

Trophic interactions under climate fluctuations: the Atlantic puffin as an example

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Co-occurrence in food requirements of offspring and food availability is a key factor determining breeding success. Prey availability is typically dependent on environmental conditions that are different from those influencing the predator's decision regarding whether or not to initiate breeding, and is not always optimal at the peak of reproduction requirements. We investigated this relationship to understand better what determines the fledging success of the Atlantic puffin (*Fratercula arctica*). Colony data from Røst (northern Norway) covering a period of 27 years were analysed with parallel data on sea temperature and the size and abundance of the puffins' main prey (the Norwegian spring-spawning herring, *Clupea harengus*). By fitting statistical models to the fledging success, we found that one effect of climate on this population of Atlantic puffins is indirect and mediated by sea temperature affecting the availability of first-year herring. The best model also demonstrates that the breeding success of the Røst puffins may be quantitatively predicted from the size of first-year herring and sea temperature.

Keywords: climate; seabirds; population dynamics; sea temperature; breeding success; trophic interactions

1. INTRODUCTION

Climate fluctuations are known to affect the ecology of plants and animals, including their distribution (Epstein *et al.* 1998; Thomas & Lennon 1999), behaviour (Post *et al.* 1999; Sparks 1999) and phenology (Beebee 1995; Forchhammer *et al.* 1998; Bradley *et al.* 1999). Among long-lived vertebrates, the influence of environmental variation has generally been most clearly demonstrated through its effects on reproductive success (Post & Stenseth 1999; Kitaysky & Golubova 2000) and early survival (Gaillard *et al.* 1998) with subsequent consequences for the size of the year classes: the cohort effect (e.g. Stenseth *et al.* 2002). To raise young successfully, birds typically adjust their breeding decisions so as ultimately to match food availability (Lack 1968). For seabirds, such as the Atlantic puffin (*Fratercula arctica*), the timing and quantity of the prey arriving in the foraging area is of utmost importance. An incorrect estimation of food resources may lead to the death of the chicks and a failure of one year's reproduction, explaining why seabird populations are closely linked to oceanographic features where resources are reliable (Hunt 1990). Although climate certainly plays a part in the ecology of Atlantic puffins (Erikstad *et al.* 1997), the more detailed influence of climate on this process is not well understood. A recent study shows that both the North Atlantic Oscillation (NAO) (Hurrell 1995) and summer temperature affect the population dynamics of the northern fulmar (*Fulmarus glacialis*) (see Thompson & Ollason 2001). Here, we develop this suggestion further by adding a food-population component and using the Atlantic puffin as an example system.

The population ecology of the Atlantic puffin has been studied since 1964 in the Røst archipelago in northern Norway (e.g. Anker-Nilssen 1992; Anker-Nilssen & Aarvak 2002). The Atlantic puffin is a pursuit-diving pelagic feeder foraging distantly at sea through the water column to a depth of 75 m (Burger & Simpson 1986; Anker-Nilssen 1992). The reproduction of Atlantic puffins at Røst depends mainly on one prey species, the first-year Norwegian spring-spawning herring (*Clupea harengus*), drifting northwards with the Norwegian coastal current from the spawning areas in southwestern Norway (Anker-Nilssen 1992; Anker-Nilssen *et al.* 1997). The Norwegian spring-spawning herring spawns at various locations along the Norwegian coast from late February to late March (figure 1). After hatching in early April, the larvae drift northwards with the coastal current, and the majority of those that survive end up in the Barents Sea (Dragesund 1970). In order to reach a good size, the young herring need good feeding conditions during this drift (Houde 1989, 1997). Their growth and survival depend on the availability of zooplankton, which, in turn, depends on the phytoplankton bloom in spring, both of which fluctuate with the climate (Corten 2001). Cold temperatures may lead to both reduced growth and increased mortality, resulting in low abundance and poor quality of young herring reaching the foraging areas of the puffins. Hence climate may influence seabirds such as the Atlantic puffin through its effect on lower trophic levels.

In order to explain this relationship we fitted several environmental descriptors (climate and food-abundance indices) to a demographic parameter—the fledging success. We provide a model showing the effect of the prey abundance in relation to climate signals on a seabird population in northern Norway.

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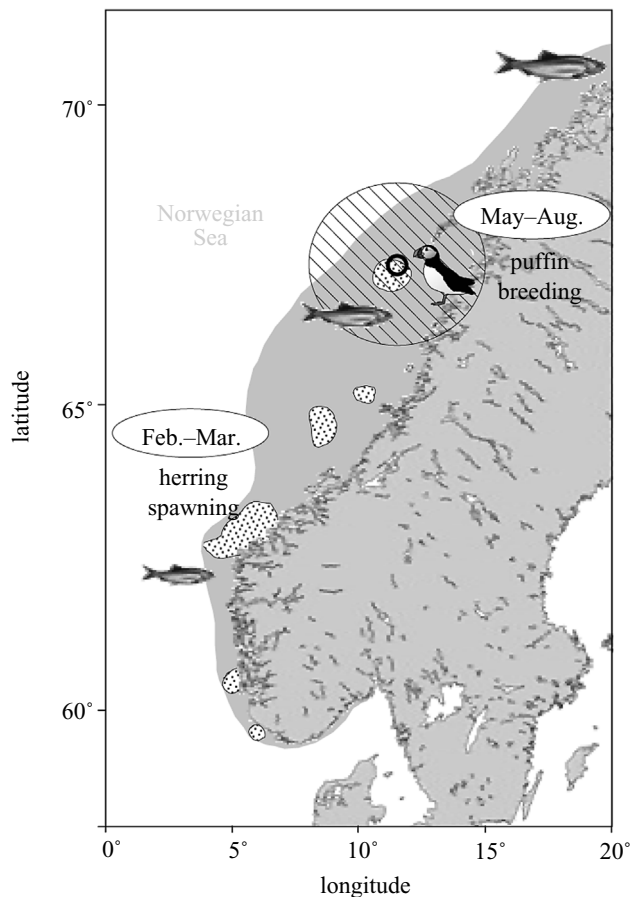


Figure 1. Interaction between Atlantic puffins at Røst and their main prey, the Norwegian spring-spawning herring (Torensen & Østvedt 2000; Sætre *et al.* 2002). The first-year herring drift passively with the Norwegian coastal current (shaded light grey), which runs northwards to the Barents Sea at depths down to 150 m. Further offshore and parallel to it runs the Norwegian Current, a prolongation of the Atlantic Current. The herring eggs hatch in spring, and the larvae smoltify and gather in schools during their drift northwards in summer. Depending on the dates of spawning and hatching, the rate of herring growth and the strength and location of the coastal current, an adequate supply of first-year herring may or may not be available for breeding puffins to ensure good reproductive success. Small black outlined circle, the puffin colony at Røst; larger hatched circle, maximum foraging area of breeding puffins; dotted areas, spawning areas of herring.

2. MATERIAL AND METHODS

(a) Study colony and data collection

The data on Atlantic puffins derive from fieldwork conducted on the island of Herynken (67°26' N, 11°52' E), which is one of the larger bird cliffs in the Røst archipelago at the tip of the Lofoten Islands. Herynken is the breeding site for *ca.* 8% of the approximately 450 000 pairs of puffins breeding in Røst in 2001 (Anker-Nilssen & Øyan 1995; Anker-Nilssen & Aarvak 2002).

In 1980–2001, an annual average of 165 puffin nests (range of 10–304 nests) were inspected regularly (at 1–6 day intervals) during the months of June to August, most frequently during hatching and periods of peak fledging and chick mortality (Anker-Nilssen & Aarvak 2002). Annual fledging success was estimated as the proportion of hatched eggs producing a fledgling. Additional data for 1975–1977 and 1978–1979 were taken

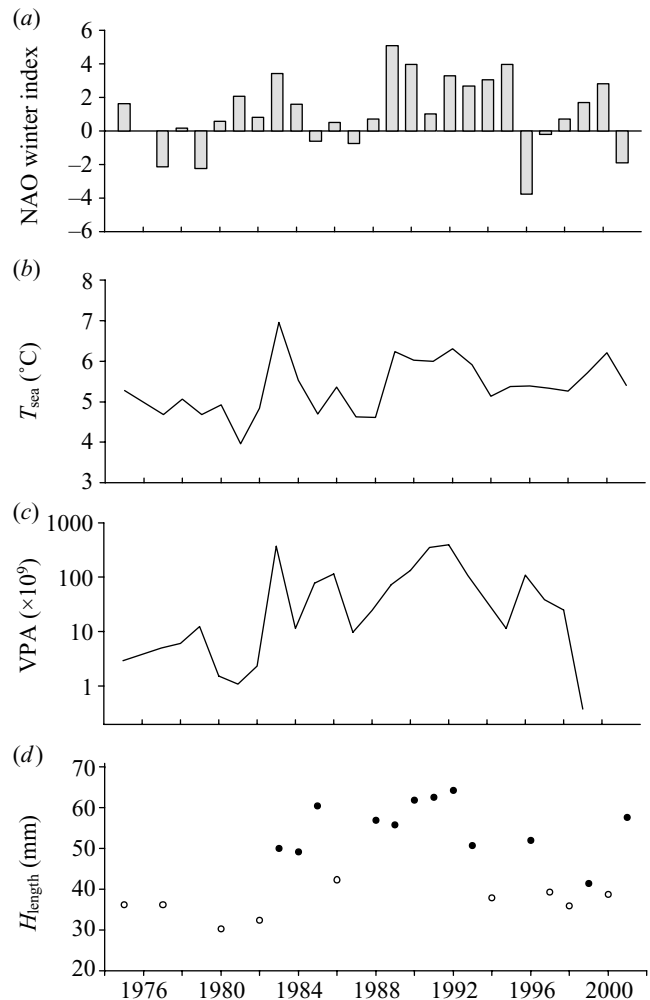


Figure 2. Time-series of the four parameters used in the study: (a) NAO index for December to March (winter index); (b) average sea temperature for the water column to a depth of 75 m during the period from March to July (T_{sea}); (c) estimate of the annual abundance of first-year herring at metamorphosis in mid-summer using a VPA; and (d) average length of herring in the puffin diet on 1 July (H_{length} ; open circles correspond to a fledging success of less than 2%).

from Lid (1981) and Tschanz (1979), respectively. Throughout the chick period, an annual average of 114 food loads (range of 6–272 loads) intended for chicks were collected regularly from adults caught in mist-nets erected in the colony. All individual prey in each load were identified to species level and their body lengths were measured to the nearest 1 mm. No dietary information was collected in 1975–1978, 1987 and 1995, and the samples from 1981 contained no herring. Further details on field methods and annual sample sizes can be found in Anker-Nilssen & Aarvak (2002) and references therein.

(b) Environmental descriptors

The NAO index is an integrated measure that reflects several climatic variables such as precipitation, wind speed and temperature over a large part of the Northern Hemisphere (Hurrell 1995; Wilby *et al.* 1997). Data on the winter NAO (December to March; figure 2a) were obtained from the Web site of James W. Hurrell of the National Centre for Atmospheric Research (<http://www.cgd.ucar.edu/~jhurrell/nao.html#winter>).

Table 1. Results of fitting a logistic equation to the variation in fledging success of Atlantic puffins at Røst, northern Norway. (The fitted equation was $y = \exp(G)/(1 + \exp(G))$ with $G = a + bx$ and x being one parameter; $p\chi^2$ is the probability obtained by ANOVA on the GLM procedure (Venables & Ripley 1999).)

parameters	d.f.	p	$F_{1,d.f.}$	r^2	$p\chi^2_{d.f.}$
food abundance (VPA)	22	0.001	24.7714	0.53	0.001
food quality (H_{length})	19	< 0.0001	43.9648	0.70	0.001
sea temperature (T_{sea})	24	0.0001	21.3952	0.47	0.005
NAO winter index	24	0.0869	3.1861	0.11	0.197

Data on sea temperature were based on continuous measurements collected in the Norwegian coastal current near Skrova (68°02' N, 14°06' E), 140 km northeast of the Røst archipelago (Aure & Østensen 1993; G. Ottersen, personal communication). From these data, we calculated, for each year, an average sea temperature (T_{sea} ; figure 2b) for the water column to a depth of 75 m (the maximum diving depth recorded for Atlantic puffins; Burger & Simpson 1986) during the period from March to July. This period was chosen because it coincides with the first period of growth for young herring, during which they drift with the Norwegian coastal current from their hatching areas to the foraging areas of chick-feeding puffins at Røst.

As an estimate of the annual abundance of the first-year herring at metamorphosis in mid-summer (i.e. at the time when herring start schooling and the Røst puffins capture and feed them to their chicks), we used the results of a virtual population analysis (VPA) (figure 2c; see Lassen & Medley (2001) and references therein for methods) for Norwegian spring-spawning herring (1907–2001). The VPA estimates the population of first-year herring by back calculation using long-term fisheries population data collected for older age classes (Toreisen & Østvedt 2000; ICES 2002) and the observed and predicted mortalities (natural and fisheries-induced) for the different age classes.

(c) Data analyses

For each year with available data ($n = 21$), the average length of herring in the puffin diet on 1 July (H_{length}) was calculated by linear regression (figure 2d; Anker-Nilssen & Aarvak 2002).

We employed generalized linear models (GLM) with binomial distribution to estimate the fledging success of the Atlantic puffins with different parameters and associations of these parameters, using the function GLM in the statistical package S-PLUS (Venables & Ripley 1999). Each fit was assessed by analyses of variance (ANOVA) to examine the validity of the model. The best model was determined using the model-selection criterion Mallow's C_p (Venables & Ripley 1999). The C_p statistic is used to compare models that are not nested. A small C_p corresponds to a better model in the sense of a smaller residual deviance relative to the number of parameters that are estimated in fitting the model.

To check for nonlinearity, we replaced the linear variable with the b-spline of the variable with one internal knot (Venables & Ripley 1999). We also checked for non-additivity. The logistic equation $y = \exp(G)/(1 + \exp(G))$, with $G = a + bx$, was then fitted to data on fledging success (y) with x being various explanatory variables (see § 3).

3. RESULTS

The fledging success of Atlantic puffins at Røst is significantly related to climate via the temperature (T_{sea}) of the explored water column (table 1). It is also related to

both quantity (VPA) and quality (H_{length}) of available first-year herring (table 1; figure 3c). However, no significant relationship was found with the NAO index. When fitting the logistic equation with one factor alone, each of the factors considered explains by itself more than 45% of the observed variation. However, the best model selected by the Mallow's C_p criterion, explaining 84% of the variation, includes only T_{sea} and H_{length} (figure 3a,b). No improvement in the model was found by replacing the linear variable by the b-spline. No improvement in the model was found by adding the NAO winter index, the effect of which was probably incorporated through T_{sea} , as the two parameters were highly correlated (table 2).

4. DISCUSSION

We have demonstrated that both sea temperature and prey quality play a major part in the breeding success of Atlantic puffins. Herring size and sea temperature (the two parameters entering our model) have clear biological or physical meaning, and their values have been measured experimentally. The effect of the abundance of Norwegian spring-spawning herring on the Atlantic puffin in northern Norway is well known (e.g. Anker-Nilssen 1992; Anker-Nilssen *et al.* 1997; Sætre *et al.* 2002), but has never before been quantified in relation to climate signals as we have done in this study. The chick growth, and consequently the breeding success, is highly dependent on the food supply (Øyan & Anker-Nilssen 1996; Cook & Hamer 1997), which in this case predominantly consists of first-year herring (Anker-Nilssen & Aarvak 2002). In our model (figure 3a), there is one clear outlier in 1999. The high success observed in that year, when there were few herring, was most probably caused by an extraordinarily good and well-timed (i.e. matched) availability of young sandeel (*Ammodytes marinus*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) during the chick period (Anker-Nilssen & Aarvak 2002).

The breeding success of the Atlantic puffin in Røst may be a rather simple on-off system: the herring is—or is not—available for the puffin chick. In this context, a discrepancy between food availability and chick requirement may be driven by the match or mismatch between herring and plankton production, as described by Cushing (1990), an idea first developed by Hjort (1914) (see also Stenseth & Mysterud 2002; Stenseth *et al.* 2002). This hypothesis stated that if recruitment–production at a given trophic level matches food availability, effective recruitment will be profound. If there is a mismatch between food requirement and food availability (in time or space), effective recruitment will be low. In other words, when herring hatching coincides with the plankton production,

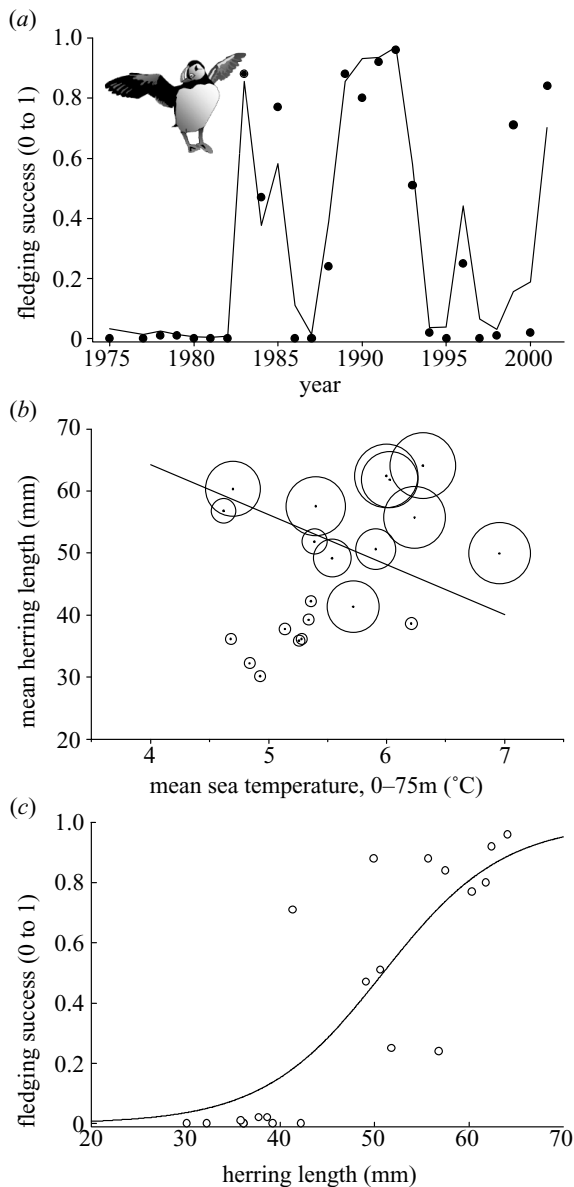


Figure 3. Relationship between environmental parameters and the fledging success (proportion of chicks surviving to fledging) of Atlantic puffins at Røst, Norway. (a) Time-series of observed fledging success (filled circles) and model prediction (line). The fitted GLM equation model is: estimated fledging success = $\exp(G)/(1 + \exp(G))$ with $G = a + bx_1 + cx_2$; a , intercept; x_1 , average sea temperature in °C for the water column to a depth of 75 m during the period from March to July (T_{sea}); and x_2 , mean herring length in mm in the chick diet on 1 July (H_{length}), where $a = -18.0167$, $b = 1.5036$ and $c = 0.1869$ ($F_{2,18} = 46.5692$, $p < 0.0001$, $r^2 = 0.84$). (b) Length of the herring in the chick diet (H_{length}) expressed as a function of the sea temperature (T_{sea}). The size of the open circles indicates the fledging success. The line is the 50% fledging success estimated using the GLM equation model. (c) Relationship between mean length of first-year herring and the fledging success (proportion of chicks surviving to fledging) of Atlantic puffins at Røst, Norway. The fitted logistic equation (line) is: estimated fledging success = $\exp(G)/(1 + \exp(G))$ with $G = a + bx_1$; a , intercept; and x_1 , mean herring length in mm in the chick diet on 1 July, where $a = -7.9886$ and $b = 0.1570$ ($F_{1,19} = 43.9648$, $p < 0.0001$, $r^2 = 0.70$).

i.e. the peak of zooplankton (copepod) biomass, which again is tuned to the phytoplankton bloom, there will be abundant food for fish larvae. In such cases, the growth and survival of young herring will be good and lead to numerous large and schooling herring arriving in the Røst area. However, the onset and peak of the plankton production in the northeast Atlantic in spring can vary from year to year by as much as six weeks (Cushing 1990). This variability may create a phenological mismatch between the hatching of herring eggs and the availability of zooplankton, resulting in depressed growth and survival of larval herring, leading to fewer, smaller and more dispersed herring being found around Røst in the chick period for the Atlantic puffins. Such a mismatch between food requirement and prey availability would lead to poor breeding success for the puffin population.

However, because the Atlantic puffin is at the upper end of the food web, the relationship with its prey appears to be more complex than the simple on-off system originally described by the match-mismatch hypothesis. Indeed, our results indicate that herring quality (H_{length}) is even more important than herring abundance for breeding success (table 1). This may be explained by the fact that the VPA estimates for first-year herring are back calculated in a model combining fisheries statistics, tagging statistics and acoustic measurements of mature herring, as well as indexed mortality parameters for larval herring. All of these input variables are based on data collected over large areas in the Norwegian and Barents Seas at very different times of year (Toresen & Østvedt 2000; ICES 2002; I. Røttingen, personal communication). Consequently, when used as an abundance measurement of first-year herring off Røst when puffins feed their young, the VPA estimates are expected to be biased by a number of factors, the most important probably being the interannual variation in drift pattern and survival of young herring between Røst and their nursery areas in the Barents Sea. By contrast, as the herring was sampled by the puffins, H_{length} was measured exactly when and where the interaction between puffins and herring takes place. In addition, because of the puffins' foraging behaviour (Axelsen *et al.* 2001), the H_{length} parameter very probably integrates both the quality and the availability of herring. This highlights the fact that, in addition to a temporal matching between herring arrival at Røst and chick rearing, there is also a food-quality factor to take into account. A match of production between herring and plankton does not necessarily imply that the food supply for the puffin chicks will not be restricted. For example, a change of sea temperature may strongly affect the development of the fish eggs (Blaxter & Hempel 1963; Hempel & Hempel 1968; Taylor 1971; Alderdice & Hourston 1985) and larvae (Sissenwine *et al.* 1984; Anthony & Fogarty 1985; Cushing 1990). Even without an expected increase of herring mortality in cold years, a slower herring growth will result in a mismatch between the chick requirement and the food availability. For example, below an average herring length of 40 mm in the chick diet on 1 July ($H_{\text{length}} < 40$ mm; figure 3b) fledging was always unsuccessful, suggesting a threshold in puffin reproduction linked to herring development. Consequently, the local conditions experienced by the young herring drifting northwards may highly influence the food supply for the

Table 2. Intercorrelations (Pearson's product moment correlation) between environmental parameters.

	VPA	H_{length}	T_{sea}	NAO
VPA	—	$r_{17} = 0.636$	$r_{22} = 0.727$	n.s.
H_{length}	$p < 0.05$	—	n.s.	n.s.
T_{sea}	$p < 0.001$	$p = 0.086$	—	$r_{24} = 0.541$
NAO	$p = 0.177$	$p = 0.523$	$p < 0.01$	—

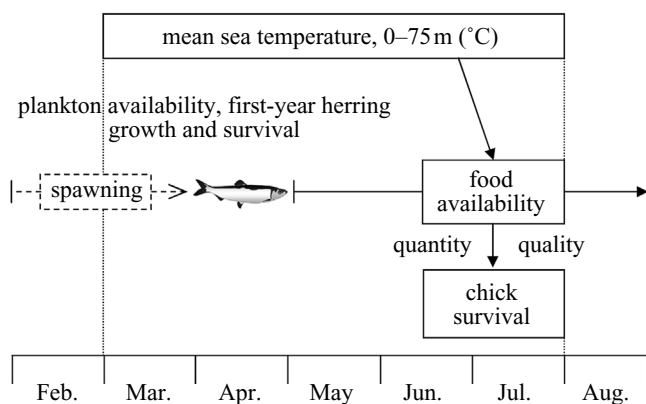


Figure 4. Hypothetical chain of mechanisms linking climate and the reproduction of the Atlantic puffin population at Røst. The movements of different water masses (Norwegian coastal current and Atlantic inflow) influence the water temperature, which strongly controls plankton abundance, which in turn influences the growth and survival of first-year herring (March to July). In years of low sea temperature, reduced food availability during the chick-rearing period of the Atlantic puffins (June to August) reduces chick survival.

puffins and, consequently, their breeding success. Indeed, our results show a strong positive relationship between the sea temperature in the Norwegian coastal current (as reflected by T_{sea}) and the breeding success of Atlantic puffins at Røst.

Figure 4 summarizes how climate may influence the performance of the Atlantic puffins through herring availability. Climate variation enters into the chain through its influence on sea temperature. While winter NAO index explains 28% of the fledging success in the northern fulmar (*F. glacialis*) (Thompson & Ollason 2001), it did not enter into our model. However, the NAO index is probably a very rough signal of changes in oceanographic conditions in the Norwegian Sea. On the scale of several months, the variations in subsurface sea temperatures in this region are largely the direct consequences of long-term fluctuations in the formation of cold water masses in the Greenland Sea many years earlier (e.g. Beverton 1993). The NAO index will also reflect this variation, but, being based on differences in atmospheric pressure, it is likely to be more affected by short-term stochastic variations in the formation of large weather systems in the North Atlantic when compared to sea temperature. Thus, for many ecosystem processes in marine environments, sea temperature is probably a better climate signal than the NAO index.

The effect of sea temperature (climate change) is expected to be most profound early in the season through its effects on lower trophic levels, which in turn influence

the prey production and consequently seabird reproduction and population dynamics. However, more work is required to examine in further detail how climate affects this important chain of trophic interactions. To undertake such a task, our results highlight the need for *in situ* measurements of the variation in arrival time and abundance of first-year herring in the foraging areas of the Atlantic puffins, and to incorporate into the analyses parallel data on the variation in timing and magnitude of the plankton blooms.

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