THE BREEDING DEMOGRAPHY AND EGG SIZE OF NORTH NORWEGIAN ATLANTIC PUFFINS *FRATERCULA ARCTICA* AND RAZORBILLS *ALCA TORDA* DURING 20 YEARS OF CLIMATIC VARIABILITY

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Barrett, R.T. 2001. The breeding demography and egg size of North Norwegian Atlantic Puffins *Fratercula arctica* and Razorbills *Alca torda* during 20 years of climatic variability. Atlantic Seabirds 3(3): 97-112. *The mean egg-laying dates of Atlantic Puffins* Fratercula arctica *and Razorbills* Alca torda *in north-eastern Norway varied between 13-30 May and 21 May-2 June respectively in the years 1980-1982 and 1988-2000. Atlantic Puffins laid on average 7 days before Razorbills, and the mean spread of laying dates each year was larger (22 days) for the former than the latter (19 days). There were significant correlations between egg-laying dates and air and sea temperatures in April and May, with lower temperatures resulting in delays in laying at a rate of 1-4 days* °C^{-1}. *Late access to nesting sites due to snow and ice in burrows might explain some of the delay in egg-laying during cold springs. Such variation should be considered when planning field trips to monitor breeding populations. There was no inter-annual variation in the mean volumes of Atlantic Puffin eggs. Although Razorbill egg volume did vary between years, it was not influenced by either sea or air temperatures. This suggests that neither species adjusted egg size in order to advance laying dates.*

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INTRODUCTION

The censusing and monitoring of breeding populations of seabirds are often timed to coincide with certain stages of the breeding cycle of the species in question (Walsh *et al.* 1995). In Norway, counts of many species are recommended at specific times during the incubation period and/or early chick-rearing period (Lorentsen 1989). The success of any monitoring scheme thus depends on prior knowledge of the laying or hatching dates of the target species so that fieldwork may be timed to coincide with the recommended stage of the breeding cycle. Such knowledge is lacking in detail for nearly all Norwegian seabird species.

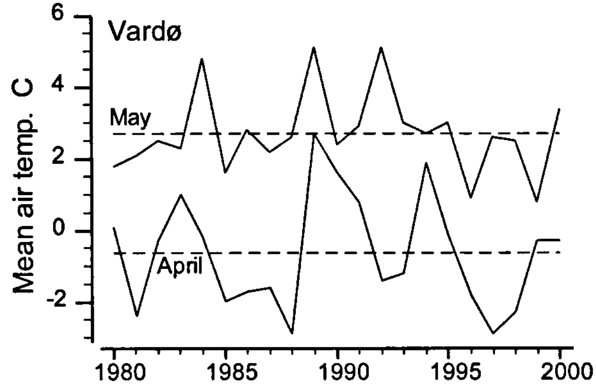
Mechanisms that determine the timing of breeding have long been a subject of discussion. Lack (1954) proposed that breeding was timed so that chicks hatched at the time of maximum food availability. However, the timing of breeding of females that lay single-egg clutches in temperate and high latitudes has since been shown to be determined also by their food requirements during egg laying and incubation (Perrins 1970; Brooke 1978). On the Semidi Islands, Alaska, Hatch & Hatch (1990a) showed that eight of 11 seabird species bred as early as environmental conditions would allow, thereby supporting Perrins' (1970) hypothesis; the three exceptions were all puffin species whose sequence of laying accorded with Lack's (1954) predictions in that their breeding schedules converged at the chick-rearing period. Furthermore, there may be selection pressure for females to breed as early as possible because the breeding success of many species declines through the season (Perrins 1970).

Weather conditions may advance or delay breeding of seabirds by many days or weeks (Hornung & Harris 1976; Lloyd 1979; Murphy & Schauer 1994; Harris & Wanless 1988; Harris *et al.* 1998). In extreme cases, inclement weather or the late break-up of ice not only delays breeding but may also result in reduced egg size, chick growth or breeding success (Nettleship *et al.* 1984; Kilpi 1992; Gaston & Hipfner 1998).

The reduction in egg-size may be the result of a trade-off between egg volume and the timing of egg laying. The production of eggs is energetically costly and late laying birds may minimize the delay in breeding due to poor food availability by laying smaller eggs (Nettleship *et al.* 1984). Alternatively, a poor food supply early in the season may cause adults to either postpone laying until there is enough food to enable them to maintain continuous incubation (Brooke 1978) or even to defer breeding until a subsequent year (Hatch & Hatch 1990b).

Among the species included in the Norwegian Seabird Monitoring Programme (Lorentsen 1989, 1999) are Atlantic Puffins *Fratercula arctica* and Razorbills *Alca torda*. One of the colonies monitored is Hornøya, Finnmark, in the southwestern Barents Sea, where their population numbers and breeding success have been monitored annually since 1980. Here, both species are near the northern limits of their ranges and, because they both nest in burrows or cavities that are blocked by ice and snow in early spring, small variations in air temperature can be expected to have major consequences on their breeding demography (Belopol'skii 1957; Sealy 1975; Rodway *et al.* 1998).

Sea temperatures might influence food availability during the pre-laying period and so could be an ultimate factor controlling the timing of egg laying (Perrins 1970). Since 1980, there have been large fluctuations in sea temperatures off the Finnmark coast as a result of major inflows of warm Atlantic water into the Barents Sea in 1982/83, 1988/89 and 1998/99 (Loeng 1999; Loeng *et al.* 1992). This inflow of Atlantic water is a major determinant



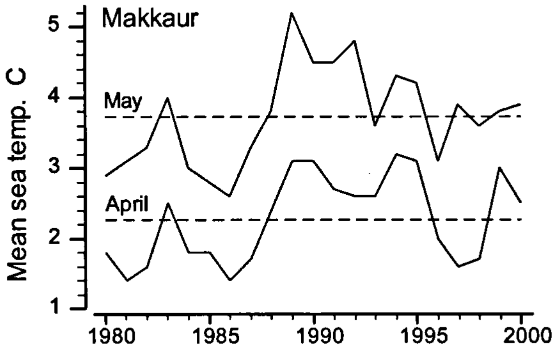


Figure 1. Variations in monthly mean air temperatures at Vardø and sea surface temperatures at Makkaur Lighthouse, East-Finnmark, in April and May 1980-2000. Dotted lines indicate the means for the period 1980-2000. Data from Norwegian Meteorological Institute.

Figuur 1. Variatie in gemiddelde maandelijkse luchttemperatuur in Vardø en zeewatertemperatuur bij Makkaur Lighthouse, Oost-Finnmarken, in april en mei 1980-2000. Data van Norwegian Meteorological Institute.

of ecological conditions at all trophic levels in the region, and its effects on seabirds breeding in the region have been described by Barrett and Krasnov (1996).

So while small changes in sea temperature may be one ultimate factor determining breeding demography, larger variations in air temperatures will have even greater short-term effects on the amount of snow and ice in and on the ground and so will affect access to breeding burrows and cavities on Hornøya. Mean monthly air temperatures during the pre-breeding period in April and May at the weather station in Vardø, c. 1 km from the colony, vary by as much as 5° C from year to year (Fig. 1). This results in large variations in snow cover on the island early in the breeding season (pers. obs.).

This aims of this study are: a) to document and discuss variations in the timing of breeding and egg size of the Atlantic Puffin and Razorbill over a 20 year period in north Norway, and b) to consider the possible effects of changes in sea and air temperature on these parameters.

METHODS

The study was carried out on Hornøya, a small (1000 x 700 m) island off the northeasternmost tip of Norway (70° 22'N, 31° 10'E) where a long-term study of colonial seabirds was initiated in 1980 (Barrett 1983, Barrett & Krasnov 1996). Approximately 5000 pairs of Atlantic Puffins and 500 pairs of Razorbills breed on the main cliff, which is otherwise dominated by c. 21 000 pairs of Black-legged Kittiwakes Rissa tridactyla (Furness & Barrett 1985; Barrett & Krasnov 1996).

In 1980-1982, c. 40-50 marked nests each of Atlantic Puffins and Razorbills were inspected once every 1-3 days during the late incubation and throughout the chick-rearing periods (Barrett 1985; Barrett *et al.* 1987). In and after 1988, the nests were checked once during the incubation period and twice during the chick-rearing period at a c. 10-20 day intervals.

In order to avoid possible interannual variations in breeding parameters due to changes in, for example, nest density, aspect, slope or distance from the cliff edge (Harris 1980; Hudson, 1982; Rodway *et al.*1998), the same nests or, when abandoned, neighbouring nests were studied each year. Scattered along the whole breeding cliff, the total sample was considered representative of the colony.

All eggs were measured (length and breadth ±0.05 mm) and their volumes were calculated using the equation $v = klb^2$, where v = volume in ml, k = 0.54 for Razorbill (Lloyd 1979) and 0.51 for Atlantic Puffin (Preston 1974), l = length in cm, and b = breadth in cm.

All chicks were weighed (±2.5 g) and their wings measured (maximum flattened chord, including down but excluding the small tuft at the end, ±2.5 mm when downy and ±0.5 mm after the eruption of the primaries or coverts) during the latter visits.

Hatching dates in 1980-1982 were determined directly during the frequent visits to the nests. In and after 1988, they were estimated using models relating wing length to age on the assumption that wing growth is less sensitive to nutrient variation than change in mass (Ricklefs & White 1975; Mauck & Grubb 1995). Despite considerable variations in chick diet during the study period (Barrett & Krasnov 1996), there was no suggestion of food shortages in any season that might have resulted in reduced somatic growth in chicks of either species (pers. obs.). The models relating wing length to age were based on data from chicks of known age, weighed and measured in two seasons in the early 1980s (Barrett 1985; Barrett *et al.* 1987), and the best model to fit each data set was determined using CurveExpert©1.2 (http://www.ebicom.net/~dhyams/cvxpt.htm). In each case, quadratic regression equations were found to be the best fit, with regression coefficients of 99.6-99.9%. These equations were then used to calculate the hatching date of each chick whose wing length was known. If a chick was measured two or more times, the hatching date was calculated for each measurement and a mean of the values used. Differences in such multiple calculations were small (means 0.7±0.7 d for Razorbills and 1.4±0.9 d for Atlantic Puffins).

Once hatching dates were estimated, any obvious outlier at the end of a hatching period was removed from the data as they were assumed to be replacement eggs. These totalled four Atlantic Puffin eggs (in 1980, 1981, 1982 and 1998) and two Razorbill eggs (1994, 1995). Laying dates were back calculated from hatching dates using incubation periods of 39 days for the Atlantic Puffin (Ashcroft 1976) and 35 days for the Razorbill (Lloyd 1979), assuming no change over the duration of the study.

Minitab® Release 12 (http://www.minitab.com) software was used for all statistical analyses. Mean values are given ±1 standard deviation.

RESULTS

The estimates of the mean hatching dates of both species varied considerably and significantly from year to year, ranging from 21 June 1989–8 July 1981 for Atlantic Puffins ($F_{15,570} = 16.0$, $P < 0.001$) and 25 June 1989–7 July 1981 for Razorbills ($F_{14,496} = 14.9$, $P < 0.001$). There was a significant correlation between the mean hatching dates of both species each year ($R^2 = 0.52$, $P = 0.002$, $n = 15$ yr). Accounting for the incubation periods, the ranges of mean laying

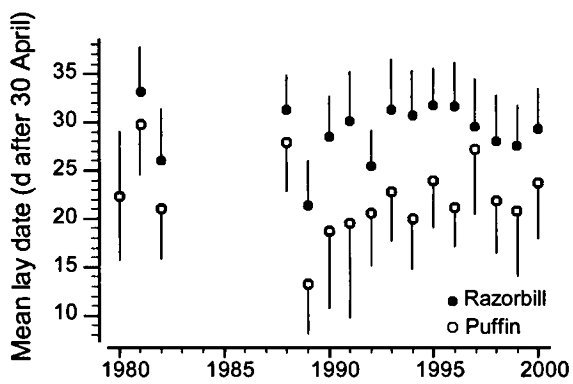


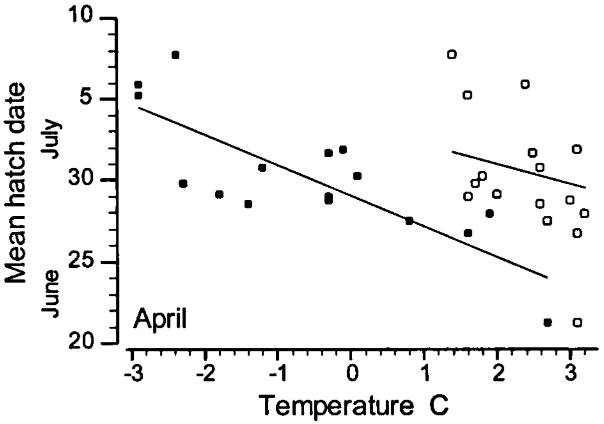
Figure 2. Mean laying dates of Atlantic Puffins and Razorbills at Hornøya, East Finnmark, 1980-2000. The dates are back-calculated from hatching dates with standard deviations (vertical lines) held constant.

Figuur 2. Gemiddelde eilegdata van Papegaaiduikers en Alken op Hornøya, Oost-Finnmarken, 1980-2000. De data zijn teruggerekend van de uitkomstdata, waarbij de standaarddeviaties (verticale lijnen) constant zijn gehouden.

dates were estimated at 13–30 May and 21 May–2 June respectively (Fig. 2). Atlantic Puffins laid on average 7 days before Razorbills (mean = 6.9±2.8 d, min = 3.2 (1997), max = 10.8 (1994), n = 15).

The spread of laying within each year on Hornøya was greater for Atlantic Puffins (mean = 22.1±4.8 d, n = 16 years) than for Razorbills (18.6±2.5 d, n = 15 years, t = 2.6, P = 0.018). The maximum variation in the mean laying dates between years for Atlantic Puffins (17 days) was also greater than that for Razorbills (12 days).

Mean sea temperatures in both April and May affected the hatching/laying dates of Atlantic Puffins with lower temperatures resulting in later laying ($R^2 = 0.32$, P = 0.022 (April), $R^2 = 0.34$, P = 0.018 (May; Fig. 3), whereas air temperatures had a similar but stronger influence in April ($R^2 = 0.65$, $P < 0.001$) but no influence in May ($R^2 = 0.12$, P = 0.18). While neither the mean air nor the mean sea temperatures in April influenced the laying dates of Razorbills, there were weak but significant effects of May temperatures, again with lower temperatures delaying egg laying ($R^2 = 0.33$, P=0.026 (air), $R^2 = 35\%$, P = 0.021 (sea); Fig. 4).



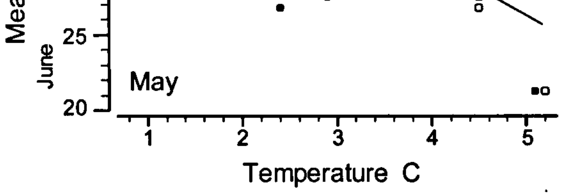


Figure 3. Correlations between mean hatching dates of Atlantic Puffin eggs and local air (solid symbols) and sea (open symbols) temperatures in East Finnmark in April and May 1980-2000. Equations for significant correlations are y = 29.1-1.85x (air, April), y = 38.7-3.54x (sea, April) and y = 43.9-3.53x (sea, May).

Figuur 3. Correlaties tussen gemiddelde uitkomstdata van eieren van de Papegaaiduiker en respectievelijk de luchttemperatuur (gesloten symbolen) en de zeetemperatuur (open symbolen) in Oost-Finnmarken in april en mei 1980-2000. Vergelijkingen voor significante correlaties zijn y = 29.1-1.85x (lucht, april), y = 38.7-3.54x (zee, april) en y = 43.9-3.53x (zee, mei).

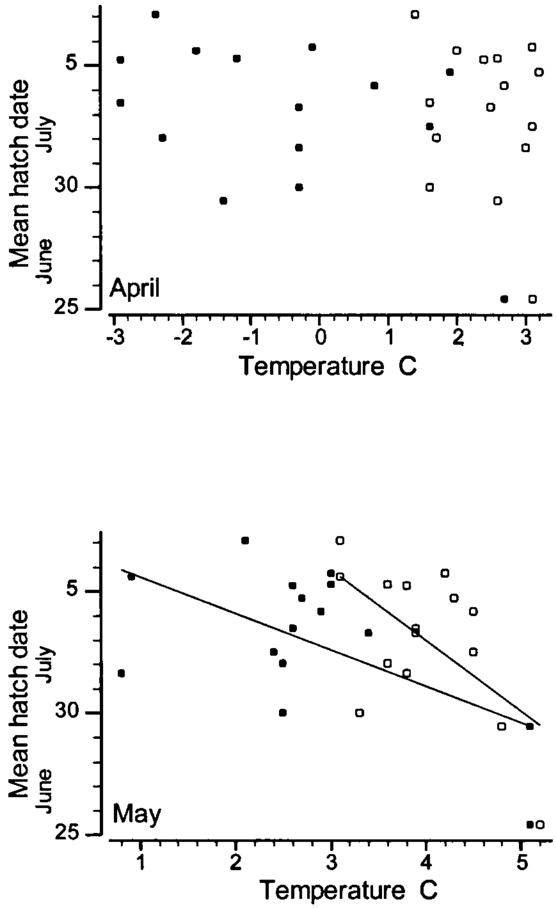


Figure 4. Correlations between mean hatching dates of Razorbill eggs and local air (solid symbols) and sea (open symbols) temperatures in East Finnmark in April and May 1980-2000. Equations for significant correlations are y = 37.1-1.47x (air, May) and y = 44.7-2.92x (sea, May).

Figuur 4. Correlaties tussen gemiddelde uitkomstdata van eieren van de Alk en respectievelijk de luchttemperatuur (gesloten symbolen) en de zeetemperatuur (open symbolen) in Oost-Finnmarken in april en mei 1980-2000. Vergelijkingen voor significante correlaties zijn y = 37.1-1.47x (lucht, mei) en y = 44.7-2.92x (zee, mei).

While the annual mean egg volumes of Atlantic Puffins did not vary among the 16 years for which data exist ($F_{15,664} = 0.8$, $P = 0.7$, mean vol. = 66.5±4.9 ml, n = 680), those of Razorbills varied within a range of 97.6±8.7 ml in 1999 to 103.5±7.6 ml in 1996 ($F_{15,762} = 1.9$, $P = 0.02$, n = 778). While there was no continuous linear trend throughout the study period, there were suggestions of an increase in volume between 1988 and 1996 followed by a decrease (Fig. 5). Neither sea nor air temperatures in April or May had any effect on the volume of eggs laid by either species. Similarly laying date had no influence on egg volumes.

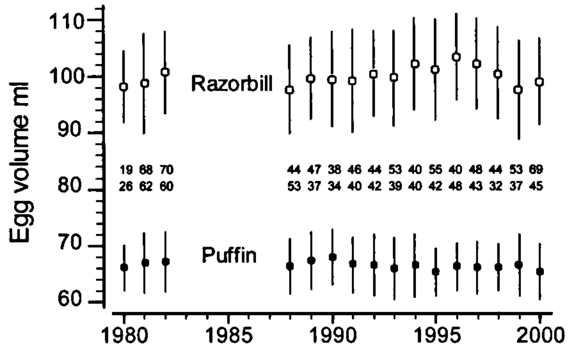


Figure 5. Mean egg volumes of Atlantic Puffins and Razorbills at Hornøya, East Finnmark, 1980-2000. Vertical lines represent standard deviations, and figures are sample sizes.

Figuur 5. Gemiddelde eivolumes van Papegaaiduiker en Alk op Hornøya, Oost-Finnmarken, 1980-2000. Verticale lijnen geven standaarddeviaties weer, getallen de steekproefgrootte.

DISCUSSION

The consistency with which Atlantic Puffins on Hornøya laid eggs earlier than the Razorbills (Fig. 2) accords with Harris (1984) in that the former are among the earliest seabirds to lay. This may be explained both by the Atlantic Puffin's long incubation and chick-rearing periods and by the fact that they require less food (in absolute terms) than most other seabirds before breeding due to their smaller size (Birkhead & Harris 1985). On Hornøya, the need to breed as early as possible is critical for species with long breeding seasons because of the short summers and the sometimes abrupt and early onset of autumn and winter.

As expected, both species laid eggs later than their conspecifics in boreal regions (Table 1) but as Birkhead & Harris (1985) point out, there is no clear latitudinal gradient in breeding demography. It is, for example, noticeable that Atlantic Puffins on the west coast of Britain and at Røst and Hornøya start laying at about the same time, whereas those on the Isle of May (east Scotland) lay earlier. Possibly, this might be related to where the adults spend the winter and when their pre-breeding moult occurs (Harris 1982; Harris & Birkhead 1985). At the north of their range, however, there appears to be a clear pattern, with Atlantic Puffins on Hornøya, Seven Islands and Novaya Zemlya laying successively later. The overall latitudinal pattern of Razorbill egg laying is also unclear with similar laying dates in Wales, Hornøya and Seven Islands, but later at Røst. These anomalies may be related to sea temperatures (Birkhead & Harris 1985) and to local hydrographical conditions (e.g. timing of upwellings) and hence feeding conditions around the individual colonies, as has been suggested to explain the similar lack of a simple relationship between latitude and laying dates among Common Guillemots *Uria aalge* in the eastern Pacific (Murphy & Schauer 1994).

The variations in the laying dates of first eggs by Atlantic Puffins at Hornøya agree well with the geographical pattern tabulated by Birkhead & Harris (1985). On the basis of few data points for five species, they suggest that the onset of laying in auks in general varies more in the Arctic than in boreal regions. This may be true for the Atlantic Puffin (and Black Guillemots *Cepphus grylle*) where the spread in first egg dates seems to be greater in Arctic colonies (12-27 d) than in boreal ones (7-11 d). However, the spread among Razorbills and Common Guillemots seems to be similar in both Arctic and boreal regions, possibly the result of the more open aspect of Razorbills and Common Guillemot breeding sites. At Hornøya, in the four years (1981, 1988, 1992 and 1997) when Atlantic Puffins laid within five days of the Razorbills, the mean April air temperatures were at the lowest recorded during the study period. There was also a clear positive correlation between the interval between the mean laying dates of both species with both sea ($R^2 = 0.38$, $P = 0.014$, $n = 14$) and air ($R^2 = 47\%$, $P = 0.005$, $n = 13$) temperatures in April.

The response by Atlantic Puffins to the mean April air temperature was by far the strongest by either species to either air or sea temperature. This probably reflects the Atlantic Puffin's need to clear out burrows before nesting. As also found by Belopol'skii (1957) on colonies to the east of Hornøya, any ice or snow blocking a burrow would delay this process until the turf had warmed up, the ice had thawed and the burrow had dried out (Hornung & Harris 1976).

Table 1. Main egg laying periods of Atlantic Puffins and Razorbills in colonies in the north-east Atlantic. Dates in italics are estimated from hatching or fledging dates assuming incubation periods of 39 and 35 days for Atlantic Puffins and Razorbills respectively, and a fledging-period of 44 days for Atlantic Puffins at St. Kilda (Harris 1984). n = number of years for which data are available.

Tabel 1. Belangrijkste eilegperiode van Papegaaiduikers en Alken in kolonies in de oostelijke Atlantische Oceaan. Gecursiveerde data zijn afgeleid van uitkomst- en uitvliegdata, uitgaand van een broedduur van respectievelijk 39 en 35 dagen voor Papegaaiduiker en Alk en een uitvliegduur van 44 dagen voor Papegaaiduiker op St. Kilda (Harris 1984). n = aantal jaren waarvan data beschikbaar zijn.

Atlantic Puffin

Locality	Period	n	Ref.
Skomer, Skokholm, Wales	2 - 22 May	2	1
Isle of May, E. Scotland	18 April-2 May	8	2
St. Kilda, W. Scotland	*8 May – 4 June*	18	3
Røst, N. Norway	*1-20 May*	19	4
Hornøya	*13-31 May*	15	5
Seven Islands, Murman	24 May-10 June	5	6
Novaya Zemlya	mid June-early July	2	7

Razorbill

Locality	Period	n	Ref.
Isle of May, E. Scotland	10-30 May	7	8,9,10
St. Kilda, W. Scotland	9-13 May	6	11
Røst, N. Norway			
Hornøya	*early June*	7	12
Seven Islands, Murman	*21 May-3 June*	14	5
Novaya Zemlya	*19 May-2 June*	6	6

References: 1. Ashcroft (1976), 2. Harris and Rothery (1985), 3. Harris *et al.* (1998), 4. Anker-Nilssen (1998), 5. This study, 6. Belopol'skii (1957), 7. Uspenski (1956), 8. Hudson (1982), 9. Plumb (1965), 10. Lloyd (1979), 11. Harris and Wanless (1989), 12. Ingold (1974).

Razorbill (and Common Guillemot) more open breeding sites are less susceptible to such blockage, might thaw more quickly due to their exposure and need less preparation. The laying dates of these species would thus be less affected by early air temperatures. The stronger response by Atlantic Puffins to temperature changes may be due not only to their earlier laying than Razorbills, but because they are smaller and therefore more susceptible to small changes in food availability caused by variations in sea temperatures early in the season.

The delay in egg-laying by Atlantic Puffins and Razorbills on Hornøya during cold springs corroborates several other studies on the same subject (summarized in Birkhead & Harris 1985). Harris & Wanless (1988) showed that a decrease of 1° C in mean sea surface temperatures off the Isle of May in March delayed Common Guillemot egg-laying by 5-6 days. Similarly, Hedgren (1979) found that a 1° C decline in spring air temperatures delayed the mean fledging date of Common Guillemots by 1 day in the Baltic, whereas Murphy & Schauer (1994) found that the same species in Alaska advanced their laying after a warm spring and hence early ice break-up. In this study, decreases in mean sea surface temperatures of 1° C in April or May delayed egg-laying in Atlantic Puffins and Razorbills by 1-4 days. A decrease in air temperatures by 1° C in April delayed Atlantic Puffins by 2 days, and in May delayed Razorbills by 1 day. Delays in breeding by Razorbills in colder weather have also been documented in Denmark, Murman and Wales (Paludan 1947; Belopol'skii 1957; Lloyd 1979). Harris *et al.* (1998) also refer to a link between early breeding and warm sea surface temperatures for several auks, including Atlantic Puffins but themselves documented the converse on St. Kilda, where breeding in the Atlantic Puffin occurred later in years when April sea temperatures were higher.

Hatch & Hatch (1990a) showed that seabird species breeding later in the season had a narrower range of laying dates and lower inter-season variability in egg-laying than those laying earlier. Such a strategy would be advantageous at high latitudes where marine production is strongly seasonal and limited to a short spring and summer period. While the spread of laying dates was indeed greater among those Atlantic Puffins that bred earlier than the Razorbills on Hornøya, there was no evidence of shorter laying periods in years of late laying in the Atlantic Puffin. For the Razorbill, the opposite seemed to be true, the correlation between length of laying period and mean laying date indicating a significantly greater spread of laying among Razorbills with later laying dates ($R^2 = 0.31$, $P = 0.03$, $n = 14$).

That sea temperatures affected both species may be a response to changeable feeding conditions prior to egg-laying, even though it did not affect egg volumes. It has been shown, for example, that the pattern of the spawning migration and the spatial location of the Barents Sea capelin *Mallotus villosus* spawning grounds along the coast of North Norway in spring is generally determined by sea temperature conditions, with more fish spawning east of the North Cape in warm years (Ozhigin & Luka 1984). Capelin might also spawn in shallower water in warmer years (Stergiou 1991). This could result in capelin, a preferred prey species of all auks on Hornøya that remain in coastal waters for the whole summer (Furness & Barrett 1985, Barrett & Krasnov 1996), being more readily available during years of higher sea temperatures, thereby facilitating an earlier breeding season. It is also possible, of course, that warmer seas produce warmer air temperatures (Fig. 1) resulting in less ice and snow on the cliff and thus earlier access to the burrows.

The lack of variation in egg volumes of either Atlantic Puffins or Razorbills on Hornøya in response to either temperatures or laying dates suggests that neither species made any attempt to reduce egg volume in order to advance egg laying as found by Nettleship *et al.* (1984). It also corroborates the studies of Birkhead & Nettleship (1987) and Gaston & Hipfner (1998), both of which failed to demonstrate any annual variation in egg volumes of guillemots despite variation in the laying periods.

Breeding populations of seabirds are generally monitored by annual counts of nests or birds at recommended periods of the breeding season, for example immediately before, during or soon after egg laying for Atlantic Puffins (Lorentsen 1989; Walsh *et al.* 1995). In the Norwegian monitoring programme, variations in the breeding demography of 12-17 days for Atlantic Puffins and Razorbills are large in relation to timing of c. 10-day monitoring field trips to remote colonies such as Hornøya. The chances of mistiming such trips may be reduced, however, by regarding sea and air temperatures prior to the field season. Although the actual monthly means are usually not available until after the field season, forecasts of temperature changes in the Barents Sea based on oceanographical measurements are published annually (Aure 1999). Knowing that increases in sea temperatures will advance the onset of breeding, these forecasts should be heeded when planning monitoring studies. Nevertheless, however well planned such a study may be, in order to avoid future problems in interpreting results arising from mistimed counts, observers should always assess and note the stage of the breeding season when counts are made.

Although this study did not provide any evidence of a long-term trend towards earlier egg laying in the Atlantic Puffin and the Razorbill that might be attributed to global climate change as has been documented for some European bird species (Crick *et al.* 1997; McCleery & Perrins 1998), its continuance will hopefully generate a sound baseline for future prediction of effects of climate change on northern seabirds (Brown 1991; Forchhammer *et al.* 1998).

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BROEDDEMOGRAFIE EN EIVOLUME VAN PAPEGAAIDUIKERS *FRATERCULA ARCTICA* EN ALKEN *ALCA TORDA* TIJDENS 20 JAAR VAN KLIMATOLOGISCHE VARIATIE

Om het beste tijdstip van inventarisatiebezoeken aan kolonies met Papegaaiduikers Fratercula arctica en Alken Alca torda in Noorwegen te bepalen is kennis nodig over de timing van de broedperiode en over de periode dat de jongen net uit het ei zijn gekropen. Op Hornøya in Noord-Noorwegen is hier in 1980-2000 een studie naar verricht. De gemiddelde eilegdata lagen in 1980-1982 en 1988-2000 tussen 13-30 mei voor Papegaaiduiker en tussen 21 mei- 2juni voor Alk (figuur 2). Papegaaiduikers legden gemiddeld 7 dagen eerder dan Alken. De gemiddelde spreiding in legdata was voor Papegaaiduiker (22 dagen) ieder jaar groter dan voor Alk (19 dagen). Eilegdata en lucht- en zeetemperaturen in april en mei waren significant met elkaar gecorreleerd (figuur 3 & 4); lagere temperaturen hadden een vertraging in legdatum met 1-4 dagen $^{o}C^{-1}$ *tot gevolg. Ontoegankelijheid van nestplaatsen als gevolg van sneeuw en ijs in holen (van Papegaaiduiker) kan een deel van de verlate in eileg in koude voorjaren verklaren. Met de gevonden spreiding in eilegdata moet rekening gehouden worden bij de planning van inventarisatiebezoeken om broedpopulaties te monitoren. Bij eieren van de Papegaaiduiker werd geen verschil in gemiddeld volume tussen de jaren gevonden (figuur 5). Hoewel het eivolume bij de Alk jaarlijks wel varieerde (figuur 5), werd het eivolume niet beïnvloed door lucht- of zeetemperatuur. Dit suggereert dat geen van beide soorten de eigrootte aanpast om de eilegdatum te vervroegen.*

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