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Sources of Breeding Season Mortality in Canadian Arctic Seabirds

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ABSTRACT. In more than 30 years of studies on marine birds in Arctic Canada, we have observed numerous instances of mortality of adults, eggs, and chicks that seem unusual when compared to known sources of mortality for seabirds breeding in temperate or tropical regions. The extreme cold weather and ice conditions of the Arctic might intuitively be expected to be a significant factor in mortality for these Arctic birds. While weather conditions led directly to seabird mortality, other factors, perhaps facilitated by typical Arctic climate features, caused more deaths. In this paper, we summarize mortality incidents that we have witnessed for nine species of Arctic marine birds, as a baseline against which future observations can be made. We also speculate on mechanisms by which climate change could increase mortality of breeding Arctic seabirds in the future.

Key words: Arctic, marine bird, mortality, predation, weather

RÉSUMÉ. Dans le cadre d'études sur les oiseaux aquatiques qui se sont échelonnées sur plus de 30 ans dans l'Arctique canadien, nous avons observé de nombreuses incidences de mortalité chez les adultes, dans les œufs et chez les oisillons, incidences qui semblent inhabituelles lorsqu'elles sont comparées aux sources connues de mortalité des oiseaux de mer qui se reproduisent dans les régions tempérées ou tropicales. Intuitivement, nous croyons que le temps froid extrême et le régime des glaces de l'Arctique peuvent représenter un facteur de mortalité important chez ces oiseaux de l'Arctique. Bien que les conditions climatiques aient directement entraîné la mort des oiseaux de mer, d'autres facteurs, qui sont peut-être déclenchés par les caractéristiques climatiques typiques de l'Arctique, ont occasionné d'autres décès. Dans ce document, nous résumons les incidents de mortalité dont nous avons été témoins pour neuf espèces d'oiseaux aquatiques de l'Arctique comme point de référence en vue d'observations futures. Nous émettons également des hypothèses à propos des mécanismes dans le cadre desquels le changement climatique pourrait accroître la mortalité des oiseaux de mer de l'Arctique en reproduction à l'avenir.

Mots clés : Arctique, oiseau aquatique, mortalité, prédation, conditions météorologiques

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INTRODUCTION

Seabirds generally share traits of low annual reproductive output, delayed maturation, and high annual survival (Lack, 1968; Schreiber and Burger, 2002; Gaston, 2004). To date, seabird research has focused on issues that influence aspects of birth and fledging, including factors affecting reproductive effort, nest failure (i.e., egg and chick mortality), and annual reproductive success (e.g., Hamer et al., 2002; Schreiber, 2002; Frederiksen et al., 2006). Mortality of adult seabirds has also received much attention, but this topic is generally more difficult to study. Most previous publications have dealt with events outside the Arctic, especially fisheries bycatch (e.g., Tull et al., 1972; Melvin and Parrish, 2001; Mallory et al., 2006a; Rolland et al., 2008), oil spills (e.g., Piatt and Ford, 1996; Wiese et al., 2004), harvest (Hansen, 2002; Priest and Usher, 2004), and mass mortality events known as seabird "wrecks" (Warham, 1996; Gaston, 2004; Bugoni et al., 2007), die-offs that are often

highly visible because numerous seabird carcasses wash ashore (Bourne, 1976; Hudson, 1985). Seabird wrecks are often linked to poor feeding conditions (usually storm-related) in winter and may kill thousands of birds (e.g., Schreiber, 2002; Anker-Nilssen et al., 2003; Gaston, 2004). Aside from these highly visible mortality events, much less is known about factors leading to other natural mortality of adult seabirds, even in the case of disease outbreaks (Friend et al., 2001).

In the Arctic, migration mortality of some marine birds has been documented, particularly for eider ducks (e.g., Barry, 1968). However, few studies have reported natural sources of mortality of adult seabirds during the Arctic breeding season, when weather conditions can be extreme and may intuitively be considered a major factor in bird mortality. Previous reports have often included brief and anecdotal evidence (e.g., Hatch and Nettleship, 1998; Gaston and Hipfner, 2000; Gilchrist, 2001; Butler and Buckley, 2002), but quantitative details of adult mortality are lacking.

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In more than three decades of studies in the Canadian Arctic, we have observed numerous instances of seabird mortality during the breeding season, much of it from causes unlikely to occur at lower latitudes. Perhaps the most obvious environmental difference faced by seabirds in Arctic Canada compared to southern waters is the presence of cold, extreme weather through much of the year. Arctic seabirds initiate nesting while the marine regions surrounding them may still be ice-covered. Ice occasionally persists into the chick-rearing period at some locations (Gaston et al., 2005; Mallory and Forbes, 2007). Moreover, temperatures at many colonies can be near or below 0°C through much of the season, and significant snowstorms can occur in any month, particularly in the High Arctic.

Given the paucity of documented and quantifiable adult mortality reported during the breeding season, we summarize published and unpublished data on mortality of adult seabirds (auks, petrels, gulls, eiders) breeding in the Canadian Arctic to provide a baseline against which future observations may be compared. Our focus was on natural mortality events that we considered "unusual," that is, mortality other than from expected predation (e.g., foxes at nests; Gaston et al., 1985). Because we were concerned with natural mortality, we also exclude a discussion of human harvest, although this is a significant mortality factor for some seabirds in the Canadian Arctic (Merkel, 2004; Wiese et al., 2004). Finally, we comment on unusual mortality of eggs and chicks to demonstrate how sources of mortality for these Arctic species may differ from those documented for seabirds nesting in temperate and tropical regions.

METHODS

The observations reported here have accrued during field research projects conducted during the May-to-August breeding season in selected years between 1975 and 2008. Opportunities to observe adult mortality during the breeding season occurred at 11 different seabird colonies (Fig. 1). Details of the years of observations and geomorphology of the sites are listed in Table 1. Observations at these colonies focused on six species, namely thick-billed murres (Uria lomvia), black guillemots (Cepphus grylle), northern fulmars (Fulmarus glacialis), black-legged kittiwakes (Rissa tridactyla), glaucous gulls (Larus hyperboreus), and common eiders (Somateria mollissima borealis), but we had occasional observations on other species during breeding (Tables 2, 3). Note also that we use the term "seabird" to include marine waterfowl (notably eiders). Our summary represents an estimated 1700 person-days of our own observations, plus records from a minimum 2000 days by our field staff (with camps of 2-12 people on each day, thereby representing an estimate of more than 7000 person-days).

For cliff-nesting Arctic seabirds (those at most locations above, except Nasaruvaalik Island and East Bay), we observed adult mortality while viewing birds breeding along cliff ledges (e.g., Gaston and Nettleship, 1981;

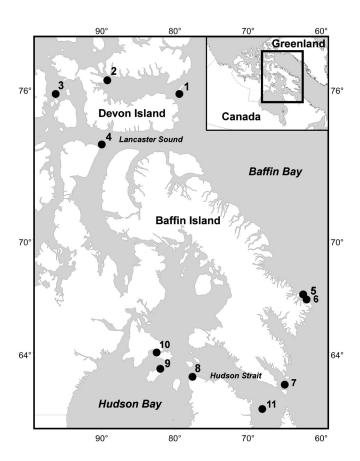


FIG. 1. Locations of marine bird colonies in Arctic Canada where seabird mortality incidents were observed between 1975 and 2008. Numbers refer to colonies listed in Table 1.

Gaston et al., 1985, 2002; Mallory and Forbes, 2007). Typically, birds were observed from discreet blinds along the top of the cliff, which overlooked long-term monitoring plots 3-300 m away. Depending on the proximity to the birds, observations were made without optical assistance, with 10×42 binoculars, or with $60 \times$ spotting scopes. Our approach to observing from blinds was similar for groundnesting colonies, although at some of those sites we walked around in order to view or check on birds (Stenhouse et al., 2001; Bottitta et al., 2003).

RESULTS AND DISCUSSION

We recorded 37 cases of unusual adult mortality during the breeding season (≥ 4500 birds; Table 2) and 13 cases of unusual egg or chick mortality (> 500 young; Table 3). Only three (6%) of these cases were reported previously.

Effects of Adverse Weather

We observed six events in which extreme weather accounted for the deaths of 40 or more adult breeding fulmars and murres (Table 2). At two colonies, Arctic fulmars with broken wings were found scattered on the sea ice or beach below the cliffs following nights of thick fog at the

Number	Colony	Lat/Long.	Years	Height and Structure
1	Coburg Island	75°50′ N, 79°25′ W	1987, 1997, 1998	Cliffs 250 m; massive metamorphic rocks
2	Cape Vera, Devon Island	76°15′ N, 89°15′ W	2003-05	Cliffs 250 m; frost-shattered, loose limestone
3	Nasaruvaalik Island	76°50′ N, 96°20′ W	2007	Island under 30 m; alluvial gravel
4	Prince Leopold Island	74° N, 90° W	1975–77, 1984, 1987, 2000–05, 2008	Cliffs 280 m; frost-shattered, loose limestone
5	Cape Searle	67°15′ N, 62°30′ W	2001, 2002	Rock towers 430 m; metasedimentary
6	The Minarets	66°56′ N, 61°46′ W	1985, 2007	Cliffs 800 m; volcanic rocks eroded into pinnacles with extensive talus areas
7	Hantzsch Island	60°25′ N, 68°08′ W	1982, 2005	Cliffs under 150 m; metamorphic
8	Digges Sound	62°15′ N, 78° W	1979–82, 1985, 1992–94, 2004	Cliffs under 250 m; sheer to sea, massive granites and metamorphics
9	Coats Island	62°57′ N, 82° W	1981, 1984-2007	Cliffs under 85 m, massive metamorphic rocks
10	East Bay, Southampton Island	64° N, 81°45′ W	1996 to 2007	Breeding sites on flat, open tundra
11	Akpatok Island	60°25′ N, 68°08′ W	1983, 1995	Cliffs under 300 m; horizontally bedded limestone

TABLE 1. Details of colonies where observations were made. Numbers refer to Figure 1.

colony. We found birds over 200 m from the cliff, and occasionally predators (probably foxes) had already eaten some of the carcasses. We never observed this type of mortality following clear evenings. Our Inuit guides had observed it often and thought that the fulmars flew into each other in the fog, breaking their wings. This seems a plausible explanation, although it is also possible that the birds collided with the cliff, broke a wing, and glided some distance before hitting the ice. We do not know whether this type of mortality also occurs at southern colonies, where injured birds might drop directly into the ocean and disappear.

We have not observed fog-related mortality in murres, but one observation suggests that flying near cliffs in fog is risky for them. On 26 July 2000 at Prince Leopold Island, the visibility was less than 50 m and wind was strong at 30–40 km/h. Approximately 20 adult murres were scared off their nests by researchers approaching the nest to measure their eggs. Murres normally return to their nest within five minutes, but on this occasion only three birds had returned after 40 minutes. When the fog dissipated to 80 m visibility, four more adults returned within one minute. This suggests that in high wind and fog, murres avoid trying to land on the cliff, presumably because of possible collision.

Heat may pose a problem for some species (Oswald et al., 2008). Gaston et al. (2002) described how unusually warm breeding seasons associated with high mosquito populations caused stress and death for breeding murres at Coats Island. Apparently some murres lack the response noted in some other seabirds (e.g., Anderson and Fortner, 1988) of abandoning the nest in reaction to either dehydration caused by heat or heavy ectoparasitism, possibly because dense swarms of mosquitoes have not been common in the evolutionary history of murres. We have not observed this response in other species, although mosquitoes are uncommon at most other colonies where we have worked.

At Coburg Island, where the colony is adjacent to a large glacier, katabatic winds with downdrafts exceeding 120 km/h struck birds as they took off from the breeding cliffs. They were driven into the sea so hard that they were killed on impact with the water. These katabatic winds flow off the nearby glaciers because air over the glacial ice sheet is colder, denser, and heavier than surrounding air. Similar

winds occur at the northern fulmar colony at Cape Vera, Devon Island. However, we have never observed mortality of fulmars due to wind, and this is perhaps attributable to their lower wing loading and greater maneuverability when compared to murres.

We recorded one case in which moving sea ice near the breeding colony trapped adult thick-billed murres and crushed them (Table 2). Abnormal ice conditions and effects of strong currents seem more likely to kill birds migrating or overwintering in polynyas (e.g., Barry, 1968; Robertson and Gilchrist, 1998), either directly or indirectly by blocking access to food resources and thus starving the birds.

Heavy storms at sea can kill young and occasionally adult breeders, such as kittiwakes and gulls (Threlfall et al., 1974), and in the Arctic, this at-sea mortality may be associated with abnormal freezing conditions, which can lead to death of fulmars and murres before the breeding season (Fisher, 1952; Tuck, 1961). However, we have not observed adult mortality at sea associated with storms in the eastern Canadian Arctic.

Collectively, the adult Arctic seabirds succumbing to the effects of harsh weather during breeding were a small proportion (~ 10%) of our observed mortality (Table 2), as expected for species adapted to breeding in the Arctic. For example, fulmars and thick-billed murres continue to incubate eggs and brood nestlings while almost completely buried in snow, with only their heads visible (pers. obs.). This snow covering could actually benefit birds by reducing wind chill while simultaneously providing protection from predators (e.g., gulls Larus spp., ravens Corvus corax). For eggs and chicks, however, the risk of mortality due to weather events is considerably higher. Eggs and chicks were often lost during bad weather, notably during heavy snowstorms and rain or freezing-rain events accompanied by high winds. In 2003 at Prince Leopold Island, 20% of the murre chicks and 32% of the fulmar chicks died at nesting areas near the tops of the cliffs during heavy August snow, apparently after being abandoned by their parents (Gaston et al., 2005). We suspect that heavy snow also explains much of the observed black guillemot chick mortality at St. Helena Island, where snow accumulation from blizzards may entomb chicks in their nesting crevices. In some years, a

large proportion of the chicks from the glaucous gulls nesting on the cliffs of Prince Leopold Island died of exposure during severe weather events (Table 3). Parent gulls often stood beside the nest rather than brood their dying chicks, probably because the young were too large to gain effective protection from the parent.

Also during major storm events, high waves at Coats Island have washed hundreds of murre eggs and chicks from nests along the lower parts of the cliff (Table 3). Similar mortality of herring gulls and kittiwake nestlings was observed by Threlfall et al. (1974) at Gull Island in Newfoundland.

Effects of Rock Fall and Avalanches

For cliff-nesting species, the main cause of adult seabird deaths during the breeding season was snow avalanches and rock falls (seven events causing 92% of deaths; Table 2). Even during events from which nesting adults escaped alive, their eggs or chicks often were crushed. This means that, after nest predation, avalanches and rock falls are probably the next main cause of reproductive failure for most Arctic seabirds (except for murres, whose poor co-ordination of incubation exchanges accounts for much egg and chick loss; Gaston et al., 1985).

Despite the frequent occurrence of avalanches and minor rock falls at the Cape Vera, Prince Leopold Island, and Cape Searle colonies (more or less daily during June and July), we observed only four occasions when snow avalanches carried nesting adult fulmars or murres to their death as they crashed on rocks or ice below the cliff (Table 2). We also saw only one instance of snow avalanches destroying nests (Table 3). Our observations seem few, given our intuition that snowstorms on cliffs should pose problems for nesting birds. The low numbers probably reflect two issues: (1) most nest sites are in locations that are sheltered from or not prone to avalanches (Gaston and Nettleship, 1981); and (2) in many years, our field observations were initiated after the period when avalanches from melting cornices were likely to occur. Colonies may also differ in their susceptibility to this phenomenon. For example, Birkhead and Nettleship (1981) noted that falling ice, accumulated as a result of freezing fog, destroyed many murre eggs and chicks at the Cape Hay (Bylot Island) colony, an apparent effect of local microclimate that has not been observed at Coburg or Prince Leopold islands.

Seabirds nesting at Arctic colonies situated on cliffs of eroding sedimentary rock appear most vulnerable to death by rock fall, which accounts for more adult and egg or chick mortality than avalanches. We saw over 1200 individuals of four species die in these events (Tables 2, 3). At Cape Vera, Prince Leopold Island, and Cape Searle, especially in July, there is a "constant chatter" as pieces of rock roll down ledges before falling to the scree slope below. At this time, temperatures are generally above 0°C, so that ice frozen into the pebbles and fissures along the cliff face thaws, releasing the rocks to the effects of gravity. Hence, mortality due

to rock fall could be considered a form of climate-related mortality. In one spectacular event, an entire cliff face at Prince Leopold Island (estimated at 25 m wide by 5 m deep by 50 m high) was released, disintegrated, and crashed to the ocean below. Hundreds of seabirds and their nests were crushed and destroyed by pieces of the rock face descending to the sea, even as they flew to escape (Table 2).

Predation in Unusual Circumstances or by Unusual Predators

Avian and mammalian predation is common at Arctic seabird colonies (Hatch and Nettleship, 1998; Gaston and Hipfner, 2000; Goudie et al., 2000). Polar bears (Ursus maritimus) can depredate the nests of an entire breeding colony of ground-nesting seabirds (e.g., Haney and Mac-Donald, 1995), and we have observed sure-footed arctic foxes (Vulpes lagopus) consuming eggs and adult murres, fulmars, kittiwakes, eiders and gulls, even on near-vertical cliff faces. However, one important aspect of predation in the Arctic is the relationship between harsh weather events and avian predation at seabird colonies. Severe weather, including extreme heat, can cause parents to leave their nests briefly, and avian predators may exploit these situations. For example, following an intense windstorm that induced temporary nest abandonment by northern fulmars at Cape Vera, glaucous gulls removed about 40% of the eggs on one nesting ledge (n = 33 nests) before the parents could return (Table 3). Storm-facilitated predation appears to be the leading cause of reproductive failure at some Arctic fulmar colonies (Mallory et al., 2009).

Glaucous gulls are effective predators at seabird colonies, with or without weather facilitation, feeding principally on eggs and chicks of a variety of species (Gilchrist, 2001). Although such cases are uncommon, we noted three situations in which gulls killed adult seabirds. First, gulls killed thick-billed murres that were already injured in rock falls (Gaston and Nettleship, 1981:103) or hit the sea ice (Table 2). We have not witnessed depredation by gulls on healthy adult murres. However, we watched gulls depredating adult black guillemots in two separate breeding seasons at St. Helena Island, near Cape Vera (Table 2). Although the defenses of a 400-gram guillemot are less effective than those of a 1000-gram murre, the gull likely incurs the greater risk of injury with this hunting behaviour. This incident occurred very early in the breeding season at a site that offered few other food resources for gulls. Similarly, we saw gulls hunting in pairs or alone to kill adult kittiwakes at Prince Leopold Island. Kittiwakes have a similar body mass to guillemots and may represent a similar, risky prey choice that is hunted when less challenging prey (eggs or chicks) are difficult to find. Regehr and Montevecchi (1997) also noted increased predation by gulls on adult kittiwakes in eastern Canada during periods of food shortage.

A second aspect of predation that is specific to the Arctic is the type of predators that can capture seabirds. We have watched polar bears use their paws to trap female eiders on

TABLE 2. Observations (minimum counts or estimates) of adult mortality among marine birds in the Canadian Arctic during the breeding seasons. Note that adult mortality during the breeding season means that the egg or chick also dies. Acronyms for predators are as follows: ARFX – arctic fox; POBE – polar bear; PEFA – peregrine falcon; GLGU – glaucous gull; CORA – common raven; REFX – red fox; GYRF – gyrfalcon; ATWA – Atlantic walrus.

Cause of Mortality Species	Date	Location	Birds Killed	Event	Comment
Species	Bute	Location	Trinica	Event	Comment
Extreme weather					
Northern fulmar	June 2001	Cape Searle	9	Fog	Wings broken; found below cliffs morning after fog
	June 2002	Cape Searle	4	Fog	Wings broken; found below cliffs morning after fog
	July 2005	Cape Vera	5	Fog	Depredated birds found on coast below cliffs following
				- 0	foggy night
Thick-billed murre	1997-99	Coats Island	12	Heat and mosquito	Gaston et al., 2002
				bites	
	July 1998	Coburg Island	> 5	Crash on ocean	Birds departing cliffs caught in katabatic downdraft
		2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	_		winds and crashed into ocean
	July 1998	Coats Island	5	Ice at cliff base	Adults trapped by loose ice pans driven into bay and
	vary 1990	Cours Island		100 40 01111 0450	crushed in ice
Avalanche and rock fall					VI 45/104 III 100
Northern fulmar	June 2001	Cape Searle	> 20	Avalanche	Caught in slide and died when hitting sea ice
rormem ramar	June 2001	Prince Leopold Island	> 2	Avalanche	Caught in slide and died when hitting sea ice
	May 2005	Cape Vera	> 7		
				Avalanche	Caught in slide and died when hitting scree slope
DI 11 11361 1	July 2005 ¹	Prince Leopold Island	~ 100	Rock fall	Nesting ledge disintegrated into massive rock fall
Black-legged kittiwake	July 1975 ²	Prince Leopold Island	5	Rock fall	Major rock fall; also carried down thick-billed murres
	July 2005 ¹	Prince Leopold Island	~ 300	Rock fall	Nesting ledge disintegrated into massive rock fall
Thick-billed murre	July 1975 ²	Prince Leopold Island	75	Rock fall	Major rock fall; also carried down black-legged
					kittiwakes
	June 1996	Coats Island	12	Avalanche	Snow cornice fell off carrying down murres to sea ice
	July 2005 ¹	Prince Leopold Island	> 800	Rock fall	Nesting ledge disintegrated into massive rock fall
Black guillemot	July 2000	Prince Leopold Island	1	Rock fall	Nesting adult in nest crevice crushed under ~2 kg rock
-	•	•			
Unusual predation					
Common eider	1996-2007	East Bay	> 5	Predation (POBE)	Polar bears can trap a nesting eider with paw and kill it
Black-legged kittiwake	June 2001	Prince Leopold Island	> 2	Predation (GLGU)	Gulls worked as team to hunt several birds
	June 2002	Prince Leopold Island	1	Predation (CORA)	Presumed predation (CORA seen on fresh kill)
	July 2008	Prince Leopold Island	1	Predation (GLGU)	Taken in flight by single gull
Thick-billed murre	June 1990,	Coats Island	> 15	Predation (ARFX)	Caught on ice after failure to get airborne while being
Thick office marie	1991, 1994	Coats Island	- 13	r reduction (r rret rr)	harassed by falcon or fox
	June 1990,	Coats Island	> 1	Predation (GLGU)	Caught on ice after failure to get airborne while being
	1991	Coats Island	> 1	Ticaation (GLGC)	harassed by falcon
	August 1991	Coats Island	1	Predation (POBE)	Caught by surfacing from below the murre
	June 1992	Coats Island	10	Predation (POBE)	Caught on ice after failure to get airborne leaving cliff
			>10	Predation (POBE)	
	August 1995	Akpatok	~10	Piedation (POBE)	Caught on beach below cliffs during chick departure
	A 4 2001	C4- I-1 1	16	D., J., (ATWA)	(J.M. Hipfner, pers. comm. 2008)
	August 2001	Coats Island	16	Predation (ATWA)	Depredated on water; Mallory et al., 2004
DI 1 31	July 2002	Coats Island	> 11	Predation (ATWA)	Depredated on water; Mallory et al., 2004
Black guillemot	May 2006	Cape Vera	3	Predation (GLGU)	Adults observed caught and eaten
	June 2007	Cape Vera	> 2	Predation (GLGU)	Adults observed caught and eaten
Disease					
Common eider	July 2004	Hudson Strait	> 100	Avian cholera	First known cases of cholera in eastern Arctic
	2005-07	East Bay	> 3000	Avian cholera	Westward expansion of cholera in eastern Arctic
Glaucous gull	August 2004	Digges Sound	3	Avian cholera	Could have scavenged infected eiders
Herring gull	2005 - 07	Hudson Strait	> 10	Avian cholera	Probably scavenged infected eiders
Navigation errors					
Thick-billed murre	1976	Prince Leopold Island	1	Flew into cliff	Bird flew into cliff at full speed, in good visibility and
					light wind; fell and disappeared
Thick-billed murre	1988	Coats Island	1	Foot stuck in crack	Bird found dead on cliff with one foot wedged in a rock
					crevice
Unknown cause					
Glaucous gull	1993-94	Coats Island	> 5	Unknown	In good condition
0	July 2005	Browne Island	1	Unknown	In good condition
Thayer's gull	~ 1994	Coats Island	1	Unknown	In good condition
Herring gull	2001	East Bay	1	Unknown	In good condition
	2001	Last Day	1	O III MIII WIII	5000 containon
Unexpected human facto	rs				
Ross's Gull	June 1985	Lancaster Sound	1	Human harvest	Shot by hunter
1000 5 Juli	May 2006	Lancaster Sound	1	Human harvest	Shot by hunter
	IVIAV ZUUU	Lancaster Sound	1	riuman nai vest	SHOL OF HUHLCI

¹ Same event.

² Same event.

TABLE 3. Observations (minimum counts or estimates) of unusual mortality of marine bird eggs or chicks in the Canadian Arctic.

Cause of Mortality Species	Date	Occurrence	Location	Chicks or Eggs Killed	Comment
Extreme weather					
Glaucous gull	1990-92	Exposure	Coats Island	> 5 C	Parents nearby but not covering young during storms
	1990–92	Drowned	Coats Island	> 5 C	Nearly fledged chicks blown off cliff by strong downdrafts while testing wings
	July and August 2001	Exposure	Prince Leopold Island	3 broods	Heavy rain, fog, and wind
	July 2002	Exposure	Prince Leopold Island	5 of 12 broods	Freezing rain, with wind and snow
Thick-billed murre	August 1993	Heavy seas	Coats Island	~ 50 C	Washed off lowest ledges by large waves
	August 2000	Heavy seas	Coats Island	> 5 C	Washed off lowest ledges by large waves
		Heavy seas	Coats Island	> 100 E, C	Washed off lowest ledges by large waves
	August 2001	Heavy seas	Coats Island	> 100 C	Washed off lowest ledges by large waves
Avalanche and rock fa	11				
Northern fulmar	July 2004	Avalanche	Cape Vera	> 5 E	Small avalanche fell on nesting ledge, removing eggs
Unusual predation					
Northern fulmar	July 2005	Gull predation	Cape Vera	> 40 E	> 100 km/h, sustained wind caused incubating birds to abandon nests; glaucous gulls removed eggs from nests before parents returned
Thick-billed murre	August 1991	Walrus predation	Coats Island	2 C	Submerged attack on swimming chicks
	July 2000	Bear predation	Coats Island	> 100 E, C	Male polar bear descended upper colony ledges
	July 2003	Bear predation	Coats Island	> 100 C	Male polar bear fed on chicks and a few adults for 3 days
	July 2005	Bear predation	Hantzsch Island	> 5	Eggshells found in polar bear scat

their nests, and have also witnessed these large predators descending cliffs, where they caught adult murres (Table 2) and consumed hundreds of eggs and chicks (Table 3). Bears and walruses may catch adult or young birds on the water by swimming beneath them and then surfacing to attack (Donaldson et al., 1995; Mallory et al., 2004; Stempniewicz, 2006). Bears, as well as foxes and gulls, may also take advantage of miscues by murres departing the cliff and prey upon birds that fail to get airborne and land on the sea ice (Table 2).

Disease

Although diseases have the potential to kill many colonial birds in a short time (Friend et al., 2001), disease outbreaks among marine birds in the eastern Canadian Arctic seem extremely rare. We have seen no obvious evidence of disease-related deaths in kittiwakes, fulmars, murres, or guillemots. Thus, it appears unusual that avian cholera has appeared at common eider colonies in northern Hudson Bay since 2004 (Table 2) and is responsible for the greatest numbers of marine bird deaths that we have witnessed. The cholera in eiders apparently moved into local scavenging birds, including herring and glaucous gulls, but to our knowledge it has not yet reached cliff-nesting colonial species, though it can infect such species (e.g., Österblum et al., 2004).

Navigation Errors

Although eiders appear prone to mortality from navigation errors during migration (Mallory et al., 2001; Merkel et al., 2006), we have witnessed only two situations in which other breeding marine birds died because of apparent errors in their flight decisions. At Prince Leopold Island, an

adult murre flew into the cliff during good weather conditions (Table 2), dropped, and disappeared below the ledge, presumably dead on impact. We have seen many situations in which murres have hit the cliff, often hard, as they came in to land at a ledge, but this was the only time when one apparently died. On three other occasions, we have observed murres with a leg trapped in a crevice on a cliff. In two cases the birds were released by researchers, but the third murre was found dead.

Unexplained Mortality

In addition to the five sources of mortality listed above, we have on four occasions found dead adult marine birds during the breeding season for which no obvious cause of death could be determined (Table 2). Interestingly, all of these birds were gulls (*Larus* spp.) that were found in good physical condition, that is, they were not emaciated as if they had starved for some time before dying, nor had they died in agonistic interactions. We have also observed dead adult murres washed ashore at Coats and Digges Island without any obvious cause of death, but we do not have detailed records on numbers or years when these were seen.

Comparison to Seabird Mortality at Lower Latitudes

Our observations suggest that Arctic marine birds experience different causes of mortality than seabirds in marine zones farther south. In warmer regions, mortality of seabird adults, eggs, and chicks during the breeding season may come from a variety of sources, including strong storms that flood or cave in burrow nests (Warham, 1990) or kill young and adults at sea (Threlfall et al., 1974), collapse of food supplies (Schreiber, 2002), ectoparasite outbreaks

(Duffy, 1983), introduced predators (Warham, 1990), fisheries bycatch (Melvin and Parrish, 2001), and disease (de Lisle et al., 1990).

In the Arctic, in contrast, many of these stressors are not significant factors in marine bird mortality, at least during the breeding season. Few Arctic marine birds nest in burrows (except possibly some Atlantic puffins Fratercula arctica at some locations; Robards et al., 2000), and rainfall is typically insufficient to flood nests, although heavy snowmelt can create flooded conditions for groundnesting species. The types of torrential storms that kill adults at sea also appear to be uncommon in the Arctic, in part because temperatures rarely vary enough to lead to dramatic weather, and because sea ice helps to moderate wave action for much of the year (ACIA, 2005). We caution, however, that we have conducted no monitoring at sea during Arctic storms, so we cannot preclude the possibility that adult mortality does occur. The Arctic marine environment is also consistently productive during the breeding season compared to southern waters (Raymont, 1976), although marine food production is low early in the season, and in some years may be delayed by late sea-ice breakup (Gaston et al., 2005). Nonetheless, Arctic marine birds rarely have to withstand the oscillations in food supplies that many seabirds in the boreal to tropical marine zones must endure (e.g., Schreiber, 2002). Ectoparasites are present in Arctic seabirds (e.g., Mallory et al., 2006b), but we have not observed any outbreaks that have led them to desert nests, or even to exhibit abnormal behaviour (e.g., excessive preening), except at the Coats Island colony in years of high mosquito abundance (Gaston et al., 2002). We are unaware of situations where invasive predators (e.g., cats or rats) may have been introduced near seabird colonies in Arctic Canada, but if they were introduced, these predators probably could not survive the extreme winter conditions (Atkinson, 1985). As noted above, some Arctic marine birds may be caught in fisheries in Davis Strait (Mallory et al., 2006a), but there is currently no significant fishing activity near most of the major colonies around Lancaster Sound or Hudson Strait. Finally, we have not observed any disease outbreaks among cliff-nesting colonial seabirds in the Arctic, although avian cholera has recently entered Low Arctic eider colonies and can lead to large mortality in a single breeding season. Excluding diseases among eiders, predators, avalanches, and rock falls appear to be the main factors killing Arctic seabirds and their young.

CONCLUSIONS

The sources of adult mortality that we observed in the Canadian Arctic differ from those reported in more temperate climates. In particular, different predators, snowstorms, and rock fall due to cliff erosion were key factors leading to the deaths of adult and young Arctic seabirds. Given the nature of these sources, we predict that climate change could accelerate mortality among adult Arctic seabirds.

If warming temperatures lead to longer, hotter summers, less sea ice cover and more frequent, intense storms, it is possible that "unusual" mortality of Arctic seabirds may increase, while at the same time causes of mortality more typical of southern latitudes may also expand to the Arctic, potentially leading to adverse consequences for populations of marine birds. For example, if the number of intense, freezing rain episodes or snowstorms increases in the Arctic (ACIA, 2005), we should expect higher levels of avalanches, nest abandonment, and consequent predation of eggs or chicks. Warmer temperatures could also intensify erosion on cliff faces, leading to increased mortality due to rock fall, particularly for colonies situated on sedimentary rock. Further, warming temperatures alone can be stressful for breeding seabirds (Oswald et al., 2008), but in concert with increased mosquito abundance or emergence, they could lead to higher mortality at some colonies (Gaston et al., 2002). As well, less severe climate in the Arctic may permit the northward expansion of populations of certain parasites and diseases (Marcogliese, 2001), which could have a dramatic impact on seabird populations that may currently have relatively weak immunity to these novel stressors (e.g., recent outbreaks of avian cholera). Finally, warmer temperatures and reduced sea ice will enhance the suitability of marine areas of the Canadian Arctic for ship-based tourism, ship transport, and industrial fisheries. Increases in all three of these activities have the potential to increase mortality of seabirds from anthropogenic activities in Arctic Canada.

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