Effects of Climate Change, Altered Sea-Ice Distribution and Seasonal Phenology on Marine Birds

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Abstract The Hudson Bay region supports internationally significant populations of marine birds (>2,000,000 individuals), particularly thick-billed murres (Uria lomvia) and common eiders (Somateria mollissima). The breeding ecology of both of these species is inextricably linked to distribution of sea ice and the timing of its breakup and freeze-up, which determine the availability and distribution of open water in which to feed. For the piscivorous murres, earlier ice breakup is creating a mismatch between the timing of breeding and the peak in food availability, and the birds have not, to date, advanced their breeding phenology to keep up with the pace of environmental change. However, at the end of the season, delayed freeze-up is extending the period that birds can remain in the Bay. Earlier ice breakup may allow migratory eiders earlier access to the benthic mollusks they require to gather nutrient resources prior to breeding, and for the non-migratory eider population in southern Hudson Bay, warmer temperatures mean more open water (i.e., larger and more numerous polynyas and floe edges) needed to gather food supplies necessary for their overwinter survival. Thus, the effects of changes in sea ice cover vary according to each species' ecological needs. We anticipate considerable changes in populations of marine birds in the Hudson Bay region in future, due to direct and indirect effects of reduced sea ice cover.

Keywords Thick-billed murre • Common eider • Arctic cod • Capelin • Sea ice • Break-up • Freeze-up • Breeding ecology • Dietary shift • Energetics

Introduction

The vast inland sea that is Hudson Bay supports some of the most important habitats for Arctic birds in North America. At least 20 "key habitat sites" for migratory birds (i.e., sites where $\geq 1\%$ of the Canadian population can be found at some

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Environment Canada, Canadian Wildlife Service, Box 1714, Iqaluit, NU XOA 0H0, Canada e-mail: mark.mallory@ec.gc.ca point during the year) have been identified in the greater Hudson Bay Region. To the public (bird hunters, bird watchers, television documentaries), the Bay is perhaps best known for its seemingly never-ending, flat coastal plains and marshes. Millions of snow geese (*Chen caerulescens*) breed in huge colonies along these coastlines, and hundreds of thousands of other waterfowl and shorebirds breed in or rely on coastal habitats as critical feeding areas during migration (Latour et al. 2008). Seven of these sites are national Migratory Bird Sanctuaries.

Perhaps less well known is the importance of the Hudson Bay Region for marine birds, that is, birds that live close to the sea and feed in the sea. This region is home to more than 2,000,000 marine birds. Arctic terns (*Sterna paradisaea*), various gulls (*Larus* spp., *Xema sabini, Rhodostethia rosea*), jaegers (*Stercorarius* spp.), guillemots (*Cepphus grylle*) and loons (*Gavia* spp.) rely on the waters of Hudson Bay for breeding and feeding annually. However, the most numerous marine birds in the Bay are thick-billed murres (*Uria lomvia*) and common eiders (*Somateria mollissima*). In fact, the two largest thick-billed murre colonies in Canada occur here, at Akpatok Island and at Digges Sound, which together support approximately 1,600,000 birds (Gaston and Hipfner 2000). Similarly, the largest, single common eider colony in Arctic Canada is found at East Bay, Southampton Island, where up to 9,000 birds breed in some years (Mallory and Fontaine 2004). Furthermore, small island archipelagoes that dot the eastern parts of the region contain widely distributed colonies that support tens of thousands of nesting eiders (Abraham and Finney 1986; Nakashima and Murray 1988).

Both murres and eiders have been the focus of conservation research in Hudson Bay for more than 20 years. Adults and eggs of both species are harvested by Inuit living in communities around Hudson Bay (Priest and Usher 2004), as well as being part of regionally important hunts in wintering areas along Newfoundland and Labrador, the northern Gulf of St. Lawrence in Quebec, and southwest Greenland (Chardine et al. 2008; Merkel and Christensen 2008). Here, we review some of the ecological needs of these species that have been revealed during these studies, with particular attention given to the relationship between sea ice and marine bird reproduction and survival.

A Tale of Two Marine Birds

It has been well-established that tracking the population size and reproductive success of marine birds serves as a strong and sensitive monitor of marine environmental conditions (Cairns 1987; Furness and Greenwood 1993, Parsons et al. 2008, Gaston et al. 2009). As well, some marine birds travel long distances to feed, with individuals sometimes feeding at different trophic levels, but they return to their colony during incubation or to rear chicks, so information integrating conditions over a geographically-large marine area can be gathered by studying birds at a single colony (Montevecchi 1993; Parsons et al. 2008).

Waters of the Arctic are covered with sea-ice for much of the year. As air-breathing predators, marine birds and mammals require open water in which to surface and

breathe while feeding. The timing of ice breakup and the position of the ice edge is a critical factor influencing the ecology of seasonally ice-covered waters (Welch et al. 1992), for two reasons. First, sea-ice forms a physical barrier for predators to be able to access marine foods. Second, breakup of sea-ice releases a food web and nutrients that developed under the ice, generating a flush of herbivorous zooplankton, which provides abundant food for upper trophic levels, and effectively "sets the clock" for the whole marine ecosystem (e.g., Le Fouest et al. 2005; Wang et al. 2005). Moreover, variation in the schedule of these events can create year-to-year variation in primary production that can affect growth and reproduction at higher trophic levels (Arrigo and van Kijken 2004; Johnston et al. 2005).

The relationships between the timing of open water availability and population size and reproductive success have been studied for both murres and eiders in Hudson Bay. These two bird species occupy very different ecological niches, and thus it should not be surprising that each tells a different story about sea-ice, climate change and the marine environment of Hudson Bay.

Thick-Billed Murres (Uria lomvia)

Natural History

Thick-billed murres are robust, black and white, pursuit diving seabirds that are found in Arctic waters (Gaston and Hipfner 2000). They resemble penguins except that they can fly (Fig. 1). Murres are long-lived (at least 29 years), and a breeding pair tends to stay "partnered" for many years (i.e., socially monogamous). Murres return to the exact same nesting location on the cliff annually, where they lay a single egg that is incubated on bare rock. They are principally pelagic piscivores, although they also consume other marine organisms like crustaceans, and evidence suggests that birds may become "specialists" on certain prey (Woo et al. 2008). Murres usually feed within 170 km of their colony, diving down to 140 m (Gaston and Hipfner 2000; Elliott et al. 2007, 2008). Because they feed relatively high in the marine food web, murres bioaccumulate various contaminants, and these concentrations differ among colonies in the Canadian Arctic (Braune et al. 2002; Braune 2009a). Both the male and the female incubate the egg and help rear the chick. During chick-rearing, murres return to their colony usually with a single fish held in their bill, which makes it easy for researchers to quantify what adult murres are feeding to their offspring (Gaston 1985; Elliott et al. 2008).

Reproduction and Climate

Murres have been studied intensively for nearly 3 decades at the Coats Island colony (62°57'N, 82°00'W) in northern Hudson Bay (Gaston et al. 2009).



Fig. 1 Thick-billed murres (*Uria lomvia*) on the breeding ledges at the Coats Island colony (Photo by Jennifer Provencher)

This site supports approximately 30,000 breeding pairs of murres, making it much smaller than Digges Sound or Akpatok Island, but the physical configuration of the colony cliffs makes working there much safer. Murres from Coats Island spend the winter in the waters of Davis Strait, Labrador Sea and off Newfoundland, and then migrate through Hudson Strait to return to their colony each spring (Gaston and Hipfner 2000). In a "normal" year, murres arrive at the colony in mid- to late May, and lay their single egg in the second half of June (Gaston and Hipfner 1998). However, in years when the sea-ice is late breaking up in Hudson Bay, murres initiate their laying by as much as a week later. This delay is attributable to the need for murres to forage and acquire resources for egg production; in years of heavy ice, open water may be too distant from the colony, and birds must wait longer before they can initiate egg formation.

Interestingly, the relationship between nest initiation and ice cover shows a parallel relationship with diet. Arctic cod *Boreogadus saida*, an ice-associated, key species in Arctic marine food webs (Bradstreet and Cross 1982) was a major component of murre nestling diet at Coats Island up to the mid-1990s. During that period murres delivered a higher proportion of cod to their chicks in years when extensive ice cover persisted later into the season (Gaston and Hipfner 1998). This situation (i.e., later ice break-up associated with a cod-dominated diet) is

thought to represent the historical norm for the Coats Island colony. However, that relationship has changed since the 1990s.

Over the past few decades, ice conditions in Hudson Bay have changed, with break-up occurring earlier and the consequent date of 50% clearing of ice cover in surrounding waters advancing approximately 17 days, especially since 1994 (Gaston et al. 2009; Fig. 2). Along with this physical change in the marine ecosystem, monitoring of thick-billed murres at Coats Island has detected biological changes. Although murre chicks were fed mostly Arctic cod from 1981 to 1990, a period of dietary transition occurred between 1990 and 1996, and since 1996, capelin (Mallotus villosus) has dominated chick diets (Gaston et al. 2003). Capelin is a fish more typical of subarctic waters, while Arctic cod is common among High Arctic areas. Thus, over the 3 decades of monitoring chick diets, there has been a shift in the marine food web towards warmer water species (Fig. 3). During the 1990s this change in diet was associated with lower adult body mass during chick-rearing than was observed in the early years of this study and with lower chick growth rates (Gaston et al. 2005). One possible reason for lower mass or growth rates comes from nutritional changes. Arctic cod and capelin have similar energy densities, but capelin delivered by adult murres tend to be smaller than cod. Consequently, chicks now receive less energy for growth than they did in the past, and adults may be working as hard or harder to deliver this energy (Gaston et al. 2005; Elliott and Gaston 2008). There is also evidence that the change in diet may be altering the exposure of these birds to different contaminants (Braune 2009b). The extent to which this may be affecting the birds is currently being explored.

Interestingly, another auk, the more typically boreal-water breeding razorbill (*Alca torda*) began appearing at the Coats Island colony coincident with an increase in the delivery of sandlance to murre chicks at this site (Gaston and Woo 2008). Sandlance is an important constituent of razorbill diet more or less throughout the species' range. The razorbills appeared in 1997, following a sharp increase in the representation of sandlance in thick-billed murre chick diets and disappeared again after 2004 as sandlance became rarer. If a long-term shift in available prey near Coats Island leads to a greater abundance of sandlance, it is likely that razorbills will colonize this site and compete for food resources with murres.

There is another route by which global warming is affecting murres, which has nothing to do with sea-ice. Coats Island supports an irritatingly abundant mosquito population which attack the incubating murres on the cliff. Mosquitoes can be so thick on the exposed feet of incubating murres that the birds look as if they are wearing fur boots. In the 1980s and early 1990s mosquitoes generally became abundant only after mid-July. Although they affected the murres on warm, still days, they appeared to have had little effect on reproduction during those years. However, by the late 1990s high mosquito activity was occurring from late June onwards. When mosquito attacks were most intense, in a few particularly hot years, the combination of mosquito parasitism and heat stress caused some incubating murres to die at their nests through a process analogous to heat stroke in humans (Gaston et al. 2002). In addition, many more birds left their breeding sites to cool off on the sea, leaving their eggs unattended. Many of these eggs were removed by

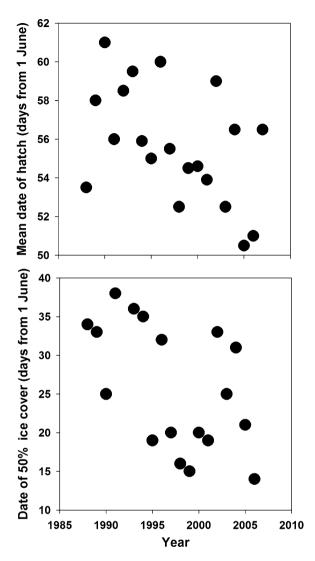


Fig. 2 Thick-billed murre hatch dates and the date at which 50% of the ice has cleared from Hudson Bay have both been advancing over the past 2 decades. In the top panel, earlier murre nesting is described by the regression: Date (days from 1 June) = -0.24*Year + 535, $r^2 = 0.23$, $F_{1,18} = 5.3$, P = 0.03. In the bottom panel, earlier ice clearing over the study period is described by the regression: Date (50% ice cover) = 1729 - 0.85(Year), $r^2 = 0.26$, $F_{1,18} = 7.6$, P = 0.01

glaucous gulls *Larus hyperboreus*, which patrol the colony constantly, on the look-out for exposed eggs or chicks, lowering the overall reproductive success of the colony. Because the first appearance and peak abundance of mosquitoes has become earlier at Coats Island over the past 3 decades (mirroring the earlier break up of sea-ice),

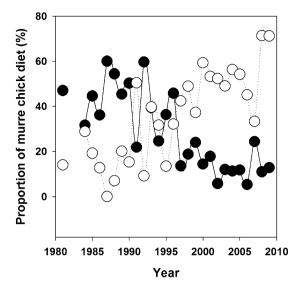


Fig. 3 The proportion of Arctic cod in the diet of thick-billed murre chicks has decreased since the 1980s (*filled circles*), while the proportion of capelin fed to chicks has increased (*unfilled circles*)

this is exposing the murre population to earlier and more prolonged mosquito attacks, creating increased mortality and lowered reproductive success.

Common Eiders (Somateria mollissima sedentaria)

Natural History

Common eiders are large, robust diving seaducks typical of cool waters (Fig. 4; Goudie et al. 2000). Like most Arctic marine birds, eiders are relatively long-lived, surviving up to 21 years, and they return to the same nesting colony in successive years, although not necessarily the same nest cup (Bustnes and Erikstad 1993). Arctic eiders lay clutches of three to six eggs in a nest cup lined with down feathers which the female plucks from her breast. Unlike murres, only the female incubates the eggs, and she departs the colony with the young when they are 1–2 days old. There is considerable variation in the size of eggs laid by eiders in different locations around Hudson Bay, presumably attributable to local differences in the genetic make-up of populations (Robertson et al. 2001; see below). Eiders dive to depths generally <20 m and feed on the ocean bottom, typically eating mollusks, sea urchins, sea stars, fish eggs and some crustaceans (Goudie et al. 2000). Like most other marine birds in the Arctic (Braune et al. 2002), common eiders exhibit



Fig. 4 A female common eider (Somateria mollissima) on her nest (Photo by Mark Mallory)

elevated levels of persistent organic pollutants (POPs) and certain toxic trace elements (Wayland et al. 2001; Mallory et al. 2004). In Hudson Bay, and notably in the Belcher Islands, eiders have relatively higher levels of certain POPs like DDT and mirex, and birds from western and northern Hudson Bay tended to have higher levels of mercury (Mallory et al. 2004).

In the Hudson Bay region, two races or subspecies of eiders inhabit coastal islands. Although the dividing line is not clear, it is thought that most eiders breeding around Hudson Strait west to Southampton Island and all areas north of that, belong to northern common eider race (*Somateria mollissima borealis*) (Abraham and Finney 1986). These eiders migrate from breeding colonies to overwinter along the west coast of Greenland, or along coastal Labrador, Newfoundland, and into the Gulf of St. Lawrence (Goudie et al. 2000; Merkel et al. 2006; Mosbech et al. 2006). Unlike murres, northern common eiders wintering in Greenland and Newfoundland do not rely on ice edges for foraging per se; they simply require open water areas over the shallow coastal mussel beds on which they feed. Sea ice has the potential to influence the timing of their spring migration, however. An earlier breakup of sea-ice in Hudson Strait, northern Hudson Bay, and Foxe Basin may initially benefit these populations by providing earlier access to food supplies as they approach their breeding colonies to nest.

Within Hudson Bay itself, from the Ottawa Islands south, most common eiders belong to the Hudson Bay common eider race (*Somateria mollissima sedentaria*); the largest race of eiders found in the world. These birds never leave Hudson Bay: they breed on coastal islands, and then aggregate in open water leads and polynyas in the Bay where they must survive the winter (Nakashima and Murray 1988; McDonald et al. 1997; Robertson and Gilchrist 1998; Gilchrist and Robertson 2000). It is these eiders that have been the focus of climate and ice research.

Overwintering and Climate

There are estimated to be more than 100,000 Hudson Bay common eiders, according to recent population surveys (Gilchrist et al. 2006). The vast majority of these birds converge on the Sleeper and Belcher Islands during the winter, to huddle together in the recurrent polynyas and the leads and floe edges that open and close with tide and currents (Nakashima and Murray 1988; Mallory et al. 2006; Fig. 5). However, the number of eiders found there in the winter fluctuates dramatically both seasonally and among years, in relation to climate and ice patterns (Nakashima and Murray 1988).

Part of this variation in numbers is attributable to climate-influenced reproductive success of nesting eiders the previous summer. For example, working in southwestern Hudson Bay, Robertson (1995a) showed that Hudson Bay eiders laid smaller eggs, delayed egg-laying and laid smaller clutches in a year following a winter of extreme ice (1991–1992), and when weather conditions were cooler prior to breeding (Fig. 6). Small eggs result in smaller chicks at hatch which typically have lower survival (Williams 1994). Thus, in particularly cold years, the combination of fewer eggs laid, and those eggs tending to be smaller means that we should expect fewer ducklings that survive to their first winter. This pattern has been observed in other Arctic waterbirds (Boyd 1996; Ganter and Boyd 2000).



Fig. 5 Common eiders huddled together in all available open water in a polynya, Belcher Islands (Photo by Grant Gilchrist)

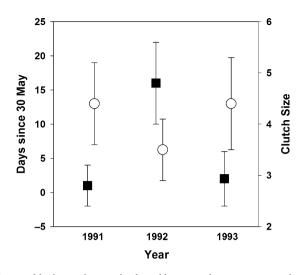


Fig. 6 Following a cold winter when sea ice lasted longer and was more extensive, eiders initiated nests later (*filled squares* \pm SD; $F_{2,312} = 27.8$, P < 0.001), and laid smaller clutches (*unfilled circles* \pm SD; $F_{2,312} = 342.3$, P < 0.0001)

Exacerbating this issue, cool spring weather in 1992 led to ice bridges remaining between islands and increased predation on clutches by arctic foxes (*Vulpes alopex*; Robertson 1995b).

However, what probably has a far larger and more lasting impact on the Hudson Bay eider population is the availability of open water during the winter, and how that constrains their access to food. This has been long-recognized by the Inuit in Sanikiluaq, as they have recorded aboriginal traditional knowledge of massive dieoffs of starving eiders during some winters (McDonald et al. 1997), notably in the winter of 1991–1992 (see Fig. 7), the same winter that preceded Robertson's (1995a) observations of reduced reproductive effort by eiders.

During "normal" winters, polynyas and leads in the sea ice are numerous around the Belcher Islands (Mallory and Fontaine 2004). During the day, eiders forage in open water areas offshore or along coastlines, where they dive through leads in the ice to feed on mussel beds. Towards the end of the day, eiders return to recurring polynyas, often in great numbers, where they roost overnight (Fig. 8). In the morning, the pattern reverses itself and eiders commute back to offshore or coastal feeding areas (Gilchrist and Robertson 2000). Ice cover is constantly shifting in the winter in this region, so the number of eiders that return to roost in the predictable open water at polynyas varies with the dynamic sea ice patterns that occur over feeding areas (Gilchrist et al. 2006). However, in years when particularly cold conditions and calm winds combine to generate heavy ice cover, many of the coastal and offshore feeding areas freeze over entirely. Under these conditions, eiders have no choice but to take refuge in the few recurrent polynyas that are kept open by strong tidal currents. If heavy ice conditions persist, all of the overwintering eider



Fig. 7 Dead common eiders along the edge of a freezing polynya, Belcher Islands (Photo by Grant Gilchrist)



Fig. 8 Common eiders hauled out to digest food along the edge of a polynya, Belcher Islands (Photo by Grant Gilchrist)

population must feed and roost at these polynyas (Gilchrist et al. 2006). Such a situation occurred in 1991–1992, when Arctic temperatures were lowered and ice was abnormally heavy in Hudson Bay, following the Mount Pinatubo eruption in 1991 (Ganter and Boyd 2000).

When eiders are trying to feed in these polynyas, they are facing three major constraints. First, there are many other eiders also trying to feed on sessile benthic prey, so competition for food in available food patches is high. For this reason, during normal winters it appears to be principally juvenile, inexperienced eiders that remain to feed at the polynyas, while more experienced, adult birds commute to open water patches where food is more abundant (Gilchrist et al. 2006). Second, strong currents, limited periods of suitable light, and freezing temperatures (which cause rapid ice formation during slack tide) mean that the amount of time available for eiders to effectively forage is actually quite limited (Heath et al. 2007). This constraint is further exacerbated by the need for eiders to have appropriate time to digest prev items, which they do when hauled out on the edge of the polynya (Gilchrist et al. 2006; Heath et al. 2006, 2007). The combination of these two constraints means that in any "normal" year some eiders die of starvation, generally inexperienced birds that are ill-equipped to withstand the winter stress. However, a third constraint emerges during years of heavy ice as occurred in the winter of 1991–1992. In these winters, thousands of eiders are forced to feed in a few polynyas, which results in rapid depletion of available prey. Mussels get eaten, and eiders then need to search for more mobile, but perhaps less nutritious, prey like urchins that move in and out of the patch. The net result is that under heavy ice conditions, food supplies are quickly depleted at polynyas and eiders begin to starve en masse. If sea ice remains extensive, mass starvation and death ensues.

In 1996, Inuit of Sanikiluaq thought that their local eider population had declined considerably since surveys conducted in the 1980s (Nakashima and Murray 1988), and they contacted government scientists to see if new surveys of known nesting islands could be initiated. The next breeding season brought favorable summer conditions, and surveys were undertaken on 426 islands where 1,414 nesting eiders were counted. In the late 1980s, these same islands had supported 5,651 eiders on nests, therefore representing a 75% decline in the local breeding population (Robertson and Gilchrist 1998). Because eiders exhibit breeding philopatry to nesting islands or island clusters, it was highly unlikely that the entire breeding population had moved. Moreover, clutch sizes were generally large in 1997, suggesting that it was also unlikely that many birds simply skipped breeding (something eiders will do in poor years; Goudie et al. 2000). However, populations of long-lived marine birds are sensitive to reductions in adult survival, and Inuit local had observed that many females had died in 1992. Subsequent collaborative research between the community and government scientists has supported the interpretation that the huge decline in the eider population detected in 1997 was a lingering result of the large die-off of the breeding population from 5 years earlier.

Collectively, research on eiders in Hudson Bay indicates that annual sea-ice conditions play a major role in regulating population size and, through occasional severe winters, structuring population demographics by entirely removing certain cohorts of birds.

What Does the Future Hold?

Multiple sources of information are showing convincingly that the Arctic climate and sea-ice are changing, and this is particularly apparent in Hudson Bay (McDonald et al. 1997; Gagnon and Gough 2005; Stirling and Parkinson 2006, this volume). What our work indicates is that the effects of these physical changes in the Hudson Bay marine environment will have quite different effects on the two key marine birds of this region.

Thick-billed murres are already experiencing dietary changes over the past 2 decades, and this has led to reduced chick growth and adult body mass, as well as altering their exposure to contaminants. However, many other factors influence murre populations, most notably human harvest and environmental conditions in wintering areas (Gaston and Hipfner 2000; Gaston 2003; Irons et al. 2008). Currently, there is no evidence that murres are being deleteriously affected at the population level by ice changes in Hudson Bay, although evidence from many murre colonies suggests a pattern of long-term population cycles in response to regime shifts in marine conditions (Irons et al. 2008). However, recent climate change may be disrupting this cycle, leading to long-term, massive changes in sea-ice patterns (Serreze et al. 2007; Comiso et al. 2008). As such, our expectation is that with continued changes to sea-ice and the prey base in the breeding and wintering areas, thick-billed murre colonies at the southern limit of their breeding range (i.e., northern Hudson Bay) will eventually decline (Gaston et al. 2005).

In contrast, Hudson Bay common eiders currently experience population-level bottlenecks or collapses in very cold years that result in persistent and extensive sea-ice cover. Not only is this a potential wildlife conservation concern, but it is an important issue for aboriginal residents of southern Hudson Bay, who rely on eiders as a key source of country food in the winter (Nakashima and Murray 1988; McDonald et al. 1997; Robertson and Gilchrist 1998; Priest and Usher 2004). Clearly this eider population has survived such natural, possibly cyclical challenges for thousands of years. Nonetheless, we expect that the non-migratory eiders of southern Hudson Bay will likely benefit by long-term reductions in sea-ice during the winter, as they should have more reliable access to open water for feeding. Then again, there are some substantial "unknowns" still to be resolved.

Despite decades of research on marine birds in Hudson Bay, there are some major gaps in our knowledge of the effects of other stressors on existing marine ecosystems that may affect future bird populations of this region, in concert with climate-induced changes. First, our knowledge of the potential sublethal effects of various contaminants on these species remains limited (e.g., Wayland et al. 2001), and requires further investigation. This may become particularly important if hydroelectric activities in Quebec alter inputs of contaminants to Hudson Bay, or alter currents that move this pollution around the Bay (McDonald et al. 1997). Second, reduced ice cover in the Bay will probably lead to increased shipping activity for community supply, industrial activity including offshore hydrocarbon

exploration, and tourism (Arctic Council 2009). The effects of these activities and their potential environmental disturbance and damage (e.g., oil spills) has not been adequately assessed. Third, climate warming will allow other competitor species to move north, and will also permit the northward movement of novel parasites and diseases into these bird populations. For example, outbreaks of avian cholera have recently appeared in northern common eiders nesting in Hudson Strait and northern Hudson Bay where they were not found previously. These have caused dramatic declines in the size of breeding colonies (e.g., Descamps et al. 2009). Finally, ongoing changes in winter habitats may be altering where, and in what proportion, Hudson Bay birds spend the non-breeding season. This can have major implications for population-level changes through anthropogenic impacts of disturbance, harvest and pollution (e.g., Merkel 2004; Wiese et al. 2004; Mosbech et al. 2006).

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