Ocean climate prior to breeding affects the duration of the nestling period in the Atlantic puffin

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Time-series covering 23 years for a long-lived seabird, the Atlantic puffin (*Fratercula arctica* L.) at Røst, northern Norway, was used to explore any indirect effects of climatic variations on chick production. By fitting statistical models on the duration of the nestling period, we found that it may be estimated using the average sea temperature and salinity at 0–20 m depth in March (having a positive and a negative effect, respectively). We propose that when the phytoplankton bloom occurs in early spring, adverse oceanographic conditions, i.e. low temperature and high salinity in March, have a negative effect on puffin reproduction by degradation of the prey availability (mainly *Clupea harengus*) for chick-feeding adults three months later.

1. INTRODUCTION

Climate fluctuations are known to affect the distribution, behaviour and phenology of plants and animals (see Stenseth *et al.* 2002). Among long-lived vertebrates, the influence of environmental variation has generally been most clearly demonstrated through effects on reproductive success and early survival that in turn affects the size of the year-classes—the cohort effect (see Stenseth *et al.* 2002 and references in Durant *et al.* 2003).

In birds with clutch size of one, reproductive success after hatching depends, among other factors (e.g. predation), on the quantity and quality of food delivered to the chick, which is determined by both the environmental conditions and the level of parental effort (i.e. the expenditure of parental resources such as time or energy for the care of offspring; Williams 1966). In addition, it might be expected that climatic conditions affect parental effort and food availability during reproduction; both these parameters in turn affect the growth of the nestling that depends on the

food provided by its parents (Bertram *et al.* 2001; Durant *et al.* 2004*b*).

A long-term population study in the Røst archipelago, northern Norway, documents that the fledging success of Atlantic puffins (*Fratercula arctica* L.) is to a large extent determined by the availability of first-year Norwegian spring-spawning herring (*Clupea harengus* L.) drifting past Røst along the Norwegian coast (Anker-Nilssen 1992; Anker-Nilssen & Aarvak 2002; Durant *et al.* 2003). In a recent study, we have suggested that the availability of herring for these puffins is affected by the environmental conditions (i.e. sea temperature; Durant *et al.* 2003). To understand better how climate affects the food availability of the puffin during reproduction, we analysed 23 years of data on the duration of the nestling period of Atlantic puffins in Røst and compared them to climatic indices expected to be relevant for this population before and during rearing.

2. MATERIAL AND METHODS

The fieldwork was conducted at Hernyken (67°26′ N, 11°52′ E) in the Røst archipelago, northern Norway. For information on field methods and annual sample sizes see Anker-Nilssen & Aarvak (2002). The duration of the nestling period (i.e. the number of days between hatching and either death in the nest or successful fledging) was determined individually for a sample of nests (annual average 64 out of 236 study nests containing an egg or chick). The average duration of the nestling period was then calculated each year from 1978 to 2001 except 1996 (100% hatching failure). It was nonlinearly related in a significant manner to the mean fledging success the same year (Gaussian function, $r^2 = 0.882$, $F_{2,20} = 83.4$, $p < 0.0001$; figure S1 in the electronic supplementary material).

(**a**) *Environmental descriptors*

As an index of general climate, we used the winter NAO (December–March) index (http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

As an index of local climate (LC), we used daily data on wind (force and direction), cloud cover and precipitation recorded at Røst since 1979 (Norwegian Meteorological Institute). For each individual nestling period, an average was calculated for each weather variable. We conducted a principal component analysis on the average data each year. The first eigenvector represented 56.9% of the total variability, whereas the second represented only 23.0%. We, therefore, decided to use the first eigenvector and principal components (wind force, cloud cover and precipitation) as indices of LC.

Following the results from a pre-analysis (table 1 in the electronic supplementary material), we used sea temperature and salinity in March (hereafter T_{sea} and *Sal*, respectively) at Eggum (68°22′ N, 13°38′ E), northeast of Røst archipelago (see references in table 1 in the electronic supplementary material).

We related the change in nestling period duration with environmental variables (tables 1 and 2 in the electronic supplementary material) using generalized additive model (GAM) formulations, as implemented in the mgcv library of R 2.2.1 (Wood & Augustin 2002). We applied a forward selection strategy, GAM regressions, based on the minimization of the generalized cross-validation (GCV), a measure of the model predictive squared error (Green & Silverman 1994). Covariates were added one at a time in the model, in the order given in tables 1 and 2 in the electronic supplementary material. A covariate was retained, if it caused a decrease in the model GCV.

For models with two variables, two-way interactions were checked. We tested whether the residuals were auto-correlated using the auto-correlation function. No correlation was found between the environmental variables used (table 3 in the electronic supplementary material).

3. RESULTS

During 1978–2001, the mean duration of the nestling period ranged from 4.9 to 48.5 days (figure 1; figure S1 in the electronic supplementary material). During the same period, the population of Atlantic puffins breeding in the Røst archipelago experienced only eight successful seasons (i.e. seasons when by far
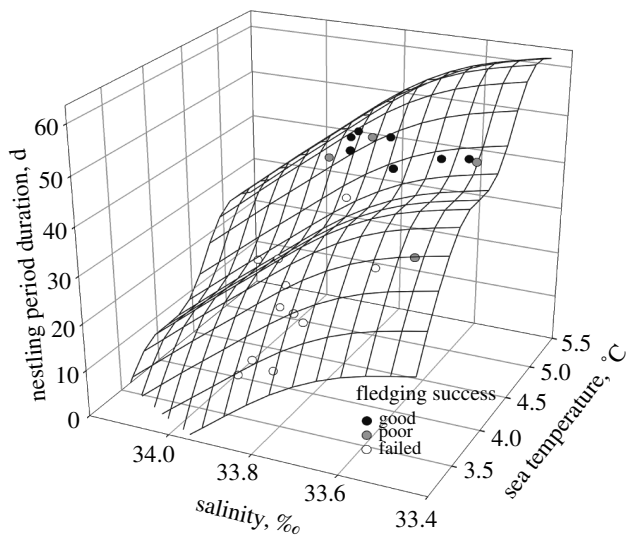
Figure 1. Physical sea characteristics as predictors of the duration of the nestling period of Atlantic puffins at Røst, northern Norway: time-series of observed mean duration of the nestling period (dots) with model prediction (grid). In addition, the overall fledging success divided into three categories (failed, 0–2%; poor, 25–51%; and good, 71–96% of the chicks fledged) is presented in different dot shadings.

most chicks (71–96%) fledged, good fledging success), whereas virtually complete breeding failures (only 0–2% fledged, failed fledging success) occurred in 11 of the remaining 15 years.

The duration of the nestling period was significantly related to two of the four climatic indices: T_{sea} and *Sal*. Neither LC nor winter NAO was significantly related to the nestling period (table 2 in the electronic supplementary material).

The best model selected by the GCV criterion includes both T_{sea} and *Sal*, with no interaction between the two (figure 1; table 2 in the electronic supplementary material). No auto-correlation was detected between the residuals.

4. DISCUSSION

Durant *et al.* (2003) showed that both sea temperature and prey quality play a major role in the breeding success of the Atlantic puffin in Røst (explaining 84% of the variation; figure 2). In the present study, we have demonstrated that the reproductive success of this seabird population as expressed by the duration of the nestling period, can be estimated using environmental variables measured well before hatching (i.e. the average sea temperature and salinity in March). These environmental variables, measured about three months before the puffin eggs hatch (which normally occurs in Late June; Durant *et al.* 2004*a*), are obviously acting indirectly on the puffins' reproductive performance and most probably through the lower trophic levels (plankton and fish). Indeed, the environmental variables used were measured during the periods of the phytoplankton bloom (starting in February) and the hatching and first growth of the herring larvae (March–April), and there is a positive relationship between sea temperatures and year-class strength of young herring (Toresen & Østvedt 2000). In addition, the absence of relationship

between nestling period duration and LC seems to indicate that the variation in the former is not due to bad weather events affecting the adults' foraging efficiency, although we cannot exclude that short events of extreme weather that would have little effect on our LC index might have had a measurable, but not a very significant effect.

Both sea temperature and salinity are influenced by common oceanographic phenomena (such as water mixing and advection). As such, they are indices of processes that in turn affect biological productivity (of plankton). Both vertical mixing of the water column and freshwater run-off from land affect salinity in the upper layers. Salinity may, therefore, represent a proxy of the nutrient conditions in spring. It may also indicate the stability of the upper part of the water column as low salinity is associated with high stability, an important factor for the phytoplankton growth (Sverdrup 1953) that in turn affects zooplankton abundance. It is then not surprising to observe a negative effect of salinity on puffin reproduction, as the increase in salinity would imply a general decrease in the feeding condition for all members of this trophic chain. In other words, for the herring, high temperature allows faster growth and lower salinity represents greater access to food making this growth possible, explaining why the fit of the model is much better with both temperature and salinity than either factor alone.

The importance of sea temperature for reproduction is well studied in seabirds and is classically interpreted in the light of food availability (see Durant *et al.* 2004*b*). For example, in the Indian Ocean, the body condition of the blue petrel (*Halobaena caerulea*) is lowered when sea-surface temperature in the preceding winter is high with effects on their breeding performance (Guinet *et al.* 1998). In the Pacific Ocean, there is a coupling between seabird reproduction and ocean temperature leading to poorer reproductive performance during warm water years for inshore species, such as the sooty shearwater (*Puffinus griseus*), and an increase in the reproductive performance during warm water years for offshore species, such as the Leach's storm petrel (*Oceanodroma leucorhoa*; Veit *et al.* 1997). In the North Pacific, high sea temperature affected negatively the nestling growth and reproductive performance of four auk species through a temperature-dependent mismatch with the copepod availability (Bertram *et al.* 2001).

Feeding success and growth of larval fish are influenced by, among other factors, variations in the onset and peak of plankton production (match–mismatch; Cushing 1990). Along the Norwegian coast, herring spawn between February and March (Dragesund 1970) when the plankton production peaks (Cushing 1990). During years with a temporal mismatch between fishes and their prey, a reduced feeding success of fish larvae is observed (Fortier *et al.* 1995). In addition, it is proposed that the recruitment–temperature relationship in fish is a proxy of food abundance for the fish during early stages (Sundby 2000). The observed relationship between oceanographic processes and the nestling period duration of puffins thus makes sense, if the latter is a proxy of the
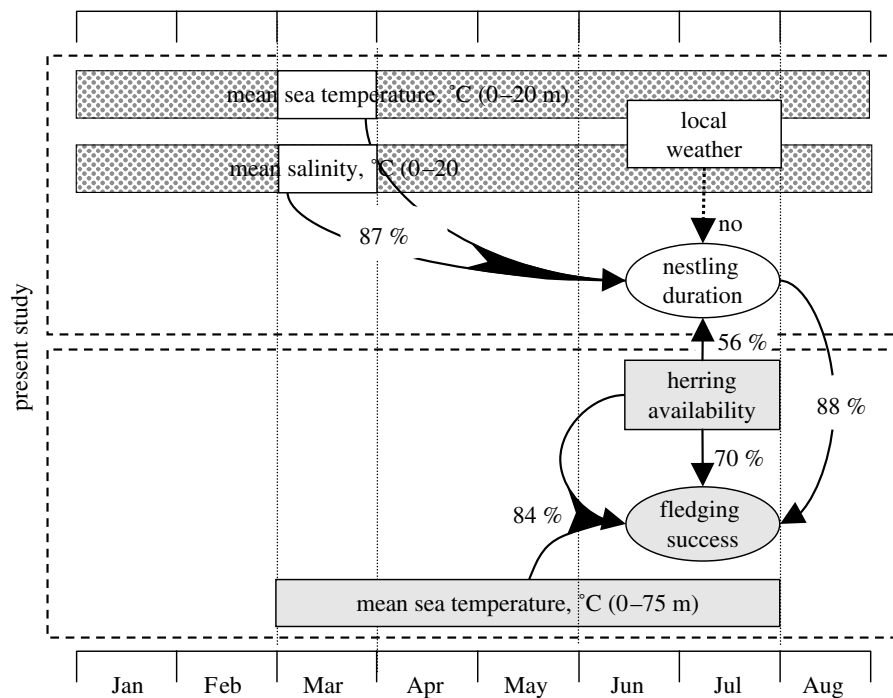
Figure 2. Hypothetical chain of mechanisms linking climate and the reproduction of the Atlantic puffin population at Røst, Norway, based on the results obtained by Durant *et al*. (2003, grey shaded area) and the complementary results of this study. Arrows represent the main relationships documented by the two papers.

food availability to the chick. During years with a plankton–herring mismatch in timing and/or abundance, the herring reaching the foraging areas of the puffins are small and unable to school due to low mobility. For a puffin, this means low accessibility and low quality of prey leading to poor growth of its chick, the duration of the nestling period falling outside its optimum range (38–44 days), and reducing the probability of successful fledging (figure S1 and table 4 in the electronic supplementary material; Durant *et al*. 2003). Identifying the importance of environmental conditions in spring is an interesting addition to previous studies of this population that document the more direct effect of herring abundance on puffin reproduction (Anker-Nilssen 1992; Durant *et al*. 2003).

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