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Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.)

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Summary

1. We compared the reproduction of a marine diving bird, Brunnich's guillemot (*Uria lomvia*), breeding at two Arctic colonies close to the northern and southern limits of the species' range in the Canadian Arctic.

2. At both colonies, timing of breeding for Brunnich's guillemots was positively correlated with summer ice cover, which was determined by winter and spring temperatures. Spring temperatures also modified the effects of ice conditions on timing of breeding.

3. At Coats Island, northern Hudson Bay, in low Arctic waters, the date of egg-laying has advanced since 1981, simultaneous with a decrease in summer ice cover in surrounding waters. Lower ice cover in this region is correlated with lower chick growth rates and lower adult body mass, suggesting that reduction in summer ice extent is having a negative effect on reproduction.

4. Conversely, at Prince Leopold Island, in the High Arctic, there has been no trend in summer ice cover and no detectable change in timing of breeding. Reproduction there is less successful in years of late ice than in years of early ice break-up.

5. Current trends suggest that continued warming should benefit birds breeding on the northern limit of the species range, while adversely affecting reproduction for those on the southern margin. The probable result will be an eventual northward displacement of the population. Although this type of effect has been widely predicted, this study is among the first to demonstrate a potential causal mechanism.

Key-words: nestling growth, range expansion/contraction, seabirds, sea-ice, timing of breeding.

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Introduction

In recent decades, climate change has been shown to be affecting many biological systems (Bradley *et al*. 1999; Crick & Sparks 1999; Hughes 2000; Inouye *et al*. 2000; Walther *et al*. 2002). Because greenhouse gas-induced global warming is predicted to be most intense at high latitudes (LeDrew 1993; Intergovernmental Panel on Climate Change 1995; Cattle & Crossley 1996), high-latitude environments may be among those most strongly affected by climate change (Brown 1991; Boyd & Diamond 1994; Boyd & Madsen 1997). Sea ice extent (i.e. the area of ocean covered by ice) has decreased at a rate of about 3% per decade since the 1970s (Parkinson *et al*. 1999). The extent of the retreat appears to be well beyond that expected as a result of natural variation in climate (Vinnikov *et al*. 1999). Earlier sea ice break-up has already caused changes in fish communities in northern Hudson Bay (Gaston, Woo & Hipfner 2003) and deterioration in female body condition among polar bears (*Ursus maritimus*) in western Hudson Bay (Stirling, Lunn & Iacozza 1999). In the same area, increasing peak temperatures and consequent increased activity of mosquitoes has been shown to cause mortality in breeding seabirds – a phenomenon not seen until 1997 (Gaston, Hipfner & Campbell 2002).

Studies in the Antarctic have shown that interyear variation in sea ice cover and distribution can be a major

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determinant of seabird reproduction and population dynamics (Smith *et al*. 1999; Barbraud & Weimerskirch 2001; Ainley 2002; Croxall, Trathan & Murphy 2002; Jenouvrier *et al*. 2003). Less dramatic, but none the less significant, effects have been detected in northern Hudson Bay by Gaston & Hipfner (1998), Alaska (Murphy, Springer & Roseneau 1991) and the Beaufort Sea (Divoky in Dickson & Gilchrist 2002).

Most predictions of the effects of climate change on wildlife assume that temperature increases will lead to contraction of species range at low latitudes, accompanied by expansion at higher latitudes (Slaymaker & French 1993; Boyd & Diamond 1994; Boyd & Madsen 1997). However, to date, demonstrations of the potential mechanisms for such a transition are lacking. To investigate this problem, we analysed data relating to reproduction in an Arctic-adapted marine bird, Brunnich's guillemot (*Uria lomvia* L.), at two breeding colonies, at opposite extremes of its climatic range in the Eastern Canadian Arctic. To develop predictions about the likely impacts of climate change, we have made inferences from indices of reproduction (timing of breeding, adult mass during incubation and chick-rearing and nestling growth rates) measured during the period 1975–2003. We relate interyear differences to variation in temperature and ice conditions in the vicinity of the two colonies.

Methods

The thick-billed murre is a circumpolar species that breeds only in the Arctic and Subarctic, wintering in the northernmost ice-free areas and feeding almost entirely in waters at less than 8 °C. Brunnich's guillemots forage underwater to depths of > 100 m, feeding on small fishes, squid and large zooplankton. They lay a single egg which is incubated constantly for about 33 days, with the parents taking turns in 12–24-h shifts. Nestlings are fed by their parents at the breeding site for 15–30 days before departing to sea (Gaston & Nettleship 1981; Gaston & Hipfner 2000).

Observations of reproduction by Brunnich's guillemots have been made intermittently since 1975 at a breeding colony of about 100 000 pairs on Prince Leopold Island (see Gaston & Nettleship 1981), and annually since 1984 at a colony of 30 000 pairs on Coats Island, both in Nunavut, Canada (Gaston *et al*. 1993, 1994). Coats Island (62° N, 82° W) experiences the highest July temperatures of any large (> 5000 pair) Canadian Brunnich's guillemot colony (July mean about 10 °C), whereas Prince Leopold Island (74° N, 90° W), has the lowest summer temperatures (about 3 °C).

TIMING OF BREEDING

Coats Island

During 1984–87 we determined median date of hatching from wing-lengths measured on a sample of 100 nestlings measured in early August, after most had hatched but none had departed from the colony. The age of each nestling was determined from the age/wing-length relationship derived from measurements of known-age nestlings. In 1988–2003 we determined dates of hatching directly, from observations of about 500 breeding pairs of Brunnich's guillemots on four or five study plots each year, using methods detailed in Birkhead & Nettleship (1980) and de Forest & Gaston (1996). These two methods for determining median date of hatching yielded estimates differing by no more than 1 day when compared for the years 1988–95 (A.J.G. unpublished data).

Prince Leopold Island

During 1975–77 and 2001–03, observations of selected colony areas (study plots) were made daily from 15 June to 15 August: the period from the beginning of egg laying to the end of hatching. These observations were used to obtain median dates of laying and hatching. In 1978, 1980, 1984, 1987, 1988, 1993, 1998 and 2000, visits were of a shorter duration (for details see Gaston 2002) and during these visits we obtained either median dates of laying or median hatching, but not both. Median dates of hatching were converted to median laying assuming an incubation period of 33 days (Gaston & Hipfner 2000). We used median laying as our primary measure of timing of breeding as, incubation period being closely constrained, date of laying fixes date of hatching and hence is the variable of interest.

ADULT MASS AND CHICK GROWTH

Coats Island

Adult Brunnich's guillemots were captured and weighed (on a Pesola spring balance, 1 g) throughout the period from the start of hatching to the start of chick departures (roughly 20 July–15 August) in 1988–2003. From 1989 onwards, if birds were not being captured as part of other research projects, a sample of 10 birds was captured every 7 days throughout the study period, except during the first 2 weeks when seven birds with eggs and seven with chicks were captured every 7 days. We recorded whether each bird was incubating an egg or brooding a chick. Yearly sample sizes ranged from 36 to 133 (mean 84).

Although the sex of most birds was not known, from 1995 onwards an attempt was made to capture both members of each pair. As a result, the representation of the sexes in our samples should have been approximately equal. Previous studies of Brunnich's guillemots have shown no systematic difference in mass between the sexes (Gaston & Nettleship 1981; Gaston & Hipfner 2000). Consequently, we have ignored sex in the present analysis.

The mean mass of all brooding birds captured before the median date of chick departures was used as an index of adult body condition for each year. Because adult mass generally showed a decline during the chick-rearing period (Gaston & Hipfnar in press), means were adjusted for date by ANCOVA, using date as a covariate, to correspond to those at the covariate mean, using the least squares method of STATISTICA Version 6·1 (Statsoft 2003).

Each year, 19–51 (mean = 41) chicks were weighed (±1 g) at 2- or 3-day intervals from hatching to departure (see Hipfner & Gaston 1999), using a 300 g Pesola spring balance. As chicks may begin to leave the colony as young as 15 days, we used the mean mass at 14 days old (extrapolated by linear interpolation for chicks not weighed on day 14) as a measure of chick growth rate in a given year.

Previous work suggested that chicks of inexperienced breeders hatch later and grow more slowly than those of experienced birds (de Forest & Gaston 1996; Hipfner & Gaston 2002). We examined the relationship between date of hatching and chick mass at 14 days to develop a method to minimize any bias caused by differences in proportion of early and late chicks in our samples. In order to combine data from different years, hatching dates were expressed in terms of 'relative hatching date' (days the median date of hatching). Mass at 14 days was found to be relatively constant over most of the range of relative hatching dates, but fell sharply after about 90% of chicks had hatched (Gaston & Hipfner unpublished data). Consequently, chicks hatching after this point of inflection (5 days after median hatch) were omitted from calculations of annual mean 14 day mass.

Prince Leopold Island

Adult mass in 2000–03 was sampled in the same way as at Coats Island. In 1975–77 and 2000–01, measures of 14 days' chick mass were obtained by the same methods as used at Coats Island. In 2003, heavy snow precluded taking such measurements and in 2001 measurements had to be halted after most chicks had reached 10 days old.

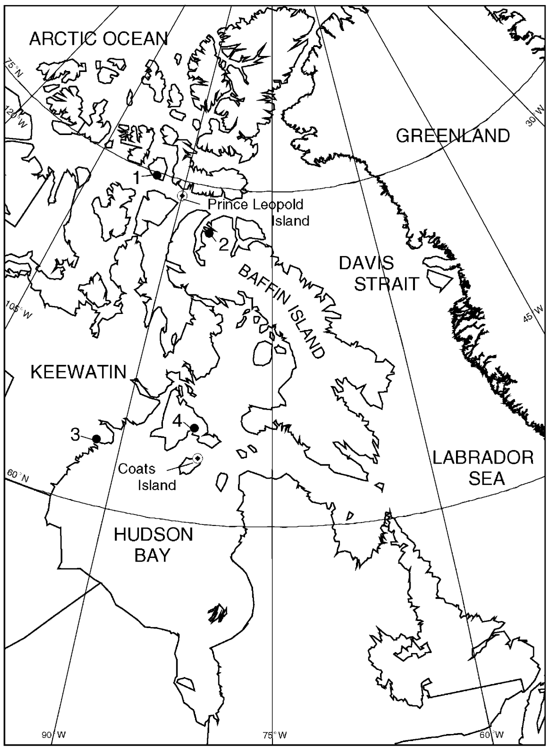

Fig. 1. Map of the area examined showing the position of thick-billed murre colonies studied and weather stations from which records were used (1 Resolute Bay, 2 Nanisivik, 3 Rankin Inlet, 4 Coral Harbour).

Table 1. Mean maximum and minimum July (warmest month) temperatures at the four weather stations used

	Latitude	Longitude	Max °C	Min °C
Resolute Bay	74°40′	94°58′	7·3	1·7
Nanisivik	72°58′	84°37′	7·6	2·6
Coral Harbour	64°11′	83°21′	14·9	5·4
Rankin Inlet	62°49′	92°07′	15·3	6·6

CLIMATE AND ICE DATA

To characterize trends in temperature and ice conditions over the period of our study we used data from 1970 to 2003. Daily temperature records were obtained from the Weather Office of Environment Canada for the nearest weather stations: Resolute Bay and Nanisivik for Prince Leopold Island; Coral Harbour and Rankin Inlet for Coats Island (Fig. 1). Mean temperature maxima and minima in July 1991–2000 at these four stations are presented in Table 1. We calculated two summary statistics for annual temperature: the sum of mean monthly maximum temperatures during January–April (hereafter 'late winter temperature') and the sum of mean monthly maximum temperatures for May and June ('spring temperature'). As temperature data were available from Nanisivik only from 1984 onwards, temperature data from Resolute Bay were used to compare with timing of laying at Prince Leopold Island, for which data extended back to 1975.

Records of ice distribution were obtained from the Canadian Ice Service in the form of weekly or bi-weekly ice maps. Waters around Prince Leopold Island (Barrow Strait, Lancaster Sound and Prince Regent Inlet) are typically completely covered by consolidated pack ice in winter. In spring, there is a clear demarcation between consolidated pack ice and open water areas ('the ice-edge'). We used the distance from the colony to the nearest ice edge on 20 June (the earliest date of laying by Brunnich's guillemots at PLI) as an annual indicator of ice conditions at the start of breeding. As ice breaks up from east to west across Barrow Strait and Lancaster Sound (Fig. 2), the position of the ice edge was expressed as km east (+) or west (–) of Prince Leopold Island.

Pack ice in the water of northern Hudson Bay adjacent to Coats Island never consolidates, remaining mobile and providing ephemeral open water areas which shift throughout the winter. Hence, we could not calculate a

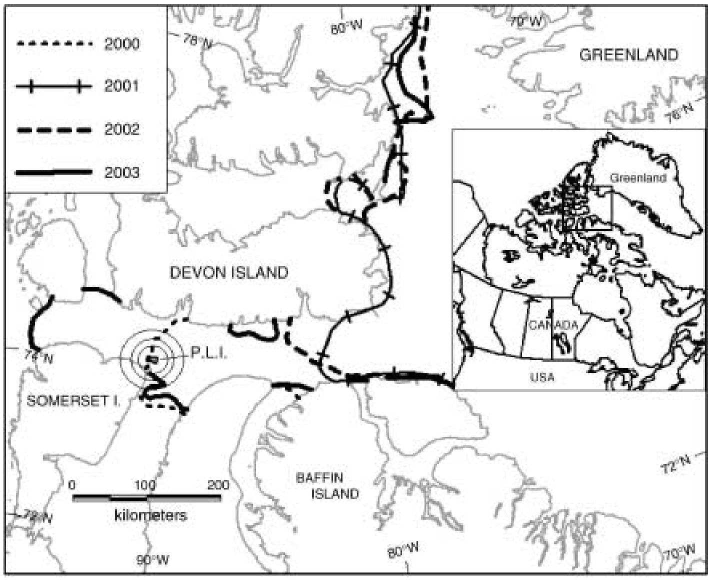

Fig. 2. Examples of ice conditions in waters adjacent to Prince Leopold Island on or about 20 June during 2000–03. The examples include years at opposite extremes (2002: ice edge 250 km E; 2003: ice edge 200 km W).

distance to open water. Instead we used the total ice cover of Hudson Bay on 26 June and 15 July ('Hudson Bay summer ice extent', km^2), provided by the Canadian Ice Service (R. Chagnon, personal communication, 1 December 2003).

STATISTICAL ANALYSIS

Trends over time and in relation to ice and climate variables were determined by linear or polynomial regression, and the independent effects of multiple variables were investigated by backwards elimination of variables in stepwise multiple linear regression (level for rejection, 0·05). All correlations given are Pearson product moment correlation coefficients. All R^2 values reported were adjusted for degrees of freedom. All statistics were performed using STATISTICA version 6·1 (Statsoft 2003).

Results

TEMPERATURE AND ICE CONDITIONS

The temperature sums of monthly means for Nanisivik and Resolute Bay were closely correlated, both in late winter (r_{24} = 0·90) and in spring (r_{25} = 0·80). The same was true for temperatures at Coral Harbour and Rankin Inlet (late winter r_{23} = 0·78, spring r_{22} = 0·83). Late winter temperatures were weakly positively correlated with spring temperatures at all four weather stations, but the correlations were not significant anywhere (maximum r = 0·32, all $P > 0·1$). During 1970–2003, only spring temperature at Coral Harbour showed a significant increasing trend (r_{32} = 0·35, P = 0·05), although trends at all other stations were positive (all $P > 0·1$).

The position of the fast ice edge in late June relative to Prince Leopold Island showed no trend during 1970–2003 (r_{32} = 0·04, Fig. 3), but Hudson Bay summer ice extent decreased significantly both for 26 June (R^2_{33} = 0·23, P = 0·002) and 16 July (R^2_{33} = 0·16, P = 0·012). Most of the decrease occurred during 1992–99, when the five years of lowest ice cover occurred (Fig. 4). A piecewise linear regression with a break-point at 1985 gave R^2_{30} = 0·79, with no trend prior to 1985 and a significant decrease subsequently (–7336 km^2/year).

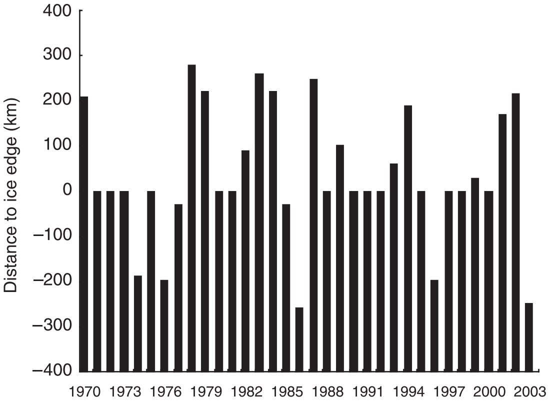

Fig. 3. Position of the ice edge in Parry Channel in relation to Prince Leopold Island [km east (+) and west (–)] during 1971–2003.

Ice conditions were correlated with late winter or spring temperatures at both Prince Leopold Island and Coats Islands. At Prince Leopold Island, late winter temperature at both Resolute Bay (Res) and Nanisivik (Nan) contributed significantly to explaining the position of the ice edge in June in a backwards stepwise regression. Cold years at Nanisivik were associated with the ice edge to the east of the colony, whereas temperatures at Resolute Bay had the opposite effect in explaining residual variation ($\mathrm{Beta}_{\mathrm{Res}}$ = 1·39, $\mathrm{Beta}_{\mathrm{Nan}}$ = –1·80, $F_{2,19}$ = 21·5, R^2 = 0·66, $P < 0·001$).

For Hudson Bay, a backwards stepwise multiple regression model including late winter and spring

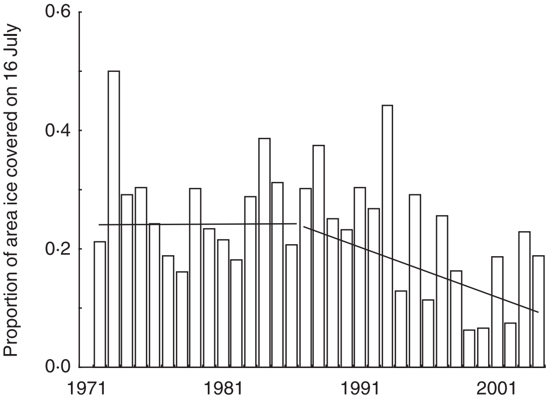

Fig. 4. Hudson Bay summer ice extent during 1971–2003 (data from Canadian Ice Service, with permission). Solid lines show piecewise linear regression.

temperatures at Coral Harbour and Rankin Inlet incorporated only late winter temperatures at Rankin inlet in explaining ice cover on 26 June (Beta$_{temp}$ = −0·68, $F_{2,20}$ = 16·8, R^2 = 0·43, P < 0·001). For ice conditions on 16 July, only spring temperatures at Coral Harbour were incorporated (Beta$_{temp}$ = −0·82, $F_{1,20}$ = 40·8, R^2 = 0·65, P < 0·001). A piecewise linear regression of spring temperature at Coral Harbour on year (R^2_{32} = 0·80), estimated a breakpoint at 1986, close to the breakpoint for summer ice extent. Temperatures were estimated increasing at 0·15 °C year^{-1} before 1986 and 0·80 °C year^{-1} afterwards.

TIMING OF BREEDING

Estimated median dates of laying varied from 19 to 28 June at Coats Island (1988–2003) and from 28 June to 18 July at Prince Leopold Island (1975–78, 1980, 1984, 1987, 1988, 1993, 2000–03). At both colonies, estimated dates of laying were influenced by both ice conditions and spring temperatures.

At Prince Leopold Island, both position of fast ice edge (ice) and spring temperature (temp) contributed significantly to variation in timing of laying in a backwards stepwise regression. In warmer years the date of laying advanced, but laying was retarded with increasing distance from the colony to open water (Beta$_{ice}$ = 0·75, Beta$_{temp}$ = −0·44, $F_{2,9}$ = 25·4, R^2 = 0·82, P < 0·001).

The effect of distance to ice edge on median date of laying was non-linear: a fitted polynomial curve became steeper as the distance to open water increased (Fig. 5). Both distance (D) and distance^2 (D2) contributed significantly to explaining variation in date of laying (t_D = 5·07, P < 0·001; t_{D2} = 2·66, P = 0·02; multiple regression, $F_{2,10}$ = 20·5, R^2 = 0·77, P < 0·001), providing a better fit than a linear equation (R^2 = 0·64).

Similarly, dates of laying at Coats Island were negatively correlated with spring temperatures at Coral Harbour (Beta = –0·85, $F_{1,13}$ = 33·4, R^2 = 0·70, P < 0·001, Fig. 6) and at Rankin Inlet (Beta = −0·87, $F_{1,14}$ = 42·4, R^2 = 0·73, P < 0·001). No other temperature variables were correlated with timing of laying. Date of laying

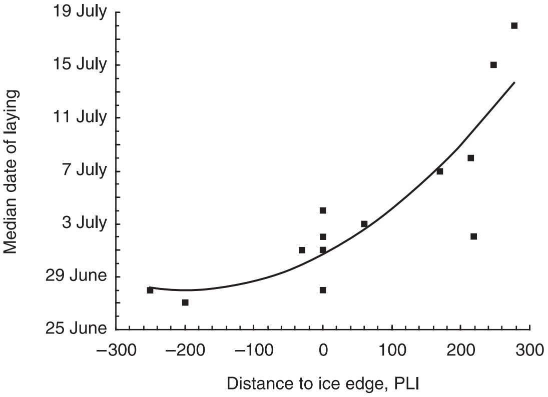

Fig. 5. Estimated median date of laying at Prince Leopold Island in relation to the distance to the ice edge (D) on 20 June in km E (+) or W (–) of the colony. Fitted polynomial function = 1 July + 0·0275(D) + 0·00007(D2).

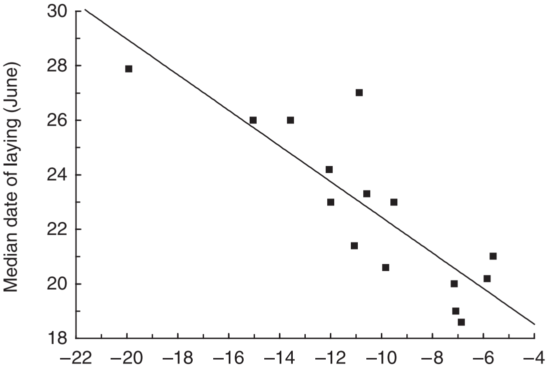

Fig. 6. Estimated median date of laying at Coats Island in relation to spring (May and June) temperatures at Coral Harbour, Nunavut.

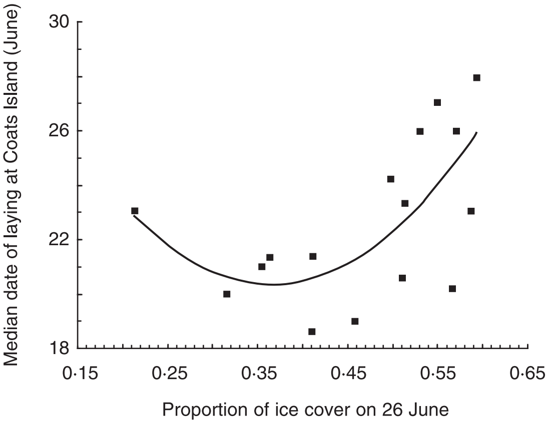

Fig. 7. Estimated median date of laying at Coats Island in relation to the extent of ice cover in Hudson Bay on 26 June.

increased with the area of ice on 26 June. The linear relationship was not significant, but there was a significant polynomial fit (t_{ice} = −1·92, t_{ice2} = 2·25; $F_{2,13}$ = 5·3, R^2 = 0·37, P = 0·02), suggesting that ice affected timing of laying only when the proportion of cover was greater than 50% (Fig. 7). When the data point for 1999

Table 2. Mean mass of breeding adult Brunnich's guillemots at Prince Leopold Island and mass of nestlings at 14 days during 2000–03. Inter-year ANOVAS: incubation $F_3 = 13{\cdot}74$, $P < 0{\cdot}001$; brooding $F_2 = 6{\cdot}71$, $P = 0{\cdot}002$; 14 d mass $F_2 = 48{\cdot}71$, $P < 0{\cdot}001$

Year	Distance to ice edge [km E (+) or W (–) of the colony]	Mean adult mass (g SD) Incubation	Brooding	Mean chick mass at 14 days (g)
2000	0	932·4 ± 64·2 (43)	908·4 ± 73·7 (19)	204·9 ± 27·3 (19)
2001	170	872·1 ± 54·6 (119)	875·0 ± 48·8 (9)	173·7 ± 15·6 (4)
2002	215	887·5 ± 64·6 (53)	840·2 ± 64·8 (32)	106·9 ± 14·1 (9)
2003	–250	930·2 ± 63·3 (26)		

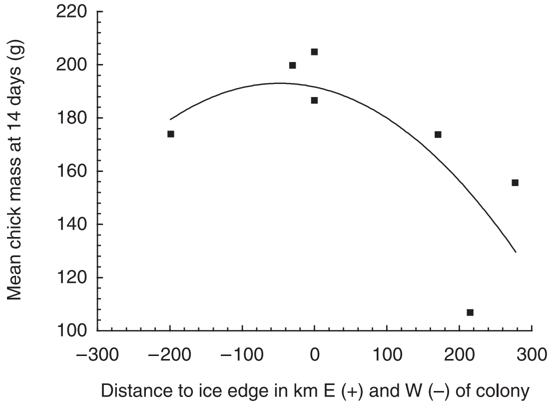

Fig. 8. Mean 14-day mass of nestlings at Prince Leopold Island in relation to the position of the ice edge on 20 June in km E (+) or W (–) of the colony. Fitted polynomial function = 191·65 – 0·0573(D) – 0·0006(D2).

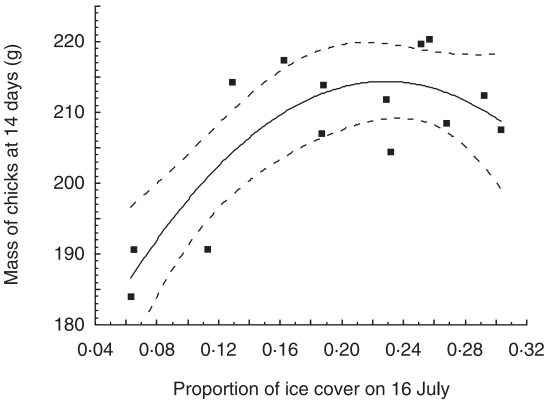

Fig. 9. Mean 14-day mass of nestlings at Coats Island in relation to summer ice extent in Hudson Bay.

was removed, a simple linear correlation was also positive and significant ($r_{14} = 0{\cdot}64$, $P = 0{\cdot}01$).

ADULT MASS AND CHICK GROWTH

Prince Leopold Island

Data on adult mass were available from Prince Leopold Island only for 2000–03, but ice conditions differed strongly among these years, with the ice edge on 20 June ranging from 215 km East of the colony in 2002 to 250 km West of the colony in 2003. Mean adult body mass during incubation was significantly higher in 2000 and 2003, when open water was present adjacent to the colony in late June, than in 2001 and 2002, when the ice edge was > 150 km to the East of the colony at that date. Mean mass during chick-rearing showed a similar pattern, but no data were available for 2003 (Table 2).

Chick growth was measured in 1975–78 and 2000–02. Chick mass at 14 days was not significantly correlated with late winter or spring temperatures at Resolute Bay ($r_7 = 0{\cdot}72$, $P = 0{\cdot}07$; $r_7 = 0{\cdot}47$, $P = 0{\cdot}28$). However, mass at 14 days was lowest in 1978 and 2002, the two years when the ice edge was farthest to the East of the colony in June. The relationship between 14 days' mass and ice edge position was best fitted by a polynomial curve (Fig. 8; Wald statistic 3·96, $P = 0{\cdot}04$). In fact, the mean value for 2002 was misleading, because 63% of chicks perished before reaching 14 days (< 10% died in other years), so presumably the sample was strongly biased towards better nourished chicks. Probably most chicks failed to fledge, but heavy snow at the end of the season prevented observations of fledging success. Nevertheless, the observed chick survival of 37% up to 14 days was lower than recorded in any other year (Gaston & Nettleship 1981; A.J.G. unpublished data). The only other year in which some chicks starved was 1978, and although more chicks survived to depart from the colony (81%) most are thought to have died after departure, owing to heavy ice that prevented them from reaching open water (Nettleship *et al.* 1984).

Coats Island

At Coats Island, data on adult body mass during incubation and chick-rearing and chick mass at 14 days were available for most years during 1988–2002. Neither ice conditions nor spring temperature were significantly correlated with adult mass at Coats Island during incubation or chick-rearing, or with chick 14 days' mass (all $N > 10$, all $P > 0{\cdot}1$). However, the three years when ice cover in Hudson Bay was lowest were the three years of lowest 14 days' mass (1995, 1997, 1998). A polynomial function provided a significant fit with ice cover on 16 July ($t_{\mathrm{D}} = 4{\cdot}42$, $P < 0{\cdot}001$; $t_{\mathrm{D}2} = -3{\cdot}87$, $P = 0{\cdot}002$; multiple regression, $F_{2,12} = 10{\cdot}7$, $R^2 = 0{\cdot}58$, $P < 0{\cdot}002$; Fig. 9). The year of maximum ice extent over the period examined was 1992, the year following the Mt Pinatubo eruption, when global temperatures dropped significantly (McCormick, Thomason & Trepte 1995). When this point was omitted, chick mass at 14 days gave a closer fit to the polynomial function ($F_{1,11} = 12{\cdot}3$, $R^2 = 0{\cdot}64$, $P = 0{\cdot}002$). It appears that 14 days' mass was little affected by ice conditions in most years, but there was a strong negative effect in the years of smallest ice extent.

Discussion

EFFECTS OF TEMPERATURE ON ICE CONDITIONS

For both areas considered, it was clear that late winter and spring temperatures had a strong effect on ice conditions in late June. Although, with the exception of spring temperatures at Coral Harbour, weather station temperatures showed no significant warming trend during 1970–2003, remote sensing observations suggest that there has been significant warming in these areas over the period considered (Jones *et al*. 1999; Comiso 2003; Jones & Moberg 2003). Similarly, although our measures of ice cover showed a significant reduction only in Hudson Bay, remote sensing observations suggest a lengthening of the open water period in both areas since 1980 (Parkinson *et al*. 1999; Parkinson & Cavalieri 2002).

The trends in seasonal sea ice cover in the eastern Canadian Arctic are part of a general decrease in Arctic sea ice since the 1970s (Johannessen, Shalina & Miles 1999; Cavalieri, Parkinson & Vinnikov 2003) and are supported by large-scale thermodynamic models (Hilmer & Lemke 2000). The connection between temperature and Arctic ice cover is predictable, given that ice thickness is determined primarily by summer melting (Laxon, Peacock & Smith 2003). Model predictions suggest that these trends are likely to intensify over the next 50 years (Gregory *et al*. 2002; Comiso 2003; Laxon *et al*. 2003).

EFFECT OF ICE CONDITIONS ON BREEDING

Ice conditions affected timing of breeding in both areas, with ice cover and distance to ice edge being positively correlated with median dates of laying. This result accords with observations for black-legged kittiwakes (*Rissa tridactyla*) at a colony in the Chukchi Sea, where variation in spring temperature, probably caused by variation in the timing of ice break-up, caused variation in the timing of laying of up to 23 days over a 15-year period (Murphy, Springer & Roseneau 1991). At Prince Leopold Island, the timing of kittiwake breeding is strongly correlated with that of Brunnich's guillemots (Gaston *et al*. 2005). The polynomial fit with ice cover for laying date at Coats Island (Fig. 7) hints that laying at that colony also may be delayed in years with very early ice clearance. However, that result is highly dependent on a single year (1999) and hence requires confirmation.

The effect of ice cover on timing of laying was modified at both sites by temperature, with increased temperature advancing date of laying. At Prince Leopold Island, the accelerating slope of the relationship between timing of laying and ice edge position (Fig. 5) suggested that conditions in extreme years were close to those in which laying, within the relatively short open-water season, would have been impossible. This late breeding was associated with lower adult mass during incubation and brooding and lower chick growth rates. The combined effect of these observations is to suggest that, at Prince Leopold Island, late ice years are associated with poor reproduction.

In 1978, the year of most extreme ice conditions, reproductive success was lower than in the preceding three years; some nestlings starved on the colony and post-fledging survival is believed to have been very low (Nettleship, Birkhead & Gaston 1984). In 2002, 63% of chicks failed to reach 14 days old, most because they starved to death. The mean mass of chicks at 14 days was the lowest among 34 colony-years reported from Canadian colonies (Gaston & Nettleship 1981; Gaston, Chapdelaine & Noble 1983; A.J.G. unpublished data). Even among chicks that left the colony, probably few survived, given their very low body mass and poor feather development (some grew no feathers at all). Ice records suggest that conditions similar to those seen in 1978 and 2002 occurred in two other years during 1970–2003. Hence, Brunnich's guillemots at Prince Leopold Island have probably suffered near or complete reproduction failure related to heavy ice conditions in 12% of years since 1970.

In contrast with the situation at Prince Leopold Island, years of heavy ice in Hudson Bay had little effect on adult condition or chick growth at Coats Island. Instead, the years of lowest adult mass and nestling 14 days' mass were those when summer ice extent in Hudson Bay was smallest. The observed trend suggests that increased temperatures, leading to reduced ice cover, will have a negative effect on nestling growth at Coats Island. Slower-growing chicks at Coats Island are less likely to be resighted at the colony as adults (U. Steiner unpublished data), suggesting that slow growth is associated with reduced survival. In fact, a generally increasing trend in the population at Coats Island from 1985 to 1997 was succeeded by a phase in which the population remained roughly stable from 1998 to 2004 (Gaston 2002 and unpublished data). As Brunnich's guillemots mainly begin to breed at 4–6 years (Gaston *et al.* 1994), the change in population trajectory between 1997 and 1998 corresponds well with the date at which post-1992 cohorts would have begun to recruit to the colony and suggests lower recruitment since 1997.

Observations of nestling diets at Coats Island since 1981 showed that a marked change occurred in the mid-1990s, with Arctic cod (*Boreogadus saida*) being progressively replaced by capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.) between 1992 and 1997. A similar decrease in Arctic cod and increase in capelin has been observed at the nearby Digges Island colony (Gaston, Woo & Hipfner 2003). This corresponds with the observed reduction in sea ice extent. Arctic cod is a characteristic species of Arctic waters and the main prey of Brunnich's guillemot at Prince Leopold Island (Gaston & Nettleship 1981), while capelin and sandlance are the predominant schooling fish in waters off Atlantic Canada (Liem & Scott 1966; Hunter *et al.* 1984; Morin & Dodson 1985; Carscadden, Frank & Leggett 2001). The change in diet indicates a switch from a predominantly high Arctic food web to one more characteristic of low Arctic waters.

Although capelin appears to be a potentially suitable replacement for Arctic cod in the diet of Brunnich's guillemot nestlings, it is notable that the mean mass of Arctic cod observed delivered to nestlings at the Coats Island colony was roughly three times that of capelin delivered (A.J.G. & K. Woo unpublished data). As Brunnich's guillemots normally deliver only one fish at a time (Gaston & Hipfner 2000), the difference in mass suggests that murres may have to commute more frequently between colony and feeding areas when only capelin are available. Moreover, although capelin are the predominant food of common guillemots (*Uria aalge*), razorbills (*Alca torda*) and Atlantic puffins (*Fratercula arctica*) in Atlantic Canada (Bradstreet & Brown 1985; Piatt 1990), they are exploited little there by Brunnich's guillemots (Birkhead & Nettleship 1987). It seems likely that the switch in prey that has accompanied diminishing summer ice cover in Hudson Bay has been responsible, at least in part, for the lower nestling growth rates observed, as suggested previously by Gaston & Hipfner (1998).

PREDICTIONS FOR THE FUTURE

The rise in temperature predicted by climate models and observed for the Canadian Arctic over the past 2–3 decades will lead to a reduction in the extent of sea ice in summer (Gregory *et al.* 2002; Comiso 2003; Laxon, Peacock & Smith 2003). Substantial changes have already taken place (Parkinson 2000; Falkingham, Chagnon & McCourt 2002). Some model scenarios for Hudson Bay predict the disappearance of sea ice altogether within the next century (Gough & Wolfe 2001). At Coats Island, in the Low Arctic, changes in the physical environment over less than 20 years have already led to a marked change in the local marine fish community (Gaston, Woo & Hipfner 2003; A.J.G. unpublished data). Trends in growth rates of nestling Brunnich's guillemots suggest that the change in fish fauna has had a negative effect on conditions for chick-rearing. As conditions continue to shift towards those characteristic of Atlantic Canada, this trend will probably intensify, while at the same time colonization of the area by species typical of the low Arctic (razorbill, common guillemot) may intensify competition.

Conversely, at Prince Leopold Island, where conditions for reproduction have been constrained by heavy ice conditions in some years since 1970, we may expect conditions for reproduction to improve. As years when the ice edge in late June remains > 200 km east of the colony become fewer, breeding should become more predictable. In addition, breeding birds should be able to maintain their body condition more consistently, perhaps enhancing post-breeding survival.

The net outcome of processes that we have identified will be to reduce recruitment at the low Arctic margin of the species range, while increasing it at the high Arctic periphery. A combination of these two processes should result in a gradual decline of the species in Hudson Bay and an expansion among the high Arctic islands. This thesis is supported by recent changes in the population trajectory at Coats Island from increasing to stable (Gaston 2002; A.J.G. unpublished data).

Our scenario of deteriorating ice conditions in the southern part of the Brunnich's guillemot range and improvement at the northern edge accords with predictions for the Adélie Penguin (*Pygoscelis adeliae*) by Smith *et al.* (1999). Like Brunnich's guillemot, the Adelie Penguin is an obligate ice-associated species, but within its range populations do best in situations of intermediate ice-cover. This type of population shift in relation to global warming has been widely predicted (Brown 1991; Boyd & Diamond 1994; Boyd & Madsen 1997), but we believe that this is one of the first cases where at least one of the population mechanisms at work has been identified.

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