



Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions

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ABSTRACT: An emerging consequence of global climate change is its potential effect on the timing of seasonal biological events. Analysis of long-term datasets reveals a high degree of plasticity in the nature of phenological responses both within and among species, and understanding these differences is central to understanding the mechanisms and implications of climate-related change. We investigated factors influencing timing of breeding (median laying date) in a colonial nesting seabird, the common guillemot *Uria aalge*, over 23 breeding seasons between 1973 and 2008. There was a trend for earlier laying over this period, and earlier laying was associated with higher average breeding success. Multiple regression models (with de-trended explanatory variables to control for linear trends over time) indicate that the timing of breeding is positively correlated with a wide-scale climatic driver, the winter North Atlantic Oscillation (WNAO), and negatively correlated with population size: guillemots lay later in years with high WNAO indices and earlier in years with larger populations. Responses to environmental conditions are probably related to indirect effects on timing or abundance of food availability, direct effects of weather or both. The mechanism(s) leading to a possible relationship between laying date and population size are less clear. They may be related to Allee-type effects associated with social stimulation, improved foraging efficiency or a density-dependent increase in breeding site quality. Given the correlative nature of these results, we are cautious about the role of non-climatic (intrinsic) factors, but we cannot exclude that they play a role alongside climatic (extrinsic) factors in influencing reproductive phenology.

KEY WORDS: Phenology · Climate change · Allee effect · Coloniality · NAO · Density dependence

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INTRODUCTION

An emergent characteristic of organisms living in seasonal environments is a shift in the timing of life-history events related to global climate change (Walther et al. 2002). For instance, many animals have altered their timing of reproduction in response to changes in the timing of peak food availability, which is linked with environmental change (Charmantier et al. 2008). The consequences and limits of this phenotypic plasticity are not fully understood, and current research indicates that responses to global climate change are highly variable both within and among

taxa (Visser & Both 2005). The reasons for this variability are not clear, but it is probably linked to spatial variation in environmental change, different life-history characteristics among taxa or other non-climate related factors that influence phenology. An important goal is to understand why this variation exists, but to date few studies have investigated the combined influence of climate change with other non-climate related effects on phenology.

For social or colonial animals, the presence of conspecifics can directly affect various important life-history tactics. Although the mechanisms are complex, key benefits of breeding in large groups include

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improved anti-predator strategies, increased reproductive facilitation, greater chance of finding a mate or improved foraging efficiency via information transfer (Courchamp et al. 2008). Together these processes can lead to a positive relationship between population growth rate and population size, collectively termed positive density dependence, or Allee effects (Courchamp et al. 2008). Although Allee effects specifically relate to effects on demographic parameters, there is also evidence that population size may have implications for other important processes such as the timing of reproduction. For example, Coulson & White (1960) found that timing of egg-laying in colonial breeding black-legged kittiwakes *Rissa tridactyla* was related to local nesting density, while controlling for the potentially confounding effects of both environmental conditions and age. Despite this, the role of intrinsic factors influencing timing of breeding remains unclear.

Here we analysed long-term data from a colonial nesting seabird, the common guillemot *Uria aalge* (hereafter guillemot), to determine the factors influencing the timing of reproduction. We simultaneously assessed whether guillemot breeding phenology is influenced by a number of environmental covariates and investigated the relationship with annual population estimates. We also investigated whether the onset of breeding is related to reproductive performance. Guillemots breed in very close proximity (i.e. at very high densities) and therefore population size and population density are likely to be closely related. We therefore investigated whether any changes in population size are related to changes in breeding density during the period of this long-term study. This is important because previous work indicates that breeding density rather than population size may play a role in altering timing of breeding (Coulson & White 1960, Coulson 2002). Understanding phenological responses to environmental factors has been the subject of much research, but it is not clear whether the effect of density-dependent factors can be excluded.

MATERIALS AND METHODS

Study site and data collection. Observations were conducted at 3 guillemot sub-colonies on Skomer Island (51° 40' N, 05° 15' W), Wales, in 23 breeding seasons between 1973 and 2008. Date of first egg laid and breeding successes were estimated by checking sites almost daily throughout the breeding period using binoculars or a telescope (Birkhead & Nettleship 1980, Hatchwell 1991a). Data on the median lay date of the 1-egg clutches laid by guillemots were collected in all 23 years of observation. Breeding success, measured as chicks fledged per breeding pair, was recorded in 17

breeding seasons during the same period. The number of breeding attempts that were followed varied during the study period (mean = 188 ± 146 SD, $n = 23$; range: 42 to 574). The whole island guillemot population (including breeders, failed breeders and immatures) was counted annually in the first half of June using standard methodologies (Hatchwell & Birkhead 1991).

Photographic records of 9 guillemot sub-colonies on Skomer (specifically, Amos sub-colonies A, B, C and D and Bull Hole sub-colonies B, C, D, E and F) were used to obtain an index of breeding density for 5 years: 1973, 1984, 1991, 1995 and 2005, spread across the study period. The location of each breeding bird was marked on photographs, and a density index was calculated as the mean number of birds within 1 bird length of all breeding individuals in each sub-colony.

Explanatory covariates. We considered 2 candidate environmental variables; winter North Atlantic Oscillation Index (WNAO; www.cgd.ucar.edu/cas/jhurrell/indices.html) and 4 major oil pollution incidents that released large quantities of crude oil into the marine environment in the wintering grounds of Skomer guillemots ('Aegean Sea', December 1992, 74 000 tonnes, La Coruña, Spain; 'Sea Empress', February 1996, 72 000 tonnes, Pembrokeshire, Wales; 'Erika', December 1999, 10 000 tonnes, Brittany, France; 'Prestige', November 2002, 63 000 tonnes, Galicia, Spain).

Guillemots feed primarily on lipid-rich shoaling fish such as sprat *Sprattus sprattus* and sandeel *Ammodytes* spp., as well as a range of different clupeid species (Hatchwell 1991b). WNAO is known to influence recruitment and timing of fish availability (Ottersen et al. 2001, Attrill & Power 2002) via changes in a suite of environmental conditions such as temperature, salinity, oxygen, turbulence and advection (Stige et al. 2006). Alternatively, WNAO may have direct effects leading to differences in foraging conditions (Finney et al. 1999). Because WNAO may influence guillemots directly via conditions in the current year or via longer-term effects on the prey base, we modelled contemporaneous WNAO as well as WNAO lagged by 1 yr. Previous studies have found variable responses of seabird reproductive phenology to NAO (Durant et al. 2004, Frederiksen et al. 2004); therefore, it was unclear whether WNAO would have positive or negative influences on lay date. The 4 major oil pollution events have been found to increase adult mortality, either because of direct effects or because of effects on the prey base (Votier et al. 2005). Moreover, reduced adult survival was associated with a concomitant increase in juvenile recruitment probability, with young birds presumably buffering adult losses (Votier et al. 2008). Therefore, major oil spills may lead to later laying because of negative effects in adult breeders or because of an increase in inexperienced breeders in the colony.

WNAO was modelled as a continuous explanatory variable, and oil pollution was modelled as a 2-level factor (i.e. whether there was an oil spill the previous winter or not). We also considered the possibility of using sea surface temperature (SST), but previous work has shown that common guillemots do not adjust timing of breeding in response to local-scale SST (Frederiksen et al. 2004). For this reason, and to reduce the number of explanatory variables given the number of years studied, we did not include SST in our regression models.

To test for possible intrinsic effects, we modelled lay date as a function of the Skomer guillemot population estimate, with a natural log (ln) transformation to correct for the fact that count data has the variance equal to the mean (i.e. the data are Poisson distributed). To determine whether the total Skomer guillemot population is related to breeding density, we modelled this as a function of breeding density measured at 9 sub-colonies. The mechanisms behind any possible density-dependent effects are likely to be linked with the presence of conspecifics, so we only modelled the current estimate of breeding density rather than consider lagged effects. Previous studies have found evidence that social stimulation from an increased number of conspecifics can facilitate earlier onset of breeding (Coulson 2002), so we *a priori* predicted that, if laying date is related to breeding density, the effect will be positive. Although population size may have negative as well as positive effects on demographic parameters (Greene & Stamps 2001, Oro et al. 2006), because of the highly social nature of guillemot colonies, we considered only the positive effects of population size.

Statistical analysis. We used multiple regression models to investigate factors influencing breeding phenology. Models were selected using Akaike's Information Criterion, corrected for small sample size (AICc; Burnham & Anderson 2002). The most parsimonious model was selected on the basis of the lowest AICc value, and AICc weights provide weight of evidence for the preferred model. Strong temporal trends in the dataset (see Figs. 1 & 4) mean that explanatory variables may be confounded by some other unmeasured variables that also co-vary with time. To control for these effects, we de-trended the response and explanatory variables by taking the Studentised residuals of their relationship with year and used these in our analysis. After removing the variation due to a linear trend with year, we found no co-linearity among explanatory variables. To reduce the effects of annual variation in the number of breeding attempts monitored, regression models were weighted by the square-root of the sample size. To reduce the number of parameters fitted, we included only 2-way interactions (we had no *a priori* reason to fit higher-order interactions).

To determine whether timing of breeding may have consequences for fitness, we modelled breeding success as a function of lay date using least square regressions, weighted by the square-root of the sample size.

We used a generalised linear mixed model (GLMM) to determine whether our measure of breeding density increased in relation to changes in the overall Skomer guillemot population. Mean breeding density (log transformed to conform to assumptions of homoscedasticity) was the dependent variable, population size a 5-level fixed factor and sub-colony included as a random factor to account for repeat observations over time. All analyses were conducted using R version 7.1 (R Development Core Team 2008).

RESULTS

The median lay date of guillemots across years did not differ significantly from a normal distribution (Shapiro-Wilk $W = 0.941$, $p = 0.188$) and became significantly earlier from 1973 to 2008 ($F_{1,21} = 5.196$, $R^2 = 0.198$, $p = 0.03$; slope $[\pm \text{SE}] = -0.172 [\pm 0.075]$; Fig. 1a). The most parsimonious model (AICc weight = 0.307) describing variation in median lay date included the additive effect of (ln) population size and lagged WNAO (Table 1) and explained 34% of the variance in lay date. After controlling for a linear trend across years, timing of breeding was positively related to WNAO with a 1 yr lag (Table 2, Fig. 1b), and was significantly earlier in years with high breeding density (Table 2, Fig. 1c). In addition, mean breeding success (which did not differ significantly from a normal distribution; Shapiro-Wilk $W = 0.934$, $p = 0.230$) was negatively correlated with laying date ($F_{1,16} = 4.53$, $R^2 = 0.221$, $p = 0.05$, slope = $-0.011 [\pm 0.005]$; Fig. 2), i.e. years of early onset of breeding were associated with higher breeding success.

Mean breeding density increased significantly as a function of the Skomer population size (GLMM: $t = 5.119$, $df = 3$, $p = 0.014$, slope = $0.396 [\pm 0.077]$; Fig. 3), indicating an increase in breeding density concomitant with increasing population size during our study.

DISCUSSION

We have shown that timing of egg-laying in a colonial seabird is positively correlated with a wide-scale climatic driver (WNAO) and negatively correlated with population size, while controlling for an effect of year (Table 1, Fig. 1). Although many studies have demonstrated phenological shifts in response to environmental cues (Visser & Both 2005), our results indicate that for colonial and social breeders, timing of breeding

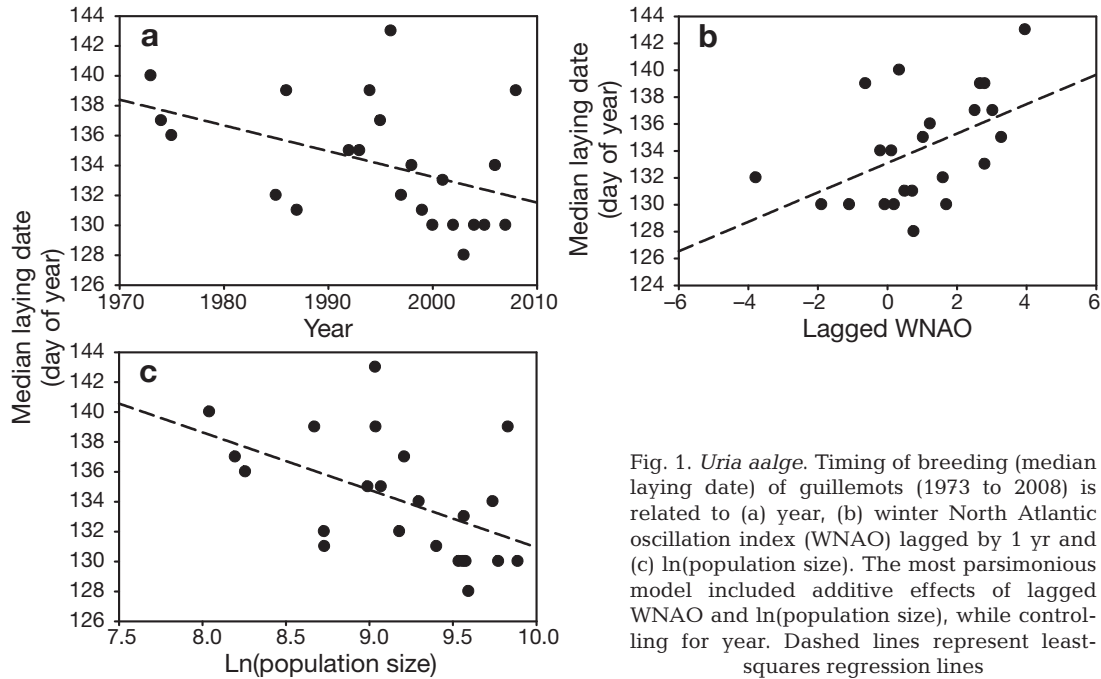


Fig. 1. *Uria aalge*. Timing of breeding (median laying date) of guillemots (1973 to 2008) is related to (a) year, (b) winter North Atlantic oscillation index (WNAO) lagged by 1 yr and (c) ln(population size). The most parsimonious model included additive effects of lagged WNAO and ln(population size), while controlling for year. Dashed lines represent least-squares regression lines

Table 1. *Uria aalge*. Model selection to estimate factors influencing timing of breeding in guillemots. Only the top 10 candidate models are shown, and the best supported model is in **bold**. df: degrees of freedom; LogLik: log likelihood; AICc: Akaike's Information Criteria (corrected); lnpop: natural log of guillemot population estimate on Skomer; WNAO: winter North Atlantic oscillation index; oil: incidence of 4 major oil pollution events

Model	df	LogLik	AICc	ΔAICc	AICc weight
lnpop + lagwnao	4	-27.376	63.895	0.000	0.307
lnpop + lagwnao + oil	5	-26.666	65.333	1.438	0.149
lnpop + wnao + oil	5	-29.655	65.476	1.581	0.139
lnpop + lagwnao + lnbreed × lagwnao	5	-26.744	65.488	1.593	0.138
lnpop	3	-29.788	66.122	2.227	0.101
lnpop + lagwnao + wnao + oil	6	-26.412	67.981	4.087	0.040
lnpop + lagwnao + wnao + oil + lnpop × wnao	7	-24.828	68.322	4.427	0.034
Intercept only	2	-32.145	68.463	4.569	0.031
lnpop + wnao + lagwnao	4	-27.165	68.474	4.580	0.031
lnpop + wnao	4	-29.666	68.512	4.617	0.030

Table 2. *Uria aalge*. Weighted multiple regression models explaining factors influencing variation in median laying date of guillemots on Skomer, Wales (1973 to 2008). The model including all main effects (but excluding interactions) and the model selected on the basis of Akaike's Information Criteria (corrected) (AICc) are presented along with slopes ± 1 SE (p-values); see Table 1 for definitions

	Full model	AICc selected model
Intercept	0.240 ± 0.230 (0.310)	0.775 ± 0.187 (0.684)
lnpop	-0.648 ± 0.222 (0.009)	-0.562 ± 0.207 (0.01)
wnao	0.132 ± 0.208 (0.533)	-
lagwnao	0.532 ± 0.220 (0.026)	0.430 ± 0.199 (0.04)
oil	-0.590 ± 0.534 (0.284)	-

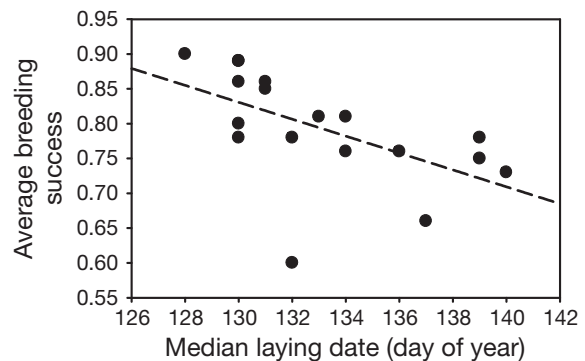


Fig. 2. *Uria aalge*. Average guillemot breeding success (number of chicks fledged per breeding pair) is negatively related to laying date in guillemots. Dashed line represents the least-squares regression line

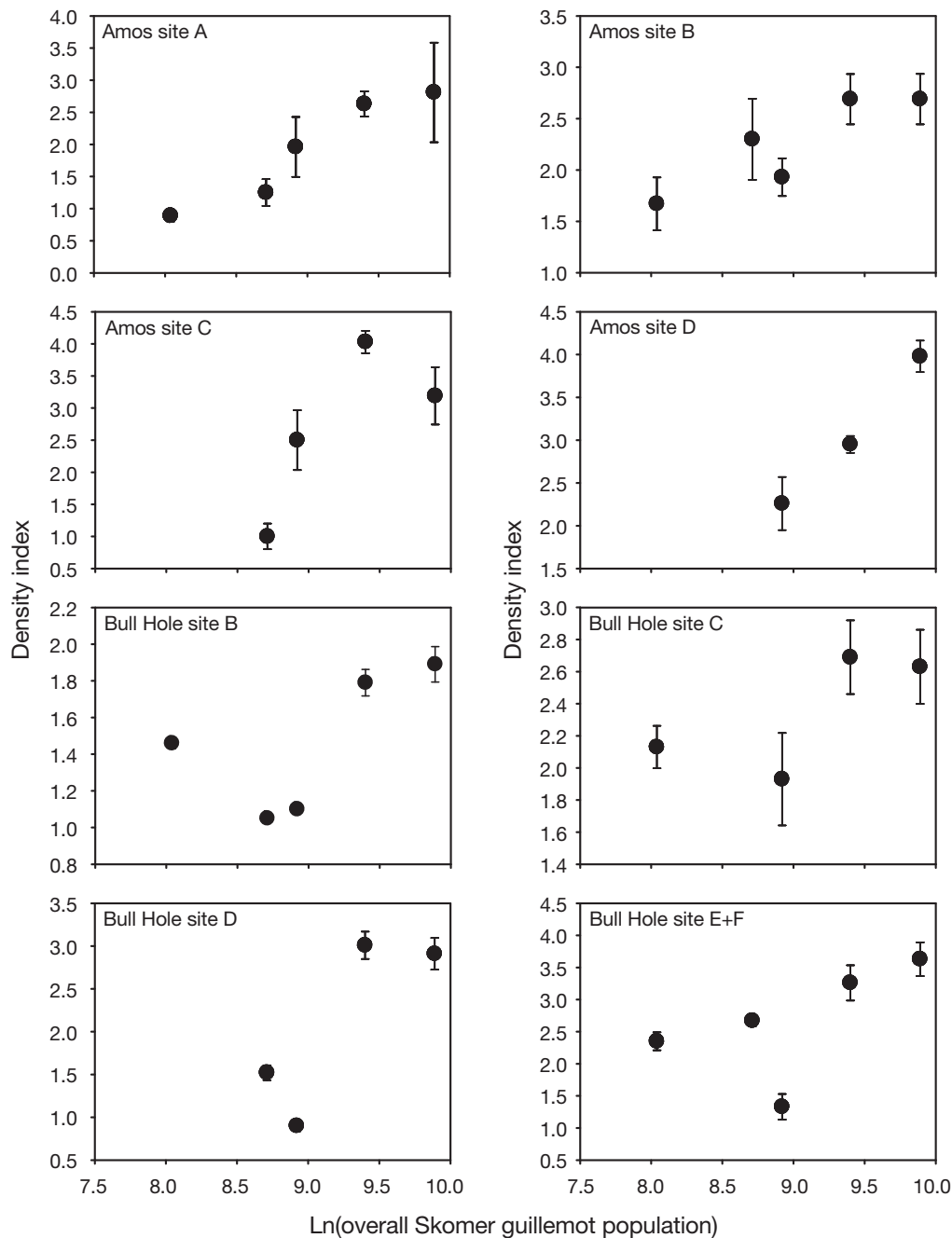


Fig. 3. *Uria aalge*. Mean breeding density ($1 \pm \text{SE}$) of guillemots at 9 sub-colonies on Skomer, Wales (1973, 1984, 1991, 1999, 2005). The density index was calculated as the mean number of birds within 1 bird length of all breeding individuals in each sub-colony. On average, density increased significantly with increasing population size

may be influenced by density-dependent factors. Possible mechanisms and alternative explanations for these findings are discussed below.

The median lay date of our study population varied in response to environmental conditions lagged by 1 yr. The WNAO index is linked to large-scale oceanographic conditions in north-western Europe, which

may affect guillemots either directly by increasing stormy conditions and therefore making foraging more difficult (Finney et al. 1999), indirectly via changes in prey fish abundance and timing (Finney et al. 1999, Ottersen et al. 2001, Attrill & Power 2002) or both. Although the direct effect of poor weather may be carried over from different periods of the annual cycle

(Sorensen et al. 2009), long-term effects from the winter 2 yr ago are unknown. Instead, the significant lagged effect probably reflects effects on the prey base. Therefore, changes in the timing of breeding most likely represent a response to changes in the timing of peak availability of forage fish (Durant et al. 2005). The inverse relationship between laying date and WNAO shown here is the opposite from a number of studies that have found positive relationships between seabird breeding phenology and WNAO in the North Sea (Durant et al. 2004, Frederiksen et al. 2004, Moller et al. 2006, Reed et al. 2006). Conversely, Durant et al. (2004) found that hatching date of Atlantic puffins *Fratercula arctica* in the Norwegian Sea was positively correlated with NAO during 1 climatic regime, although timing of breeding was independent of NAO following a regime shift. Such inter-population variation in the response of seabird reproductive phenology to the NAO are not well understood but probably reflect the complex nature of bottom-up effects of environmental conditions on fish population dynamics, including spatial differences in the effect of NAO on environmental conditions (Hallett et al. 2004, Stige et al. 2006) and non-linear effects of NAO (Durant et al. 2004). Further study of the relationship between the demographics and timing of peak abundance of forage fish at broad spatial scales might reveal more about the way in which different populations of top marine predators respond to environmental change.

To account for the trend for median lay date to become earlier during the course of this study (Fig. 1a), WNAO would have to show a negative trend over this period, but instead it did not change significantly with time ($F_{1,21} = 0.355$, $R^2 = 0.017$, $p = 0.558$, slope $[\pm SE] = -0.023 [\pm 0.039]$; Fig. 4). SST showed a linear increase over the duration of this study (Fig. 4), but was not correlated with lay date ($F_{1,21} = 0.087$, $R^2 = 0.004$, $p = 0.087$, slope $[\pm SE] = -0.059 [\pm 0.201]$). Therefore, some other factor must be influencing the long-term trend for earlier breeding in guillemots.

Early onset of breeding in guillemots was associated with higher population size in the current year (Tables 1 & 2). However, because our data are correlative, they do not necessarily show a causal relationship, and alternative explanations exist. For instance, years of high food availability may coincide with early breeding and an increase in breeder numbers at the colony. Guillemots exhibit delayed maturity and a protracted 2-stage recruitment (Votier et al. 2008), so breeder numbers change slowly over time and are relatively insensitive to annual fluctuations in food availability. However, the pre-breeding component of the population may be able to respond rapidly to environmental change and start breeding at a younger age in

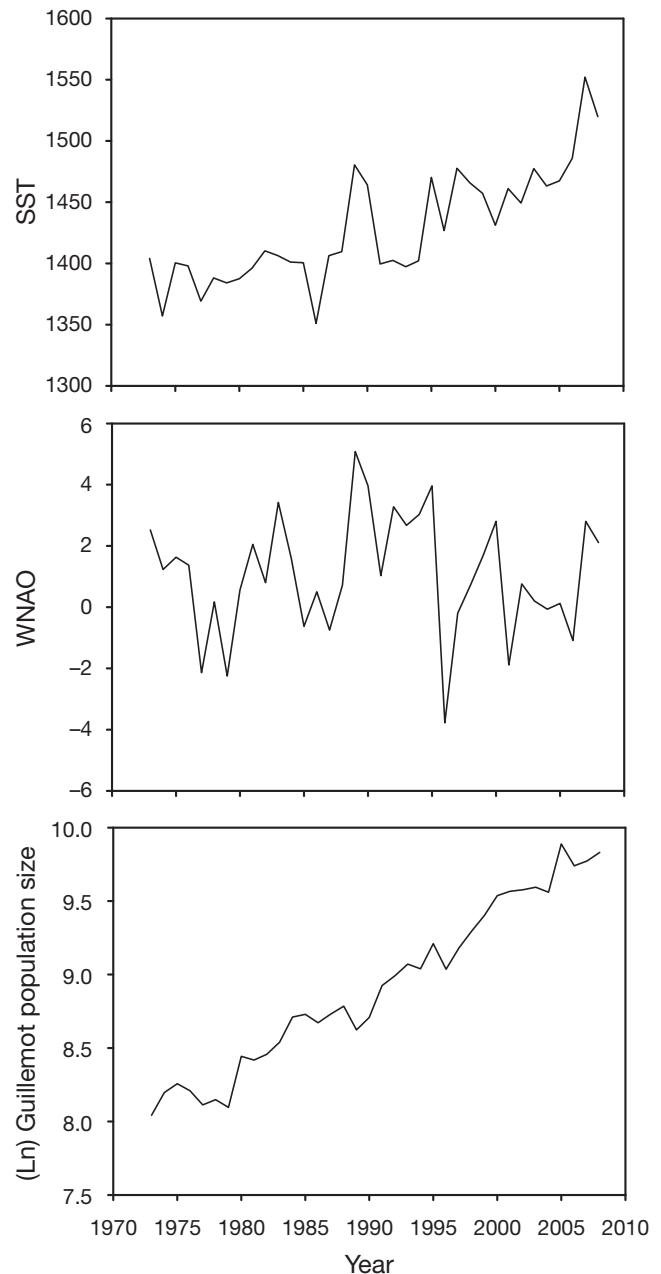


Fig. 4. Variation in explanatory variables used in the analysis (WNAO and population size), as well changes in SST, between 1973 and 2008

good years, and it has been shown that recruitment of this age class is negatively related to population size (Crespin et al. 2006) and is higher following increased oil-related adult mortality (Votier et al. 2005, 2008). On the other hand, young birds tend to lay later than older, more experienced birds (Hatchwell 1991a), and a growing population necessarily includes a number of inexperienced breeders, so increased recruitment of young birds would not necessarily be expected to drive

earlier laying. Furthermore, we found no significant effect of major oil spills on the timing of breeding (Table 2), an effect that would have been predicted under this scenario. An alternative explanation is that the proportion of sexually mature birds that breed each year is sensitive to variation in their social or ecological environment. If late breeders are less likely to breed at higher population sizes, the median lay date would be earlier in years when population size is large. Again, this idea is incompatible with the fact that the mean breeding density, as well as the overall population size, has increased over the study period (Fig. 3). Another potentially confounding factor is the possibility that detection probability of eggs laid early may increase with population size (Tryjanowski & Sparks 2001). Once again this explanation seems improbable. By using median laying date, we reduced the statistical influence of early or late laid eggs, and, given the intensive nature of the long-term study at Skomer, such methodological detection issues are doubtful. Finally, the trend for earlier breeding could be explained by the trend in population size. There is a negative relationship between population size and laying date (Fig. 1c) combined with a positive trend in population size ($F_{1,21} = 859.86$, $R^2 = 0.98$, $p < 0.001$, slope = $0.050 [\pm 0.002]$; Fig. 4), but despite this, we cannot exclude the influence of some other unmeasured factor. In summary, given the large number of possible alternative explanations for our findings, and without direct measures of prey availability, we cannot be certain that population size is causally linked with the timing of breeding in common guillemots.

Despite the uncertainty for a direct influence of density-dependent effect on timing of breeding, it is helpful to consider likely proximate causes of earlier laying in larger populations. Guillemots are present at the colony for several months prior to egg-laying (Birkhead 1978a), providing opportunity for much interaction, and the most plausible influence of increasing population size on phenology is a link with Allee-type density dependence, mediated in 2 possible ways. Firstly, social stimulation by conspecifics could lead to advancement in the timing of reproduction. Darling (1938) hypothesised that social stimulation among colonial-nesting birds could lead to an acceleration and synchronisation in reproduction. While the 'Fraser Darling effect' remains hypothetical, there is some evidence that local density, rather than population size, can influence laying date in black-legged kittiwakes (Coulson & White 1960, Coulson 2002). At Skomer, a significant increase in local breeding density is concomitant with an increase in overall population size on Skomer (Fig. 3). Secondly, increasing numbers of conspecifics may facilitate food location, improving average body condition and therefore leading to earlier

onset of breeding. Colonies may act as information centres to enhance foraging efficiency (Sonerud et al. 2001, Wright et al. 2003) and although this has not been demonstrated at the colony level for seabirds, there is evidence of positive density dependence in foraging success at sea, mediated via local enhancement (Grünbaum & Veit 2003, Silverman et al. 2004). Alternatively, since strong stabilising selection favours synchronous breeding in this species (Reed et al. 2006), which is probably closely linked with social constraints (Birkhead 1978b), other components of social behaviour linked with synchrony may also be important. Finally, the increase in density at Skomer (Fig. 3) would also result in an increase in breeding site quality, because site quality in guillemots is positively related to density through its effect on communal defence against predators (Birkhead 1977, Hatchwell 1991a). Thus, if an earlier onset of egg-laying is linked to population size, this may be via inverse density dependence.

Given the reliance on correlative studies for this type of research, assessing the role of density-dependence on timing of breeding will require a more detailed body of evidence than that currently available to us. Latitudinal studies from a range of colonies with different breeding densities could prove fruitful, as could similar longitudinal studies from other sites as that presented here. As mentioned, there is already evidence that timing of breeding is related to breeding density in the colonial-nesting black-legged kittiwake (Coulson & White 1960, Coulson 2002), and work suggests that chinstrap penguins *Pygoscelis antarctica* nesting in large colonies in the South Shetlands have earlier hatching dates compared to those nesting in small colonies (Barbosa et al. 1997). Conversely, long-term trends in later laying of northern gannets *Morus bassanus* in the eastern Atlantic (Wanless et al. 2008) are associated with increasing population sizes of this species (Mitchell et al. 2004). With so few studies, it is not possible to draw any firm inference, so we urge other researchers conducting similar phenological studies to consider the effects of density dependence to test this further.

It is generally the case that an early onset of avian breeding leads to improved reproductive performance within seasons (Spear & Nur 1994). Guillemots are characterised by a high degree of breeding synchrony, and pairs that breed later than average have lower breeding success than the rest of the population (Birkhead 1977, Hatchwell 1991a, Reed et al. 2006). Thus, there is strong stabilising selection that should limit intra-population variation in timing of breeding (Reed et al. 2006). Here, we found that guillemot breeding success was negatively correlated with median lay date across years (Fig. 2) as well as within years (Birkhead 1977, Hatchwell 1991a). However, we think it

unlikely that this between-year relationship is also mediated by reproductive synchrony, because previous studies have suggested that synchrony operates at the level of the sub-colony, so that timing relative to neighbours is the key determinant of breeding success (Birkhead 1977, Hatchwell 1991a).

To conclude, our results indicate that timing of guillemot laying date is influenced by environmental conditions linked with the NAO, but this does not explain a long-term trend for earlier breeding. This trend may in part be explained by an increase in population size or breeding density, but because our findings are open to multiple interpretations, and given problems with collecting experimental data to test the robustness of these findings, they are equivocal. Nevertheless, we urge other researchers conducting phenological studies to consider the influence of both climate- and non-climate-related factors to better understand the effects of global change.

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