

# C A (*Uria lomvia* L

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**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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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 temper-

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adult mass generally showed a decline during the chick-rearing period (Gaston & Hipfner in press), means were adjusted for date by  $\text{ANCOVA}$ , using date as a covariate, to correspond to those at the covariate mean, using the least squares method of  $\text{ANCOVA}$  Version 6.1 (Statsoft 2003).

Each year, 19–51 (mean = 41) chicks were weighed ( $\pm 1$  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.

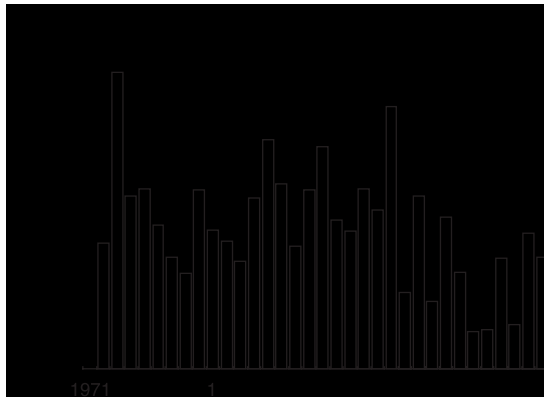
Previous work suggested that chicks of inexperienced breeders hatch later and grow more slowly than those of experienced birds (de Forest & Gaston 1996; Hipfner & Gaston 2002). We examined the relationship between date of hatching and chick mass at 14 days to develop a method to minimize any bias caused 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-0.0959 Tw.1996; Hipfner &

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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<sup>2</sup>), provided by the Canadian Ice Service (R. Chagnon, personal communication, 1 December 2003).



temperatures at Coral Harbour and Rankin Inlet incorporated only late winter temperatures at Rankin inlet in explaining ice cover on 26 June ( $\text{Beta}_{\text{temp}} = -0.68$ ,  $F_{2,20} = 16.8$ ,  $R^2 = 0.43$ ,  $P < 0.001$ ). For ice conditions on 16 July, only spring temperatures at Coral Harbour were incorporated ( $\text{Beta}_{\text{temp}} = -0.82$ ,  $F_{1,20} = 40.8$ ,  $R^2 = 0.65$ ,  $P < 0.001$ ). A piecewise linear regression of spring temperature at Coral Harbour on year ( $\beta = 0.80$ ), estimated a breakpoint at 1986, close to the breakpoint for summer ice extent. Temperatures were estimated increasing at  $0.15 \text{ }^\circ\text{C year}^{-1}$  before 1986 and  $0.80 \text{ }^\circ\text{C year}^{-1}$  afterwards.

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 ( $\text{Beta}_{\text{ice}} = 0.75$ ,  $\text{Beta}_{\text{temp}} = -0.44$ ,  $F_{2,9} = 25.4$ ,  $R^2 = 0.82$ ,  $P < 0.001$ ).

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<sup>2</sup> (D<sup>2</sup>) contributed significantly to explaining variation in date of laying ( $t_D = 5.07$ ,  $P < 0.001$ ;  $t_{D^2} = 2.66$ ,  $P = 0.02$ ; 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 ( $\text{Beta} = -0.85$ ,  $F_{1,13} = 33.4$ ,  $R^2 = 0.70$ ,  $P < 0.001$ , Fig. 6) and at Rankin Inlet ( $\text{Beta} = -0.87$ ,  $F_{1,14} = 42.4$ ,  $R^2 = 0.73$ ,  $P < 0.001$ ). No other temperature variables were correlated with timing of laying. Date of laying

increased with the area of ice on 26 June. The linear relationship was not significant, but there was a significant polynomial fit ( $t_{\text{ice}} = -1.92$ ,  $t_{\text{ice}^2} = 2.25$ ;  $F_{2,13} = 5.3$ ,  $R^2 = 0.37$ ,  $P = 0.02$ ), 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





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 sand-lance 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 murrens may have to commute more frequently between colony and feeding areas when only capelin are available. Moreover, although capelin are the



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