



Climate change and phenological responses of two seabird species breeding in the high-Arctic

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ABSTRACT: The timing of breeding is a life-history trait that can greatly affect fitness, because successful reproduction depends on the match between the food requirements for raising young and the seasonal peak in food availability. We analysed phenology (hatch dates) in relation to climate change for 2 seabird species breeding in the high-Arctic, little auks *Alle alle* and black-legged kittiwakes *Rissa tridactyla*, for the periods 1963–2008 and 1970–2008, respectively. We show that spring climate has changed during the study period, with a strong increase in both air temperature (TEMP) and sea surface temperature (SST) and a decrease in sea ice concentration. Little auks showed a trend for earlier breeding over the study period, while kittiwakes showed a non-significant trend for later breeding, demonstrating different phenological responses in these 2 species. Little auks and kittiwakes adjusted their timing of breeding to different environmental signals. Spring TEMP was the best predictor of little auk phenology, with a significant negative effect. Spring SST was the strongest predictor of kittiwake phenology, with a non-significant negative effect. Spring sea ice concentration and the North Atlantic Oscillation (NAO) winter index had a low relative variable importance. Furthermore, in kittiwakes, years with late breeding were associated with low clutch size and mean annual breeding success, indicating poor investment and food availability. This study identifies some spring environmental factors important for regulating the timing of breeding in the high-Arctic, most likely through effects on snow cover limiting access to nest sites and the development of the polar marine food web. It remains to be investigated whether environmental factors are reliable predictors of marine prey phenology, and whether the decision to start breeding is constrained by food availability.

KEY WORDS: Phenology · Climate change · Seabirds · Match-mismatch · Svalbard · Sea ice · Temperature · Timing of breeding

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INTRODUCTION

Some of the strongest evidence for the effects of climate change on organisms comes from studies of phenology (e.g. Stenseth et al. 2002, Walther et al. 2002).

Phenology is the timing of seasonal activities of animals and plants, and long-term trends for changes in arrival dates and breeding dates of birds have been regarded as 'fingerprints' of the ongoing climate change (Parmesan & Yohe 2003, Root et al. 2003).

In regions where food availability is highly seasonal, reproduction is only possible during a short time period, usually during the spring and summer. The timing of the peak in food availability varies between years. Hence, the timing of breeding is crucial in order to match the energy requirements of breeding to the actual food availability (the temporal match-mismatch concept; Cushing 1990, Edwards & Richardson 2004, Frederiksen et al. 2004, Durant et al. 2005). Thus, the timing of breeding is among the key factors for successful reproduction in birds (Dunn 2004, Reed et al. 2009).

The decision to start breeding is under endocrine control, and the hormone levels involved in this control are influenced by a combination of fixed (photoperiod) and variable environmental cues (climatic factors, food availability; Wingfield 1983, Gwinner 1986). Birds experience variable environmental cues on different spatial and temporal scales, and evidence suggests that birds use these cues in optimal decisions on when to initiate breeding (e.g. Frederiksen et al. 2004). The decision is done before the peak in food availability occurs, so optimal decisions are possible if the environmental cues are reliable predictors of the peak in food availability (Visser & Both 2005). In addition, initiation of breeding could be constrained by the food availability during the pre-breeding period that is needed for investment in eggs. In extreme cases, egg production relies on endogenous reserves built up before and during migration ('capital breeders'; Drent & Daan 1980). However, most birds produce their eggs from resources acquired at the breeding grounds ('income breeders'; Drent & Daan 1980).

The Arctic region is currently undergoing a dramatic climate change, with a 2-fold higher increase in temperature compared to the global increase, a trend that is expected to continue (Kattsov et al. 2005, IPCC 2007). Advancement in the onset of spring is already evident, with the timing of snow melt becoming 15 d earlier over the last decade in Greenland (Høye et al. 2007). Furthermore, sea ice extent has decreased linearly by 3 to 9% per decade in the Arctic Ocean (Serreze et al. 2007), with substantial effects on polar marine ecosystems (Gaston et al. 2003, Moline et al. 2008). The development of the polar marine food web on which seabirds depend is closely linked to the timing of removal of sea ice and the warming and stratification of the surface waters to allow for a spring bloom. Consequently, there is a need to assess the effects of climate change on Arctic seabirds. With some exceptions, however, there are very few published long-term studies on breeding phenology from the Arctic. In the Canadian Arctic, years with low sea ice cover and early sea ice break-up were related to early breeding of Brünnich's guillemots *Uria lomvia* (Gaston et al. 2005a). While low sea ice cover negatively affected breeding success of the low-Arctic population, breeding success of the high-Arctic

population was positively affected by early sea ice break-up (Gaston et al. 2005a). In East Antarctica, a decrease in sea ice cover and an increase in the length of the sea ice season were associated with a trend for later breeding of adelic penguins *Pygoscelis adeliae* and cape petrels *Daption capense* (Barbraud & Weimerskirch 2006). These studies suggest that sea ice affects seabird breeding phenology and breeding success in high-latitude regions. They also underline the fact that climate change has not affected all parts of the polar regions to the same extent or in the same direction (Vaughan et al. 2001).

In the present study, we analysed long-term data on breeding phenology of 2 high-Arctic breeding seabirds, black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') and little auks *Alle alle*, breeding at Ny-Ålesund and Hornsund, respectively, on the western coast of Svalbard (Fig. 1). These data cover the periods 1970–2008 and 1963–2008 for kittiwakes and little auks, respectively, and offer a great opportunity to detect long-term changes in the timing of breeding in relation to climate change in the high-Arctic and to test whether environmental conditions at different scales explain the variability in the timing of breeding. Migratory seabirds may use the winter conditions to initiate the spring migration (Frederiksen et al. 2004), and we used the North Atlantic Oscillation index (NAO) as a large-scale proxy for winter conditions. Our study populations spend the winter in the North-west Atlantic Ocean, close to Greenland according to ring recoveries (Bakken et al. 2003). If they use the winter conditions to initiate the spring migration, and this in turn affects the timing of breeding, we expected NAO to affect the breeding phenology of both species.

When the seabirds arrive at the breeding grounds in spring, they may use local environmental cues or food availability to further adjust the timing of breeding (Frederiksen et al. 2004). Both of these birds are 'income breeders'. Just after arrival at their breeding grounds, kittiwakes and little auks feed at different trophic levels (Karnovsky et al. 2008). In the early part of the breeding season, little auks are primarily zooplanktivorous: they feed at a low trophic level on copepods (e.g. Karnovsky et al. 2003, 2008). Little auks from West Greenland have been known to arrive at their breeding grounds just when copepods such as *Calanus hyperboreus* rise to the surface waters to feed on the spring phytoplankton bloom that is linked to stratification of the water column (Karnovsky & Hunt 2002). In contrast, kittiwakes feed at a higher trophic level on fish, amphipods and krill (Hop et al. 2002, Karnovsky et al. 2008). We used spring sea surface temperature (SST) and sea ice concentration (ICE) to represent the environmental conditions in the foraging areas at sea, and we expected both species to breed earlier in years

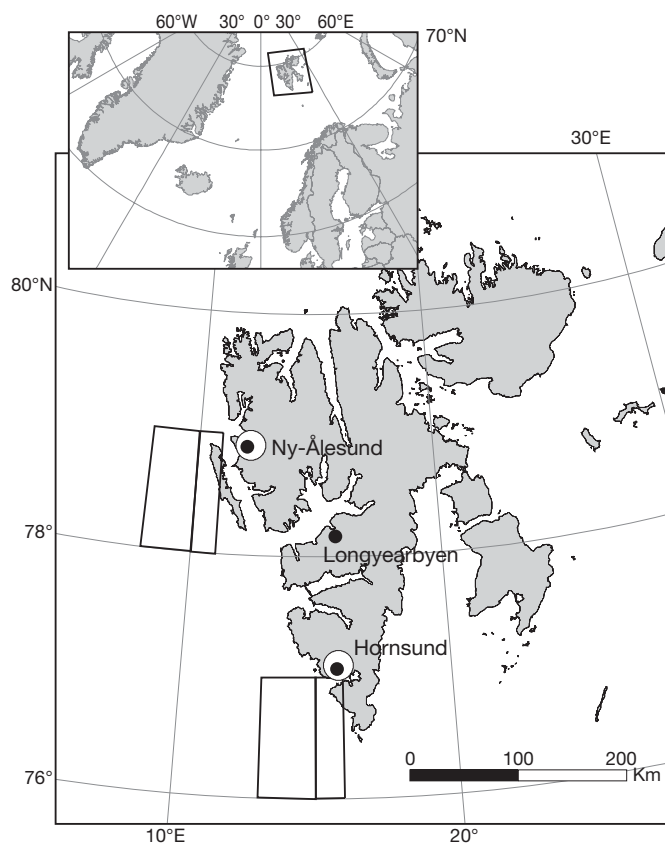


Fig. 1. Study area on Spitsbergen, Svalbard. Kittiwakes were studied at Ny-Ålesund and little auks in Hornsund, and large white circles indicate the 2 study colonies. Meteorological stations (small black circles) in Ny-Ålesund, Longyearbyen and Hornsund provided data on air temperature. The boxes show the areas from which data on sea surface temperatures (SST) and sea ice concentrations (ICE) were obtained (see 'Materials and methods: Environmental parameters')

with low ICE and high SST (Gaston et al. 2005a, Barbraud & Weimerskirch 2006).

The ground-nesting little auks breed in a rocky slope that is covered by snow during spring. Hence, access to the nests is only available when the snow cover has melted sufficiently. However, snow does not block access to nests for the cliff-nesting kittiwakes. By using spring air temperature (TEMP) as an indicator of timing of snow melt, we expected TEMP to affect little auk but not kittiwake phenology. Furthermore, in kittiwakes, we also tested the hypothesis that inter-annual variation in the timing of breeding would be related to fecundity and breeding success.

MATERIALS AND METHODS

Breeding phenology. Data on median hatch date of little auks was obtained in a large colony (~10 000 breeding pairs) at the Arieakammen slopes (77° 00' N,

15° 33' E) in Hornsund, Svalbard (Fig. 1). Published (Stempniewicz 2001, Harding et al. 2004) and unpublished data on median hatch date were obtained for 18 years in the period 1963–2008 (1963–65, 1974–75, 1980, 1983–84, 1986–87 and 2001–08). Hatch date was determined by regular visual inspections of 17 to 261 nests in the same area of the colony for all years, except for one. In 2003, hatch date was back-calculated from the median date of fledging (departure of 857 fledglings during 14 nights of observation that covered the whole fledging period; Wojczulanis et al. 2005) and the length of the nesting period (27 d; Stempniewicz 1981).

Median hatch dates of kittiwakes were obtained in the colony Krykkjefjellet (78° 54' N, 12° 13' E) in Kongsfjorden, 6 km from Ny-Ålesund in Svalbard (Fig. 1). Since 2002, we included a second colony (Irgensfjellet; 79° 00' N, 12° 07' E). It is located only 10 km away from the other and comprises approximately the same number of nests. This was done to maintain robust sample sizes after a substantial decline in the population size (during 1997–2003), and to maintain high precision in the measure of hatch date. Published (Mehlum 2006) and unpublished data were obtained for 18 years in the period 1970–2008 (1970–71, 1982–85 and 1997–2008). The median hatch dates for 2004–2008 were determined by regular visual inspections of ~180 nests, and in 1997–2000 we inspected ~100 nests. In 2002 and 2003, we used hatch dates of chicks (2002, N = 18; 2003, N = 5) that were hatched in an artificial egg incubator (A90, J. Hemel; T = 37.5–38°C, relative humidity 55–75%), because breeding was extremely late and the hatching occurred when the field workers were not present. The chicks originated from eggs that were collected in the colony, insulated with wool and brought to the laboratory in Ny-Ålesund within 1 h upon collection. Median hatch dates for 1970–1971, 1982–1985 and 2001 were determined from counts of hatched eggshells under the bird cliff in the same colony (Krykkjefjellet) by Mehlum (2006). We did a methodological study and observed hatch dates in the nests and counted hatched eggshells under the same nests (covering 112 nests). This showed that counts of hatched eggshells produced a 0.5 d later median hatch date, compared to direct observations in the nests. Accordingly, we adjusted the hatch dates obtained from Mehlum (2006) by –0.5 d.

Breeding success. For kittiwakes, data on clutch size and a measure of breeding success (number of chicks >12 d old per active nest) were obtained for all years in the period 1997–2008 (51 to 139 active nests), except for 2001. Data on breeding success of little auks were only available for a few years, and consequently were not analysed.

Environmental parameters. We used the NAO as a large-scale measure of winter conditions and 3 local measures of spring conditions (SST, ICE and TEMP).

Monthly NAO indices, standardised by the 1950–2000 base period monthly means and SD, were obtained from the National Oceanic and Atmospheric Administration (NOAA; www.cpc.ncep.noaa.gov) to produce a winter index (NAO_w, averaged over December to March). Measures averaged for April–May were used for local spring conditions, because both kittiwakes and little auks return to the breeding grounds in Svalbard in April, and egg-laying occurs in June.

Data on TEMP (°C) were obtained from the weather stations in Ny-Ålesund and Longyearbyen (Norwegian Meteorological Institute, DNMI) and Hornsund (Polish Polar Station Hornsund; Fig. 1). Data on TEMP from Ny-Ålesund were used in the analyses of kittiwake phenology. In analyses of little auk phenology, we used data on TEMP from Hornsund for the period 1979–2007 and estimated data on TEMP for Hornsund for the period 1963–1979. By using the estimates from a linear regression, we made a reliable estimate of TEMP for Hornsund from TEMP Longyearbyen ($\text{TEMP Hornsund} = -0.36 [\pm 0.27] + 0.794 [\pm 0.037] \times \text{TEMP Longyearbyen}$), because these measures were highly correlated (1979–2008, $N = 30$, $r = 0.97$, $p < 0.0005$). The conclusions drawn in this study did not differ if we entirely used TEMP Longyearbyen to represent TEMP Hornsund. Furthermore, we expected the timing of snow melt to influence the breeding phenology of little auks. Data on snow depth or snow cover, however, do not exist for the appropriate time scales, so we used TEMP as a proxy for the timing of snow melt.

ICE (%) was extracted with the software ArcGIS Arcinfo (9.2) from sea ice maps. DNMI has produced daily maps (1979–2008) and weekly maps (1963–1979) by manual interpretation of satellite data and *in situ* observations. Sea ice maps were unavailable for May 1964 from Hornsund. We therefore estimated ICE May from ICE April ($\text{ICE May} = 0.59 \times \text{ICE April} - 0.127$, $F_{1,41} = 25.5$, $p < 0.001$). Maps were unavailable for April and May in 1964 and 1965 for Ny-Ålesund. The sea ice cover at the western coast of Spitsbergen typically consists of different types of drift ice, ranging from 'very close drift ice' to 'open water', with 90–100% and 0–10% ice concentrations, respectively.

Data on sea temperature at 5 m depth were used as SST (°C). These data were obtained from the Carton-Giese SODA v2.0.2-4 database (Carton & Giese 2008) via the IRI/LDEO Climate Data Library (<http://iridl.ldeo.columbia.edu>). The SST data from Carton-Giese SODA v2.0.2-4 covered the whole study period except for the last year. SST for 2008 was therefore estimated from SST obtained from Reyn_Smith OIv2 (Reynolds et al. 2002) via the IRI/LDEO Climate Data Library. We simply multiplied the SST from 2007 by the 2008/2007 SST ratio from Reyn_Smith OIv2.

We used ICE data from the 1° box bounded by 78–79°N and 10–11°E for the kittiwakes breeding at Ny-Ålesund (Fig. 1) and by 76–77°N and 15–16°E for the little auks breeding in Hornsund (Fig. 1). The sea ice is more extensive close to the coast compared to farther west, so data from these areas are the best to reflect the sea ice conditions. We used SST data from the 2° boxes bounded by 78–79°N and 8–10°E and by 76–77°N and 13–15°E for the kittiwakes and the little auks, respectively (Fig. 1). We chose these boxes to cover a relatively large area that included both the shelf and the area to the west of the shelf break. From GPS-tracking, we know that this geographical sector corresponds well to the foraging areas during the pre-breeding period for the kittiwakes breeding at Ny-Ålesund (O. Chastel unpubl. data). We do not have knowledge about the foraging grounds of the little auks during the pre-breeding period. However, the chosen area corresponds well to the foraging areas during the breeding period (Karnovsky et al. 2003).

Statistical analyses. Linear regressions and Pearson moment-product correlations were used to test for temporal trends in environmental factors and timing of breeding. We followed the approach by Frederiksen et al. (2004) to test how environmental variables affected breeding phenology. We entered TEMP, ICE, SST, NAO_w and YEAR as predictor variables in multiple linear models where median hatch date was the response. We used diagnostic plots (QQ, residuals versus fitted, residuals versus leverage) to assess whether the data sufficiently met the assumptions of the linear model. We fitted 32 models for each species and included no interactions. The selection of the best models was based on Akaike's Information Criterion adjusted for small samples size (AIC_c ; Burnham & Anderson 2002). To avoid models with very limited support, we selected a redefined set of candidate models with $\Delta\text{AIC}_c < 4$ and calculated AIC_c weights. AIC_c weight is the likelihood of the model given the data and the set of candidate models, and evidence ratios summarise this for each predictor variable. Thus, AIC_c weight and evidence ratio represent the relative importance of a model and a predictor variable, respectively. Evidence ratios > 10 indicate moderately strong support (Lukacs et al. 2007, Frederiksen et al. 2008). The effect of each environmental variable on breeding phenology was estimated using model-averaged estimates that were calculated using AIC_c weights according to Burnham & Anderson (2002). Hence, the effects were adjusted for model selection uncertainty.

It was important to include YEAR in these analyses, because some of the environmental variables showed a linear trend over time (Fig. 2, Table A1 in Appendix 1). Other predictor variables also correlated with each other (Table A1), so we carefully compared models

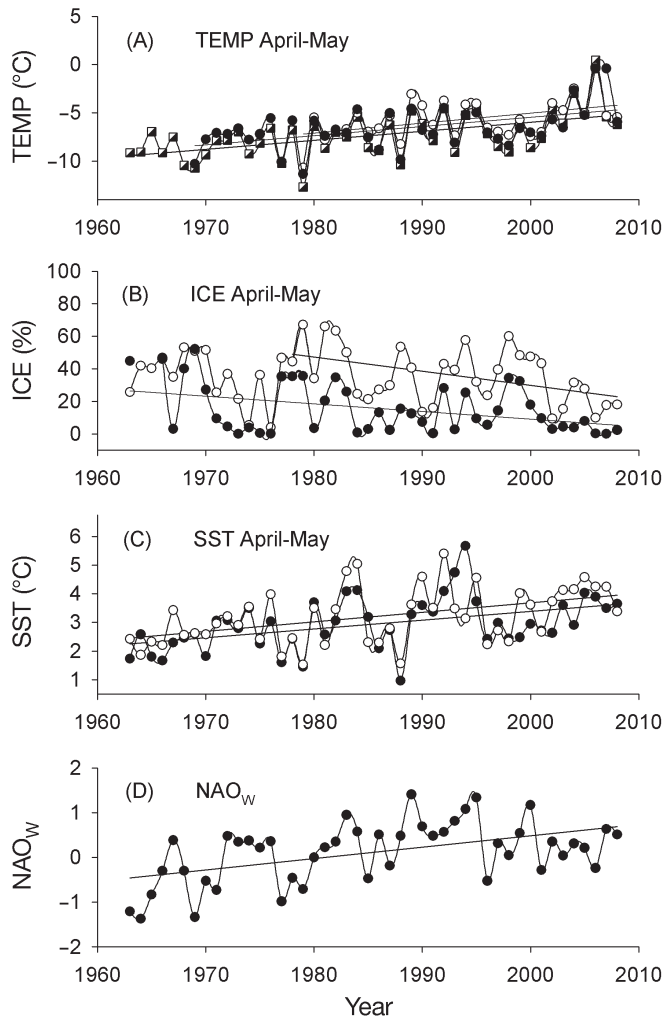


Fig 2. (A) Air temperature (TEMP), (B) sea ice concentration (ICE) and (C) sea surface temperature (SST) at (●) Ny-Ålesund, (○) Hornsund and (■) Longyearbyen as a function of year. (D) North Atlantic Oscillation winter index (NAO_w) as a function of year. The data on TEMP are from the periods 1963–2008, 1969–2008 and 1979–2008 from Longyearbyen, Ny-Ålesund and Hornsund, respectively. Regression lines indicate significant linear relationships. (A) TEMP Longyearbyen = $-194.3 (\pm 42.4) + 0.094 (\pm 0.021) \times \text{year}$; TEMP Ny-Ålesund = $-196.6 (\pm 53.3) + 0.096 (\pm 0.027) \times \text{year}$; TEMP Hornsund = $-213.3 (\pm 76.2) + 0.104 (\pm 0.038) \times \text{year}$; (B) ICE Ny-Ålesund = $958.8 (\pm 333.7) - 0.475 (\pm 0.168) \times \text{year}$; ICE Hornsund = $1775.8 (\pm 617.4) - 0.873 (\pm 0.310) \times \text{year}$; (C) SST Ny-Ålesund = $-57.8 (\pm 18.2) + 0.031 (\pm 0.009) \times \text{year}$; SST Hornsund = $-63.1 (\pm 19.0) + 0.034 (\pm 0.010) \times \text{year}$; (D) NAO_w = $-50.7 (\pm 13.0) + 0.026 (\pm 0.007) \times \text{year}$

containing only 1 variable to those of multiple variables. The SEs of the estimates were not severely inflated when multiple variables were included in the same models, so the conclusions drawn from these analyses are not assumed to be influenced by problems related to multiple collinearity.

The analyses could potentially be affected by the fact that different methods had been used to obtain hatch dates. For kittiwakes, data from 2002 and 2003 were special because hatch dates were obtained from eggs in incubators, and because these years were extremely late and poor. For little auks, data from 2003 was special because hatch date was back-calculated from fledging dates. We therefore performed reanalyses to test how environmental variables affected breeding phenology when these years were excluded. However, the results from these reanalyses did not change the conclusions drawn from the full analyses with all years included. The statistical analyses were performed with the software R 2.6.0 (R Development Core Team 2007). The seabird and environmental data used in this study are given in Appendix 1, Table A2.

RESULTS

Spring TEMP increased in Svalbard over the study period (1963–2008), with TEMP becoming $0.9 (\pm 0.2)^\circ\text{C}$ warmer per decade in Longyearbyen ($F_{1,44} = 19.4$, $p < 0.001$, Fig. 2A). The strongest increase in TEMP took place during the later part of this period, with an increase of $0.47 (\pm 0.18)^\circ\text{C}$ per year from 1997 to 2008 ($F_{1,10} = 6.9$, $p = 0.03$, Fig. 2A). The increase in TEMP was similar for Hornsund and Ny-Ålesund (Fig. 2A). This trend was accompanied by a decrease in spring ICE and by an increase in spring SST. During the whole study period, the decrease in ICE was significant for Ny-Ålesund ($F_{1,42} = 8.0$, $p = 0.007$, Fig. 2B), but not entirely for Hornsund ($F_{1,44} = 2.3$, $p = 0.14$, Fig. 2B). During the last 30 yr, however, it was significant for both locations (1978–2008, $F_{1,29} > 5.5$, $p < 0.02$, Fig. 2B). SST increased significantly over the study period for Ny-Ålesund ($F_{1,44} = 11.2$, $p = 0.002$, Fig. 2C) and Hornsund ($F_{1,44} = 12.1$, $p = 0.001$, Fig. 2C). The NAO_w also increased significantly during the study period ($F_{1,44} = 15.3$, $p < 0.001$, Fig. 2D).

Little auks showed a significant trend for earlier breeding ($F_{1,16} = 4.5$, $p = 0.05$, Fig. 3); median hatch date became $4.5 (\pm 2.1)$ d earlier over the study period. The kittiwakes showed a trend for later hatching, but it was not significant ($F_{1,16} = 1.7$, $p = 0.21$, Fig. 3). For the years with data from both species, there was no correlation between the median hatch dates of kittiwakes and little auks ($r = 0.06$, $df = 8$, $p = 0.86$), indicating that the 2 species have shown different phenological responses over time.

Different environmental factors were related to the breeding phenology of little auks than kittiwakes (Tables 1 & 2). The best models were TEMP for little auks and SST+ICE for kittiwakes (Table 1), with coefficients of determination (R^2) of 0.40 and 0.30, respec-

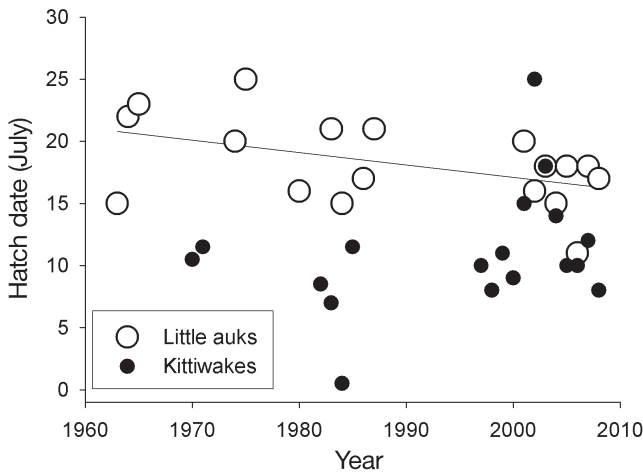


Fig 3. *Alle alle* and *Rissa tridactyla*. Median hatch dates in July of little auks (open circles) and kittiwakes (filled circles) breeding in Svalbard, as a function of year (kittiwakes, 18 yr, 1970–2008; little auks, 18 yr, 1963–2008). The regression line represents a significant linear trend for earlier breeding of little auks; hatch date = 217.2 (±93.7) – 0.100 (±0.047) × year

Table 1. *Alle alle* and *Rissa tridactyla*. Rank of linear models explaining breeding phenology of little auks and kittiwakes based on Akaike’s Information Criterion corrected for small sample size (AIC_c). *k* is the number of parameters, and *w* is the Akaike weight calculated from the set of models with ΔAIC_c < 4. See ‘Materials and methods: Environmental parameters’ for an explanation of model parameters

| | Rank | Model | <i>k</i> | ΔAIC _c | <i>w</i> |
|-------------|------|-----------------------------|----------|-------------------|----------|
| Little auks | 1 | TEMP | 2 | 0.0 | 0.33 |
| | 2 | TEMP, ICE | 3 | 0.1 | 0.31 |
| | 3 | TEMP, SST | 3 | 2.6 | 0.09 |
| | 4 | TEMP, YEAR | 3 | 3.3 | 0.06 |
| | 5 | TEMP, NAO _w | 3 | 3.4 | 0.06 |
| | 6 | TEMP, ICE, SST | 4 | 3.5 | 0.06 |
| | 7 | TEMP, ICE, NAO _w | 4 | 3.9 | 0.05 |
| | 8 | ICE | 2 | 3.9 | 0.05 |
| Kittiwakes | 1 | SST, ICE | 3 | 0.0 | 0.34 |
| | 2 | SST, ICE, YEAR | 4 | 1.9 | 0.13 |
| | 3 | SST, YEAR | 3 | 2.2 | 0.11 |
| | 4 | intercept only | 1 | 2.3 | 0.11 |
| | 5 | SST | 2 | 2.7 | 0.09 |
| | 6 | YEAR | 2 | 3.3 | 0.06 |
| | 7 | YEAR, NAO _w | 3 | 3.6 | 0.06 |
| | 8 | SST, ICE, NAO _w | 4 | 3.9 | 0.05 |
| | 9 | SST, ICE, TEMP | 4 | 3.9 | 0.05 |

tively. TEMP was the best predictor of little auk phenology, while SST was the best predictor of kittiwake phenology (Tables 1 & 2). High TEMP was associated with early breeding of little auks, while high SST was associated with early breeding of kittiwakes (Table 2). For little auks, TEMP had an evidence ratio that indicated moderately strong support relative to the other predictor variables (Table 2), and the confidence inter-

Table 2. *Alle alle* and *Rissa tridactyla*. Effects of environmental variables on breeding phenology of little auks and kittiwakes. Effects are model-averaged slope estimates derived from the models in Table 1. Variables are ranked according to the evidence ratio (ER), which reflects their relative importance. Shown are unconditional SEs and 95% confidence intervals. ER was calculated as the summed Akaike weights of all models including the variable divided by the summed weight of models not including the variable. ER > 10 indicates moderate to strong support. Units are °C for TEMP and SST and % for ICE. See ‘Materials and methods: Environmental parameters’ for an explanation of model parameters

| Variable | Effect | SE | 95% CI | ER |
|------------------|--------|-------|---------------|------|
| Little auks | | | | |
| TEMP | -1.02 | 0.45 | -1.89, -0.14 | 19.0 |
| ICE | 0.04 | 0.06 | -0.07, 0.16 | 0.9 |
| SST | -0.09 | 0.22 | -0.51, 0.34 | 0.2 |
| NAO _w | 0.02 | 0.14 | -0.26, 0.30 | 0.1 |
| YEAR | -0.001 | 0.005 | -0.010, 0.008 | 0.1 |
| Kittiwakes | | | | |
| SST | -3.54 | 2.66 | -8.75, 1.67 | 3.3 |
| ICE | -0.13 | 0.14 | -0.39, 0.14 | 1.3 |
| YEAR | 0.05 | 0.08 | -0.11, 0.22 | 0.6 |
| NAO _w | -0.20 | 0.57 | -1.33, 0.92 | 0.1 |
| TEMP | -0.003 | 0.032 | -0.066, 0.060 | 0.1 |

val of the model-averaged slope estimate did not overlap with 0 (Table 2). Hence, TEMP seemed to have an important negative relationship with breeding phenology of little auks. For kittiwakes, however, the model-averaged slope estimate for SST overlapped slightly with 0 and the evidence ratio was relatively low (Table 2), and we cannot conclude firmly about the effect or the relative importance of the variable.

Although ranked second best, ICE had low relative variable importance, and the effects were highly uncertain (Table 2). Furthermore, NAO_w and YEAR had the lowest evidence ratios, and the model-averaged slope estimates were very close to 0 (Table 2). Notably, the significant correlation between YEAR and little auk phenology (Fig. 3) disappeared when TEMP was included in the models (Table 2). Hence, it seems likely that the trend for increased spring TEMP (Fig. 2) has caused the trend for earlier breeding of little auks (Fig. 3).

In kittiwakes, clutch size ($r = -0.84$, $df = 9$, $p = 0.001$, Fig. 4) and breeding success ($r = -0.80$, $df = 9$, $p = 0.003$, Fig. 4) were negatively correlated to median hatch dates. When breeding success was calculated as the number of chicks per egg laid, instead of the number of chicks per active nest, the negative correlation with phenology was still significant ($r = -0.83$, $df = 9$, $p = 0.001$). Thus, late breeding was associated with low clutch size and poor breeding success (Fig. 4). These relationships, however, were strongly driven by the 2 extremely late years, i.e. 2002 and 2003, and the correlations were not significant when these years were excluded.

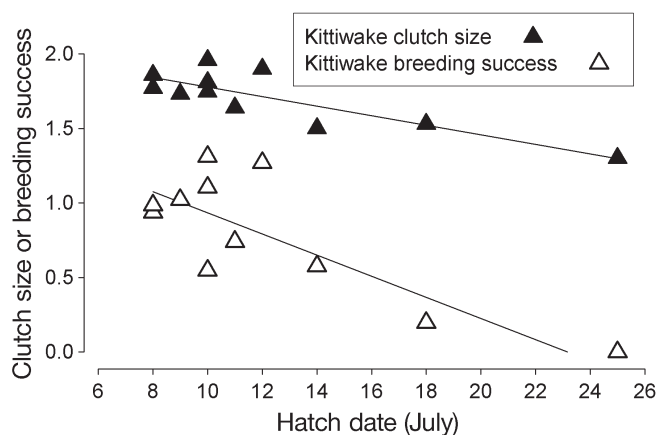


Fig. 4. *Rissa tridactyla*. Mean annual clutch size (filled triangles) and breeding success (number of chicks >12 d old per active nest; open triangles) of kittiwakes in relation to median hatch date (in July) during the breeding seasons 1997–2008 (N = 11, no data on clutch size or breeding success in 2001). Regression lines indicate significant linear relationships

DISCUSSION

The main findings of this study were that (1) median hatch date of little auks advanced during the study period, while hatch dates of kittiwakes tended to become later (albeit not significantly); (2) spring TEMP was a strong environmental predictor of little auk phenology, while spring SST tended to be an important environmental predictor of kittiwake phenology; and (3) clutch size and breeding success of kittiwakes was negatively related to the timing of breeding. Kittiwakes and little auks thus showed some different phenological responses.

Temporal trends in the timing of breeding

To our knowledge, this is the first little auk study with long-term phenology data and, consequently, the first to detect a trend for earlier breeding. The timing of breeding advanced by 4.5 d during 1963–2008. Another alcid species, Brünnich's guillemot, advanced breeding by 5 d during 1988–2007 in the Canadian low-Arctic but showed no trend in the high-Arctic (Gaston et al. 2005a, 2009). The trend for later breeding of kittiwakes, although not significant, is in accordance with trends for later breeding of British kittiwake populations (Frederiksen et al. 2004, Wanless et al. 2009). The finding that kittiwakes and little auks showed different

phenological responses adds to a diverse picture of seabird phenology in polar and temperate regions. Studies have reported trends for earlier (*Catharacta maccormicki*, *Fratercula cirrhata*, *Sterna paradisaea*, *Uria lomvia*) and later breeding (*Daption capense*, *Fulmarus glacialis*, *Pygoscelis adeliae*, *Rissa tridactyla*, *U. aalge*), as well as no detectable trends (*Aptenodytes forsteri*, *Fratercula arctica*, *Fulmarus glacialis*, *Pagodroma nivea*, *Ptychoramphus aleuticus*, *U. aalge*, *U. lomvia*; e.g. Gjerdrum et al. 2003, Abraham & Syde-man 2004, Durant et al. 2004, Frederiksen et al. 2004, Gaston et al. 2005a, 2009, Barbraud & Weimerskirch 2006, Møller et al. 2006, Wanless et al. 2008, 2009, Reed et al. 2009). This diverse pattern may indicate that the phenology of specific seabird species is regulated by different environmental factors (e.g. Frederiksen et al. 2004, Barbraud & Weimerskirch 2006), or that climate has changed in different degrees or directions in different parts of the world (e.g. Vaughan et al. 2001). Hornsund and Ny-Ålesund are located relatively close (Fig. 1) and are strongly correlated environments (Table 3, Fig. 2), and it is not likely that the different trends are caused by climate change having acted differently on Hornsund and Ny-Ålesund. Rather, we think that the different ecologies of the 2 species have created the different phenological responses.

Environmental predictors of seabird phenology

TEMP and SST in combination with ICE were the highest ranked models explaining little auk and kittiwake phenology, respectively (Table 1), and TEMP and SST were the variables with the highest relative importance (Table 2). Conditional on the candidate models and the data, this suggests that local environmental factors during spring are the most important predictors of timing of breeding in these 2 high-Arctic populations. Indeed, we think spring TEMP is strongly linked to the timing of snow melt and to the time when ground-nesting little auks can have access to snow-

Table 3. Mean and SE of environmental variables (TEMP, SST and ICE) of Ny-Ålesund and Hornsund in April–May of the periods 1963–2008 (SST and ICE) and 1979–2008 (TEMP). Shown are the correlations of the environmental variables between the 2 locations and a comparison of the means (paired *t*-test). The difference in SST between the locations was reversed if data on SST were obtained closer to the coast

| | Ny-Ålesund | | Hornsund | | Correlation | | | Paired <i>t</i> -test | |
|------|------------|------|----------|------|-------------|------|-------|-----------------------|-------|
| | Mean | SE | Mean | SE | N | r | p | <i>t</i> | p |
| TEMP | -6.5 | 0.43 | -5.7 | 0.37 | 30 | 0.84 | <0.01 | -2.3 | 0.03 |
| SST | 2.9 | 0.13 | 3.2 | 0.14 | 46 | 0.71 | <0.01 | -2.4 | 0.02 |
| ICE | 15.4 | 2.31 | 35.6 | 2.42 | 44 | 0.70 | <0.01 | -10.5 | <0.01 |

free nest sites in the rock debris colony slope. Unfortunately, we do not have appropriate data on snow cover, but behavioural observations and temperature measurements at Hornsund in 2006 strengthen this interpretation. The little auk colony was constantly occupied by birds in the colony only after the ground temperature and the nest temperature were permanently above 0°C (Fig. 5). The little auks then occupied nests as soon as the snow cover melted sufficiently to allow access to the nests. Therefore, the timing of egg-laying seemed to be strongly determined by temperature and snow melt in the colony (Fig. 5), consistent with a study on ground-nesting auklets (*Aethia pusilla*, *A. cristatella*, *Cyclorhynchus psittacula*) in Alaska (Sealy 1975). Effects of spring snow cover and TEMP on phenology have also been reported in other ground-nesting bird species in the high-Arctic, such as waders (*Calidris alba*, *C. alpina*, *Arenaria interpres*; Meltofte et al. 2007), greater snow geese *Chen caerulescens atlantica* (Bêty et al. 2003, Dickey et al. 2008) and pink-footed geese *Anser brachyrhynchus* (Madsen et al. 2007). In addition to effects via snow cover, temperature could also directly impose energetic constraints on little auk phenology. Temperatures are often below the

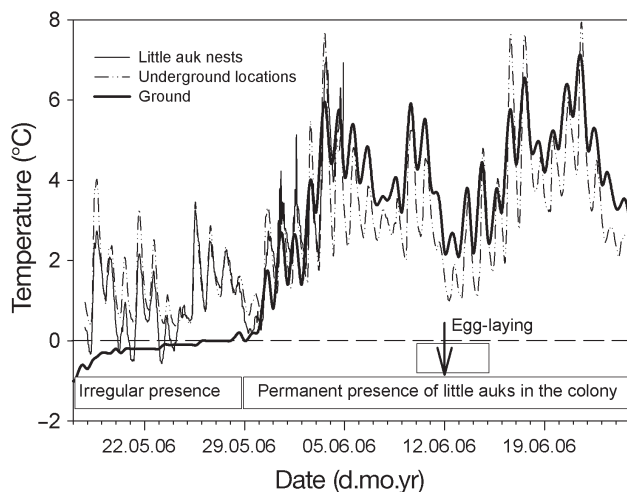


Fig. 5. *Alle alle*. Temperature (°C) in little auk nests (solid line), underground locations in the colony slope (broken line) and ground (measured ~20 cm above flat tundra; thick solid line) as a function of date in 2006. 'Irregular presence' means that the colony attendance alternated between periods without any birds and periods with many birds in the colony. 'Permanent presence' means that the colony was constantly attended by little auks. The arrow indicates median egg-laying date in 2006, and the box indicates the egg-laying period. Ground temperature was measured 3 times d^{-1} . Temperature was measured every hour in 3 nests and 4 underground locations, and this graph presents the hourly means for these 3 nests and 4 underground locations, respectively. Temperature loggers in the 3 nests were removed on 4 June, i.e. before egg laying occurred

thermoneutral zone (TNZ) when they lay eggs (TNZ >4.5°C, Gabrielsen et al. 1991), and costs of egg production and incubation are elevated under such conditions (Stevenson & Bryant 2000).

SST correlated negatively to kittiwake phenology, but we cannot conclude firmly that SST had an effect, because the confidence intervals of the model-averaged slope estimate slightly overlapped with 0 (Table 2). This is in accordance with studies of kittiwakes (Frederiksen et al. 2004) and tufted puffins *Fratercula cirrhata* (Gjerdrum et al. 2003) at lower latitudes. Those studies reported significant negative correlations with local SST, but they disappeared when a longer time series was analysed for the kittiwakes (Frederiksen et al. 2004, Wanless et al. 2009) and when all years were included in the tufted puffin data (Gjerdrum et al. 2003). Wanless et al. (2009) reported long-term phenology data for British seabirds, and SST did not correlate significantly to phenology of any of the 11 investigated species. Hence, the effect of SST on seabird phenology seems weak or unclear.

Studies from the Arctic and the Antarctic have shown that seabirds breed later in years with more sea ice or a longer sea ice season (Gaston et al. 2005a,b, Barbraud & Weimerskirch 2006). Extensive ICE could force arctic seabirds to forage in more distant waters and make early breeding energetically expensive, and late disappearance of sea ice and development of the polar marine food web could delay the optimal timing of breeding (Moline et al. 2008). However, we did not detect a clear effect of ICE on phenology, as the signs of the model-average slope estimates differed between kittiwakes and little auks and the confidence intervals considerably overlapped with 0 (Table 2). This result is somewhat unexpected, especially for little auks breeding at Hornsund, because the sea ice cover can be rather extensive in this area (Fig. 2B, Table 3).

We used NAO_w as a large-scale proxy for winter conditions, and detected no effect on phenology (Fig. 2). However, we cannot rule out the possibility that kittiwakes breeding in the high-Arctic assess their winter conditions to adjust the timing of breeding, as reported for kittiwakes, common guillemots *Uria aalge*, Atlantic puffins *Fratercula arctica* and razorbills *Alca torda* breeding in Great Britain (Frederiksen et al. 2004, Wanless et al. 2009). Kittiwakes and little auks are likely to disperse over a large area in the North Atlantic during winter, and the evidence for wintering close to Greenland is sparse (Bakken et al. 2003). Because the correlation between NAO and local climate (e.g. SST) is highly spatially variable, it is not clear how well NAO_w captures the winter conditions of kittiwakes and little auks.

Our phenological time series covered substantial time periods (1963–2008, 1970–2008, Fig. 3). However,

data were not available for all the years within these periods, and the time series had some substantial gaps (Fig. 3). Complete time series would have provided (1) better precision in the descriptions of the temporal trends in the timing of breeding and (2) more statistical power to detect potential relationships between environmental factors and timing.

It is not clear whether kittiwakes and little auks use the environmental cues in optimal decisions on when to initiate breeding. We have no data on phenology of the main prey items of little auks and kittiwakes (copepods versus fish/amphipods/krill). Therefore, we are consequently unable to test whether specific environmental variables are reliable predictors of marine prey phenology (Visser & Both 2005). We do not think TEMP is a direct predictor of marine prey phenology. SST and ICE could be such predictors through their effects on the timing of spring bloom and phenology of phytoplankton and zooplankton (Edwards & Richardson 2004, Scott et al. 2006, Moline et al. 2008). Alternatively, the ability of kittiwakes and little auks to initiate breeding could be constrained by food availability, because they rely on food acquired at the breeding grounds for investment in their eggs. Reed et al. (2009) reported that fish abundance affected phenology of common guillemots in California, but appropriate data to test this for our populations do not exist. Thus, our results are not conclusive on whether breeding phenology is regulated by optimal decisions or constrained by food availability.

Breeding success and phenology

Kittiwake clutch size and breeding success were significantly negatively related to the timing of breeding (Fig. 4), indicating poor investment and poor food availability in years with very late breeding. The same relationship has been found for other Arctic kittiwake populations in Alaska (Murphy et al. 1991) and Canada (Gaston et al. 2005b), but not at lower latitudes in Scotland (Frederiksen et al. 2004). The Arctic summer is very short, so this relationship could indicate that a late peak in food availability is associated with a very short peak or a very low peak in food availability, and that the low breeding success achieved in the late years is the best possible in these years. However, we do not know how well kittiwakes are able to match the peak in food availability.

CONCLUSIONS AND FUTURE CONSIDERATIONS

The spring climate is currently undergoing big changes in this part of Svalbard. The increase in air

temperature and SST and the decrease in sea ice concentration are consistent with rapidly advancing spring and timing of snow melt in Greenland (Høye et al. 2007). Thus, further advancements in the timing of breeding could be expected for little auks and other ground-nesting high-Arctic species. A possible consequence of an earlier snow melt is the opening of new breeding grounds at the limits of the species' range (Jensen et al. 2008), with a displacement of the population towards the colder areas (e.g. Gaston et al. 2005a, Stempniewicz et al. 2007). Although SST tended to have some importance, it is not sufficiently clear how kittiwake phenology is affected by environmental factors to make sound future predictions.

We investigated seabird phenology in the high-Arctic in relation to environmental factors. Local environmental factors during spring seem to be stronger predictors than winter conditions, but it is unclear how well the considered variable (NAO_w) captures the winter conditions. It remains to be investigated whether specific environmental variables are reliable predictors of marine prey phenology, whether the initiation of breeding is constrained by food availability, and how well seabirds are able to match the peak in food availability in the high-Arctic. Since phenology, abundance and composition of marine prey species may change as climate changes (Edwards & Richardson 2004, Wassmann et al. 2006), this is important for understanding the fitness consequences of future climate change.

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Appendix 1. Data used in models of phenology for little auks *Alle alle* and black-legged kittiwakes *Rissa tridactyla* and of climate change in Svalbard

Table A1. *Rissa tridactyla* and *Alle alle*. Correlation matrix of predictor variables used in the linear models analysing hatch date in relation to environmental variables (Table 1). Pearson's product moment correlations are presented with p-values in parentheses. See 'Materials and methods: Environmental parameters' for an explanation of model parameters

| | | YEAR | NAO _w | TEMP | SST |
|--------------------------------------|------------------|--------------|------------------|--------------|--------------|
| Kittiwakes (1970–2008) N = 18 | NAO _w | 0.38 (0.12) | – | | |
| | TEMP | 0.47 (0.05) | 0.14 (0.57) | – | |
| | SST | 0.23 (0.36) | 0.31 (0.20) | 0.44 (0.07) | – |
| | ICE | –0.39 (0.11) | 0.12 (0.62) | –0.58 (0.01) | –0.50 (0.04) |
| Little auks (1963–2008) N = 18 | NAO _w | 0.54 (0.02) | – | | |
| | TEMP | 0.65 (0.004) | 0.20 (0.43) | – | |
| | SST | 0.57 (0.01) | 0.66 (0.003) | 0.53 (0.03) | – |
| | ICE | –0.40 (0.10) | –0.23 (0.35) | –0.40 (0.10) | –0.31 (0.21) |

Table A2. *Alle alle* and *Rissa tridactyla*. Seabird and environmental data used in the study. See 'Materials and methods' for details on data collection, calculations, units and abbreviations. HD: hatch date; BS: breeding success; CS: clutch size; NA: data not available

| YEAR | Little auk | | | Hornsund | | | Kittiwake | | | Ny-Ålesund | | | Longyearbyen | |
|------|------------|--------|-------|----------|------|------|-----------|--------|-------|------------|--------|------------------|--------------|--|
| | HD | TEMP | ICE | SST | HD | BS | CS | TEMP | ICE | SST | TEMP | NAO _W | | |
| 1963 | 15 | -7.66 | 25.60 | 2.42 | NA | NA | NA | NA | 44.86 | 1.73 | -9.15 | -1.21 | | |
| 1964 | 22 | -7.58 | 41.86 | 1.87 | NA | NA | NA | NA | NA | 2.58 | -9.05 | -1.38 | | |
| 1965 | 23 | -5.91 | 40.35 | 2.32 | NA | NA | NA | NA | NA | 1.80 | -6.95 | -0.83 | | |
| 1966 | NA | NA | 45.92 | 2.20 | NA | NA | NA | NA | 46.78 | 1.66 | -9.15 | -0.30 | | |
| 1967 | NA | NA | 35.05 | 3.43 | NA | NA | NA | NA | 3.08 | 2.29 | -7.50 | 0.38 | | |
| 1968 | NA | NA | 53.09 | 2.55 | NA | NA | NA | NA | 40.08 | 2.46 | -10.45 | -0.30 | | |
| 1969 | NA | NA | 50.93 | 2.62 | NA | NA | NA | -10.30 | 52.14 | 2.60 | -10.75 | -1.34 | | |
| 1970 | NA | NA | 51.58 | 2.58 | 10.5 | NA | NA | -7.75 | 27.21 | 1.82 | -9.35 | -0.53 | | |
| 1971 | NA | NA | 25.43 | 2.95 | 11.5 | NA | NA | -7.10 | 9.43 | 3.05 | -7.90 | -0.73 | | |
| 1972 | NA | NA | 36.84 | 3.21 | NA | NA | NA | -7.20 | 4.47 | 3.08 | -7.85 | 0.48 | | |
| 1973 | NA | NA | 21.51 | 2.90 | NA | NA | NA | -6.65 | 0.05 | 2.79 | -6.95 | 0.35 | | |
| 1974 | 20 | -7.74 | 5.33 | 3.55 | NA | NA | NA | -7.80 | 3.80 | 3.49 | -9.25 | 0.37 | | |
| 1975 | 25 | -6.86 | 36.25 | 2.41 | NA | NA | NA | -7.20 | 0.48 | 2.26 | -8.15 | 0.21 | | |
| 1976 | NA | NA | 3.95 | 3.98 | NA | NA | NA | -5.55 | 0.17 | 3.03 | -6.60 | 0.36 | | |
| 1977 | NA | NA | 46.66 | 1.81 | NA | NA | NA | -10.10 | 35.27 | 1.60 | -10.25 | -0.99 | | |
| 1978 | NA | NA | 44.45 | 2.45 | NA | NA | NA | -5.80 | 35.32 | 2.42 | -6.80 | -0.46 | | |
| 1979 | NA | -10.70 | 67.18 | 1.53 | NA | NA | NA | -11.35 | 35.62 | 1.45 | -12.70 | -0.71 | | |
| 1980 | 16 | -5.50 | 34.10 | 3.50 | NA | NA | NA | -5.85 | 3.45 | 3.70 | -6.40 | 0.00 | | |
| 1981 | NA | -7.80 | 66.03 | 2.20 | NA | NA | NA | -7.40 | 20.43 | 2.57 | -8.70 | 0.22 | | |
| 1982 | NA | -6.80 | 63.41 | 3.45 | 8.5 | NA | NA | -6.75 | 34.75 | 3.06 | -7.00 | 0.35 | | |
| 1983 | 21 | -6.70 | 50.08 | 4.79 | 7 | NA | NA | -7.10 | 25.92 | 4.08 | -7.50 | 0.95 | | |
| 1984 | 15 | -5.03 | 24.56 | 5.04 | 0.5 | NA | NA | -4.65 | 0.85 | 4.12 | -5.45 | 0.58 | | |
| 1985 | NA | -6.99 | 21.31 | 2.30 | 11.5 | NA | NA | -7.55 | 2.94 | 3.19 | -8.60 | -0.48 | | |
| 1986 | 17 | -6.62 | 27.26 | 2.29 | NA | NA | NA | -8.85 | 13.10 | 2.10 | -8.90 | 0.51 | | |
| 1987 | 21 | -5.30 | 29.81 | 2.79 | NA | NA | NA | -5.05 | 2.41 | 2.73 | -6.25 | -0.19 | | |
| 1988 | NA | -8.25 | 53.49 | 1.56 | NA | NA | NA | -9.85 | 15.43 | 0.96 | -10.40 | 0.48 | | |
| 1989 | NA | -3.05 | 40.63 | 3.62 | NA | NA | NA | -4.60 | 12.49 | 3.27 | -4.80 | 1.41 | | |
| 1990 | NA | -4.25 | 13.49 | 4.59 | NA | NA | NA | -6.80 | 7.31 | 3.60 | -6.10 | 0.69 | | |
| 1991 | NA | -6.25 | 15.99 | 3.51 | NA | NA | NA | -7.25 | 0.28 | 3.37 | -7.90 | 0.48 | | |
| 1992 | NA | -3.75 | 42.95 | 5.40 | NA | NA | NA | -4.50 | 28.21 | 4.09 | -4.60 | 0.57 | | |
| 1993 | NA | -7.35 | 39.30 | 3.48 | NA | NA | NA | -8.10 | 2.65 | 4.74 | -9.10 | 0.81 | | |
| 1994 | NA | -4.15 | 57.70 | 3.14 | NA | NA | NA | -5.20 | 25.37 | 5.67 | -5.25 | 1.08 | | |
| 1995 | NA | -4.05 | 32.03 | 4.55 | NA | NA | NA | -5.00 | 9.41 | 3.73 | -4.65 | 1.34 | | |
| 1996 | NA | -6.55 | 23.68 | 2.24 | NA | NA | NA | -7.05 | 5.47 | 2.42 | -7.15 | -0.53 | | |
| 1997 | NA | -6.95 | 39.52 | 2.72 | 10 | 1.10 | 1.81 | -7.70 | 14.29 | 2.98 | -8.50 | 0.32 | | |
| 1998 | NA | -7.30 | 60.07 | 2.33 | 8 | 0.94 | 1.77 | -8.40 | 34.38 | 2.43 | -9.05 | 0.05 | | |
| 1999 | NA | -5.70 | 48.33 | 4.01 | 11 | 0.74 | 1.64 | -6.60 | 32.42 | 2.48 | -6.30 | 0.54 | | |
| 2000 | NA | -7.45 | 47.50 | 3.62 | 9 | 1.02 | 1.73 | -7.05 | 17.94 | 2.94 | -8.60 | 1.17 | | |
| 2001 | 20 | -7.00 | 43.39 | 2.67 | 15 | NA | NA | -7.40 | 9.62 | 2.71 | -7.65 | -0.29 | | |
| 2002 | 16 | -4.00 | 9.36 | 3.73 | 25 | 0.00 | 1.30 | -5.70 | 2.95 | 2.63 | -4.70 | 0.35 | | |
| 2003 | 18 | -4.75 | 15.29 | 4.13 | 18 | 0.25 | 1.53 | -6.55 | 4.40 | 3.59 | -6.05 | 0.04 | | |
| 2004 | 15 | -2.50 | 31.46 | 4.15 | 14 | 0.58 | 1.50 | -2.70 | 3.88 | 2.90 | -3.00 | 0.31 | | |
| 2005 | 18 | -5.05 | 27.71 | 4.58 | 10 | 1.31 | 1.96 | -5.25 | 7.90 | 4.03 | -5.15 | 0.21 | | |
| 2006 | 11 | -0.25 | 9.89 | 4.24 | 10 | 0.55 | 1.74 | -0.40 | 0.21 | 3.89 | 0.45 | -0.24 | | |
| 2007 | 18 | -5.33 | 17.67 | 4.24 | 12 | 1.27 | 1.90 | -0.40 | 0.00 | 3.49 | -5.40 | 0.63 | | |
| 2008 | 17 | -5.45 | 18.02 | 3.38 | 8 | 0.98 | 1.86 | -5.95 | 2.39 | 3.65 | -6.20 | 0.51 | | |

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