (2) most were four years old, which is the median observed age of first recapture for individuals banded as chicks on Cooper Island; and (3) most were two years old, since black guillemots of this age disperse farther from the natal colony than older birds (Petersen, 1981), potentially prospecting for nest sites. We ran models reflecting the three possibilities and chose the assumption exhibiting the best fit to our dataset (based on AIC).

Goodness-of-fit tests of the multi-state capture–recapture model were performed in U-CARE (Choquet et al., 2009a). Minimization of the likelihood in E-SURGE

2.1.4 (Choquet et al., 2009b) was done with a hybrid algorithm, composed of four cycles of 20 iterations of an Expectation–Maximization followed by 200 iterations of a quasi-Newton algorithm, to obtain an acceptable convergence and avoid local minima.

Demographic parameters modeled using the capture histories of MBG did not provide a full understanding of the population dynamic, which also depends on immigration and emigration. The survival estimated using capture histories was the apparent survival, thus taking into account death and permanent emigration of adults. Immigration was not considered in the capture–recapture analysis and is needed to model the growth rate of the population. Immigration rate (i) was calculated for each year as the number of immigrants (individuals banded as adults for the first time in the colony) divided by the number of adult residents (adults that were already seen at least once in the colony).

Matrix population model and LTRE analysis

We created a projection matrix that modeled the annual population growth rate from 1980 to 2019 based on the demographic parameters determined earlier. The number of age/state classes and estimates of demographic parameters (ϕ , β , γ , and δ) were determined by the capture–recapture modeling of the entire dataset, including individuals banded as adults. Immigration was included in the projection matrix by creating the state “immigrant.” The number of immigrants at year $t + 1$ was determined by applying the immigration rate multiplied by the survival rate to each state and age at year t . The number of immigrants at year $t + 1$ by age and state was then computed for different ages and states according to the proportion of captured returning chicks (see Appendix S1: Figure S2). We then used the values of the demographic parameters of residents to estimate their contribution to the population at $t + 2$. Appendix S1: Figure S3 presents a life cycle graph of this projection matrix. All of the demographic parameters were collected into a parameter vector, noted θ .

The first five years (1975–1979) of monitoring the colony were excluded from this model analysis for two reasons: (1) individuals originally captured as adults in those years could be immigrants as well as the few locals fledging in breeding seasons before banding was initiated in 1975 (see *Field methodology*), and (2) most environmental covariates were obtained by satellite and not available before 1980. It is important to note that exclusion of those years omits a period of rapid increase in the breeding population from 38 birds in

1975 to 150 in 1980 in response to the provision of nest sites. Additionally, this model does not include observations from 2020 to 2021, obtained after modeling was completed.

Using the R package *popbio*, the dominant eigenvalue of the projection matrix was extracted, giving the growth rate of the population λ . The relative influence of each demographic parameter on growth rate, that is, their sensitivity $\delta\lambda/\delta\theta$, as well as their elasticity, that is, the relative sensitivity, were also computed. Using the same package and applying the Caswell method (Caswell, 2001) on the projection matrix, we also measured generation time, that is, the mean time for a generation to be replaced by the next one. Immigrant state was excluded from the matrix when computing this metric.

To model the population long-term trajectory (Figure 2) we identified four periods for the years included in the model:

1. 1980–1990: last part of initial growth followed by reduced growth due to nest-site availability;
2. 1990–1998: initial decline and start of period with nest-site availability not constraining growth;
3. 1998–2006: minor increase and plateau; and
4. 2006–2019: recent and ongoing decline.

We estimated demographic parameters for each period independently to better understand temporal variations in population growth rate. We also performed a LTRE to determine the contribution of each demographic parameter to variation of population growth rate for each period. LTRE was performed by considering the growth rate over the entire monitoring period (1980–2019) as the reference. The difference between the growth rate of a given period (λ_t) and the reference growth rate (λ_r) can be approximated by

$$\lambda_t - \lambda_r \approx \sum_i (\theta_i^t - \theta_i^r) \times \frac{\partial \lambda}{\partial \theta_i},$$

with θ_i being one demographic parameter out of the parameter vector θ and sensitivity being calculated at the mean of the demographic parameters for the focal period and reference period (Hunter et al., 2010). Each term in the summation corresponds to the contribution of the demographic parameter to the difference between the growth rate of a given period and the growth rate of the whole monitoring period.

The time until quasi-extinction for the colony was calculated by simulating future population growth using the package *popbio* (Stubben & Milligan, 2007).

Quasi-extinction analysis estimates the probability of decline of a population below a pre-defined threshold (Ginzburg et al., 1982) or population size at which extinction becomes inevitable. It is a widely used risk metric for species conservation and management (Riquelme et al., 2020; Vincenzi & Mangel, 2014). *Cephus guillemots* are semicolonial, regularly breeding as single pairs and colonies frequently with <10 pairs, complicating the selection of a quasi-extinction threshold. We chose two thresholds of 5 pairs and 25 pairs, to determine timing to an 88% or 98% decline in the population from its peak in 1990 (Figure 2). Our objective was to estimate the timing of the colony reaching certain thresholds if colony decline continued at its current rate. We assumed an independently and identically distributed but stochastic environment and based our simulation on projection matrices obtained from 2006 to 2019. Projection matrices considered population structured in age and state, with the initial vector using the known repartition in age and state of the 2019 captured birds. The number of inexperienced nonbreeders recruiting after 2019 was estimated by summing fledglings from previous years that had not yet been seen as adults and applying appropriate survival rates.

Relationship of environmental demographic variables

Environmental variables

We considered 17 environmental covariates presumed to affect the population dynamic of MBG (Table 1). These included annual values for six meteorological covariates (air temperature, wind speed, snow disappearance), eight oceanographic variables (SIC, distance and extent and prey availability), two colony metrics (nestling abundance and loss of egg and young to predators and nest competitors) and a single atmospheric teleconnection, the Arctic Oscillation.

Environmental covariates were summarized over periods considered biologically meaningful in the MBG's annual cycle: *Incubation*—laying of the first egg to last hatching; *Nestling*—first hatching to last fledging; *Departure*—first fledging to 21 days later to include the period birds are moving north to the sea ice and also molting; *Fall*—end of the Departure period to 30 November, the approximate date birds leave the Chukchi Sea through the Bering Strait with the MIZ (Divoky et al., 2016); *Winter*—1 December to 15 April, the approximate date when birds begin a directed migration north to the Arctic Basin (Divoky et al., 2016). Table 1 details the period

considered for each environmental covariate, as well as the corresponding demographic parameter variation to be explained.

Meteorological observations were obtained from the National Weather Service (NWS) station in Utqiagvik, 30 km northwest of Cooper Island for breeding season covariates and from the Nome NWS station for the Bering Sea wintering area (NOAA/National Centers for Environmental Information [NCEI] www.ncdc.noaa.gov/). SIC data were obtained from the National Snow and Ice Data Center's (NSIDC) 25-km resolution Sea Ice Index version 3 (Fetterer et al., 2017) to determine the distance from the study colony to the closest pixel with SIC > 30% directly north of the island during that year's Nestling and Departure (fledging) periods. The species primarily occupies ice concentrations of 30%–60% in the MIZ (Divoky et al., 2016), which has concentrations of 15%–80% (Strong & Rigor, 2013). SIC data was also used to determine the proportion of days during the Incubation and Nestling periods that sea ice was present (>0% concentration) within 25 km of the colony.

August SIC adjacent to Herald Island, in the Chukchi Sea ~700 km west of the study colony, was obtained to assess oceanographic conditions during chick provisioning at the largest MBG colony in the Western Arctic (Artukhin, 2016; Birdlife International, 2021; Stishov, 2004) and the likely source colony for most immigrants to Cooper Island. Proximity of sea ice to the study colony during the nestling stage is positively correlated with breeding success and quality and parental energy expenditure (Divoky et al., 2015, 2021). August SIC adjacent to Herald Island was obtained from the Historical Sea Ice Atlas (Walsh et al., 2019) and averaged for the previous three years to obtain a proxy for the number of potential immigrants of breeding age for a given year. Sea ice extent for the Chukchi and Bering Sea was obtained from the NSIDC Daily Sea Ice index (Fetterer et al., 2017). The winter (December–March) Arctic Oscillation Index (Thompson & Wallace, 1998) was provided by the NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml).

Three biological covariates were used in the model. Nest Disturbance was the percentage of nests with eggs or chicks eaten or destroyed by nest predators, primarily Arctic fox (*Vulpes lagopus*) or polar bear (Cox et al., 2017) or broken or killed by a nest competitor, the horned puffin (*Fratercula corniculata*) (Divoky, 1982). Nestling abundance was the number of nests with nestlings where hatching occurred, and was a measure of the annual attractiveness of the colony to prospecting birds, potentially affecting immigration rate the following year (Boulinier et al., 1996). Arctic cod availability in the Bering Sea wintering area was measured with the percentage of

TABLE 1 Environmental variables used in analyses of Mandt's black guillemot demographic parameters.

| Covariate | Period | Code | Survival | | Breeding | | Success | | 2 chicks | | Immigration | |
|---------------------------|--------------|---------------------|----------|--------------|-----------|---------------|------------|----------------|------------|----------------|---------------|-------------------|
| | | | ϕ_t | ϕ_{t+1} | β_t | β_{t+1} | γ_t | γ_{t+1} | δ_t | δ_{t+1} | ι_{t+1} | $\iota_{t+(1-3)}$ |
| Cooper Island | | | | | | | | | | | | |
| Snow disappearance | Prebreeding | Melt date | ● | | ● | | ● | | ● | | | |
| Air temperature (avg) | Incubation | Incub AirT | | ● | ● | | ● | | ● | | | |
| Ice concentration | Incubation | Incub SIC | | ● | ● | | ● | | ● | | | |
| Air temperature | Nestling | Nestl. AirT | | ● | | ● | | ● | | | | |
| Wind speed (max) | Nestling | Nestl. Wind | | ● | | | | | | | | |
| Ice concentration | Nestling | Nestl. SIC | | ● | | ● | | ● | | | | |
| Ice distance from colony | Nestling | Nest Ice dist | | | | | | ● | | | ● | |
| Nestling abundance | Nestling | Nestl Abund. | | | | | | | | | | ● |
| Nest disturbance | Nestling | Disturb. | | ● | | | | ● | | ● | | |
| Ice distance from colony | Departure | Dept. Dist | | ● | | | | | | | | |
| Herald Island | | | | | | | | | | | | |
| Ice concentration | Nestling | Herald SIC | | | | | | | | | | ● |
| Chukchi Sea | | | | | | | | | | | | |
| Ice extent (max) | Fall staging | Fall Sea ice extent | | ● | | | | | | | | ● |
| Bering Sea | | | | | | | | | | | | |
| Air temperature (avg) | Wintering | Winter AirT | | ● | | | | | | | | |
| Wind speed (max) | Wintering | Winter Wind | | ● | | | | | | | | |
| Ice extent (max) | Wintering | Winter SIE | | ● | | | | | | | | ● |
| Polar cod freq. | Wintering | Winter A. Cod | ● | | | | | | | | | |
| Other | | | | | | | | | | | | |
| Winter Arctic Oscillation | All periods | Winter AO | | ● | | ● | | ● | | ● | | |

Note: t denotes a measurement from same year as the demographic parameter estimation. $t + 1$ denotes a measurement from the previous year. $t + (1-3)$ denotes a measurement averaged over the three preceding years. See *Environmental variables* for the explanation of these lags.

sampling stations with Arctic cod in NOAA's Eastern Bering Sea Shelf Groundfish Bottom Trawl Survey, 1982 to 2019 (NOAA, 2019). The surveys occur primarily in June and July, 2–3 months after MBG are present in the Bering Sea.

Demographic parameters were related to environmental covariates by considering periods before or during the breeding season. Demographic parameters measured in year t were related to Departure, Fall, and Winter covariates of year $t - 1$. In some cases, especially when investigating the cost of reproduction on some demographic parameters, a lag of one year was also applied on incubation and nestling covariates.

Most environmental databases utilized began in the late 1970s with the advent of satellite monitoring and analyses conducted with these data only considered demographic parameters from 1980 to 2019. Arctic cod occurrence in the Bering Sea was tested from 1982 to 2019. All environmental covariates were scaled

(i.e., mean 0 and SD 1) to assess their relative effect on demographic parameters.

Effect of environmental variables on demography

The effects of environmental covariates on apparent survival, breeding probability, success probability, and probability to fledge two chicks were tested by constructing models that would include, for each demographic parameter, the model structure best describing the state/age variations (see *Modeling demographic parameters*) to which one covariate effect was added in interaction with every state/age class of the model. All relationships between covariates and demographic parameters were fitted using a logit link function: $\text{logit}(\theta) = b + a \times X^t$, where θ is the demographic trait, b is an intercept parameter, a is a slope parameter, and X^t is the value of the covariate at

year t . Models were built with the program E-SURGE V 2.1.4 (Choquet et al., 2009b).

We examined which demographic parameters were influenced by an environmental covariate by determining if the 95% CI of the slope parameter excluded zero. If so, we performed an analysis of deviance (ANODEV) for each coupled demographic parameter—environmental covariate (Grosbois et al., 2008). ANODEV allows assessment of the fit of a covariate model (Mcov) relative to that of the constant (Mcst) and the time dependent (Mt) models, and a test of the significance of each relationship. This was computed as:

$$\text{ANODEV} = \frac{\frac{\text{Deviance}(\text{Mcst}) - \text{Deviance}(\text{Mcov})}{J-1}}{\frac{\text{Deviance}(\text{Mcov}) - \text{Deviance}(\text{Mt})}{n-J}},$$

where J is the number of parameters involved to explain the relationship between θ and the covariate in Mcov (2 in our case) and n is the number of parameters involved to explain the relationship between θ and the time in Mt (40 in our case, from 1980 to 2019). In the few cases where Mt did not perform better than Mcov likely due to local minima, ANODEV was not computed (Grosbois et al., 2008). Applying the appropriate Fisher–Snedecor test on the obtained ANODEV gave a p value assessing the significance of a covariate on a demographic parameter. Because the number of tests between demographic parameters and environmental covariates was high, the p values obtained were adjusted following the multiple test procedure proposed by Benjamini and Hochberg (1995).

The part of deviance explained by each environmental covariate (R^2_{Dev}) was calculated as Grosbois et al. (2008):

$$R^2_{\text{Dev}} = \frac{\text{Deviance}(\text{Mcst}) - \text{Deviance}(\text{Mcov})}{\text{Deviance}(\text{Mcst}) - \text{Deviance}(\text{Mt})}.$$

The effects of environmental covariates on immigration rate were tested through generalized linear models in R (R Core Team, 2018). To ensure that the results of those tests were consistent with those performed on other demographic parameters, each covariate was tested independently with the immigration rate as a response variable, and with a logit link function. The significance of each test was assessed through likelihood-ratio χ^2 tests, and p values were also corrected for multiple testing using the Benjamini and Hochberg procedure.

Models used to estimate the effect of covariates on immigration rate prevented us from performing the exact same R^2 calculation based on deviance. We thus calculated a pseudo- R^2 by using the McFadden method

(McFadden, 1977), which also relies on the ratio of likelihood between a constant model and a model with covariate:

$$R^2_{\text{McF}} = \frac{\ln(\text{Likelihood}(\text{Mcst})) - \ln(\text{Likelihood}(\text{Mcov}))}{\ln(\text{Likelihood}(\text{Mcst}))}.$$

Because in some cases the correction for multiple testing on tests corresponding to demographic parameters to which the population growth rate was most sensitive resulted in values slightly >0.05 , we considered an environmental covariate to be significantly impacting a demographic parameter if the p value was <0.07 .

The relative influence of each significant environmental covariate on demographic parameters, that is, their sensitivity $\delta\theta/\delta X$, was calculated using the partial derivative of the link function (Horswill et al., 2014):

$$\frac{\partial\theta}{\partial X} = a(\hat{\theta} - \hat{\theta}^2).$$

When several covariates were found to be significant for the same demographic parameter, the slope parameter used to calculate their sensitivity was calculated from a composite multi-state capture–recapture model that included every significant covariate.

The contribution of each significant environmental covariate to variation in population growth rate was estimated using the same computation as for LTRE. Sensitivity of growth rate to environmental covariates $\delta\lambda/\delta X$ was calculated as the product of $\delta\lambda/\delta\theta$ and $\delta\theta/\delta X$. Those sensitivities were calculated by averaging demographic parameters between the focal and reference periods (Urban et al., 2016). The contribution of each environmental covariate to population growth rate variation for a given period was calculated as:

$$(X^t - \hat{X}) \times \frac{\partial\lambda}{\partial X}.$$

RESULTS

Overview of colony population dynamics

During the first 15 years of our study, the breeding population of MBG on Cooper Island exhibited a 10-fold increase followed by a 30-year episodic and ongoing decline of over 60% (Figure 2). Our creation of approximately 200 nest sites in the 1970s and early 1980s allowed the colony to increase from <20 pairs in 1975 to over 200 pairs in 1986–1990, and with some nest sites accommodating two breeding pairs, and a large number of birds

prevented from breeding due to lack of nest sites. This was followed by a precipitous decline from 1991 to 1997, reducing the colony to >125 pairs in 1997, with the total colony (breeders and nonbreeders) declining from >600 birds in the late 1980s to <300 in the late 1990s. After plateauing at an average of approximately 120 pairs from 1997 to 2001, the breeding population increased slightly to approximately 140 pairs from 2002 to 2010 before declining to <50 pairs in 2020 to 2021. Observed annual population growth (λ_{obs}) during 1976–1990 was 1.38 ± 0.02 before declining to 1.04 ± 0.04 after 1982 when nest-site occupancy exceeded 95% and limited colony growth (Figure 2). Lambda for the subsequent periods was as follows: 1980–1990: 1.17; 1991–1998: 0.94; 1999–2006: 1.03; 2007–2019: 0.97.

A major increase in the occurrence of nonbreeding by established pairs in 2018 resulted in major fluxes in lambda, as a measurement of breeding population size. While the number of nonbreeders was only 13% of the colony for the first three years it increased rapidly to an average of 35% during 1982–1991. For the entire study period the number of nonbreeders was negatively correlated (Spearman correlation, $\rho = -0.53$, $p < 0.001$) with nest vacancies (i.e., nest sites that were not occupied by breeders). The total number of birds, breeders and nonbreeders, attending the colony annually, underwent a remarkable increase of 600 birds in nine years, from 42 in 1975 to a peak of 642 in 1984. After a decline to 276 in 1998, there followed an increase to 363 in 2006 followed by a long-term decline to 190 birds in 2019. The percentage of the breeding population composed of native birds was <10% from 1982 to 1987, increased to nearly 50% in 2001 and, after declining to 32% in 2007–2008, increased to nearly 60% in 2019.

Demographic parameters, population dynamics, and effects of the environment

Demographic parameters

The goodness-of-fit test for the Jolly Movement model performed on the fledgling dataset showed signs of significant overdispersion ($p < 0.001$), associated with significant transience (test 3G.SR, $p < 0.001$). This was caused by the large difference in survival rate between chicks and older birds. Indeed, the goodness-of-fit test was not significant once we removed the first encounter of our data ($p > 0.999$). Because bird age was explicitly taken into account in our model, we thus performed our modeling procedure without including a variance inflation factor.

Model selection revealed an effect of previous breeding state for all demographic parameters, and an effect of age for all parameters but the probability to fledge two chicks. Demographic parameter estimates accounting for age and previous breeding state effects are presented in Figure 3. Overall, apparent survival was higher in breeders than in nonbreeders. Age affected breeding probability and the probability of success, with, in general, lower probabilities for younger individuals. However, success probability of young inexperienced birds (i.e., aged 3) was poorly estimated since the number of birds belonging to this category was very low. Survival probabilities were the lowest for the youngest birds (ages 1–2, 0.504), and highest for birds of intermediate age (3–8, 0.855 for nonbreeders and 0.889 for breeders). The latter values exceeded the survival probability of oldest birds (age ≥ 9 , at 0.746 and 0.860 for nonbreeders and breeders, respectively). Breeding probability varied between previous breeding states, being >0.80 for experienced breeders 4 years and older, under 0.40 for experienced nonbreeders of the same age and under 0.40 for inexperienced nonbreeders. Success probability was also higher for birds that had been successful the previous year (>0.50). The probability to fledge two chicks was lower for first-time breeders (0.470) than for experienced breeders (0.554). Model selection supported the assumption that immigrants banded as adults were 4 years old at capture ($\Delta\text{AIC} = 56.23$). Immigration rate from 1981 to 2019 ranged from 0 to 0.521, with a mean of 0.107 (0.019 SE).

Detection probability increased until birds reached 6 years. It was higher for experienced breeders, averaging 0.998 for birds of 6 years and older, than for experienced nonbreeders (0.859) and inexperienced nonbreeders (0.540). Detection probabilities were also highly year-dependent.

Modeling population dynamics

While the breeding population experienced a 290% increase and a subsequent 270% decline, the overall population growth rate from 1980 to 2019 estimated using the projection matrix was 1.004, very similar to the observed population growth rate (0.998). This value ignores the major fluctuations in population over the 45-year study period. In the four periods delineated for our modeling analysis (Figure 4), population growth rate was highest during 1980–1990, at 1.12, before decreasing to 0.91 during 1990–1998. It increased slightly during 1998–2006, to 1.07, before declining to 0.95 during 2006–2019. The modeled population growth rates of each period were extremely close to the observed growth rates for the respective periods—1.12, 0.90, 1.03, and 0.95.

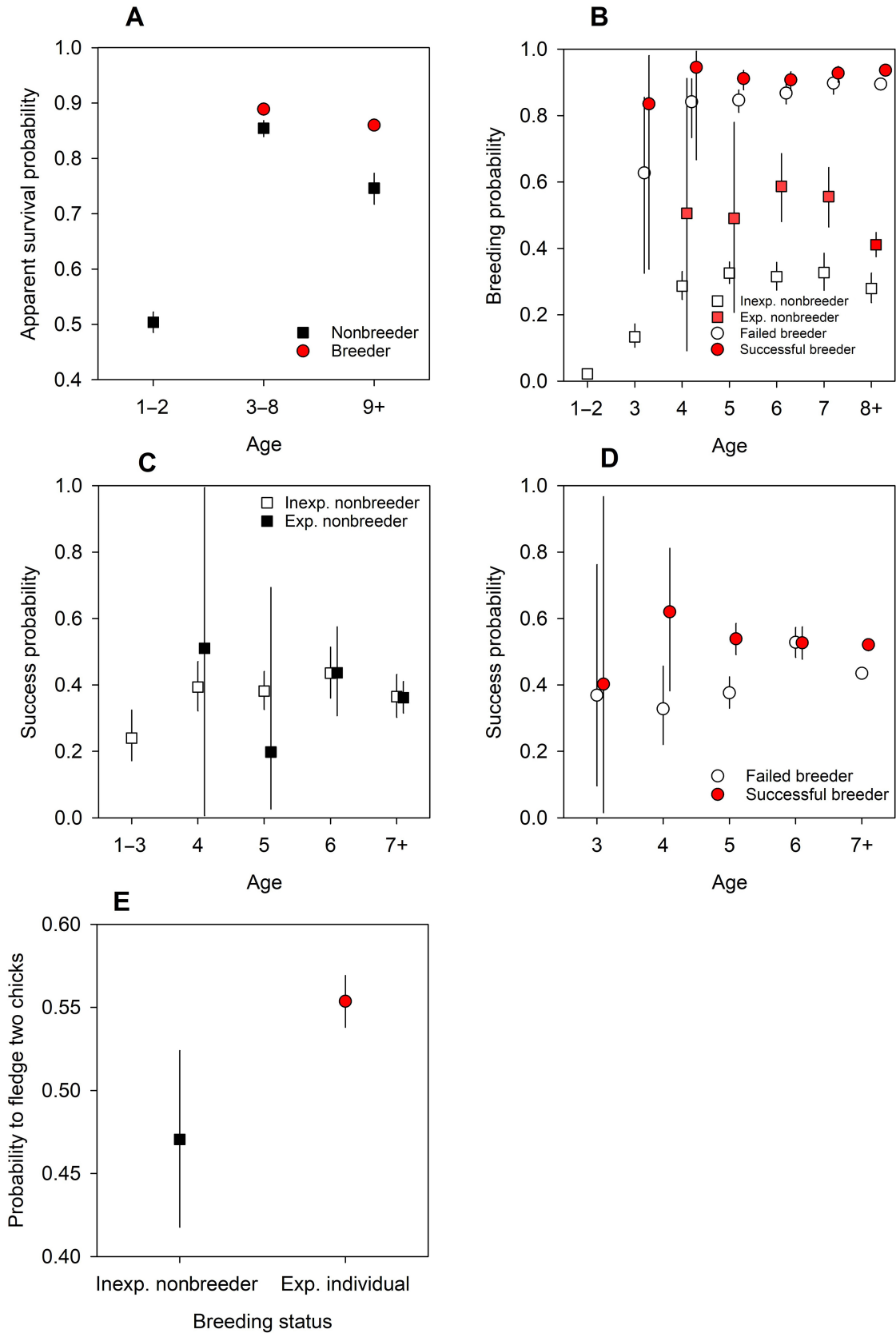


FIGURE 3 Legend on next page.

The prospective analysis from the matrix population model indicated that immigration rate and apparent survival of breeders and nonbreeders had the highest sensitivities, 0.86, 0.72, and 0.53, respectively (Appendix S1: Table S1). Our analysis of population growth rate using the matrix population model for the years 1980–2019 allowed examination of demographic variables affecting growth rate. Importantly, it did not include the period of rapid population growth ($\lambda_{\text{obs}} = 1.30$) from the first five years of the study (1975–1979) when recruitment opportunities were not limited by nest occupancy. The LTREs revealed that immigration rate and apparent survival (of breeders and nonbreeders) were the primary demographic drivers of annual variation in population growth rate from 1980 to 2019 (Figure 4A). The population increase from 1980 to 1990 was primarily the product of immigration (Figure 5) which accounted for 89.3% of growth rate variation. The initial decrease in breeding population size (1990–1998) was due to decreased immigration, survival, and breeding success probability, respectively accounting for 60.9%, 23.8%, and 17.3% of the growth rate variation. The subsequent population growth from 1998 to 2006 was mainly due to relatively high survival, which explained 78.6% of growth rate variation. The current decline is associated with a decrease in both immigration and survival, explaining 77.4% and 35.8% of growth rate variation, respectively. The breeding probability, despite being higher than in the past, is not sufficient to reverse the decline (−15.1% of growth rate variation).

Environmental effects on demography

Twelve of the 17 environmental covariates included in the model were found to significantly impact at least one demographic parameter of MBG for a total of 41 significant relationships (Figure 6). Immigration, the demographic parameter most influencing growth rate was positively correlated with Chukchi Sea fall ice extent the previous year, the number of nestlings in successful nests at the colony during the previous year, and the SIC around the presumed source colony, Herald Island, during the three previous years (Figure 7D). It was decreased by high (warm) values of the WAO and distance between sea ice and the colony during the previous year. Overwinter survival of breeders

aged 3–8 was sensitive to and positively correlated with ice extent in the Chukchi Sea in fall (Figure 7A) and negatively correlated with the WAO of the current year.

Breeding probability was higher for years having earlier snow melt, warmer temperatures during incubation, and with less sea ice. The probability of fledging at least one chick (defined in our model as breeding success) was only reduced by loss of eggs and chicks to nest predators (polar bears and Arctic fox) and competitors (horned puffin) (Figure 7C). It is important to note that nest disturbance was highly episodic annually and caused a major reduction in breeding success in only 9 of the 45 years. It has been greatly reduced since 2011 when the original wooden nest sites were replaced with plastic nest cases. No environmental factor significantly impacted the probability of fledging at least one chick. Environmental conditions did have a large influence on the probability of successfully fledging two chicks. More nests fledged two chicks in years with higher SIC, pack ice in closer proximity and colder atmospheric temperature during the incubation and nestling periods (Figure 7B).

Altogether, all the significant environmental covariates explained 76.8% of population growth variation between the model's initial growth period (1980–1990) and the average growth rate, and 66.6% of variation between the most recent period (2007–2019) and the average growth rate. For the two intermediate periods the variation from the average growth explained by environmental covariates was lower, being 20.2% and 28.1% for 1990–1998 and 1998–2006, respectively (Figure 4B).

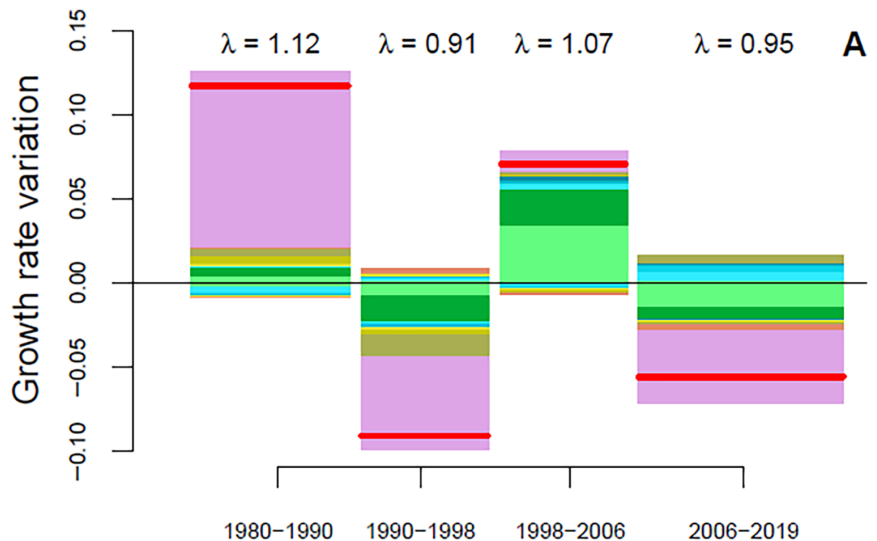
While 12 environmental covariates significantly affected one or several demographic parameters, only six were of importance in explaining the overall growth rate variation when the interaction between environmental covariates and the demographic parameters' sensitivity to growth rate was considered. Three of these were sea ice variables and were the primary drivers of growth rate variation. Distance to ice during the nestling period, Chukchi fall ice extent, and ice concentration adjacent to Herald Island, the presumed source colony during the nestling period (Figure 8) explained 64.4% of the population growth rate variation for 1980–1990, and 76.8% for 2006–2019.

The effect of two other environmental covariates, the WAO and date of spring snow melt, was less. The WAO was correlated with population growth rate variation for

FIGURE 3 Model probability estimates of effect of age and previous year's breeding state on demographic parameters (mean and 95% CI) for Mandt's black guillemot on Cooper Island. (A) age effects on apparent survival probability; (B) age, experience, and previous state effects on breeding probability; (C and D) age and previous state effects on the probability of fledging at least one chick; and (E) previous state effect on the probability of fledging two chicks. Estimates from the final model were obtained through model selection with no time effect on parameters (see Appendix S1: Table S4). Some CIs were too small to be visible.

Demographic parameters

- Apparent survival
 - φ Nonbreeder
 - φ Breeders
- Reproduction probability
 - β Juvenile
 - β Adult nonbreeder
 - β Failed breeder
 - β Successful breeder
- Breeding success
 - γ Juvenile
 - γ Adult nonbreeder
 - γ Failed breeder
 - γ Successful breeder
- Two fledges probability
 - δ Juvenile
 - δ Adult
- Immigration
 - Total immigration



Environmental covariates

- Global index
 - Arctic Osc.
- Air Temperature
 - Incub. AirT.
 - Nestling AirT.
 - Winter AirT.
 - Melt date
- Sea ice concentration
 - Incub. SIC
 - Nestling SIC
 - Herald SIC
- Sea ice retreat
 - Nestling Dist.
 - Fall SIE
- Biotic interaction
 - Nest Feeding
 - Nest Disturb.

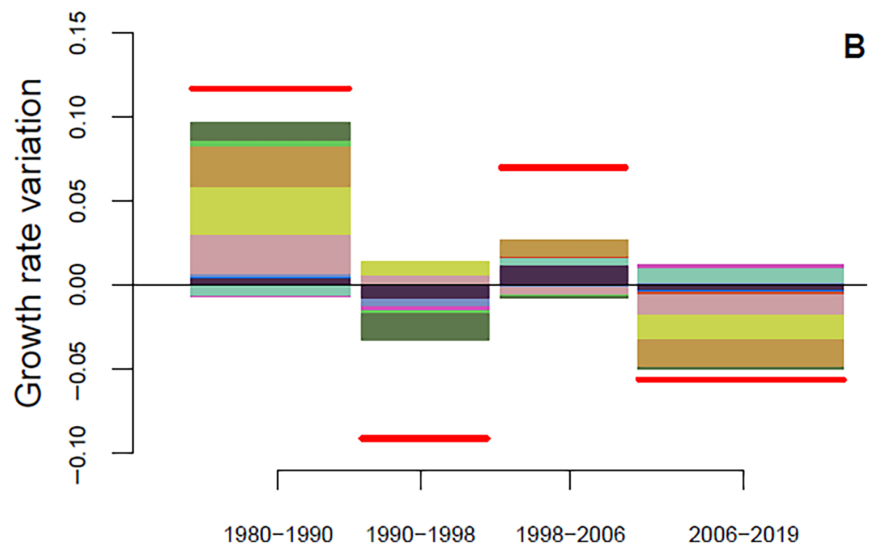


FIGURE 4 Projected growth rate variation (horizontal red lines) of Mandt's black guillemot on Cooper Island in the four modeling periods compared with overall observed growth rate (1.004) and the contribution of (A) demographic parameters and (B) environmental covariates to the variation. The four periods correspond to the initial increase (1980–1990), first decline (1990–1998), second increase (1998–2006), and recent decline (2006–2019). Parameters indicate demographic state the previous year and environmental covariates with a time lag dependent on the demographic parameters (see Table 1). SIC, sea ice concentration.

each of the four periods and the entire study period. For the two periods of population increase, 1980–1990 and 1998–2006, it accounted for 3.7% and 17.1%, respectively, and for the two periods of population decline, 1990–1998 and 2006–2019, it accounted for 9.2% and 6.1%, respectively. The effect of spring snowmelt varied, negatively influencing population growth from 1980 to 1990 (−5.3%) but having a positive effect from 2006 to 2019 (15.3%).

The nonclimatic environmental variable, nest disturbance resulting from egg loss and chick mortality from nest predators and competitors also contributed to temporal variation in population growth rate. It was low during the initial period of population growth and high

during the subsequent period of decline, reflecting the distribution shifts in those species in response to loss of sea ice since 1990. It accounted for 16.9% of population growth rate variation from 1990 to 1998.

Quasi-extinction

A simulation of future population trajectory based on the observed decline to 2019 predicts quasi-extinction, that is, a reduction to 5–25 pairs likely between 2040 and 2070 (Figure 9). There is a 95% probability that the population would be reduced to 10 breeders or less in 2073.

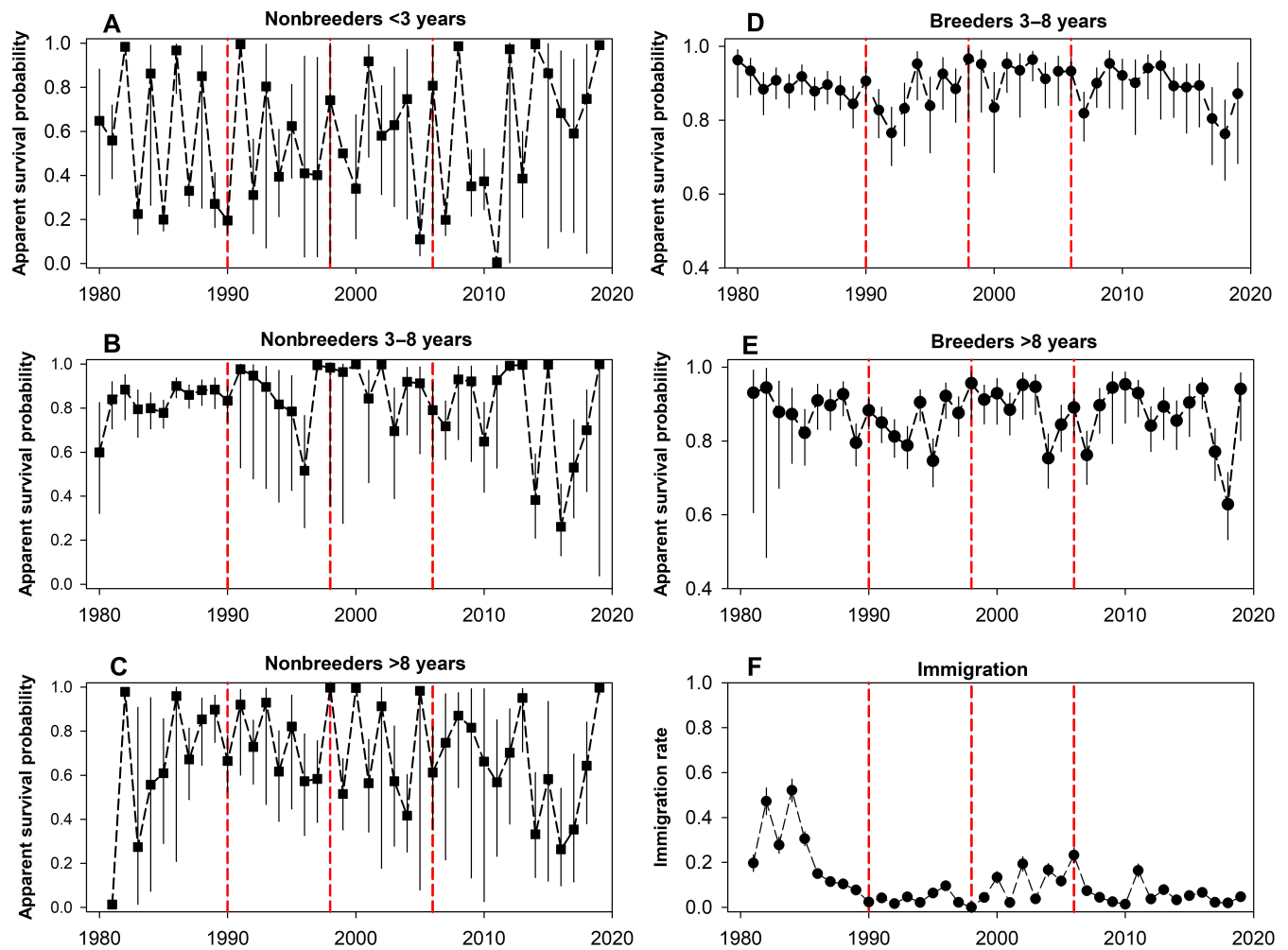


FIGURE 5 Model probability estimates for annual survival and immigration, the demographic parameters with greatest influence on population growth rate variation of Mandt's black guillemot on Cooper Island. Annual variation in apparent annual survival as a function of age for (A–C) nonbreeders and (D, E) breeders. (F) Annual rate of immigration. Error bars indicate 95% CI for survival and ± 1 SE for immigration rate. Vertical dashed red lines delimit the colony's initial increase (1980–1990), first decline (1990–1998), second increase (1998–2006), and recent decline (2006–2019). Annual variation of other demographic parameters presented in Appendix S1: Figures S4–S6.

DISCUSSION

During the course of our study, the Western Arctic has experienced some of the greatest increases in atmospheric temperature in the world, over 4°C since 1979 (GISTEMP Team, 2023; Lenssen et al., 2019), causing major reductions and alternations in the cryopelagic ecosystem supporting MBG. Our study population's rapid growth, during an initial period with no significant trend in summer sea ice extent, and the subsequent long-term major decline during three decades of major reductions in ice extent and volume, is indicative of a recent major decrease in the availability of cryopelagic prey.

While limited to a single colony, the robust nature of our data, allowing the inclusion of immigration in the demographic analysis, allows conclusions to be made

about the status of the regional metapopulation over the last half century. The importance of immigration to colony growth and its variation in response to sea ice variables provides evidence that the changes in sea ice and oceanography that have affected the prey availability and success of the study colony (Divoky et al., 2015, 2021) are also occurring at the source colonies in the Siberian-Chukchi-Beaufort metapopulation, where similar environmental change has occurred.

Importantly, our findings indicate a multi-decadal and widespread decrease in the availability of Arctic cod, the Arctic's primary forage fish, and a keystone species in the cryopelagic food web. This decrease could be expected to have major impacts on the piscivorous marine predators in the Western Arctic, all of which have a major dependence on Arctic cod. Use of a seabird species as an ecological monitor requires consideration of the species' ecology,

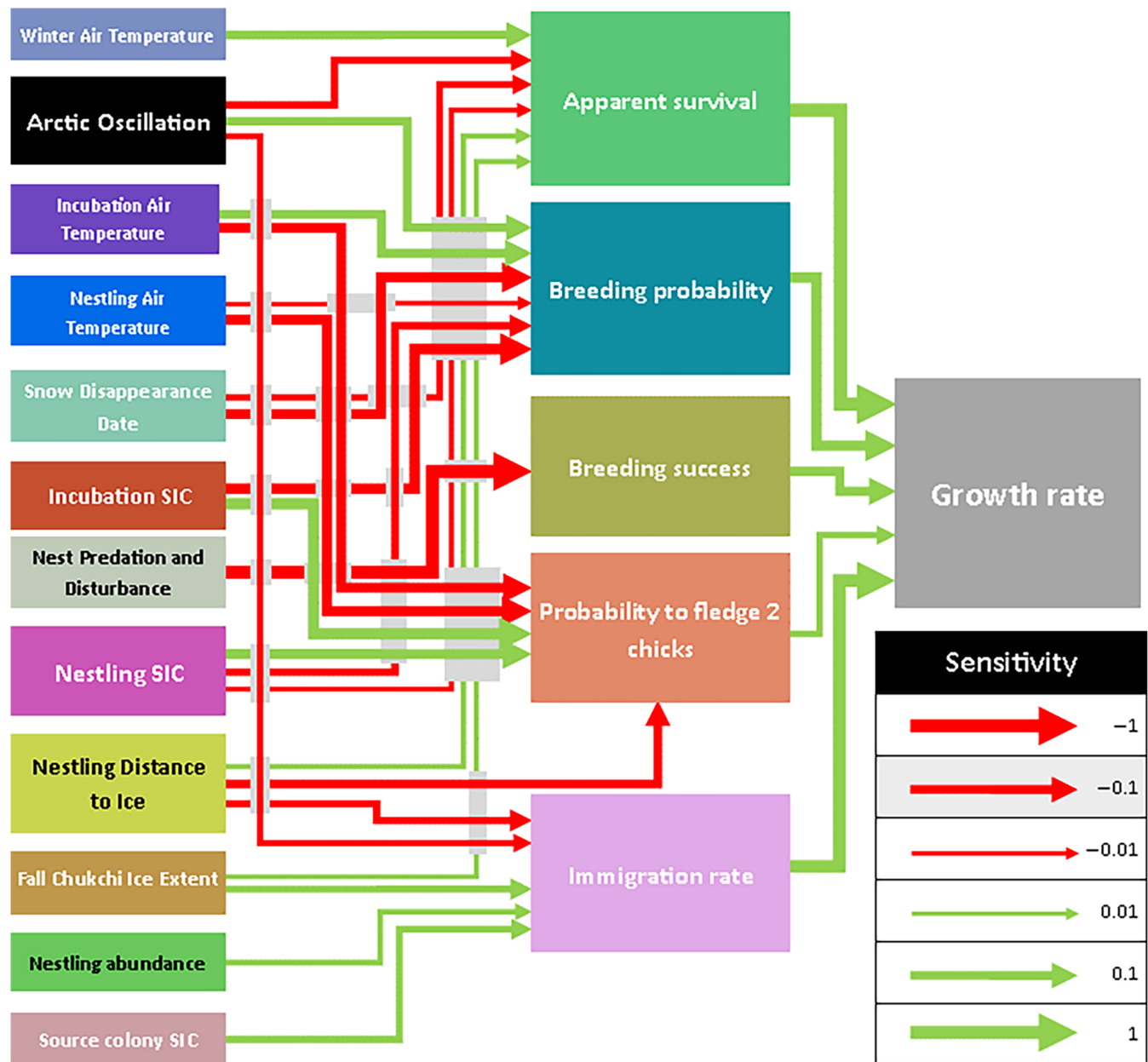


FIGURE 6 Diagram summarizing effects of environmental covariates on Mandt’s black guillemot demographic parameters and resulting population growth rate. Green and red arrows indicate a positive or negative correlation, respectively. Arrow width indicates sensitivity of demographic parameters to environmental covariates. Relationships not statistically significant are not shown. For univariate models, sensitivities of demographic parameters to each covariate were summed for every age class and breeding state. Sensitivities of population growth rate to each demographic parameter were summed for every age class and breeding state. Sensitivity values taking into account interactions between covariates (composite models) and distinguishing age class and reproductive status are found in Appendix S1: Tables S1 and S2. SIC, sea ice concentration.

however, when drawing inferences about larger ecosystem processes (Durant et al., 2009). Chief among these for MBG is its extremely shallow dive depth, averaging <5 m in both the breeding and nonbreeding season and rarely exceeding 20 m (Divoky et al., 2021; unpublished data), precluding inferences about prey availability deeper in the water column. Arctic cod are regularly found down to 250 m (Geoffroy et al., 2023).

Evidence for a decrease in Arctic cod at depth in the Western Arctic would best be provided by temporal changes in two cryopelagic mammals, ringed seal (*Pusa hispida*) and beluga (*Delphinapterus leucas*), both able to dive to >500 m (Ogloff et al., 2021; Storrie et al., 2022). While there are no time series of abundance for either species in our study region, both have had a reduction in body condition in the eastern Beaufort Sea,

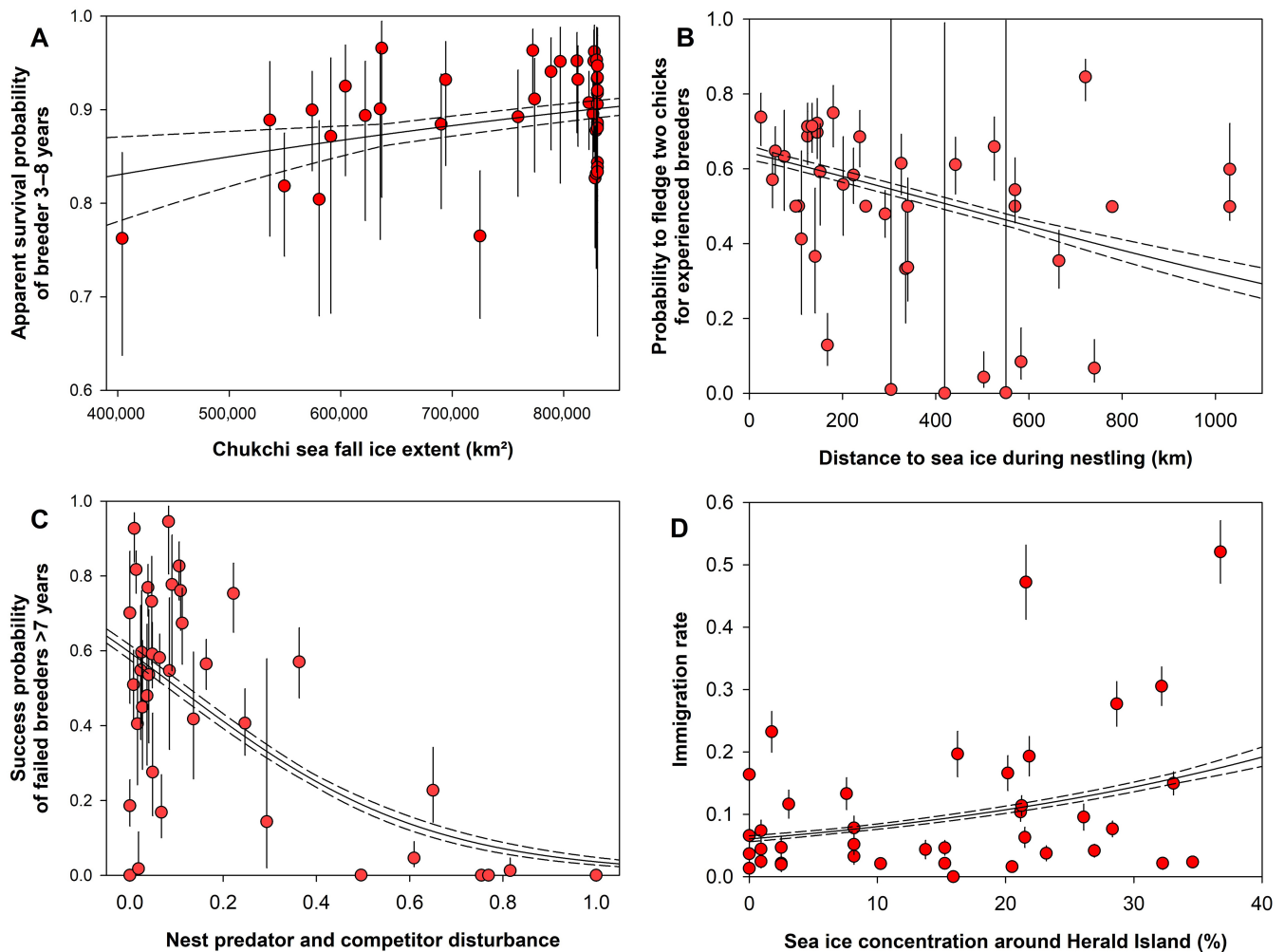


FIGURE 7 The effect of (A) Chukchi Sea fall ice extent effect on the probability of apparent survival of breeders 3–8 years, (B) distance to sea ice during nestling on the probability of experienced breeders fledging two chicks, (C) nest predator and competitor disturbance on the success probability of failed breeders >7 years, (D) sea ice concentration around Herald Island, presumed source colony, on immigration rate on Mandt's black guillemot on Cooper Island. Effects (solid line) with 95% CI (dashed line) were estimated through univariate models. Annual estimates (solid circles with 95% CI) were obtained from the time-dependent model.

which for beluga was associated with a decrease of Arctic cod in the diet (Choy et al., 2017, 2020; Harwood et al., 2012, 2015, 2020). In the Chukchi Sea, ringed seals had no decrease in body condition, growth, or reproduction between the late 20th and early 21st century (Crawford et al., 2015) but this may have been due to the foraging plasticity of the species, as analysis of stomach contents in the first two decades of the 21st century found a decrease in Arctic cod consumption accompanied by an increasing frequency of two subarctic fish, rainbow smelt (*Osmerus mordax*) and capelin (Quakenbush et al., 2020). Additional evidence of no major change in the abundance of Chukchi Sea ringed seals is the health of the regional population of polar bear, a major predator on ringed seals (Regehr et al., 2018; Rode et al., 2021). Evidence for an Arctic Basin-wide reduction in near-surface availability

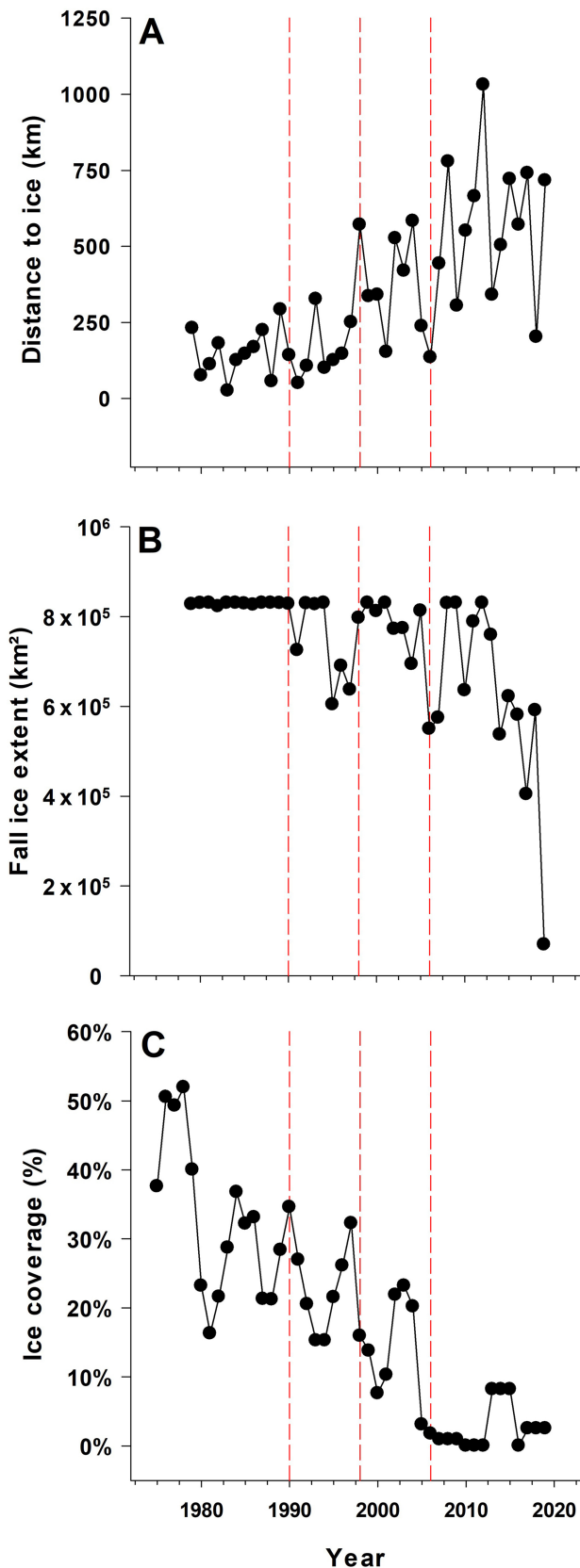
of Arctic cod is provided by the only other cryopelagic Arctic seabird, the ivory gull (*Pagophila eburnea*), which is most abundant in the Eastern and Atlantic Arctic (Gilg et al., 2010). A surface feeder highly dependent on Arctic cod (Divoky, 1976), it has experienced a major decline in recent decades (Chardine et al., 2004; Gilchrist & Mallory, 2005; Strøm et al., 2020) and is considered endangered in Canada (COSEWIC, 2006).

The population trajectory

Colonization and initial growth

Mandt's black guillemot initially benefited from the atmospheric warming of the 20th Century as it caused

earlier snowmelt and a resulting longer annual period with the ground free of snow providing sufficient annual access to ground-level nests to allow a breeding range



expansion to northern Alaska (Divoky et al., 1974; MacLean & Verbeek, 1968). Females require access to a snowfree nest cavity for ovulation, as do other cavity-nesting alcids (Sealy, 1975) and earlier annual snowmelt (Stone, 1997; Stone et al., 2002, 2005) provided access to ground-level nest cavities for >80 days (Cox et al., 2017), the minimum period required for successful breeding.

Cooper Island, without the debris left by an earlier occupation, is a flat sand and gravel bar with no habitat for cavity-nesting birds. The rapid growth of the study population in response to provisioning nest sites in the 1970s and 1980s can be attributed to conditions in the Western Arctic in the mid-20th century and the characteristics of the study species. Nest sites were provided at a time when extensive summer ice throughout the region supported extremely large, and apparently productive, source colonies to produce immigrants, while conditions near and at the colony were attractive to prospecting nonbreeders, with oceanographic conditions providing his availability of Arctic cod.

While natal philopatry (returning to the natal colony to breed) was long considered a central tenant of seabird biology, with low emigration and immigration rates, recent studies have shown high rates of natal dispersal (Coulson, 2016). *Cephus* guillemots have several traits that would select for increased prospecting by prebreeders and lead to higher natal dispersal and emigration/immigration rates compared to more colonial species. First, as a cavity nester, *Cephus* colonies are frequently nest-site limited, reducing the benefits of natal philopatry. Moreover, as semicolonial cavity nesters, frequently breeding as individual pairs or in small colonies, high natal philopatry would increase inbreeding. Unlike colonial seabird species, which can focus on aggregations of conspecifics when prospecting, *Cephus* guillemots could be expected to investigate any shoreline habitat that might provide nest cavities, as they can successfully breed as single pairs. Also, the utilization of nearshore habitats allows nonbreeders to encounter potential breeding sites more frequently than more pelagic species. High rates of immigration for the

FIGURE 8 Temporal variation in environmental covariates explaining the majority of variation in population growth of the Mandt's black guillemot colony on Cooper Island. (A) Distance to ice in nestling period, (B) Chukchi Sea fall ice extent, and (C) Herald Island (presumed source colony of immigrants) ice concentration in August. Vertical dashed red lines delimit the four periods used in population modeling: Initial increase (1980–1990), first decline (1990–1998), second increase (1998–2006), and recent decline (2006–2019). The annual variation of other environmental parameters is presented in Appendix S1: Figure S7.

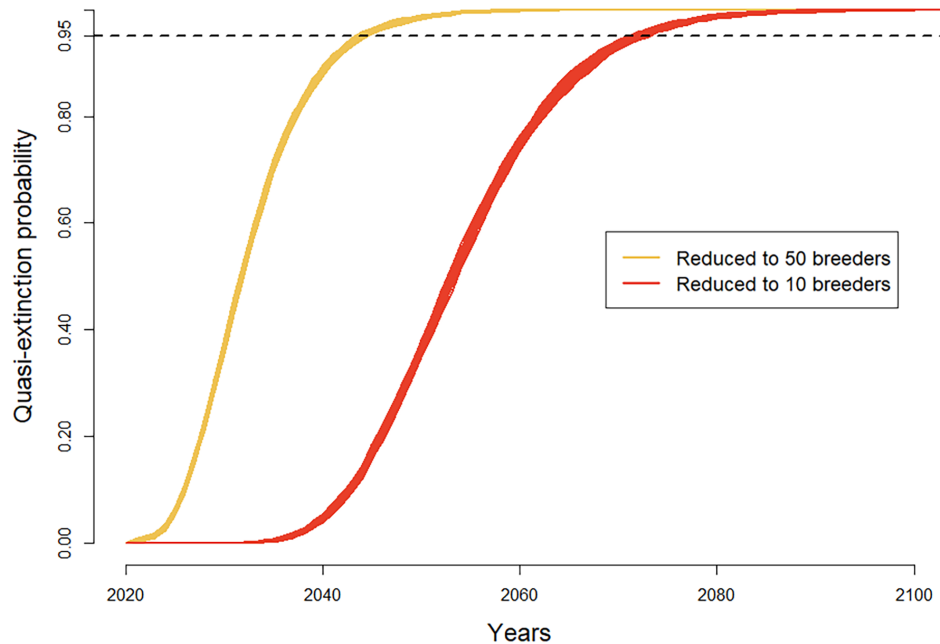


FIGURE 9 Quasi-extinction probabilities (reduction to 50 and 10 breeders) for Mandt’s black guillemot colony on Cooper Island after 2019 with environmental stochasticity similar to 2006–2019. The dashed line indicates 0.95.

species, such as found in our study, have been noted elsewhere. An Icelandic colony also underwent a rapid population increase (Petersen, 1981) having immigrants constitute an estimated 50% of the breeders (Frederiksen & Petersen, 2000).

The location of our study colony was also a factor in the rapid population growth as there were few alternate locations with potential nesting cavities in northern Alaska providing recruitment opportunities while there were two extremely large colonies in the Siberian Arctic to produce fledglings and ultimately emigrants. The Western Arctic metapopulation of MBG breeds mainly on rocky islands north of Siberia with <5% breeding in the North American Arctic (Seabird Information Network, 2019). Cooper Island lies in the middle of a 1600-km stretch of shoreline, extending from Cape Lisburne to Cape Parry, consisting of low eroding tundra bluffs, with potential nest sites limited to cavities in manmade debris. The 200 nest sites added in the 1970s and 1980s to the original 10 active sites of our study colony in 1972, provided the vast majority of recruitment opportunities for the eastern part of the metapopulation’s range.

Those sites were provided at a time when the number of potential immigrants in the region was high. Two locations in the Siberian Chukchi Sea, approximately 750 km west of Cooper Island, supported an estimated combined population of 70,000–80,000 MBGs. Herald Island had an estimated 60,000–70,000 birds and was likely the largest colony in the world (Stishov, 2004), and Wrangel Island

an estimated 10,000 more (Stishov et al., 1991). Together they comprised over 95% of the MBG population estimated to be breeding in the Western Arctic in the mid- to late 20th century and almost certainly provided the majority of emigrants and nonbreeders found on Cooper Island.

Local oceanographic conditions also increased the likelihood of the increase at the study colony. In the 1970–1980s, the MIZ in the Chukchi Sea extended longitudinally from the Siberian source colonies east to Point Barrow (Walsh et al., 2019) remaining in close proximity to both the source colonies and study colony for the entire breeding period. The high productivity of the MIZ and its importance to pagophilic species is well known (Hamilton et al., 2017; Hop & Gjosaeter, 2013). The resulting availability of Arctic cod provided by the cryopelagic system not only amply supplied the source colonies and study colony, but it also increased the likelihood that source-colony “floaters” and prebreeders would encounter the study colony. An estimated 70,000 birds occupied the MIZ in the Alaskan Chukchi in the 1970s (Divoky, 1987). Prospecting nonbreeders could be expected to concentrate in the waters adjacent to Point Barrow and north of Cooper Island due to higher densities of Arctic cod (Forster et al., 2020; Logerwell et al., 2018) associated with oceanographic conditions created by the confluence of Alaska Coastal Water and Pacific Water in the vicinity of Barrow Canyon that supports high densities of other Arctic cod predators (Citta et al., 2020; Logerwell et al., 2018). Guillemots have

historically occupied the waters off Point Barrow (Bailey, 1948), well before colonizing the area in the late 20th century. Recruitment to the colony was also likely facilitated by the increased seasonal access to nest sites with increasing atmospheric temperatures expanding the annual period when nest sites were free of snow (Cox et al., 2017).

The long-term decline

The atmospheric conditions that facilitated rapid growth of the colony until 1989, almost exclusively negative WAOs retaining sea ice in the Western Arctic, ended abruptly with a switch to an extreme positive WAO in 1989/1990. The switch initiated a three-decade and ongoing period of positive WAOs that, in conjunction with warming from anthropogenic carbon emissions, caused major decreases in the sea ice habitat of MBGs. The three environmental covariates that best explained colony growth variation (distance to ice during the nestling period, August ice concentration at the presumed source colony, and Chukchi fall ice extent) all had inflection points in 1990, with no significant annual trend prior to the 1989/1990 WAO shift but showing significant ice reduction trends for the remainder of the study. Distance to sea ice from the study colony at fledging, a covariate not included in our final model results due to its high correlation with distance during the nestling period, had a similar pattern.

While a large decrease in a population of an ice-obligate seabird would be expected in response to the extensive loss of sea ice during our study, the immediacy of the decline in breeding pairs at the study colony, starting directly after the beginning of the sea ice decrease initiated by the 1989/1990 WAO, is not easily explained. While reductions in sea ice and increases in SST reduces prey availability for provisioning parents resulting in decreased breeding productivity (Divoky et al., 2015), a decrease in the breeding population would not be expected to occur for 2–3 years when affected cohorts reached breeding age.

Immigration was the primary demographic factor affecting colony growth and the changes in sea ice beginning in 1990 could have affected immigration rates in several ways; decreased prey reducing production of potential emigrants, a northward movement of the MIZ in summer reducing the incidence of prospecting nonbreeders at the study colony, or decreased attractiveness of the study colony to prospecting nonbreeders.

Decreases in sea ice and associated ocean warming in the Western Arctic could be expected to affect all aspects of MBG's life history, the decrease in summer ice adjacent

to breeding colonies and its negative effect on breeding parameters (breeding probability, probability to fledge two chicks), survival and immigration would have the greatest effect on the region's metapopulation. Observations at the study colony demonstrate how decreases in ice concentration and proximity result in increased SST in the parental foraging area and decreased availability of the preferred prey, Arctic cod. The result is a decrease in nestling quality and survival and increased foraging effort by provisioning parents (Divoky et al., 2015, 2021). From 1975 to 2002, Arctic cod was the dominant (>90%) prey returned to nestlings at the study colony. However, in 2003 the distance to the nearest sea ice and SST adjacent to the island both underwent a shift from the 1982 to 2002 means, with distance to sea ice in early August increasing nearly 100 km and SST increasing 1.9–3.3°C. That year (2003) was the first year with a seasonal shift from Arctic cod to nearshore demersals, primarily fourhorn sculpin (*Myoxocephalus quadricornis*) during provisioning of nestlings (Divoky et al., 2015). Subsequent documentation of the daily prey composition provided to nestlings, in conjunction with SST obtained with temperature/depth recorders deployed on provisioning parents, found Arctic cod typically constituted 100% of the prey at SST < 2°C with percentage of cod declining at 2°C, comprising 50% at 3.5°C, continuing to decline with increasing SST and with parental foraging effort increasing with increasing SST (Divoky et al., 2021).

Seabirds, like MBG, with short foraging ranges while provisioning nestlings one prey item per foraging trip (single-prey loaders), are more sensitive to temporal and spatial variation in prey availability during chick provisioning than seabirds provisioning chicks by regurgitation of stomach contents (Gaglio et al., 2018; McLeay et al., 2009; Monaghan et al., 1992). The switch from Arctic cod to nearshore demersal prey was associated with increased starvation of nestlings, brood reduction, and lower fledging quality (Divoky et al., 2015).

Reductions in the presence of Arctic cod at the study colony were not seen until 2003 indicating decreased sea ice and increased SST had a more immediate impact on the source colonies or the pelagic waters occupied by summering nonbreeders. While breeding productivity of Chukchi colonies could be expected to decline with loss of sea ice, as it did at the study colony, the reduction in immigration to the study colony would not be expected to be as immediate and large as what was observed, given that recruiting immigrants would be >2 years of age. The timing of the beginning of the decrease, immediately after the WAO shift, is indicative of decreased immigration due to changes in the location or quality of the sea ice habitat occupied by young prebreeders in summer. However, the distance to sea ice variables in our model showed no shift in the early 1990s, although there could

have been changes in ice concentration in the MIZ that would have birds summering further from the study colony. Changes in sea ice and SST affecting availability of Arctic cod near the colony did not occur until the late 1990s and early 21st century (Divoky et al., 2015) so no clear change in the attractiveness of the study colony occurred during the period of major decline in the 1990s. The immediacy of the shift could also be due to decreases in adult survival, as survival of nonbreeders <3 years was low in 1989 and 1990 and survival of breeders was relatively low in 1992 and 1993, which could also indicate a decrease in immigration from source colonies.

Tipping points and the AO

While our sensitivity analysis, based on the matrix population model and functional relationships between year-to-year variations in demographic parameters and the WAO, indicated that the WAO had a modest contribution to interannual variation in population growth rate, its influence on population growth rate appeared more obvious when considered by multi-year periods. During the 19 years in the two periods of population increase (1980–1989 and 1999–2006) the WAO was negative in 79% of the years, while in the 21 years in the two periods of decline (1991–1998 and 2007–2019) the WAO was negative in 29% of the years (Appendix S1: Figure S8). The observed population growth rate for each of the four periods was highly correlated with the percentage of years with a negative AO for that period ($r^2 = 0.99$, $p = 0.01$). The WAO was found to affect another cryopelagic species in the region as Chukchi Sea polar bears had an increased frequency of yearlings in years with a negative WAO (Rode et al., 2021).

The initiation of population declines also coincided with three recognized “tipping points” or major transitions in the region’s sea ice, occurring in 1990 (Danielson et al., 2020; Rigor & Wallace, 2004), 2007 (Livina & Lenton, 2013; Moore et al., 2022; Sumata et al., 2023) and 2017 (Ballinger & Overland, 2022) (Figure 10). The beginning of the initial population decrease was correlated with the results of the extremely positive winter WAO in 1989/1990 and changes in the Bering Sea inflow through the Bering Strait. The post-2007 population decline, beginning after a period of minor population growth and plateau from 1999 to 2006, occurred after a then-record low September ice extent for the entire Arctic in 2007 that led to decreases in extent and thickness in subsequent years (Livina & Lenton, 2013; Moore et al., 2022; Sumata et al., 2023). Most recently the winter of 2017/2018, which saw a regime shift to warmer temperatures and decreased sea ice in the Bering Sea

wintering area (Stabeno & Bell, 2019) and resulting ecosystem impacts (Baker et al., 2020; Duffy-Anderson et al., 2019; Huntington et al., 2020; Stabeno & Bell, 2019), is strongly suspected to be the reason for increased overwinter mortality and the first observations of large-scale nonbreeding.

Effects of environmental change on demography

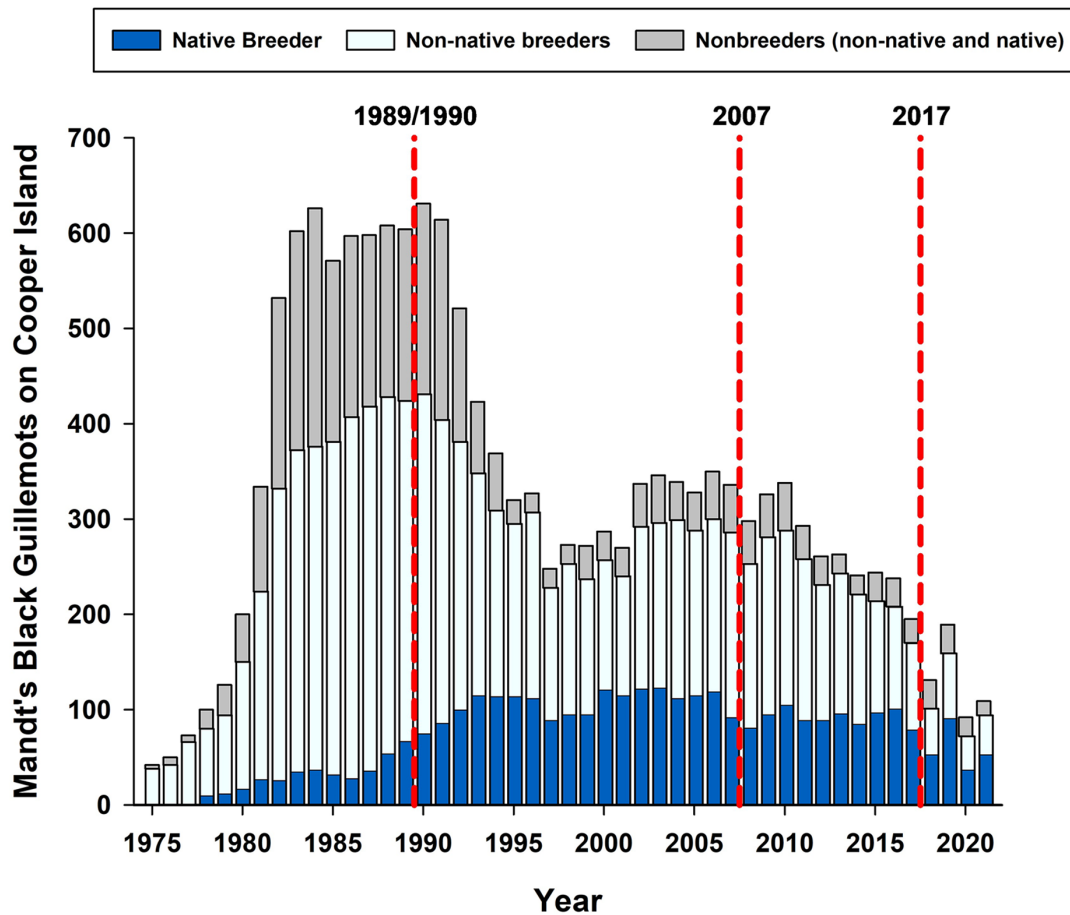
The two demographic parameters contributing the most to the variation of the population growth rate were immigration and survival which are discussed below.

Immigration

Immigration rate was found to be the demographic parameter most influencing population growth rate, with its large variation having a major influence on the size of the colony. While decreased breeding productivity at the source colonies due to decreased ice concentration during the nestling period in August could be expected to be the biggest factor in the decreased immigration, the loss of sea ice adjacent to the study colony could also decrease immigration in several ways. By decreasing chick survival, it would make the colony less attractive to prospectors, whose recruitment can be facilitated by indications of high breeding success (Boulinier et al., 1996; Danchin et al., 1991). While this might be less developed in *Cepphus* guillemots, as they frequently breed as single pairs, nonbreeding birds at the study colony are frequently seen following parent birds carrying fish to the nest and aggregating near nests containing nestlings. As mentioned above, prebreeding MBG in summer would be most abundant in areas of high prey density, and decreases in prey near the study colony would reduce the probability potential immigrants would encounter the colony. The annual extent of sea ice in the Chukchi Sea could affect immigration as a northward retreat of the MIZ could decrease the chances of nonbreeders encountering the study colony. During the summer, nonbreeding birds (primarily prebreeders) occupy the MIZ in the Chukchi Sea and the adjacent Beaufort Sea (Divoky, 1984, 1987) with Chukchi summer population estimated at 70,000.

Survival

As expected for a long-lived seabird (Lebreton & Clobert, 1991), MBG population growth rate was most sensitive to adult survival, which had the highest sensitivity and



| Identified Climatic Tipping Points | | |
|------------------------------------|--|-------------------------------|
| Year | Event | Ref. |
| 1989/1990 | Beginning of long-term ice decrease | Lindsay and Zhang (2005) |
| | Increase in Bering Strait inflow temp and amount | Danielson et al. (2020) |
| 2007 | Record low September ice extent | Livinia and Lenton (2013) |
| | High ice melt and export with low replenishment | Babb et al. (2023) |
| 2017 | Record low Bering Sea March ice extent | Ballinger and Overland (2022) |

FIGURE 10 Size and composition of Mandt’s black guillemot colony on Cooper Island showing three recognized tipping points in sea ice and oceanography occurring in the Western Arctic.

elasticity among demographic parameters. Despite the fact it is expected to be the life history trait least sensitive to climate variability through environmental canalization (Gaillard & Yoccoz, 2003), the LTRE indicated that adult survival accounted for a large part of the variation in population growth rate, from 5.7% to 78.5% depending on the period considered. This suggests the factors affecting survival have been harsh enough to overcome environmental canalization.

The causes of variation in annual survival for seabirds are generally thought to be related to prey availability, either due to low prey abundance or

meteorological or oceanographic conditions hindering access to prey or foraging ability in the nonbreeding period (winter) which is when most mortality of adult seabirds occurs (Newton, 1998). The recent decline of the colony has been associated with years of high adult mortality, affecting all age classes and breeding states, and unprecedented occurrences of large-scale nonbreeding by surviving birds (particularly 2018 and 2020) indicating that recent record decreases in sea ice in the Bering Sea wintering area (Ballinger & Overland, 2022; Stabeno & Bell, 2019) are reducing prey availability.

Environmental factors

While 12 environmental covariates were found to be significantly linked to demographic parameters, fewer actually explained the majority of the observed variation in growth rate (Figure 4). Air temperature measurements, for example, were significant but explained little of the variation in growth rate, varying from 1.3% to 4.1% in our four analysis periods. This is likely a product of: (1) our avoiding overlap between covariates when explaining growth rate variation by performing composite models; and (2) an environmental factor having a significant effect on a demographic parameter that had little effect on overall growth rate. Our model was best at explaining the environmental factors affecting the initial period of colony growth (1980–1990) and the recent decline (2007–2019), both influenced by variation in sea ice covariates, but explaining far less of the variation in population growth rate for the two intervening periods. Our model shows the primary environmental factors affecting colony growth were sea ice metrics at the source and study colony and in the Chukchi Sea, the primary summering and fall staging areas for the species in the Western Arctic. The major changes in these environmental factors affected immigration and survival, the vital rates found to most affect colony growth.

While decreased availability of Arctic cod from the loss of sea ice and associated increased SST was likely the primary effect on population growth, breeding success was negatively affected by the long-term reduction in sea ice affecting the distribution of horned puffin, a subarctic nest competitor that displaced MBG eggs and killed nestlings, and polar bear, a nest predator that disturbed nests and ate eggs and nestlings. This nest disruption and predation contributed to variation in population growth primarily during 1990–1998 when nearly 17% of the growth variation was explained by these interspecific interactions. Polar bears were rare visitors to the study colony in the 20th century but have been regular since 2002 (Cox et al., 2017) as loss of summer sea ice has had bears moving to terrestrial environments (Wilson et al., 2017). Horned puffins prospected MBG nests at the study colony since the 1970s and began breeding there in 1986 (Divoky, 1982). The occurrence of both polar bears and horned puffins on the island increased in the first decade of the 20th century with increasing loss of sea ice. From 2002 to 2011, 281 nestlings were eaten by polar bears and 175 killed by prospecting horned puffins, resulting in the loss of 26% of the nestlings for that period. Replacement of the original wooden nest sites with plastic nest cases in 2011 resulted in minimal loss of nestlings to disturbance and predation from 2011 to 2019, <2% of nestlings, and has acted to reduce the rate of decline of the colony.

It is important to note that our analysis of breeding success by age and experience does not take into account environmental and nest disturbance effects that reduce breeding success but are unrelated to an individual's demographic status. Chief among these factors is nest predation by Arctic fox and polar bear both of which would be greatly reduced starting in 2011 when the original wooden nest sites were replaced by more secure plastic nest cases.

The colony's future

Our quasi-extinction model was useful in predicting future population trajectories, but of less utility in determining the threshold below which persistence of the colony is possible. It is important to note the limitations of applying a quasi-extinction model to a semi-colonial seabird like *Cephus guillemots*. Unlike colonial seabirds that require a certain nesting density for successful breeding, MBG regularly breed as single pairs and in small (<10 pairs) colonies. While our model predicts a reduction to <25 pairs by 2050, it is possible that single pairs or a small colony could persist on Cooper Island well into the future. As is currently occurring on Cooper Island, a small number of pairs (20–30; G. Divoky, unpublished data) can breed successfully given sufficient populations of nearshore demersals for provisioning nestlings. In the 20th century, both the study and source colonies were supported by Arctic cod that were part of much larger populations existing under and adjacent to sea ice that maintained high prey densities in the MBG limited foraging range throughout the breeding season. The loss of sea ice in the Western Arctic that began in the early 1990s is continuing with all three seas occupied by the Western Arctic population of MBG predicted to be ice-free (SIC < 15%) in summer and ice-free in fall by the end of the century (Årthun et al., 2020). The persistence and abundance of the species in the Western Arctic depends on its ability to display foraging plasticity with the ongoing changes in nearshore fish populations. The current alternative prey provided to nestlings, fourhorn sculpin, is becoming less abundant in the Beaufort nearshore while more subarctic fish, sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and saffron cod (*Eleginus gracilis*) are increasing in the Arctic (Pedro et al., 2020; Von Biela et al., 2022). Fish surveys conducted adjacent to Cooper Island have found capelin to be common (Johnson et al., 2010; Vollenweider et al., 2018) but rarely fed to nestlings (<1% of feeds). In the eastern Arctic, climate-driven dietary shifts from Arctic cod to capelin have been found in thick-billed murre (*Uria lomvia*) and black-legged

kittiwake (*Rissa tridactyla*) (Gaston & Elliott, 2014; Vihtakari et al., 2018). Both of those species have primarily subarctic distributions and may have more foraging plasticity than the High Arctic ice-obligate MBG.

Future MBG populations, or other Arctic subspecies of black guillemot, will likely never be of the magnitude present in the mid-20th century, however, when high densities of ice-associated Arctic cod supported colonies of >10,000 birds. Future breeding densities in the Western Arctic will likely be similar to those of subarctic *Cephus* populations dependent on nearshore prey (Divoky et al., 2021).

Given the species' clear dependence on sea ice and with the certainty of a continuing decline of sea ice given current and projected atmospheric conditions (Douglas & Atwood, 2017), our quasi-extinction estimates are quite optimistic. An adaptive (heritable) response to the loss of sea ice is unlikely given the generation time of the species relative to the rate of sea ice decline, and the multiple ways in which loss of sea ice is affecting the subspecies' life history. Loss of sea ice in the Bering Sea wintering area has lagged CO₂ emissions but is accelerating, and the conditions required for a complete loss of Bering Sea ice may already exist (Clement Kinney et al., 2022). While loss of summer sea ice in the Arctic has had a major effect on breeding success and population growth since the 1990s, since 2018 decreased sea ice in the Bering Sea wintering area has been associated with decreased survival and conditions of adult birds.

Of more concern and greater uncertainty is the future trajectory of the Western Arctic MBG metapopulation, of which the Cooper Island colony is a part. It extends from Herschel Island, Canada, west to at least the Wrangel and Herald Island in the Chukchi sea and perhaps the New Siberian Islands in the East Siberian Sea. The importance of the metapopulation to the establishment, initial rapid growth and continued maintenance of the Cooper Island colony is clear as shown by our results. In the last four decades all colonies in the metapopulation have experienced changes in sea ice and SST during the period of chick provisioning, like those that have reduced Arctic cod availability and breeding success at Cooper Island. Evidence that the decline observed on Cooper Island is part of a region-wide reduction is seen in the decreased immigration rate, indicating the assumed source colonies in the western Chukchi Sea are also decreasing in numbers and productivity. Cape Lisburne, in the Alaska Chukchi Sea, has been censused irregularly and declined from 85 pairs in 1977 to 20 pairs in 2019 (Dragoo et al., 2020). Additionally, the only other colony in the metapopulation that has been regularly monitored, Herschel Island, has a population trajectory very similar to the study colony, rapidly increasing

from the 1970s to early 1990s followed by a major decline with the colony now consisting of a few nonbreeding birds (Eckert, 2018) (Appendix S1: Figure S9).

Poleward range expansions in response to increasing temperatures have been predicted and documented for Arctic species (Brommer et al., 2012; Burnham et al., 2014). While changes in breeding distribution of MBG in response to spatial variation in sea ice have been documented for populations in the Canadian Archipelago (Prach & Smith, 1992), the Western Arctic lacks potential nesting islands north of 72° N that would allow birds to breed adjacent to the retreating sea ice.

CONCLUSIONS

Our half a century of study of an upper trophic-level predator dependent on the cryopelagic ecosystem demonstrates the sensitivity of MBG to variation in sea ice in the Western Arctic caused by changes in the region's cryosphere driven by major alterations in the region's atmosphere and oceans. Our analysis provides a unique detailed multi-decadal examination of the response of an upper-trophic level marine predator to changes in the availability of Arctic cod, a keystone species of the Arctic's cryopelagic system. While our study involved only a single colony, the major importance of variation in immigration to colony growth and decline strongly suggests the entire metapopulation is in decline. More importantly, as an Arctic cod specialist, our documentation of a region-wide decline is evidence of a substantial reduction in the availability of the primary forage fish in the Arctic Basin.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Divoky et al., 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.c.7079446>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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