

Fluctuations in circumpolar seabird populations linked to climate oscillations

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Abstract

We found that synchronous fluctuations of two congeneric seabird species across the entire Arctic and sub-Arctic regions were associated with changes in sea surface temperatures (SST) that were linked to two climate shifts, in 1977 and again in 1989. As the SST changes linked to climate shifts were congruent at the scale of ocean basins, fluctuations of these species occurred similarly at continental or basin scale. Changes in colony sizes were examined for a decade following climate shifts. The magnitude of the SST shift was more important than its direction in determining the subsequent rate of population change. Seabirds declined when the SST shift was large and increased when the shift was small, although the effect differed between the Arctic-breeding species and the more temperate-breeding congener. The Arctic species, Thick-billed Murre (*Uria lomvia*) increased most rapidly when SST warmed slightly, while the temperate species, Common Murre (*Uria aalge*) showed most rapid increase with moderate cooling. Both showed negative trends with large temperature shifts in either direction. This pattern was replicated during both climate oscillations. Negative population trends in seabirds presumably indicate the alteration of underlying food webs. Hence, similar widespread fluctuations in response to climate shifts are likely for other ecosystem components (marine mammals, fish, and invertebrates).

Keywords: circumpolar Arctic, climate change, Common Murre, population change, seabirds, Thick-billed Murre, *Uria aalge*, *Uria lomvia*

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Introduction

Recent climate trends and general climate models point toward an increase in global temperatures over the next

century (Stott & Kettleborough, 2002; ACIA, 2005). This realization has focused attention on the effects of global climate change on populations and ecosystems (Stenseth *et al.*, 2002; Chavez *et al.*, 2003; Parmesan & Yohe, 2003). Three general obstacles have hindered the documentation of these effects for widely distributed marine species. While climate change is a global

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phenomenon, most analyses of its ecological consequences, to date, have been local in scale. Additionally, although global temperatures are generally increasing (Stott & Kettleborough, 2002), superimposed on this long-term warming trend are cyclical patterns created by decadal climatic oscillations, like those in the North Pacific (Francis *et al.*, 1998; Hare & Mantua, 2000), North Atlantic (Wilby *et al.*, 1997; Hurrell *et al.*, 2003) and Arctic (Deser, 2000; Wallace, 2000) regions. Furthermore, a massive and profound alteration of marine ecological systems by the loss of top trophic levels owing to overfishing, pollution, and the introduction of exotic species cause the baseline for comparisons to be a moving target (Pauly & Maclean, 2003).

The Pacific Decadal Oscillation (PDO), the North Atlantic Oscillation (NAO), and the Arctic Oscillation (AO) are three common climate indices often referred to while describing decadal climatic oscillations in the mid to high latitudes of the northern hemisphere. The PDO is a leading principal component of North Pacific sea surface temperature (SST) variability (Francis *et al.*, 1998; Hare & Mantua, 2000), the NAO is the dominant mode of winter climate variability in the North Atlantic region and is based on sea level pressure anomalies (Wilby *et al.*, 1997; Hurrell *et al.*, 2003), and the AO is a leading mode of high latitude variability also based on sea level pressure (Deser, 2000; Wallace, 2000). All these oscillations fluctuate between a positive and negative state every two or three decades. These oscillations, all of which seesaw at a basin-scale, are associated with periodic shifts in wind patterns, which in turn affect ocean mixing and SST trends. Changes in SST have often helped explain large changes in marine fish (Francis *et al.*, 1998; Hare & Mantua, 2000) and bird populations (Schreiber, 2002; Durant *et al.*, 2004). Two shifts in the state of these oscillations, called regime shifts (Francis *et al.*, 1998; Hare & Mantua, 2000), with parallel shifts in SST, have occurred since 1970. During the same period, much information has been accumulated on seabird population trends (Gaston & Hipfner, 2000; Ainley *et al.*, 2002; Dragoo *et al.*, 2003; ICES, 2003; Lorentsen, 2005; Mavor *et al.*, 2005).

Because seabirds are abundant, as visible top predators they are good indicators of change in the marine ecosystem, and their habit of breeding on land allows them to be studied relatively easily as compared with many other marine organisms. Recently, seabirds have been found to respond to long-term climatic changes at local to regional scales in the North Atlantic (Aebischer *et al.*, 1990; Thompson & Ollason, 2001; Durant *et al.*, 2003, 2004; Harris *et al.*, 2005), the North Pacific (Veit *et al.*, 1997; Anderson & Piatt, 1999), and the Southern Ocean (Weimerskirch *et al.*, 2003). To develop a larger-scale global view of the relationship between seabirds

and climate change, we combined population trend data on Common and Thick-billed Murres (*Uria aalge*, *Uria lomvia*) from 10 countries of the circumpolar Arctic. Between them, these two congeners inhabit most of the temperate and polar waters of the northern hemisphere, breeding in colonies of up to one million birds (Nettleship & Evans, 1985; Anker-Nilssen *et al.*, 2000; Gaston & Hipfner, 2000; Ainley *et al.*, 2002). The Thick-billed Murre tends to be associated with colder water than the Common Murre, and is particularly associated with areas of seasonal and sometimes extensive sea-ice cover. Both species feed on fish and large zooplankton throughout the year (Gaston & Hipfner, 2000; Ainley *et al.*, 2002) and are abundant throughout their ranges, which overlap extensively in the Pacific and less so in the Atlantic (Fig. 1). Their populations are easy to assess because birds usually nest in the open on cliffs or bare rocky islets, thereby providing good subjects for investigating large-scale phenomena. Murres, like many seabirds, have delayed maturation, are long-lived, and lay only a single egg. Survival rates for Thick-billed Murres range from 87% to 90% (Gaston & Hipfner, 2000) and for Common Murres range from 87% to 97% (Ainley *et al.*, 2002). Because murres are long-lived, population size tends to be slow in changing (Gaston & Hipfner, 2000; Ainley *et al.*, 2002; Dragoo *et al.*, 2003; Mavor *et al.*, 2005) as compared with short-lived animals, like many of their prey.

A basic tenet in ecology and evolutionary biology is that organisms adapt to their environment. Under stable conditions, populations are expected to achieve equilibrium. However, if the conditions shift rapidly, populations may be unable to adjust in the short-term and may consequently decline (e.g. Ainley *et al.*, 1994). The pooling of data from the entire circumpolar north presented us with the unusual opportunity to examine how ocean-atmosphere events at the scale of the hemisphere affected seabird populations throughout most (Common Murre) or all (Thick-billed Murre) of their range. In addition, because the two species differ with respect to their preferred water temperatures, comparing their reactions to SST changes should provide insights into their competitive relationship.

A fundamental expectation of the effect of climate change on a single seabird colony would be a monotonic, linear model that could be positive or negative. However, if populations before a shift reflected favorable SST conditions for these species, then we might anticipate that a large, rapid change would have negative population effects, irrespective of the direction of change. In that case, by combining data from many colonies in different climatic regimes, we anticipate a hump-shaped (quadratic), rather than a linear, response to climate change, with some colonies positively



Fig. 1 Distribution and size of Thick-billed and Common Murre colonies in the circumpolar countries: Iceland, Greenland, Canada, USA, Russia, Finland, Sweden, Norway, Great Britain, and the Faroe Islands.

affected and others negatively affected. Here, we examine how decadal regime shifts in climate, as measured by SST, have influenced population change in these two seabird species across their entire circumpolar ranges.

Methods

Sea surface temperature data

We examined the timing of shifts in three indices of climate oscillations: the PDO, NAO, and the AO. In all cases, we used SST as a proxy for the accompanying oceanographic changes. These indices fluctuate from positive to negative deviations on a decadal scale, and all indices made a shift in the 1970s and another shift in the 1980s (Hare & Mantua, 2000; Hurrell *et al.*, 2003). The concurrent shifts in SST in the Pacific matched well with the timing of the shifts in SST in the Atlantic, resulting in coherent and synchronous shifts of SST for

both oceans. We used the PDO shifts recognized in 1977 and 1989 (Hare & Mantua, 2000) and the adjacent decades to define the boundaries of three periods for investigation: 1965–76, 1977–88, and 1989–97.

To examine changes in ocean temperatures from one period to the next, annual winter SST data were used because winter storms mix surface waters and winter SST therefore reflects water column temperature, which is what we were most interested in but was not available, better than summer SST (PICES, 2005). The SST changes from one period to the next were characterized for the area within a 100 km radius of each colony, the approximate maximum foraging range of breeding murre (Gaston & Jones, 1998). Within each range, we did this by averaging SST data for 1° latitude/longitude blocks for the January–March period available from the Hadley Centre Global Sea Ice and Sea Surface Temperature (HadISST) Analyses of monthly long-term global SST (Hadley Centre for Climate Prediction and

Research, The Met Office, UK). The SST data were collected by satellites, buoys, and ships. Winter SST data were not available for seven Thick-billed Murre colonies located where the ocean was frozen all winter. For those colonies, we used July–September SST data, the period of least ice. These data were analyzed along with the winter data. Annual and then period means were calculated for each colony site. Period means were subtracted to find the change in SST between periods. This combination of winter SST at most colonies and summer SST at a few ice-bound colony sites were used throughout the paper to characterize changes in SST at murre colonies. However, we also used a long-term (50 years) average of annual SST for each colony to indicate the range of habitats used by these birds for breeding sites.

Murre data

Murre data were collected throughout the entire circumpolar Arctic and sub-Arctic regions of the northern hemisphere. In the western hemisphere, murre colonies ranged from about 52° to 69° north latitude in the Pacific and Arctic oceans. In the eastern hemisphere, colonies ranged from about 49° to 79° north latitude in the Atlantic and the Arctic Oceans. Although many colonies were situated in the Arctic Ocean, we refer only to the Atlantic and Pacific oceans when comparing colonies in the eastern and western hemisphere. Those in the Arctic Ocean were included within one or other sector.

Population changes were assessed by counting the number of adult murres, directly on cliffs or from photographs, either in sample plots or entire colonies (Birkhead & Nettleship, 1980). Sample plots were generally counted multiple times (four to seven) per year and entire colonies were counted once during the incubation or chick-rearing periods. Some colonies were monitored annually, others only intermittently. We calculated an annual rate of change by using the slope of the line obtained by linear regression using the natural log of the number of murres and the years when murres were counted. When sufficient data were available, we calculated an annual rate of change for each colony during each of the two climate regime periods following a regime shift. Such rates were estimated only if there were at least two data points, 5 or more years apart within the period. In a few cases, the first or last data point used occurred slightly before or after the climatic shift of the period of interest. To examine variability in population estimates, coefficients of variation (CV) were calculated for colonies that had 5 or more years of data. Murre colonies generally do not vary much from year to year, the average CV for Thick-billed and Common Murres were 15.12%, SD \pm 8.49%, range 26.02, $N = 14$; and 23.13%, SD \pm 13.39%, range

53.93, $N = 31$, respectively. Only colonies with >50 pairs were included in the analysis, and data from colonies less than 100 km apart were treated as if from a single colony.

We analyzed data from 32 Common and 21 Thick-billed Murre colonies, encompassing the entire circumpolar region. As 10 sites supported both species, 43 different study areas were represented. Data covering both periods, 1977–88 and 1989–97, were available for 19 Common and nine Thick-billed Murre colonies. In all, there were 295 colony-years of data for Common Murres and 123 for Thick-billed Murres.

Although many factors other than climate change affect murre populations, we omitted colonies only when there was compelling evidence that obvious factors other than climate had caused the observed population change, specifically, (1) three colonies affected by the *Exxon Valdez* oil spill; (2) nine colonies in decline due to excessive hunting; and (3) four colonies where unusual mortality of adults occurred due to a single, possibly fisheries-related, event.

Once we had determined the mean rate of change for each murre population during a period, we compared these rates, expressed as change per annum, with the difference in mean SST from one period to the next. As we used the colony-period as our sample unit, some colonies were featured twice when data were available for both time periods.

Analyses of murre population trends and changes in SST

We examined the relationship between changes in SST and changes in murre populations. We used the timing of climatic regime shifts as boundaries for our analyses. We ran a linear regression model that was consistent with a monotonic effect of climate change on murre populations. However, inspection of the residuals revealed that structure remained. We next ran a quadratic regression model that was consistent with the idea that too much change in the environment, either warming or cooling would be detrimental for murres. For both murre species, the parameter estimate for the quadratic term was significantly different from zero (Common Murres, $P = 0.013$; Thick-billed Murres, $P = 0.006$), and fitted the data much better than the linear model (Common Murres linear regression: $r^2 = 0.18$, quadratic regression: $r^2 = 0.28$; Thick-billed Murres linear regression: $r^2 = 0.16$, quadratic regression: $r^2 = 0.37$); consequently, we have plotted results from only the quadratic regression models.

Results

The SST around murre colonies in the northeast Atlantic cooled in the late 1970s while the SST around murre

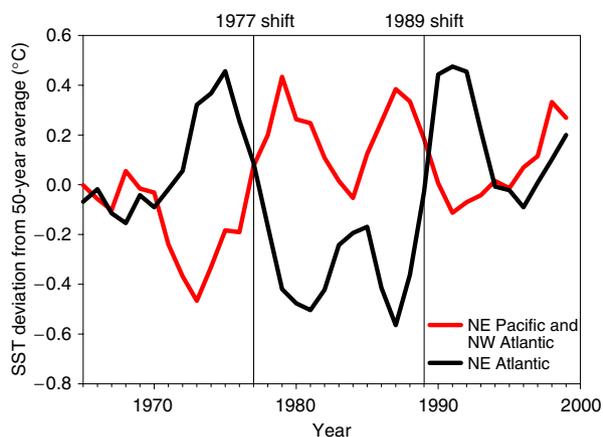


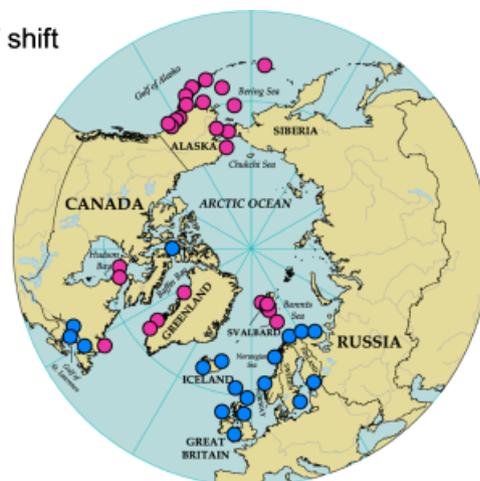
Fig. 2 Deviation of sea surface temperature (SST, 3-year running average) from a 50-year average around murre colonies in the NW Atlantic and the NE Pacific/NW Atlantic that were monitored for population change. The timing of the 1977 and the 1989 climatic regime shifts are indicated. NE Pacific and NW Atlantic were combined and compared with the NE Atlantic. Alaska represents the NE Pacific; Greenland and NE Canada represent the NW Atlantic; and Norway (excluding Svalbard), Sweden, Finland, and Great Britain represent the NE Atlantic.

colonies in the northeast Pacific warmed (Figs 2 and 3). Further, SST trends in the northwest Atlantic colonies were the opposite of trends in the northeast Atlantic colonies and similar to those at the Pacific colonies (Figs 2 and 3). The magnitude of the mid-1970s regime shift, expressed in terms of change in SST, was larger than the relatively small shift in 1989 (Fig. 2). The mean absolute value of the SST shift around murre colonies in 1977 was 0.46°C as compared with 0.32°C in 1989 (t -test: $t = 2.61$, $df = 79$, $P = 0.011$). Following the large 1977 regime shift, SST warmed at 58% of the colonies and cooled at 42% (Fig. 3a). It warmed at 47% and cooled at 53% of the sites after the relatively small shift in 1989 (Fig. 3b).

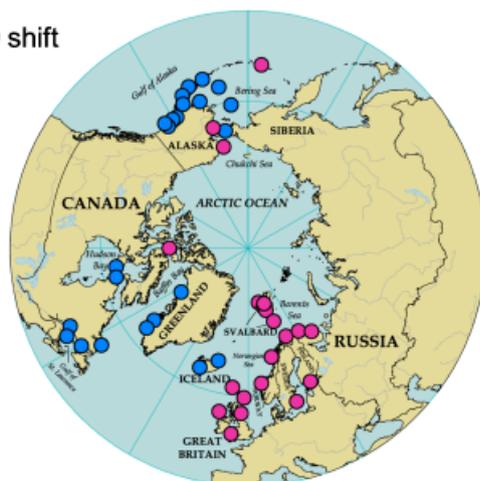
Also, the range of changes in SST from one regime to the next was smaller at the more northerly situated Thick-billed Murre colonies than at the more temperate Common Murre colonies. The range of changes in SST at Thick-billed Murre colonies was only 1.1°C from -0.4 to 0.7°C , while the range of changes in SST at the Common Murre colonies was 2.3°C from -1.0 to 1.3°C .

Murre colonies throughout the circumpolar north responded to the regime shifts. The responses were not linear, but quadratic, with increases in populations when the shift was small and decreases when the shift was large (Fig. 4). However, the model indicates that the range of SST changes (-0.95 to 0.50°C) allowing most Common Murre colonies to increase was about 60% larger than the corresponding range for Thick-billed Murres (-0.22 to 0.69°C). This difference in sensitivity

(a) 1977 shift



(b) 1989 shift



Change in average sea surface temperature

● Colder ● Warmer

Fig. 3 Direction of decadal change in average sea surface temperature after the 1977 climatic regime shift (a), and after the 1989 shift (b), at murre colonies that were monitored for population change.

is commensurate with the difference in total range of SST shift at the colonies of the two species, which was about twice as large for Common Murres than Thick-billed Murres (Fig. 4).

In addition, the entire quadratic response curve for the two species was offset, with Thick-billed Murre colonies increasing fastest after a positive SST shift of about 0.25°C and Common Murre colonies increasing fastest after a negative SST shift of about -0.20°C (Fig. 4). Thus, Thick-billed Murres seem to be more acceptable of warmer water and less adaptable to cooler changes, whereas Common Murres are likely to decline more quickly when the water warms than when it cools. The maximum rates of change observed for the colonies

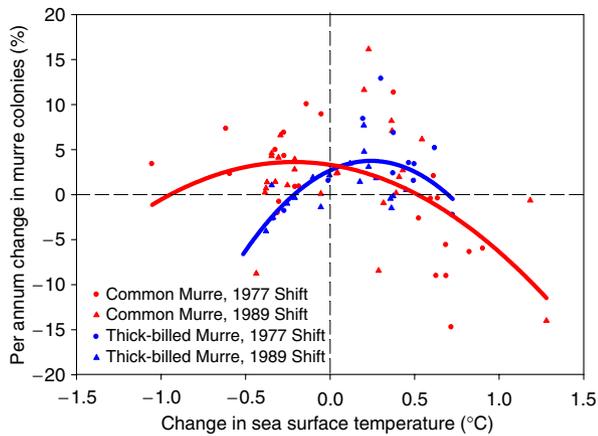


Fig. 4 Relationship between per annum change in the size of murre colonies during the 12 years after the 1977 climatic regime shift and during 9 years after the 1989 shift, and changes in sea surface temperatures around the colonies from one decadal regime to the next. Population data are from 32 Common and 21 Thick-billed Murre colonies, encompassing the entire circumpolar region. As 10 sites supported both species, 43 different study areas were represented. Quadratic functions were fitted to the data (Thick-billed Murres $P = 0.002$, $df = 27$, $r^2 = 0.370$; Common Murres $P < 0.001$, $df = 48$, $r^2 = 0.280$).

in our sample were notable in that it takes only about 7 years for a population to be doubled or halved if its changing by a rate of +10% or -10% per annum, respectively. Hence, many populations changed substantially from one regime shift to the next.

Although the SST shifted markedly from one regime to the next, the variation in SSTs among colony locations for each species was far greater than temporal variation between regimes. The SST at colonies in cold-water currents was substantially more frigid than SST at colonies in warm water currents. Mean annual SSTs for the period of the study varied over a range of 11 °C (1.3–12.4 °C) for Common Murre colonies and 9 °C (-1.0 to 8.0 °C) for Thick-billed Murre colonies (Fig. 5). In contrast, the mean winter (summer for a few ice-bound colonies) SST change at any particular colony between periods averaged only 0.4 and 0.3 °C, respectively (0.4 and 0.1 °C for summer temperatures).

Discussion

In the 1970s, both the North Pacific and the North Atlantic climatic oscillations shifted from a negative to a positive regime (Wilby *et al.*, 1997; Francis *et al.*, 1998; Hare & Mantua, 2000; Hurrell *et al.*, 2003) with parallel but opposite shifts in SSTs. When the northeast Atlantic cooled in the late 1970s, the northeast Pacific warmed. This atmospheric teleconnection, mediated by atmo-

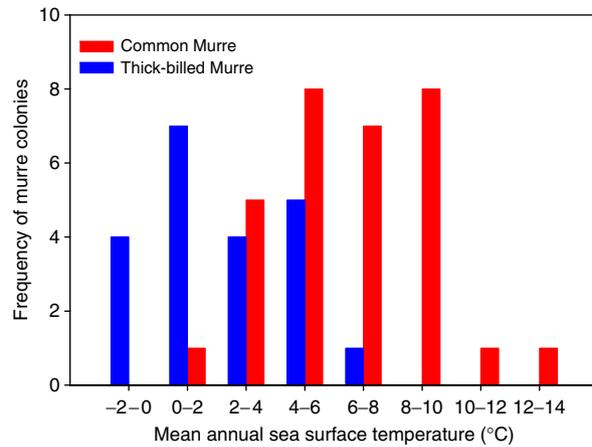


Fig. 5 Distribution of Common and Thick-billed Murre colonies with respect to the mean annual sea surface temperature within a 100 km radius of each colony.

spheric pressure, acted like a complementary transpolar seesaw during our study period. However, this uniformity in timing of PDO and NAO shifts has not always occurred (Wilby *et al.*, 1997; Hare & Mantua, 2000; Hurrell *et al.*, 2003). The mid-1970s regime shift was the largest recorded in the northern hemisphere (Visbeck *et al.*, 2001; Hurrell *et al.*, 2003), whereas the shift in 1989 was relatively small (Hare & Mantua, 2000) (Figs 2 and 3).

Murre populations throughout their entire range were affected by these changes in climate. Because shifts in SST occurred at the same time throughout the Arctic, there was a circumpolar pattern in the timing of changes of seabird populations throughout the northern hemisphere. While many factors cause seabird populations to vary, climate change is likely the only factor that affects seabird populations at the scale of a hemisphere. Such widespread patterns can of course only be recognized when data from around the world are brought together for analyses.

The convex response curves of murre colonies to decadal SST changes demonstrate a very important aspect of how climatic change can affect seabirds. Murre populations increased with little or no SST change but declined when the SST shift was large, irrespective of the direction of the temperature change (Fig. 4). The shape of these response curves could be derived in two ways. First, if murres at each colony throughout their range are adapted to local environmental conditions they may be unable to cope with changes caused by large, abrupt changes in water temperature. In this case, we would expect that colonies declined throughout the range of each species. Or second, because species are generally thought to do

better in the center of their range than at the edges, an 'edge effect' might cause birds at the edge of their range to be more sensitive to climate change. In this case, large declines would be expected to occur more often at the edges than in the centers of these species' ranges. We, therefore, examined the colonies that declined to see if they were at the edge of their ranges. Because there is not a clear range-wide latitudinal gradient, we used both latitude and long-term average SST (the average of 50 years SST data) as coarse proxies for the position of each colony within the species range. We found for both Thick-billed Murres and Common Murres, colonies that declined were generally not at the edges of their ranges. We, therefore, suggest that the reaction to climate change by murres is caused because murres are sensitive to abrupt change in the environment throughout their ranges.

The mechanisms behind the changes in murre colonies are more likely related to changes in prey availability than to changes in temperature *per se*. The decadal SST changes observed were very small compared with variation in temperature over the species' ranges (Figs 4 and 5). However, murre diets differ throughout their range in accordance to distinct water temperatures (Nettleship & Evans, 1985; Venrick *et al.*, 1987; Gaston & Hipfner, 2000; Ainley *et al.*, 2002). In the north Atlantic, Arctic cod (*Boreogadus saida*) and sculpins (Cottidae) are important prey items of Thick-billed Murres in the high Arctic areas, while capelin (*Mallotus villosus*) and gadoid species such as Atlantic cod (*Gadus morhua*) dominate their diet in the low Arctic. Atlantic Common Murres depend largely on capelin in the low Arctic, while those breeding in the boreal zone prey much on herring (*Clupea harengus*), and sandlance (*Ammodytes* spp.) (Bradstreet & Brown, 1985). The situation in the north Pacific is similar, with capelin, herring, and sandlance being the most important prey for Common Murres at low latitudes and Arctic cod the more important for both species at higher latitudes (Dragoo *et al.*, 2003). These results suggest that each colony has adapted to the average long-term conditions for that area and members prey on species that are abundant and similar in ecotype, (i.e. small schooling clupeoid or clupeoid-like species).

Fish populations are known to be sensitive to regime shifts and long-term climate changes (Francis *et al.*, 1998; Anderson & Piatt, 1999; Hare & Mantua, 2000; O'Brien *et al.*, 2000; Toresen & Østvedt, 2000; Visbeck *et al.*, 2001). Changes in populations of fish-eating seabirds are likely to be proximately mediated by changes in their prey base. The large fluctuations in the stock of Norwegian spring-spawning herring during the 20th century were caused by variations in the survival of recruits released from significant top-down forcing

owing to the depletion of upper trophic level fish and whales, and again largely corresponded to parallel variations in the temperature of the inflowing water masses to the region (Toresen & Østvedt, 2000). The climate-affected oscillations in predator abundance (herring and cod) have also contributed to repeated collapses of the Barents Sea capelin (Hjermann *et al.*, 2004), another important prey of murres. Similarly, capelin almost disappeared in the Gulf of Alaska after the regime shift in 1977 (Anderson & Piatt, 1999) and underwent substantial changes in distribution off Atlantic Canada following the 1989 regime shift (Frank *et al.*, 1996; Carscadden *et al.*, 2001). Our results suggest that relatively large climate shifts, irrespective of direction, may have had negative consequences for marine food webs and hence for murre populations.

The effects of decadal shifts in climatic and oceanic conditions on circumpolar seabird population dynamics have important implications. Because the peak population growth rates of the two murre species are offset with respect to changes in atmospheric pressure and ocean circulation as manifested in ocean temperature, a small climate shift to the warm phase favors Thick-billed Murres and a small shift to the cold phase favors Common Murres, demonstrating that small climate change may have disparate effects on closely related species. More importantly, large rapid change appears to have a negative impact irrespective of the direction of change. However, because of the offset peak population growth rates, the decline of Thick-billed Murres was large when temperatures cooled and small when temperatures warmed, while the effect on Common Murres was opposite; their decline was large during warming and small during cooling.

The difference between the two species accords with what we might expect if their current population levels and distributions are determined partly by competitive interactions and partly by physical constraints. Thick-billed Murres are an Arctic species that are likely limited by abiotic factors such as sea ice prohibiting feeding (Gaston *et al.*, 2005). Common Murres are a temperate species generally associated with dense schools of forage fish (Piatt, 1990) that are common in cold, energy-rich water. We suggest that part of the reason that Thick-billed Murres do best when water warms up is that there are longer ice-free periods, which allows better foraging and higher reproductive success. Common Murres may do better when it cools slightly because those are the prey-rich conditions that they have become adapted to, but recent global warming has changed that. Competition would result in the realized range of Thick-billed Murres lying in colder waters than might be the case without competition, while the range of Common Murre would, on average,

be warmer. In that case, we should anticipate that SST reduction within the range of Thick-billed Murres should have negative population consequences, whereas SST reduction within the range of Common Murre would be more likely to have positive consequences. That is precisely the pattern that we see.

If the amplitudes of ocean climate fluctuations continue to be large (Wilby *et al.*, 1997; Visbeck *et al.*, 2001), or increase with global warming and depletion of top-trophic fish and cetacean predators continues (Pauly & Maclean, 2003; ACIA, 2005; Salinger, 2005), future climate shifts are likely to have large-scale negative consequences for seabirds, presumably through the disruption of underlying food webs. Hence, similar negative consequences are likely for other ecosystem components (marine mammals, fish, and invertebrates). Widespread decline of these resources would have far-reaching consequences to Arctic and sub-Arctic communities and rural cultures, as has been demonstrated for other cultures in the past (Bowen, 2005).

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