



Discontinuous change in ice cover in Hudson Bay in the 1990s and some consequences for marine birds and their prey

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Arctic ice cover has changed strikingly since the mid-1990s, with the minimum ice extent in the northern hemisphere diminishing by 8.5% per decade since 1981. In the Canadian Arctic, ice cover in June and November showed a step change in the mid-1990s, with little reduction before that. There was a similar step change in northern Hudson Bay. A long-term dataset on marine birds at Coats Island, Nunavut, revealed that many changes in seabird biology also exhibited an abrupt change at, or soon after, the change in ice conditions. This applied to their diet that switched in the 1990s from one dominated by Arctic cod, *Boreogadus saida*, to one dominated by capelin, *Mallotus villosus*. Evidence from the proportion of Arctic cod in adult diets suggested that the length of the open-water season may be a good predictor of the switch between Arctic cod and capelin. Other changes, in nestling growth and population trend, may relate to the same ecosystem changes that led to the switch in diet. Abrupt changes, as in the breeding biology of murrelets at Coats Island, would seem to be characteristic of ecosystem alterations driven by climate change.

Keywords: Arctic cod, capelin, diet, Hudson Bay, nestling growth, regime shift, sea ice, step change, thick-billed murre.

Introduction

A rapid reduction in the extent of summer ice cover in the Arctic has taken place over the past two decades (Comiso *et al.*, 2008; Parkinson and Cavalieri, 2008; Perovich and Richter-Menge, 2009), with an overall rate of change in September ice cover of –8.5% per decade between 1981 and 2010 (<ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/Sep/>, last accessed 24 August 2011). In Hudson Bay, minimum ice cover decreased by –11%/decade during the period 1968–2008 (Tivy *et al.*, 2011). This trend has been accompanied by an advance in the date of ice breakup and clearance (Gagnon and Gough, 2005; Hochheim *et al.*, 2010). In the Canadian Arctic, the change in dates of breakup and clearance (as exemplified by ice cover on fixed dates during the breakup) advanced rapidly after 1994 (Figure 1), coincident with a sharp reversal in the North Atlantic Oscillation Index (NAOI; Figure 2). No trend in ice breakup was apparent during the years 1971–1994 (Figure 1). In addition, ice conditions in the region are known to be affected also by *El Niño*–Southern Oscillation (ENSO) episodes (Mysak *et al.*, 1996). Both NAO and ENSO are characterized by changes in ocean-basin-scale pressure differentials, affecting wind patterns and, for ENSO, consequent ocean upwellings (Hurrell, 1995;

Enfield and Mayer, 1997). Both have been shown to affect sea and ice conditions in the NW Atlantic and Hudson Bay (Mysak *et al.*, 1996; Mehta *et al.*, 2000).

The timing of ice breakup has a strong influence on the timing and intensity of ecosystem processes in ice-affected waters, regulating production by under-ice algae, and influencing the distribution and abundance of open-water plankton (Sibert *et al.*, 2010). These changes in lower trophic levels in turn influence the timing of life-history events for upper trophic level organisms including seabirds and marine mammals (Moline *et al.*, 2008). Non-linear or “stepped” changes in ice conditions can therefore contribute to abrupt changes in the ecology of these higher trophic level organisms. Although difficult to predict, these abrupt regime shifts are increasingly viewed as an important consequence of global climate change (Overland *et al.*, 2010).

Different regions of the Canadian Arctic have shown variations in the timing of the step change in ice conditions, but the signal is clear for Hudson Bay and adjacent waters (see “Results” section). Using data collected at a breeding colony of thick-billed murrelets (*Uria lomvia*) at Coats Island, northern Hudson Bay (Nunavut, Canada; Figure 3), we examined the consequences of this abrupt change in ice conditions for seabirds and their prey. It was

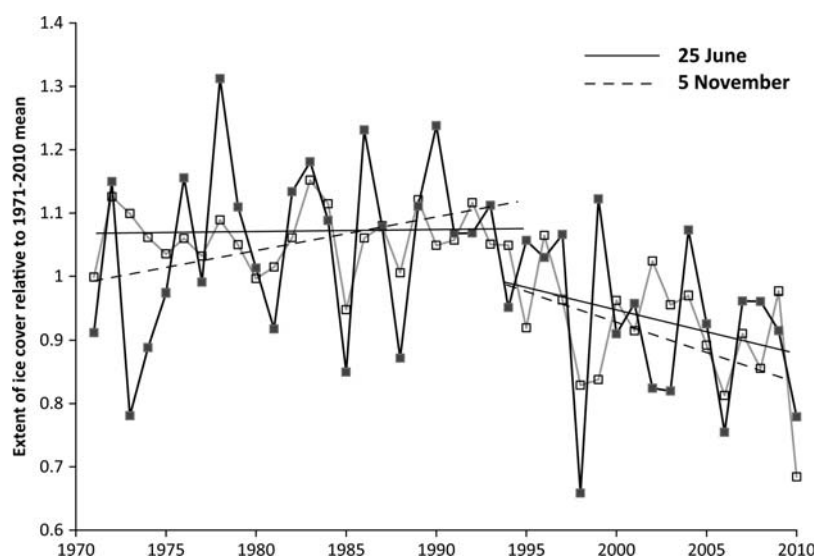


Figure 1. Changes in the extent of ice cover (1971–2010 means = 1) over Canadian Arctic waters approximately midway through typical breakup (25 June) and freeze-up (5 November) periods. The breakpoint (1994/1995) derives from the Statistica 7.0 (Statsoft, 2004) piecewise linear regression procedure. The data are derived from the Canadian Ice Service Icegraph2 (<http://dynaweb.cis.ec.gc.ca/IceGraph20/>) for the Northern Canadian Waters region (see website for map). There is a significant correlation between year and ice cover only for 25 June ice after 1994 ($r^2 = 0.20$, $F_{1,15} = 5.08$, $p = 0.03$).

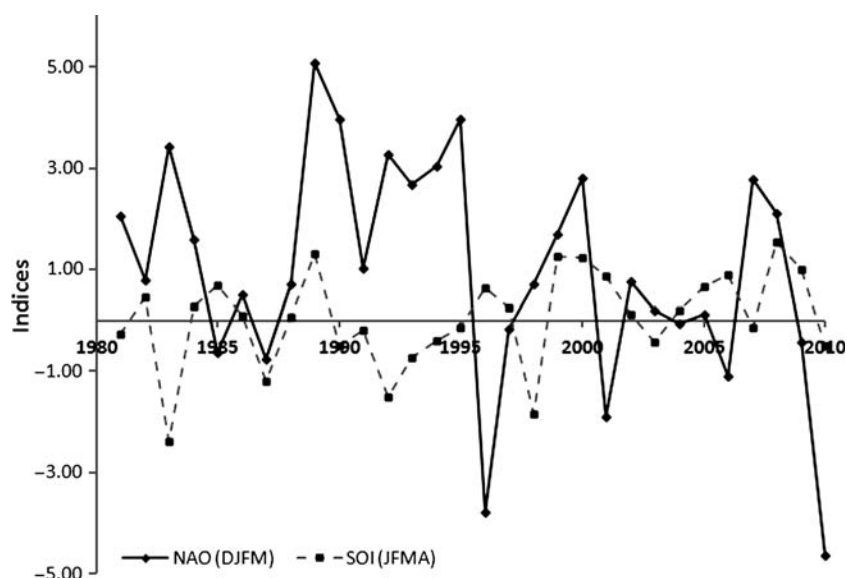


Figure 2. Winter NAOI [NAO (DJFM) CGD: <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>] and January–April mean Southern Oscillation Index [SOI (JFMA); NOAA: <http://www.cpc.ncep.noaa.gov/data/indices/soi.3m.txt>]. Note the very strong downturn in NAO between 1995 and 1996 and a similar downturn in the years 2008–2010.

expected that abrupt changes in ice conditions would be reflected in similarly abrupt changes in biological variables, perhaps with some lags. We compared several models for time-trends, including linear, breakpoint (=changepoint), and polynomial regressions to identify critical periods of change in both ice cover and biological variables. In addition, diet data from several colonies across the eastern Canadian Arctic were used to explore the role that the length of the ice-free season plays in driving these changes.

Methods

Thick-billed murres breeding at Coats Island are the westernmost breeding locality for the species in the low Arctic, and the colony is relatively small (30 000 breeding pairs) compared with others in Nunavut (Gaston, 2002). Birds arrive near the colony in May (Gaston *et al.*, 2011), and egg-laying commences from mid-June on (Gaston and Hipfner, 1998). At that date, land-fast ice is usually present next to the colony, and the surrounding waters

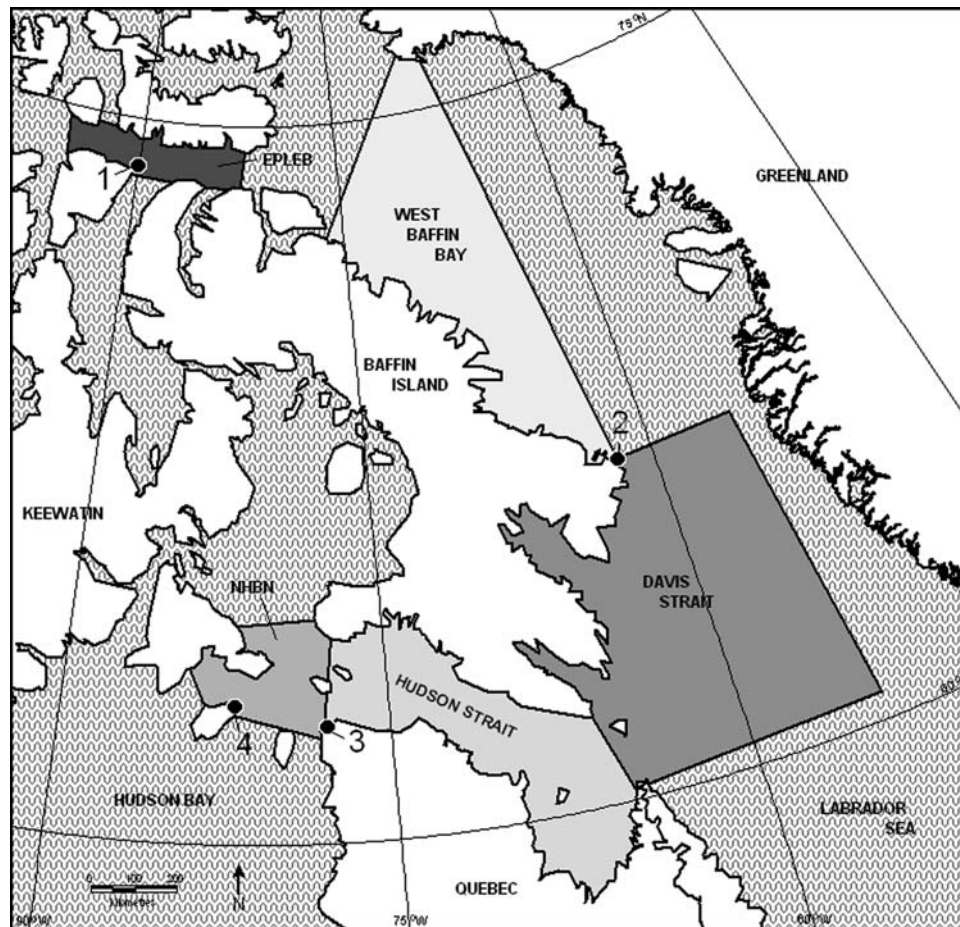


Figure 3. The position of the study colonies and boundaries of the regions used for ice analysis. 1, Prince Leopold Island; 2, The Minarets; 3, Digges Sound; 4, Coats Island; NHBN, North Hudson Bay Narrows; EPLEB, Eastern Parry Channel/Lancaster Sound and East Barrow Strait.

of Evans Strait are partially to completely ice-covered (pers. obs.). The waters within sight of the colony are generally ice-free by mid-to late July, although this has been becoming earlier in recent years (see “Results” section). Incubation takes 30–34 d, and the nestlings are fed at the breeding site for 15–30 d before departure (mean ~ 21 d; Gaston and Hipfner, 2000). Consequently, little or no sea ice is present near the colony while nestlings are being reared.

Data

We examined the timing of ice clearance and the duration of the open-water season for waters next to the colonies, using the region defined as “North Hudson Bay Narrows” (NHBN; Canadian Ice Service, Icegraph 2.0, <http://dynaweb.cis.ec.gc.ca/IceGraph20/>, last accessed May–June 2011). The concentration of ice cover (% water covered in ice) on 25 June each year (1981–2010) was used as a measure of the timing of breakup. This date is close to the date of 50% cover in parts of Canadian Arctic waters completely ice-covered in winter. The same data were used by Hochheim *et al.* (2011) in discussing changes in ice breakup in Hudson Bay. For comments on the use of these data, see Tivy *et al.* (2011). For comparison with timing of breeding, the date of 50% ice cover in spring, by interpolation from the weekly data (<http://dynaweb.cis.ec.gc.ca/IceGraph20/>), was used. Ice cover on 25 June and date of 50% ice cover were closely

correlated ($r_{28} = 0.88$). As a measure of the open-water period in different regions, we used the difference between the dates of 50% ice cover in spring and autumn (following Gagnon and Gough, 2005) interpolated as above. The winter NAOI [NAO (DJFM)] was obtained from the Climate and Global Dynamics Division of US National Centre for Atmospheric Research (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) and the January–April mean Southern Oscillation Index [SOI (JFMA)] from NOAA (<http://www.cpc.ncep.noaa.gov/data/indices/soi.3m.txt>).

The breeding biology and the diet of thick-billed murre breeding at Coats Island have been studied intensively since 1981 (e.g. Gaston *et al.*, 1994; Gaston and Hipfner, 1998). Year-to-year variation and trends in several breeding biology variables were analysed over the period 1981–2010. Sample sizes differed among variables, because not all information was obtained in all years (see below).

- (i) Timing of breeding—Determination of the median date of hatching was made using the method of Gaston *et al.* (1983). This involved recording, for a sample of sites, the presence each day of an egg or a chick. Changes in this measure of timing of breeding were compared with changes in the date of 50% ice cover in adjacent waters

(NHBN). Timing of breeding data were available for the period 1986–2010.

- (ii) Nestling diet—This was recorded as described by Elliott and Gaston (2008) during round-the-clock watches for food delivered by chick-rearing pairs. Normally, parents deliver a single prey organism at each visit, but occasionally several small items may be delivered. The annual indices used were the proportion of deliveries of each identifiable taxon (e.g. Arctic cod, *Boreogadus saida*; capelin, *Mallotus villosus*; and decapod shrimp, *Lebbeus*, *Argis*) as a percentage of all identified deliveries (not all identified organisms; some deliveries included more than one organism, but always of the same species). Data were available for 1981 and 1984–2010 and the mean sample size was 340 deliveries (range 50–1224).
- (iii) Nestling growth—This was measured as described by Hipfner and Gaston (2002) by weighing a sample of chicks at 2–3-d intervals from hatching to departure from the colony (mean sample 41 chicks, range 17–91). The data, available for the years 1986–2010, were analysed using mean mass at 14-d old (14-d mass, in g), and the mean mass at departure from the colony (departure mass in g, available for 19 years from 1988). Nestling mass at a given age is an indicator of year-to-year variation in the availability of food during the chick-rearing period and is especially sensitive during the later part of the growth period, when nestling food demands are greatest (Gill *et al.*, 2002; Lyons and Roby, 2011).
- (iv) Population trend—Daily counts of adult murres present on predetermined study plots at a fixed time of day were carried out to determine the number of adult birds in attendance each day (Gaston, 2002). Thick-billed murres make no nest, so one adult is invariably present at each breeding site, along with a variable number of mates and non-breeding birds. As breeders and non-breeders cannot be distinguished without prolonged watching, we used the total number of birds counted on an area as an index of the breeding population. The annual indices used here represent the mean of daily counts expressed as a percentage of the 1990–1992 average (years when counts were made throughout the season) for each date. The number of days of counts made each year varied, but was always >14 d. Data were available for the period 1986–2010 and annual means ranged from 1423 to 2232 (mean 1845).

In the period 2007–2009, adult thick-billed murres were collected in waters next to four Arctic colonies (Prince Leopold Island, The Minarets, Digges Sound, and Coats Island; Figure 3) for diet analysis and comparison with historical collections made in the 1970s and 1980s (Provencher *et al.*, 2012). Birds were frozen within 24 h of collection, and the digestive tracts were subsequently removed in the laboratory, their contents flushed out, and all individual organisms or recognizable parts (e.g. otoliths, squid beaks) enumerated (see Provencher *et al.*, 2012, for further detail of the methods). The proportion of Arctic cod among fish identified in the stomachs was compared with the length of the open-water period for adjacent waters (measured as above, for Prince Leopold Island—using ice data from the eastern Parry Channel, The Minarets—Davis Strait and West Baffin Bay [aggregated], Digges Sound—Hudson Strait, Coats Island—NHBN) during summer of collection.

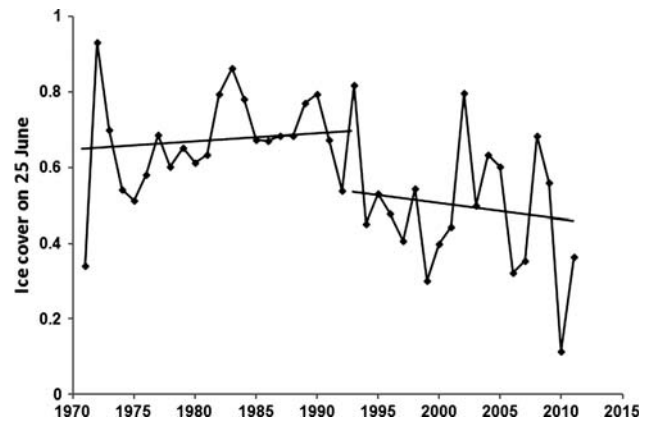


Figure 4. Trends in ice conditions on 25 June for NHBN from Icegraph 2.0 (<http://dynaweb.cis.ec.gc.ca/IceGraph20/>). Fitted lines are the linear least-squares regression of ice cover on year for the periods 1971–1994 and 1995–2010. None is statistically significant (all $p > 0.1$); they are shown to illustrate the “step”.

All statistical tests were carried out in Statistica 7.0 (Statsoft, 2004). All time-series were tested for autocorrelation (Statsoft ARIMA procedure), but significant autocorrelation was found only for the count data (see below). Breakpoints were determined using the non-linear estimator “piecewise linear regression” procedure of Statistica 7.0, which fits two linear regressions split at a breakpoint estimated by the program to minimize residual variation. Relative support for linear and breakpoint regressions was inferred from comparisons of AIC values determined using the programme TRIM version 3.53 (Statistics Netherlands, 2006), fixing the breakpoint where it had been estimated by piecewise linear regression. We accepted the breakpoint model as better supported than the linear model if the AIC value was lower by >2 (Burnham and Anderson, 2002). The difference in the AIC value between linear and breakpoint models is given, and the results from the best-supported model are discussed.

Results

Ice conditions

Based on least-squares regression on year, the date of 50% ice in NHBN advanced by 22 d between 1986 and 2010 (0.92 d year^{-1} ; $r_{23} = -0.60$, $p = 0.001$), the period for which most of our biological time-series were available. The step feature in date of ice clearance identified for Canadian Arctic waters as a whole for the 1990s (Figure 1) was clearly detectable in the data for ice concentration on 25 June for NHBN, with the breakpoint at 1993/1994 (Figure 4). The ΔAIC value for the model incorporating a breakpoint at 1993/1994 was -70 (linear trend = 0). Ice extent on 25 June was positively correlated with the NAOI ($r^2 = 0.20$, $F_{1,23} = 5.68$, $p = 0.03$), but not with the SOI ($p = 0.6$).

Timing of breeding

During the years 1986–2010, there was a marginally significant advance in the date of hatching ($r_{23} = -0.39$, $p = 0.05$), but a linear, least-squares regression estimated only a 4-d advance over the entire period. No breakpoint could be identified. Because ice conditions changed rapidly over the same period, the difference between the median date of hatching and the timing of ice breakup increased significantly ($r_{23} = 0.57$, $p = 0.01$), with the

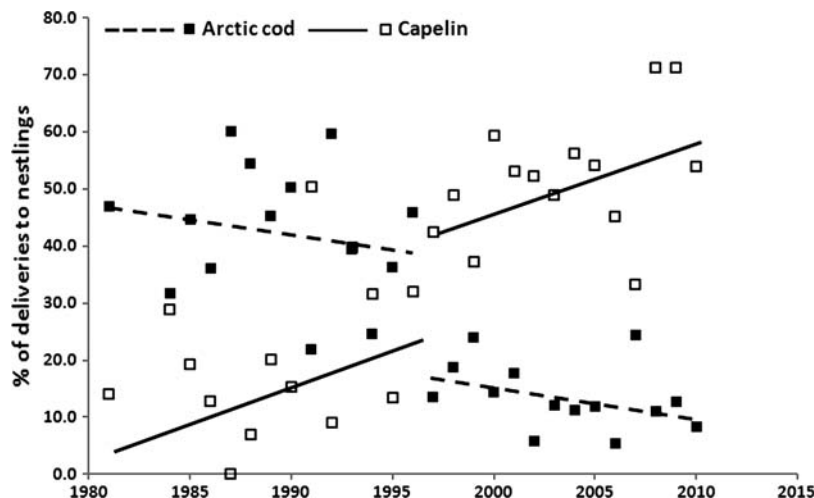


Figure 5. Trends in the proportion of Arctic cod and capelin delivered to nestling thick-billed murres at Coats Island during the years 1981–2010. Lines are fitted with least-squares regressions for years before 1997 (<97) and from 1997 on (97>). None of the fitted relationships are statistically significant (all $p > 0.1$); they are shown to illustrate the “step”.

regression suggesting an increase of 19 d from 1986 to 2010. A breakpoint was identified at 1998/1999 ($r^2 = 0.80$), and the ΔAIC value for this model was -15.7 (linear trend = 0).

Nestling diet and growth at Coats Island

As documented previously (Gaston *et al.*, 2003), there was a decline in the proportion of Arctic cod in the nestling diet and an increase in capelin since 1981. The decline in Arctic cod was best represented by piecewise regression with a breakpoint at 1997/1998 ($r^2 = 0.86$, ΔAIC relative to linear trend -5.2). Arctic cod represented an average of $>40\%$ of items delivered before the break and $\sim 15\%$ after the break (Figure 5). Although a breakpoint was also detectable for capelin, there was a significant increasing trend in both periods, and the breakpoint accounted for a smaller change than for Arctic cod (18%, Figure 5). The proportion of benthic prey (Stichaeidae, Pholidae, Cottidae, Agonidae) also diminished over the study period ($r_{23} = -0.53$, $p = 0.007$), and the proportion of sandlance *Ammodytes* spp. showed no significant change ($r_{23} = 0.36$, $p > 0.05$).

In contrast to earlier findings based on the period up to 1996 (Gaston and Hipfner, 1998), nestling mass at 14 d was not correlated with year or ice conditions ($p > 0.1$) in the dataset, but nestling mass at departure decreased by 20 g between 1988 and 2010 (9% of 1988 mean, $r^2 = 0.25$ for mass on year, $F_{1,17} = 5.80$, $p = 0.03$). The change in mass between 14 d and departure fell from about $+11\%$ of 14 d mass at the start of the study to $+4\%$ of 14 d mass by 2010, with a breakpoint between 1998 and 1999 (breakpoint $r^2 = 0.82$, ΔAIC relative to linear trend -14.4 ; Figure 6).

Changes in numbers attending the colony

The mean numbers of birds counted on the study plots at the colony rose by 45% between 1986 and 2010 (Figure 7; 1.6% year $^{-1}$). No breakpoint could be identified ($\Delta AIC < -2$ from linear fit), probably because the data showed significant autocorrelation, especially up to 2000. However, there was a significant increasing trend up to 2000 ($r^2 = 0.64$, $F_{1,13} = 23.1$, $p < 0.01$, trend $+2.63\%$ year $^{-1}$), but thereafter a non-significant trend ($p > 0.1$, $+0.7\%$ year $^{-1}$).

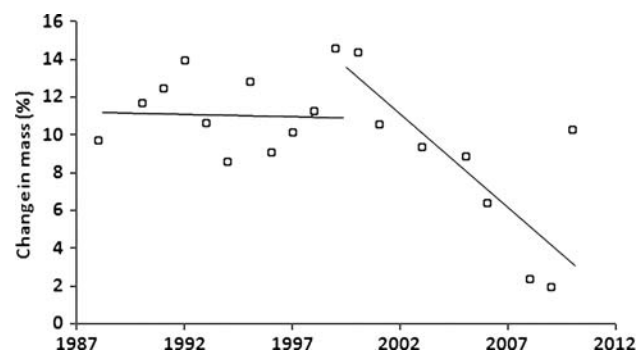


Figure 6. Changes in the weight added by nestling thick-billed murres at Coats Island between 14 d of age and colony departure, on average at 21-d old. Solid lines show the linear least-squares regression of change in chick mass on year for the periods 1988–1997 and 1998–2010.

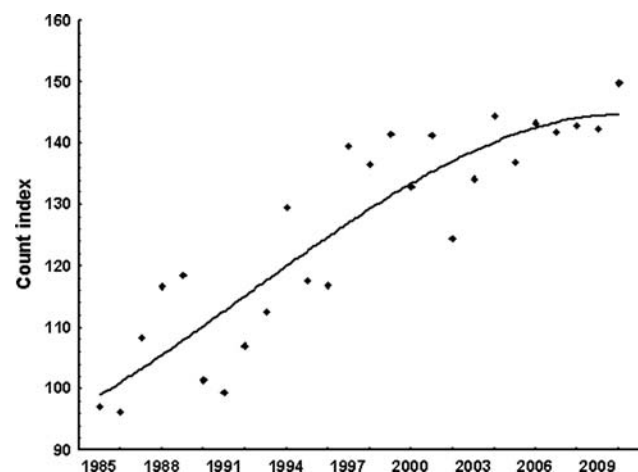


Figure 7. Change in murre count index at Coats Island between 1985 and 2010. The regression ($y = 20\,078\,000 - 30\,241.26x + 15.182x^2 - 0.0025x^3$) was fitted using the polynomial regression module of Statistica 7.0.

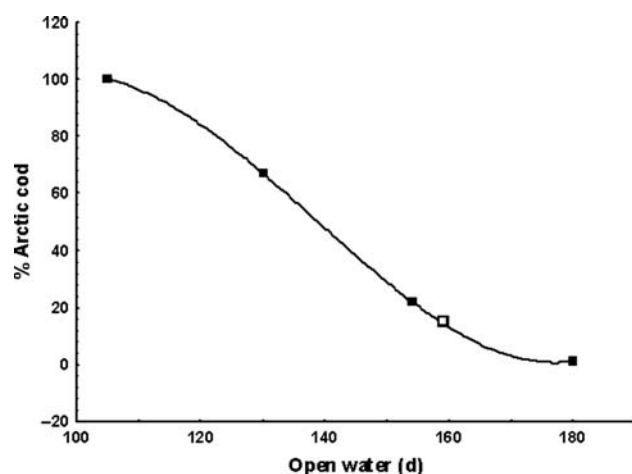


Figure 8. Proportion of Arctic cod in the diet of adult thick-billed murres during the period 2007–2009 in relation to the duration of open water in the region next to the colony. The white square shows data for Digges in the period 1980–1982 (Gaston and Noble, 1985). The regression ($y = 0.0004x^3 - 0.1776x^2 + 22.645x - 814.51$) is fitted to 2007–2009 points only using the polynomial regression procedure of Statistica 7.0.

Arctic cod in adult diets

The proportion of Arctic cod among fish remains in murre stomachs from the four colonies sampled from 2007 to 2009 ranged from close to zero at Digges Sound to almost 100% at Prince Leopold Island. When the proportions were plotted against the length of the open-water period in the region next to each colony, the relationship suggested that the proportion of Arctic cod in adult diets falls from 100% where open water is present for <110 d to near 0% where the open-water season exceeds 175 d (Figure 8). Earlier collections at Digges Sound (1980–1982) contained 15% Arctic cod (Gaston and Noble, 1985) at a period when the open-water season in Hudson Strait was 165 d, lending support to this interpretation (Figure 8).

Discussion

A breakpoint or inflexion in the mid-1990s could be determined in all the time-series analysed except for date of hatching, which showed little change over the period considered, and the mean count of adult birds. The coincidence between the breakpoint in ice conditions and the other breakpoints strongly suggests a causal connection. Although ENSO episodes have been identified as a contributory factor in determining ice cover in the region (Mysak *et al.*, 1996), it appears that this phenomenon contributed little to the change in ice conditions since 1981 (Figure 2). Conversely, the NAOI, which was significantly correlated with ice conditions in northeastern Hudson Bay, showed a very sharp downturn just before the breakpoint in ice conditions. An association between the state of the NAO and ice conditions in the North Atlantic has been identified previously (Bader *et al.*, 2011).

Spring ice conditions in Hudson Bay are strongly affected by regional surface air temperatures (SATs) in September–November and April–June, which together explain 62–75% of the variation in ice concentration at week 25 (Hochheim *et al.*, 2011). Regional spring SAT anomalies surrounding Hudson Bay increased from 1960 to 2005 from 0.26 to 0.30°C per decade. Moreover, mean regional SAT anomalies were positive from 1995 to 2005 and

significantly different from earlier decadal periods (0.78–1.26°C warmer), as were autumn mean SATs (1.4°C warmer; Hochheim and Barber, 2010). As Hudson Bay is unlikely to be affected by major ice movements from other regions or by warm-water intrusions, it seems likely that the trends in ice cover identified here were driven by regional SATs.

As Arctic cod is strongly associated with seasonally ice-covered waters (Fortier *et al.*, 2006), and capelin have a more Subarctic distribution (Rose, 2005; Orlova *et al.*, 2010), it seems likely that the diet change for nestling murres reflected a change in the relative availability of these two schooling fish species, brought about by changes in the duration of ice cover. This interpretation is supported by the relationship between the proportion of Arctic cod in adult diets and the duration of the open-water period (Figure 8).

Between 1981 and 1997, the open-water period near the Coats Island colony (NHBN) region averaged 123 ± 19 d (SD), whereas the average in later years was 152 ± 17 d (SD). Based on Figure 8, Arctic cod should have been an important element in adult diets at Coats Island in the earlier period, and this is suggested by the importance of Arctic cod in nestling diets before 1997 (Figure 5). Although adult diet at Coats Island was not measured directly in the earlier period, there is a correlation between adult and nestling diets (Woo *et al.*, 2008).

The step change in the proportion of Arctic cod delivered to nestlings seems to have taken place 1–2 years after the step change in ice conditions. A similar 2-year lag between changes in ice conditions and changes in the percentage of Arctic cod in murre diets was detected by Smith and Gaston (2012). This could indicate that birds took a few years to adjust to catching new prey or that it took time for the foodweb to adjust to a decrease in Arctic cod. Woo *et al.* (2008) demonstrated that about half of all adult murres tend to specialize in particular prey. Those specializing on rare prey mainly continued to do so: only those using unspecialized foraging behaviour were involved initially in the switch to capelin (AJG, unpublished data). The behaviour associated with finding Arctic cod and capelin differs substantially (Elliott *et al.*, 2008). For some of these birds, the search for new foraging areas and the deployment of different underwater foraging strategies relating to the optimal capture of capelin may have taken more than one season, resulting in lowered chick growth during most years from 1993 to 1997 (the period of the switch; Figure 6). In fact, up to 1990, Arctic cod was the most abundant component of chick diets in every year. During the years 1991–1996, Arctic cod was the most abundant fish eaten in 3 years, capelin in 2 years and they were equal in 1 year (1993), with some alternation. Assuming that the changes in diet reflected changes in the relative availability of the two species, the feeding behaviour of the murres would have required substantial switching between successive years. However, after 1996, capelin were the most abundant prey delivered in every year, so the relative value of different foraging patterns would have stabilized, creating a more predictable foraging environment for the murres. The step change in the proportion of Arctic cod in the diet may represent some threshold in the balance of availability between Arctic cod and capelin, with their relative availability being close to the threshold in the period 1991–1996, after which the balance remained firmly in favour of feeding on capelin.

Gaston and Hipfner (1998) used data obtained at Coats Island up to 1996 to show a significant negative correlation between ice concentration and the mass of 14-d thick-billed murre nestlings.

The contradiction between their finding and that reported here, based on data up to 2010, could have resulted from initial difficulties experienced by adult birds in making the switch to capelin, depressing feeding rates to a level where 14-d mass was affected. The end of the period analysed by Gaston and Hipfner (1998) coincided with the period when birds would have been adjusting their foraging behaviour. However, after 1996, new recruits to the colony would have been more likely to specialize in capelin from the outset, leading to an increasing proportion of capelin specialists as time went on and accounting for the recovery in nestling growth rates.

The diet, or the availability of prey species, appears to have been less suitable for rearing thick-billed murre chicks at Coats Island from 2000 on, because mean mass at departure decreased sharply thereafter (Figure 6). This decline in the fledging condition of the nestlings appears to be linked to the degree of mismatch between the date of laying and the date of ice breakup (as represented by the date of 50% ice; Gaston et al., 2009), but the causal mechanism involved is unknown. It is worth noting that the breakpoint predicted for this dataset is probably unduly influenced by the very high post-14-d increases recorded in 1999 and 2000 and the very low increases in 2008 and 2009. It seems likely that, as ice breakup gets further divorced from the timing of chick-rearing, the effects of ice conditions may decrease relative to other environmental factors and consequently the unexplained variation will increase.

The observed change in population trend, with an increase during the years 1985–2000 followed by a levelling off through to 2010, suggests that the decrease in nestling mass at colony departure may have had demographic consequences for the murre, perhaps reducing the proportion of young birds surviving to recruit to the Coats Island population. The fact that young birds do not return to the colony until their second year and do not usually breed until 4 or 5 years old (Gaston et al., 1994) means that we would expect a lag between a change in post-departure survival and a change in the number of birds at the colony. The observed flattening out of the population trend after 2000 (Figure 7) seems to indicate the existence of such a lag. Although the change in population trajectory was not statistically significant, the coincidence with the reduced condition of chicks at departure after 2000 suggests that conditions after that date became less favourable for the population. We have no way of determining whether the population effects were driven by reduced recruitment or by reduced adult survival, although no significant trend in adult survival at Coats Island has been detected to date (Smith and Gaston, 2012).

Ice breakup in Hudson Bay in springs of 2010 and 2011 were the earliest on record, and winters of 2010/2011 and 2011/2012 have shown record late freeze-up in that region (see Canadian Ice Service <http://dynaweb.cis.ec.gc.ca/>). Along with the very steep decrease in the winter NAOI over the same 2 years (Figure 2), these may provide an indication that we are seeing the start of another step change, in the same direction as that identified in the 1990s. If that is the case, it will be important to pursue monitoring of the Coats Island thick-billed murre to provide further evidence on foodweb changes in a region for which other information on the marine ecosystem is sparse.

The occurrence of step changes (at a larger scale known as regime shifts; Drinkwater et al., 2010; Spencer et al., 2011) in physical and biological systems in the ocean is well-known and is one of the likely consequences of climate change (Overland et al., 2010).

Recently, Kirby and Beaugrand (2009) argued that, even without regime shifts in physical processes, smooth changes in physical variables such as temperature can produce step effects through trophic amplification. A similar step change in seabird reproduction was reported for the common murre, *Uria aalge*, in Newfoundland (Regular et al., 2009), and a similar step change in capelin stocks affecting seabirds was recorded for the Gulf of Alaska (Anderson and Piatt, 1999). We suggest that, in analysing any long-term datasets, investigators should look for such abrupt changes in indicators, because identifying breakpoints or inflexion points can help in interpreting causal relationships.

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