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**Citation for published version:**

Keogan, K, Daunt, F, Wanless, S, Phillips, RA, Alvarez, D, Anker-Nilssen, T, Barrett, RT, Bech, C, Becker, PH, Berglund, P-A, Bouwhuis, S, Burr, ZM, Chastel, O, Christensen-Dalsgaard, S, Descamps, S, Diamond, T, Elliott, K, Erikstad, KE, Harris, M, Hentati-Sundberg, J, Heubeck, M, Kress, SW, Langset, M, Lorensten, S-H, Major, HL, Whalley, H, Mallory, M, Mellor, M, Miles, WTS, Moe, B, Mostello, C, Newell, M, Nisbet, I, Reiertsen, TK, Rock, J, Shannon, P, Varpe, Ø, Lewis, S & Phillimore, AB 2022, 'Variation and correlation in the timing of breeding of North Atlantic seabirds across multiple scales', *Journal of Animal Ecology*, vol. 91, no. 9, pp. 1797-1812. <https://doi.org/10.1111/1365-2656.13758>

**Digital Object Identifier (DOI):**

[10.1111/1365-2656.13758](https://doi.org/10.1111/1365-2656.13758)

**Link:**

[Link to publication record in Edinburgh Research Explorer](#)

**Document Version:**

Peer reviewed version

**Published In:**

*Journal of Animal Ecology*

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# Variation and correlation in the timing of breeding of North Atlantic seabirds across multiple scales

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**Author contributions**

46 The study was conceived by KK, FD, SW, RAP, SL and ABP. KK was responsible for  
47 developing the methods, running analyses and drafting the ms, with support from ABP, SL  
48 and FD. All authors contributed data and/or commented on the ms.

49

## 50 Summary

51 1. Timing of breeding, an important driver of fitness in many populations, is widely studied  
52 in the context of global change, yet despite considerable efforts to identify environmental  
53 drivers of seabird nesting phenology, for most populations we lack evidence of strong  
54 drivers. Here we adopt an alternative approach, examining the degree to which different  
55 populations positively covary in their annual phenology to infer whether phenological  
56 responses to environmental drivers are likely to be (i) shared across species at a range of  
57 spatial scales, (ii) shared across populations of a species, or (iii) idiosyncratic to populations.

58 2. We combined 51 long-term datasets on breeding phenology spanning 50 years from nine  
59 seabird species across 29 North Atlantic sites and examined the extent to which different  
60 populations share early versus late breeding seasons depending on a hierarchy of spatial  
61 scales comprising breeding site, small-scale region, large-scale region and the whole North  
62 Atlantic.

63 3. In about a third of cases we found laying dates of populations of different species sharing  
64 the same breeding site or small-scale breeding region were positively correlated, which is  
65 consistent with the hypothesis that they share phenological responses to the same  
66 environmental conditions. In comparison we found no evidence for positive phenological  
67 covariation among populations across species aggregated at larger spatial scales.

68 4. In general we found little evidence for positive phenological covariation between  
69 populations of a single species, and in many instances the inter-year variation specific to a

70 population was substantial, consistent with each population responding idiosyncratically to  
71 local environmental conditions. Black-legged kittiwake (*Rissa tridactyla*) was the exception,  
72 with populations exhibiting positive covariation in laying dates that decayed with the distance  
73 between breeding sites, suggesting that populations may be responding to a similar driver.  
74 5. Our approach sheds light on the potential factors that may drive phenology in our study  
75 species, thus furthering our understanding of the scales at which different seabirds interact  
76 with interannual variation in their environment. We also identify additional systems and  
77 phenological questions to which our inferential approach could be applied.  
78

79

## 80 Introduction

81 Predicting how organisms will respond to changing climate presents one of the greatest global  
82 challenges for ecologists. Some of the key responses that have been observed are changes in  
83 timing of seasonally recurring events (Parmesan & Yohe, 2003), which are often sensitive to  
84 environmental conditions, most notably temperature (Cohen, Lajeunesse, & Rohr, 2018;  
85 Thackeray et al., 2016). Timing of reproduction in relation to the timing of resource availability  
86 is expected to affect fitness, with mistiming expected to be detrimental (Varpe, 2017; Visser &  
87 Both, 2005). In order to respond to fluctuating environments, an individual may maximise its  
88 fitness if it can adjust timing of breeding to coincide with suitable conditions by responding to  
89 environmental drivers that cue the future arrival of a favourable environment (McNamara,  
90 Barta, Klaassen, & Bauer, 2011). Breeding phenology may be adjusted in response to one or  
91 multiple environmental cues and/or constraints, such as temperature (Chambers, Cullen,  
92 Coutin, & Dann, 2009), photoperiod (Dawson, King, Bentley, & Ball, 2001), wintering  
93 conditions (Dobson, Becker, Arnaud, Bouwhuis, & Charmantier, 2017), or resource  
94 availability, potentially mediated by body condition in the pre-breeding season (Daunt et al.,  
95 2014; Love, Gilchrist, Descamps, Semeniuk, & Bêty, 2010). The extent to which these different  
96 environmental drivers combine or interact to elicit a phenological response may differ between  
97 species and regions, hampering our ability to make general predictions regarding population  
98 responses to environmental change (Cohen et al., 2018; Thackeray, 2016; van de Pol et al.,  
99 2016).

100

101 Determining the conditions that drive phenological responses and the spatiotemporal scales at  
102 which they act requires both long-term data on phenology and fine-scale data on candidate  
103 environmental variables, and often involves comparison of environmental sensitivities across

104 a range of time-windows (van de Pol et al., 2016). While identifying a set of candidate  
105 environmental conditions and spatial scales is relatively straightforward for ectotherms that  
106 respond directly to temperature (Visser & Both, 2005) and species that are rooted/sessile or  
107 have small year-round ranges (Lindestad, Wheat, Nylin, & Gotthard, 2018), species at higher  
108 trophic levels and that are wide-ranging present a much greater challenge. For instance, wide-  
109 ranging species may respond to cues or conditions in the area where they breed (Frederiksen  
110 et al., 2004), at their wintering areas (Dobson et al., 2017; Szostek, Bouwhuis, & Becker, 2015),  
111 or both (Harrison, Blount, Inger, Norris, & Bearhop, 2011).

112

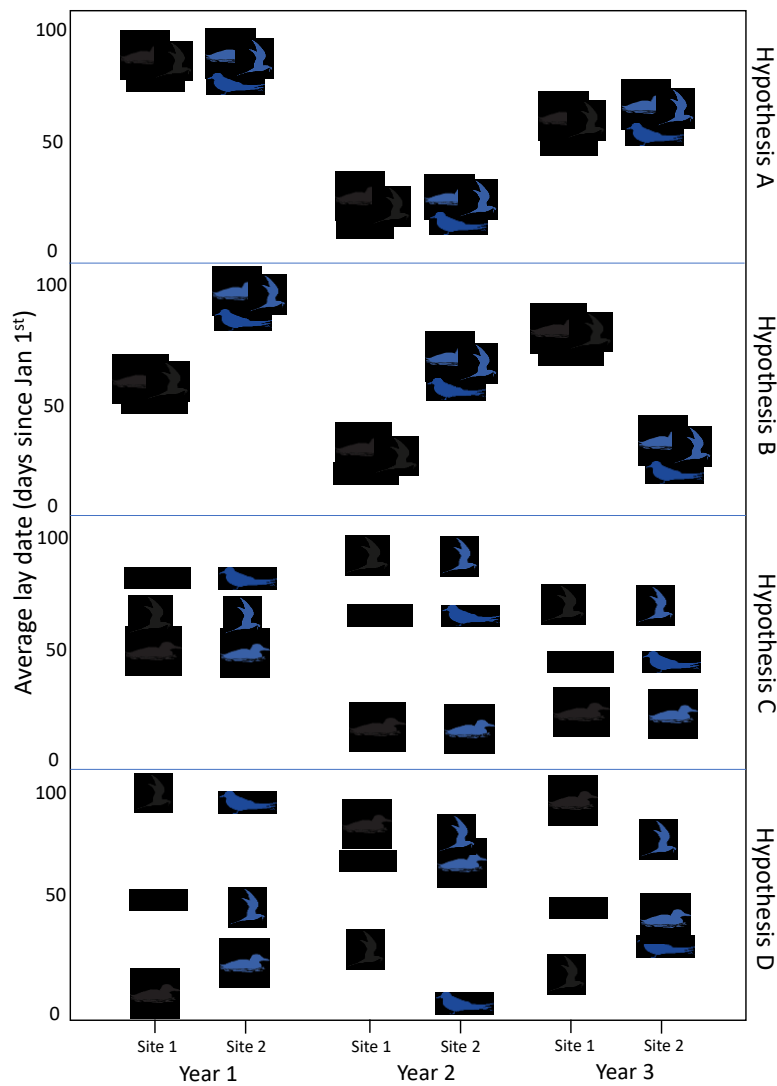
113 Identifying environmental drivers of phenology has proven especially challenging for seabirds.  
114 Globally, seabirds on average show no phenological trend over time or with spring sea surface  
115 temperature (Descamps et al., 2019; Keogan et al., 2018), in stark contrast to the pronounced  
116 phenological responses over time and with respect to temperature in the preceding months  
117 found in extra-tropical terrestrial systems (Thackeray et al. 2012; 2016; Cohen et al. 2018). The  
118 fact that some seabird populations exhibit substantial year to year variation in the timing of  
119 breeding (Burr et al., 2016; Keogan et al., 2018; Youngflesh et al., 2018), is consistent with  
120 populations responding to variation in their environment. Timing of breeding may be  
121 determined by climate or diet-related drivers, immediately prior to breeding or as carry-over  
122 effects from preceding months, either at breeding or winter grounds. However, the nature of  
123 the environmental drivers, when they occur and where they occur remains to be established.  
124 Most seabirds occupy higher trophic levels, and the breeding ranges of many species span large  
125 spatial gradients in environmental conditions. They can forage at great distances from the  
126 breeding site during the breeding season, and have some of the longest migrations known in  
127 the animal kingdom (Egevang et al., 2010). Although many seabird species winter far from  
128 their colonies, many also spend time at the breeding site before egg laying commences, such

129 that conditions at both breeding (Frederiksen et al., 2004; Love et al., 2010) and wintering  
130 grounds (Dobson et al., 2017; Szostek et al., 2015) may affect breeding phenology.

131

132 Identifying the environmental conditions that drive the phenology of each seabird population  
133 is critical because timing of breeding is strongly correlated with productivity, with earlier years  
134 more successful than later years (Durant et al. 2007; Ramirez et al. 2016; Keogan et al, 2020).

135 However, the combination of an extensive set of potential environmental drivers and the short  
136 duration for the average time series (Keogan et al. 2018) makes this identification a huge  
137 challenge. As an alternative, we seek to identify the extent to which different seabird  
138 populations exhibit similar phenological responses to shared environmental drivers, which we  
139 predict should manifest in positively correlated phenological time series. This approach has the  
140 potential to greatly reduce the set of candidate environmental variables (see hypothetical  
141 scenarios and deductions in Figure 1).



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**Figure 1.** Schematic representation of interannual (co)variation in phenology across populations of four seabird species at two sites. Below we represent four hypotheses A-D. A. *Cross-species spatial effect*: A positive correlation in the phenological time series across all populations may arise if populations respond similarly to a shared environmental variable. B. *Cross-species site effect*: A positive correlation across populations of different species at a site (but not between sites) may arise if populations respond similarly to local environmental conditions which are uncorrelated between sites. C. *Species spatial effect*: A positive correlation across sites (but not species) may arise if environmental drivers of phenology are shared across sites, but the nature of the drivers or responses to them are species-specific. D. *Idiosyncratic population effect* Interannual variation in phenology but no correlation across sites or species may arise if each population responds to a different driver or idiosyncratically to the same local driver.



154 In this study, we aimed to identify the extent to which 51 populations (defined as a species  
155 breeding at a particular site) of nine seabird species breeding in the North Atlantic show  
156 positively correlated timing of breeding across years. We test four hypotheses. 1. *Cross-species*  
157 *spatial effect*: Phenology covaries positively across time for populations of all species found in  
158 the same geographic region during breeding or wintering season (defined at three spatial scales  
159 from the entire North Atlantic down to small-scale regions where breeding populations were <  
160 120 km apart). Evidence for this would indicate that species and populations share a  
161 phenological response to a driver or drivers that show correlated interannual change across the  
162 geographic region. 2. *Cross-species site effect*: Phenology covaries positively across time for  
163 populations of different species at a site (but not between sites). Evidence for this would  
164 indicate that these populations are responding similarly to local environmental conditions that  
165 are uncorrelated between sites. 3. *Species spatial effect*: Phenology covaries positively across  
166 all populations of a species in either the North Atlantic or that share a breeding or wintering  
167 region. Evidence for this would indicate that populations of a species share a phenological  
168 response to a driver or drivers that show correlated interannual change across the focal spatial  
169 scale. 4. *Idiosyncratic population effect*: The phenology of a population does not positively  
170 covary with other populations in the same region or of the same species. Evidence for this  
171 would indicate that populations of different species are responding to different drivers or  
172 idiosyncratically to the same local environmental drivers. In *lieu* of identifying the  
173 environmental drivers themselves, we can use estimates of positive correlations between  
174 phenological time series to deduce the likely attributes of environmental drivers and direct  
175 future examination.

176

## 177 Methods

### 178 Data collection

179 We compiled phenological data (annual average breeding times) on nine North Atlantic seabird  
180 species for which multiple populations have been studied (black-legged kittiwake (*Rissa*  
181 *tridactyla*), common tern (*Sterna hirundo*), roseate tern (*Sterna dougallii*), Arctic tern (*Sterna*  
182 *paradisaea*), European shag (*Phalacrocorax aristotelis*), razorbill (*Alca torda*), Atlantic puffin  
183 (*Fratercula arctica*), common guillemot (*Uria aalge*), and Brünnich's guillemot (*Uria*  
184 *lomvia*)). A study population was defined as a species breeding at a particular site. For each  
185 study population, annual data on breeding phenology during the period from 1968 to 2017 were  
186 selected in the following order of preference: median lay date (n = 24 populations); mean lay  
187 date (n = 5); median hatch date (n = 6); mean hatch date (n = 12); first hatch date of the study  
188 population (n = 4), in units of ordinal days. Our rationale for this order of preferences was  
189 threefold. First, we preferred median to mean values as this measure is less sensitive to whether  
190 the distribution of breeding date is normal. Second, we preferred average dates over first dates  
191 as the former will be less sensitive to interannual variation in sample size. Third, lay date is  
192 preferred over hatch date since it includes all study nests whereas hatch dates excludes those  
193 that failed during incubation, which may show bias with respect to timing of breeding. We used  
194 only one measure of phenology for each population, and where only hatch date was available,  
195 we back-calculated lay date using information on the average incubation period (Sources in  
196 Table S1). All time series were a minimum of eight years, although the years did not need to  
197 be consecutive.

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199 In addition to breeding site, we consider three larger spatial-scales: (i) North Atlantic: Includes  
200 all populations. (ii) Large Marine Ecosystem (LME): Populations were assigned to one of  
201 eleven breeding LMEs to assess covariance at a smaller spatial scale (Figure 2a, Table 1). The  
202 wintering LMEs of individuals for each population was determined from available published

203 tracking data. If tracking studies suggested a population may overwinter in several locations,  
204 the area where the highest proportion of birds from a population spent the winter was used to  
205 define that population's wintering ground. Across all populations, eleven potential wintering  
206 grounds were identified in total (Figure 2b, Table 1, see Table S1 for sources). As this was a  
207 population level analysis, we assumed that the individuals in a population shared a wintering  
208 region. We identified wintering region in different ways depending on the tracking data  
209 available for a population. For most populations information came from published papers (cited  
210 in Table S1), which identified the most common locations used overwinter for each species.  
211 For 11 Norwegian and two Scottish breeding populations, we used information from  
212 [seatrack.seapop.no/map/](http://seatrack.seapop.no/map/), which presents wintering distributions from multiple years in kernel  
213 distribution maps. Based on visual inspection of the maps we assigned a wintering distribution  
214 as the location where highest percentage of individuals within a population spent the winter  
215 across all years available. (iii) Small-scale region: comprised of breeding sites that were < 120  
216 km apart. We chose 120 km based on average foraging ranges during the breeding season of  
217 the study species, which are generally markedly less than this value (Thaxter et al., 2012). This  
218 classification allowed us to estimate the average positive covariance between populations  
219 within a small-scale region. In addition, for each time series we collated information on the  
220 latitude and longitude of the breeding site, and categorised sites as being either east (< 35° W)  
221 or west (> 35° W) coast of the North Atlantic Ocean.

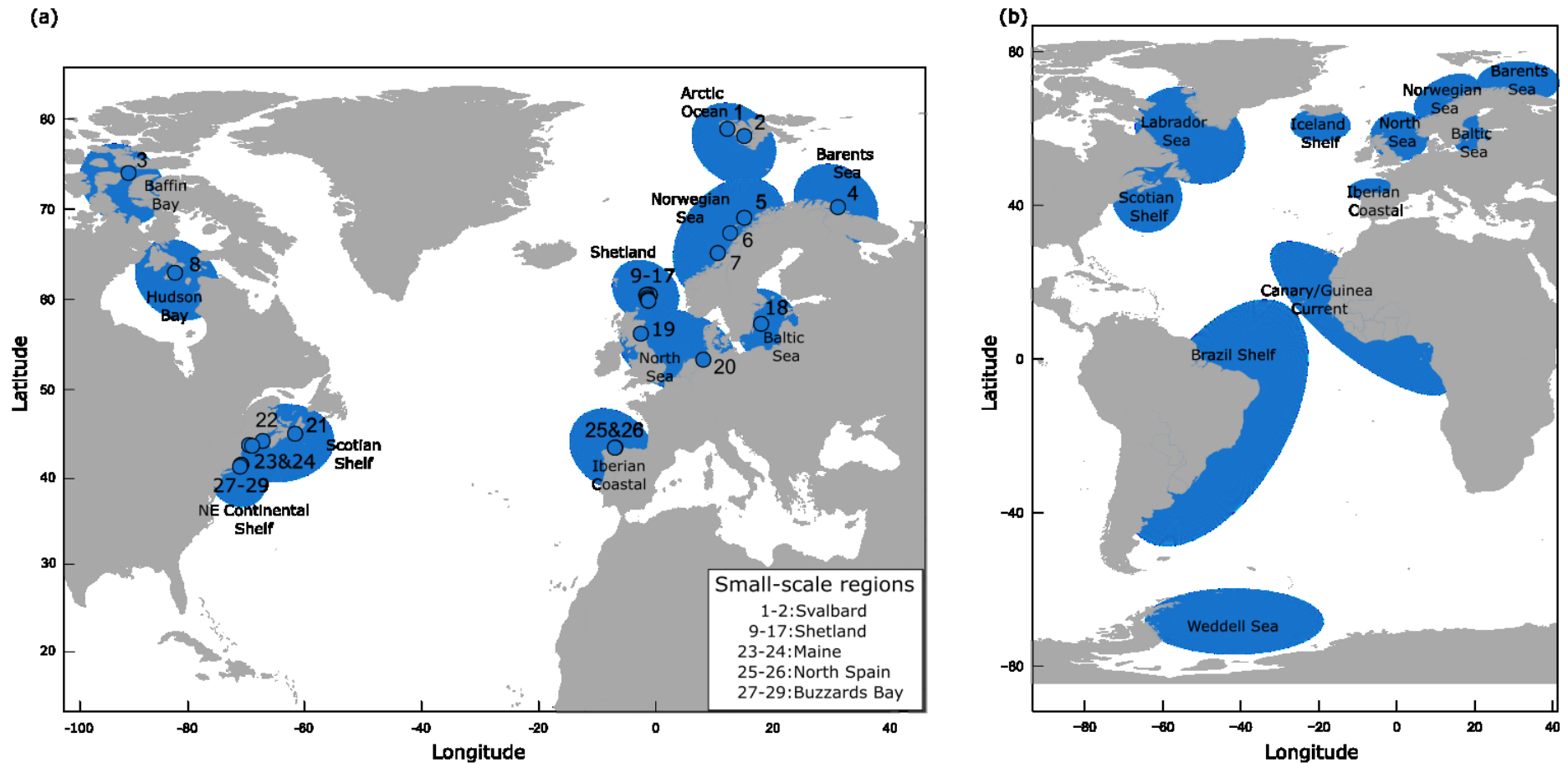
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 228 **Figure 2.** Map of sites in the North Atlantic included in the analyses. a) during the breeding season. Blue shading represents the Large Marine  
 229 Ecosystem (LMEs) classification. Numbers correspond to the breeding sites named in Table 1, numbered in order of decreasing latitude. Only  
 230 LMEs and small-scale regions (sites <120km apart) in which data for more than one site were available were included in the analysis of the  
 231 annual covariance. b) during winter. Wintering LMEs represent the location where highest percentage of individuals within a population spend  
 232 the winter. For further information, sources and site coordinates see Table S1.  
 233

234 **Table 1.** List of breeding sites and species included in the analyses in order of decreasing latitude, with breeding and wintering regions indicated.  
 235 Site numbers on the left correspond to those in Figure 2a. Species are as follows: KI = black-legged kittiwake, CT = common tern, RT = roseate  
 236 tern, AT = Arctic tern, SH = European shag, RA = razorbill, AP = Atlantic puffin, CG = common guillemot, BG = Brünnich's guillemot, with  
 237 numbers in parenthesis indicating the number of populations of each species included in the analyses. Multiple wintering LMES listed in a single  
 238 row appear in the same order as the species' listed at each breeding site. A term was only included in the analysis of annual covariance when data  
 239 for more than one population were available.

	AP (6)	RA (3)	CG (4)	BG (2)	SH (6)	KI (16)	AT (3)	CT (7)	RT (4)	Breeding site	Breeding small-scale region	Breeding LMES	Wintering LMES
1						x				Kongsfjorden	<b>Svalbard</b>	(Arctic Ocean)	<b>Labrador Sea</b>
2						x				Grumantbyen	<b>Svalbard</b>	(Arctic Ocean)	<b>Labrador Sea</b>
3				x		x				<b>Prince Leopold Island</b>	(Prince Leopold Island)	(Baffin Bay)	<b>Labrador Sea</b>
4	x	x	x			x				<b>Hornøya</b>	(Hornøya)	(Barents Sea)	<b>Barents Sea / Norwegian Sea / Barents Sea / Labrador Sea</b>
5	x					x				<b>Anda</b>	(Anda)	<b>Norwegian Sea</b>	<b>Iceland Shelf / Labrador Sea</b>
6	x				x	x				<b>Røst</b>	(Røst)	<b>Norwegian Sea</b>	<b>Iceland Shelf / Norwegian Sea / Labrador Sea</b>
7	x				x					<b>Sklinna</b>	(Sklinna)	<b>Norwegian Sea</b>	<b>Iceland Shelf / Norwegian Sea</b>
8				x						<u>Coats Island</u>	( <u>Coats Island</u> )	( <u>Hudson Bay</u> )	<b>Labrador Sea</b>
9						x				Burraoec	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
10						x				Esha Ness	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
11						x				Westerwick	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
12						x				Ramna Geo	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
13						x				Kettla Ness	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
14						x				No Ness	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
15						x				Troswick Ness	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
16						x				Compass Head	<b>Shetland</b>	<b>North Sea</b>	<b>Labrador Sea</b>
17			x		x	x				<b>Sumburgh Head</b>	<b>Shetland</b>	<b>North Sea</b>	<b>North Sea / North Sea / Labrador Sea</b>
18			x							<u>Stora Karlsö</u>	( <u>Stora Karlsö</u> )	( <u>Baltic Sea</u> )	<u>Baltic Sea</u>
19	x	x	x		x	x				<b>Isle of May</b>	(Isle of May)	<b>North Sea</b>	<b>North Sea / North Sea / North Sea / North Sea / Labrador Sea</b>

20			x	Banter See	(Banter See)	<b>North Sea</b>	<b>Canary or Guinea Current</b>
21			x x x	<b>Country Island</b>	(Country Island)	<b>Scotian Shelf</b>	(Weddell Sea) / <b>Brazil Shelf</b> / <b>Brazil Shelf</b>
22	x x		x x	<b>Machias Seal Island</b>	(Machias Seal Island)	<b>Scotian Shelf</b>	<b>Gulf of Maine</b> / Unknown / (Weddell Sea) / <b>Brazil Shelf</b>
23			x	Eastern Egg Rock	<b>Maine</b>	<b>Scotian Shelf*</b>	<b>Brazil Shelf</b>
24			x	Matinicus Rock	<b>Maine</b>	<b>Scotian Shelf*</b>	(Weddell Sea)
25		x		A Forcada	<b>North Spain</b>	(Iberian Coastal)	<b>Iberian Coastal</b>
26		x		As Pantorgas	<b>North Spain</b>	(Iberian Coastal)	
27			x x	<b>Bird Island</b>	<b>Buzzards Bay</b>	(North East U.S Shelf)	<b>Brazil Shelf</b>
28			x x	<b>Ram Island</b>	<b>Buzzards Bay</b>	(North East U.S Shelf)	<b>Brazil Shelf</b>
29			x x	<b>Penikese Island</b>	<b>Buzzards Bay</b>	(North East U.S Shelf)	<b>Brazil Shelf</b>

240 Terms in bold represent effects for which year (co)variance was estimated. Terms in brackets represent effects which are confounded because the  
241 same combination of populations is grouped at another spatial scale, see main text for details. Confounded terms were not included in the model  
242 unless specified in the main text. Underlined terms were not included in estimates of site year (co)variance, in either one or both of the breeding  
243 and wintering models, as data for only one population available and covariance could therefore not be estimated. \*Usually classed as North East  
244 U.S. Shelf but grouped here as Scotian Shelf.

245 **Table 2.** Hypotheses and how they relate to the structure of random terms used to capture year (co)variances  
 246 ( $\sigma^2$ ) for groupings of populations in the analyses. We use the among year variance for a grouping of  
 247 populations as an estimate of the among year covariance between populations in the group. B indicates terms  
 248 included in the breeding model, W indicates terms included in the wintering model.

Hypothesis and Description	Year (co)variance structure (where levels are unspecified see table 1 for levels that variances correspond to)	Model
1.1 <i>Cross-species spatial effect (North Atlantic scale):</i> Characterises the among-year variance in the mean annual average phenology means or medians across all populations breeding in the North Atlantic. Provides an estimate of the magnitude of a shared response to a trans North Atlantic driver.	$\mathbf{V}_{\text{global}} = \sigma_{\text{global}}^2$	B, W
1.2 <i>Cross-species spatial effect (Breeding LMEs scale):</i> Characterises among- year variance in the average phenology of all populations in the breeding Large Marine Ecosystem. This accounts for populations sharing a phenological response to a common broad scale regional driver during the summer.	$\mathbf{V}_{\text{breeding LMEs}} = \begin{bmatrix} \sigma_{1,1}^2 & 0 & 0 \\ 0 & \sigma_{2,2}^2 & 0 \\ 0 & 0 & \sigma_{3,3}^2 \end{bmatrix}$ Where 1 – 3 correspond to different breeding LMEs	B
1.3 <i>Cross-species spatial effect (Winter LME scale):</i> Characterises among- year variance in the average phenology of all populations that share the same winter LME. This accounts for populations sharing a phenological response to a common regional driver during the winter.	$\mathbf{V}_{\text{wintering LMEs}} = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{8,8}^2 \end{bmatrix}$ Where 1 – 8 correspond to different wintering LMEs	W
1.4 <i>Cross-species spatial effect (small-scale, i.e. breeding colonies within 120km):</i> Characterises among year variance in the average phenology of all populations found in the same local area. This accounts for a shared phenological response to small-scale regional conditions.	$\mathbf{V}_{\text{local}} = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{12,12}^2 \end{bmatrix}$ Where 1 – 5 correspond to different small-scale regions.	B
2 <i>Cross-species site effect:</i> Characterises among year variance in the average phenology of all populations found at the same breeding site. This accounts for a shared phenological response to very local conditions.	$\mathbf{V}_{\text{site}} = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{12,12}^2 \end{bmatrix}$ Where 1 – 12 correspond to different breeding sites.	B
3.1 <i>Species spatial effect (North Atlantic scale):</i> Characterises among year variance in the average phenology of all populations that belong to the same species. This accounts for the potential for species to share a phenological response to a spatially consistent driver.	$\mathbf{V}_{\text{species}} = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{9,9}^2 \end{bmatrix}$ Where 1 – 9 correspond to different species	B,W
3.2 <i>Species spatial effect (Winter LME scale):</i> Characterises among year variance in the average phenology of all populations of the same species that share the same wintering LME. This accounts for populations of the same species sharing a phenological response to a common driver encountered in the same wintering LME	$\mathbf{V}_{\text{species wintering}} = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{4,4}^2 \end{bmatrix}$ Where 1 = Northern North Sea European shag, 2 = Northern North Sea Common guillemot, 3 = Brazil Shelf Roseate tern, 4 = Brazil Shelf Common tern	W

3.3 *Species spatial effect (breeding colonies within 120km)*: Characterises among year variance in the average phenology of all populations within a small-scale region that belong to the same species. This takes into account the potential for members of a single species to share a phenological response to conditions at breeding sites within 120km.

$$\mathbf{V}_p = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{3,3}^2 \end{bmatrix}$$

B,W

Where 1 = Shetland Black-legged kittiwake, 2 = Buzzards Bay Roseate tern, 3 = Buzzards Bay Common tern

4. *Idiosyncratic population effect*: Allows for the residual among year variance to be heterogeneous across all populations. High residual variance implies that phenology is largely determined by a driver and/or response that is idiosyncratic to the population.

$$\mathbf{V}_{\text{population}} = \begin{bmatrix} \sigma_{1,1}^2 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma_{51,51}^2 \end{bmatrix}$$

B,W

Where 1-51 correspond to different populations



250

## 251 [Statistical Analyses](#)

252 We used the *MCMCglmm* package (Hadfield, 2010) in R (v 3.5.1; R Core Team 2018), to fit  
253 linear mixed-effect models in a Bayesian framework. In these models, the Gaussian response  
254 variable was the yearly breeding phenology of each population. Random effects were used to  
255 (i) control for differences in mean/median timing among populations and (ii) identify the  
256 sources of positive covariance in phenology among populations (see Table 2 for full list of  
257 terms used). Estimating the unstructured 51 x 51 covariance matrix for annual timing among  
258 all populations was unfeasible given the number of observations we had. While methods to  
259 capture the major aspects of this among population covariance exist (Warton et al., 2015), our  
260 approach reduced the dimensionality of the problem by only estimating positive among year  
261 (co)variances where we hypothesised *a priori* they may exist and assuming other covariances  
262 = 0 (see Appendix 1). We used separate models to distinguish the positive (co)variance among  
263 populations that share breeding LMES (core model) versus wintering LMES (wintering  
264 model). An additional core model (fixed effects model) included latitude and the continental  
265 coast of the breeding site (east or west Atlantic Ocean) as fixed effects to account for broad  
266 geographic trends in the long-term mean/median phenology of populations.

267

268 We used random terms in two ways. First, we controlled for variation in the multi-year  
269 mean/median phenology of the time series' in each group by including species, LMES  
270 (breeding or wintering), small-scale region (groups of sites that are < 120 km apart), species  
271 within small-scale region, site, and population (site:species) as random terms. The year random  
272 term estimated the overall between-year (co)variance in timing of breeding across all  
273 populations. Secondly, we allowed the among-year variance to be heterogeneous across spatial  
274 and taxonomic groupings of populations (Table 2). For example, heterogenous year variance  
275 structure was applied at the species level to nine species groupings, which estimates a 9x9

276 matrix of among year (co)variance, where the annual variance of each species is along the  
277 diagonal and the dimensionality of the problem is reduced by fixing the off-diagonals  
278 (covariances between species) at zero. The year variance estimated for a species is equivalent  
279 to the among-year covariance among populations of that species (Figure 1, Table 2, see  
280 Appendix 1 for further explanation). For each of the year variances estimated for a grouping of  
281 populations, a high value indicated positive covariance among associated time series, such that  
282 populations within the grouping had similar patterns of early or late breeding years (Figure  
283 1a,b,c). Conversely, low covariance indicated no tendency for shared early or late breeding  
284 events among the population time series within a grouping (Figure 1d). We only allowed for  
285 heterogeneity in year variance where data were available for two or more populations in each  
286 grouping. We also allowed the among-year residual variance to be heterogeneous across  
287 populations. For all random terms, effects were drawn from a normal distribution with mean =  
288 0 and with the variance estimated from the data. As the sample sizes on which annual  
289 population averages varied among populations and years this introduced heterogeneity in the  
290 measurement error across observations. To control for measurement error we allowed for a  
291 slope of  $\sqrt{1/n}$  (where  $n$  = annual sample size for a population) to vary across observations.

292

293 Given the five alternative random terms in the core model, the combination of populations was  
294 sometimes the same for more than one spatial scale. For example, both populations of European  
295 shag in North Spain were located < 120 km apart and were therefore included in the same  
296 small-scale region, and this same combination was found in the breeding LMEs, Iberian  
297 coastal. Where an identical set of populations were grouped by more than one random effect,  
298 only the level in which populations were in closest proximity (i.e., site, then small-scale region,  
299 then LME) was included. In such cases, the spatial-scale at which positive covariance arise  
300 cannot be distinguished and we highlight such cases in the results.

301

302 In the wintering model (Table 2), we tested for positive covariance among populations that  
303 share a wintering LMES. Year, species, population, and heterogeneous year variances across  
304 species and populations were retained as random terms from the core model. We also retained  
305 the species small-scale regional effect to control for similar responses of adjacent populations  
306 of the same species (e.g., nine populations of kittiwakes from Shetland) that may travel to the  
307 same wintering LMES. In addition to estimating positive covariance in phenology among all  
308 populations wintering in the same LMES, we also estimated the species-specific positive  
309 covariance among populations across years.

310

311 All models were run for 1,200,000 iterations, discarding the first 100,000 as burn-in and  
312 sampling every 100<sup>th</sup> iteration. For the residual priors we used an inverse-Wishart distribution.  
313 To improve mixing, for the remaining variance random terms we adopted parameter-expanded  
314 priors (Gelman, Van Dyk, Huang, & Boscardin, 2008), which give a scaled F distribution with  
315 numerator and denominator degrees of freedom = 1 and scale parameter = 1000 (Gelman,  
316 2006). Trace plots of posterior distributions were examined to assess autocorrelation and model  
317 convergence. Statistical significance of fixed effects was inferred where 95% credible intervals  
318 (CIs) did not span zero. As variance estimates are bounded at zero, we infer that a random term  
319 is significant where visual inspection of posterior showed that the 2.5% CI was removed from  
320 zero.

321

322 The method we employed assumes that between grouping covariances are zero and that all  
323 non-zero covariances are positive. In appendix 2 we outline *post hoc* tests designed to assess  
324 model adequacy. To examine how properties of the data (effect size, replication, number of  
325 overlapping years, etc.) affected the accuracy and power of our approach for estimating

326 (co)variances, we conducted simulations of phenology based on the original data structure of  
327 the core model (Appendix 2). Simulations revealed that our method for estimating population  
328 covariance had good power to detect a (co)variance of 40 and moderate power to detect a  
329 (co)variance of 20. Power to detect a non-zero covariance was reduced when time series were  
330 short and care should be taken in interpreting covariance estimates with very broad credible  
331 intervals, as this may reflect low power rather than a true absence of a covariance.

332

333

334

335

336

## 337 Results

338

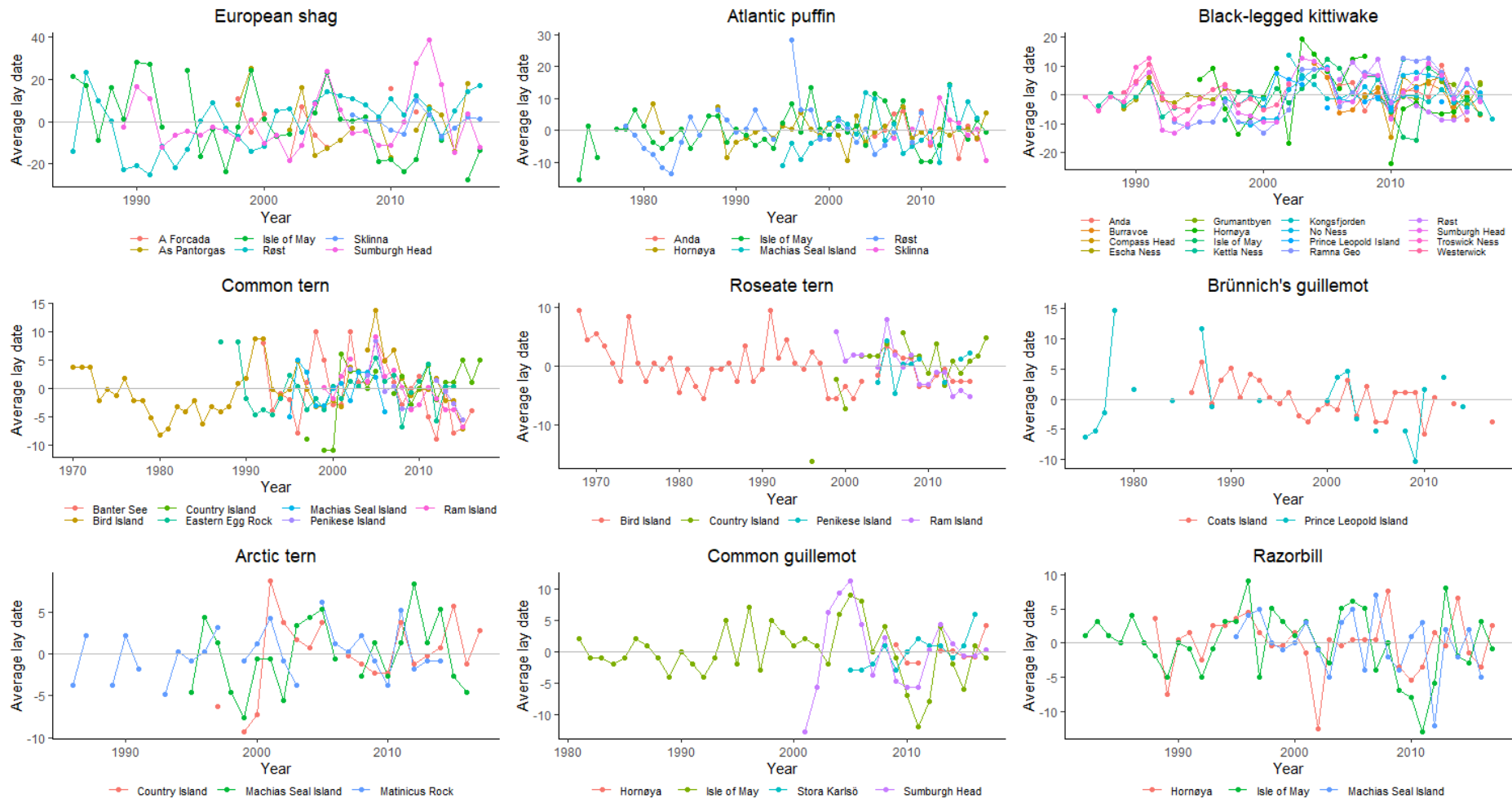
### 339 *Phenological time series*

340 The full dataset of 1041 phenological observations (annual means or medians) spanned 50 years and  
341 51 populations across nine species and 29 breeding sites, with more recent years represented by more  
342 time-series than earlier years (Figure S1, Table S1). From visual inspection of population time series  
343 from the same species (Figure 3) or site (Figure 4) there were some instances where population  
344 responses appeared to be correlated (e.g., Black-legged kittiwake, Ram Island) and other instances  
345 where the time series appeared to be entirely uncorrelated (e.g., European shag).

346

### 347 *Large-scale geographic trends*

348 All model parameter estimates correspond to those obtained from the core breeding model unless the  
349 wintering model is specified. Average lay date was delayed with latitude ( $b = 1.782 \text{ days lat}^{-1}$ , 95%  
350 CI = 0.879, 2.678), and, controlling for latitude, laying in the west Atlantic was 38 days later (95%  
351 CI = 16.119, 58.164) than the east Atlantic.



352  
 353  
 354  
 355

**Figure 3.** Annual lay dates of populations of all species included in the analysis. The grey line represents the line of central tendency of laying for each species.



356  
357  
358

**Figure 4.** Annual lay dates of populations at twelve sites for which more than one time series was available for analysis. The grey line represents the central tendency of laying at each site.

359

360 *Cross-species spatial and site effects*

361 To test whether the phenology of populations in the North Atlantic Ocean basin varies in a

362 similar way from year to year we tested for covariance in timing between years across all time

363 series'. Variance (in units of days<sup>2</sup>) of the *cross-species spatial effect* at the North Atlantic scale

364 was very low ( $\sigma^2 = 0.173$ , 95% CI = 0.000, 1.077, years = 49) in comparison to the average

365 interannual variance in lay date shown by each population (Table S2), indicating that for North

366 Atlantic seabirds in general, early and late years were not shared across all of the populations.

367

368 To assess *cross-species spatial effects* (LMEs scale) we estimated among year phenological

369 covariance between populations sharing similar breeding or wintering LMEs. We detected no

370 statistically significant cross-species covariance of populations that share a breeding LME

371 region (Figure 5e, Tables S2, S3), although in the Norwegian Sea and the North Sea the credible

372 intervals were wide. In the wintering model, significant covariance was found only for

373 populations in the North Sea ( $\sigma^2 = 18.236$ , 95% CI = 10.014, 29.438, time series = 6, Figure

374 S3b, Table S4), with the estimated variance corresponding to the shared phenological effects

375 being in the range of  $\pm 8.3$  days in 95% of years. The posteriors for inter-year variance in

376 phenology for populations that wintered in three additional LMEs (Gulf of Maine, Iceland

377 Shelf and Barents Sea) were somewhat removed from zero, although the 2.5% CI was

378 approximately 0. In the case of populations that winter on the Iceland Shelf, the posterior

379 median for the among-year variance was large, but there was high uncertainty in the variance

380 estimate (Figure S3b).

381

382 We estimated *cross-species spatial effects* for five small scale regions (each made up of sites

383 within 120 km) and found among-year variance to be quite high in North Spain, Shetland and

384 Svalbard, but only estimated well for Shetland ( $\sigma^2 = 32.688$ , 95% CI = 14.502, 59.032, time



385 series = 11, Figure 5c, Table S2). Of the 29 breeding sites, 12 held more than one species,  
386 allowing estimation of *cross-species site effects* (Figure 4 and 5b), with among year variance  
387 significant for only three sites: Country Island, Hornøya, and Prince Leopold Island. For these  
388 sites the 95% limits for the expected annual deviations are in the range  $\pm 10.5$  days,  $\pm 7.1$  days  
389 and  $\pm 9.2$  days, respectively. The peaks of the posterior distribution for inter-year variance for  
390 five additional sites (Bird Island, Isle of May, Machias Seal Island, Ram Island and Sumburgh  
391 Head) were removed from 0, but the 2.5% CI was approximately 0 (Figure 5b).

392

393

#### 394 *Species effects*

395 We tested for among year phenological covariance between populations of the same species to  
396 test the hypothesis that there are environmental conditions that drive species-specific  
397 responses. The *species spatial effect (North Atlantic scale)* was only significant for black-  
398 legged kittiwakes ( $\sigma^2 = 10.723$ , 95% CI = 2.927, 22.228, time series = 16, Figure 5a, Table S2).  
399 Under a normal distribution with mean = 0 and variance = 10.723, the shared annual deviations  
400 in timings were expected to lie in the range  $\pm 6.4$  days in 95% of years. All other species  
401 covariance effects were small with the 97.5% quantile of the posterior for seven of the species  
402  $< 6$  (Table S2). For three species we estimated *species spatial effects* within small scale regions.  
403 We found a suggestion of positive covariance for common terns at Buzzards Bay (Figures 5d  
404 & S4c, Tables S2, S3), whereas for Roseate terns in this small-scale region the covariance was  
405 low. For kittiwakes across Shetland covariance was poorly estimated, making it unclear  
406 whether there is a species-specific response to a small-scale driver, in addition to the North  
407 Atlantic scale species effects and small-scale (Shetland) cross species effects that this species  
408 will be affected by. We found no evidence that breeding phenology of populations of the same  
409 species within a wintering region covaried (Figure S3d, Table S4), although for Roseate terns

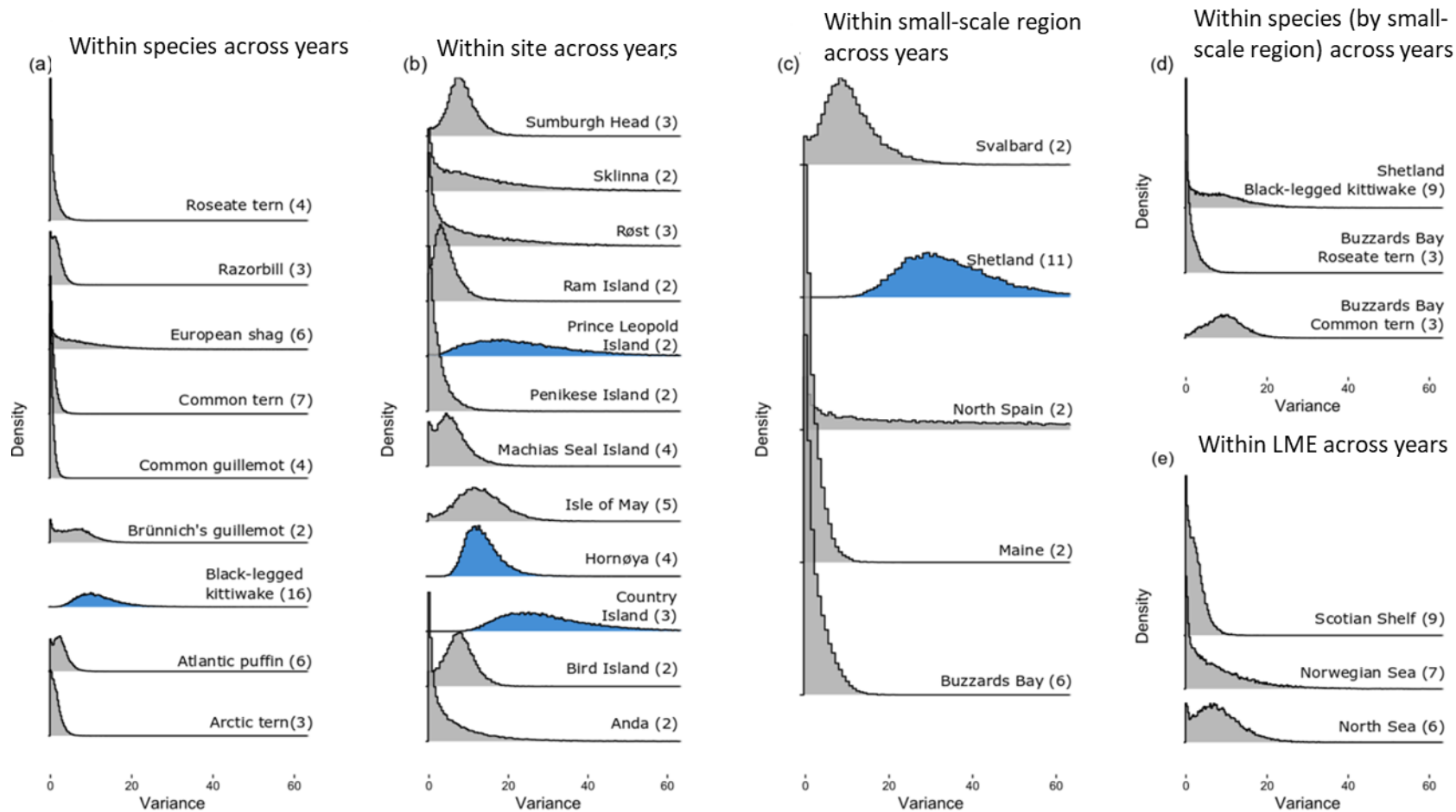
410 at Brazil Shelf and Common guillemots at the Northern North Sea credible intervals were very  
411 broad.

412

413 *Idiosyncratic population effects*

414 Residual annual variance was significant for all of the 51 populations (Table S2) and varied  
415 substantially among species (Table 3), being particularly pronounced in European shags.

416 Averaged across populations, the residual term explained substantially more of the annual  
417 (co)variance than any other term.



418  
 419 **Figure 5.** (Co)variance in timing of breeding of seabird populations across years during the breeding season. Plotted from the posterior  
 420 distribution of the core random-effects model, representing shared variance across years according to (a) species, (b) site, (c) small-scale region  
 421 (< 120 km apart), (d) species within small-scale region (i.e. populations of the same species within a group of nearby sites), and (e) Large Marine  
 422 Ecosystem. On the y axes labels, values in parenthesis indicate the number of populations associated with each term. For interpretation, narrower  
 423 histograms indicate a posterior distribution that has been estimated with higher precision (i.e. a tighter credible interval), and histograms with a  
 424 centre of mass further removed from zero represent more posterior support for a positive (co)variance. Groups for which significant positive  
 425 covariance was estimated (i.e. where 2.5% credible interval was removed from 0) are shaded in blue.

426 **Table 3.** Median residual variance for the nine species included in the analysis in order of decreasing  
 427 variance. Residual variance is calculated from the core random effects model, and species are placed  
 428 in order from highest to lowest values. Numbers in brackets indicate 95% credible intervals for the  
 429 species medians. 95% range in days corresponds to the 0.025 and 0.975 quantiles of a normal  
 430 distribution of mean = 0 and  $\sigma$  calculated from the residual variance.

Species	Median among-year residual variance	95% range in days
European shag	143.31 (45.55 – 278.17)	± 23.46 days
Atlantic puffin	25.12 (4.63 – 54.67)	± 9.82 days
Black-legged kittiwake	18.83 (3.59 - 41.92)	± 8.50 days
Razorbill	7.72 (1.24 - 15.07)	± 5.45 days
Brünnich's guillemot	7.38 (0.00 – 20.65)	± 5.33 days
Roseate tern	7.08 (0.00 – 17.48)	± 5.21 days
Common tern	5.31 (1.34 – 12.40)	± 4.52 days
Arctic tern	5.05 (1.05 – 11.03)	± 4.40 days
Common guillemot	4.65 (0.55 – 12.27)	± 4.23 days

431

432

### 433 Model diagnostics

434

435 The model which allowed for negative covariance between two populations at a single local  
 436 site (Anda) estimated a non-significant negative covariance between populations at this site  
 437 (Appendix 2: Table S6). Allowing for this negative correlation led to no substantial changes to  
 438 other (co)variance parameters that these populations contributed to (Appendix 2, compare  
 439 Tables S2&3 with S6).

440

441 For four species with data for > 5 populations (Black-legged kittiwake, common tern, Atlantic  
 442 puffin, European shag) we compared pairwise correlations estimated from the raw data against  
 443 those from the posterior distribution of the core random effects model as a diagnostic of the  
 444 performance of the mixed-model approach. The model-based estimates corresponded well with  
 445 estimates from pairwise correlations using the raw data and captured a spatial decay in pairwise  
 446 correlations (Appendix 2, Figure S4). While estimates obtained via both approaches converged  
 447 on zero as distance increased, a minor difference was that those from the model were always  
 448 positive, whereas those estimated pairwise from the data were both positive and negative.

449 Intraspecific pairwise Pearson's correlations of annual phenology between populations of  
450 black-legged kittiwakes, Atlantic puffins, and European shags all decreased with increased  
451 distance (black-legged kittiwake: Mantel statistic [between distance and 1-correlation]  $r =$   
452  $0.515$ ,  $p = 0.004$ ; Atlantic puffin:  $r = 0.803$ ,  $p = 0.025$ ; European shag:  $r = 0.526$ ,  $p = 0.006$ .  
453 Appendix 2, Table S7, Figure S4).

454

455 The *a posteriori* quantile-quantile plot for pairwise population correlations revealed an  
456 excellent correspondence between empirical and model-based quantiles (Appendix 2, Figure  
457 S5). Model-based *a posteriori* simulations yielded a similar frequency of negative pairwise  
458 correlations between populations to that which we observe, indicating that the observed  
459 frequency of negative phenological correlations is consistent with what we would expect to  
460 observe by chance in the absence of any true negative covariances.

461

## 462 Discussion

463 Timing of breeding is often used as an indicator of response to environmental change, yet for  
464 many species the drivers of phenology and the spatiotemporal scale at which they operate  
465 remain unclear. We collated phenology from a diverse group of North Atlantic seabird  
466 populations and examined to what extent populations share early versus late breeding seasons  
467 between sites, species, breeding and wintering regions. We found no evidence that across  
468 species all populations in the North Sea collectively breed early or late, suggesting that if there  
469 is a common driver of phenology in the North Atlantic, such as sea surface temperature or  
470 North Atlantic Oscillation, it either does not exhibit correlated annual variation across this  
471 region and/or does not elicit a consistent response across populations. However, we did identify  
472 a pronounced difference in the median timings between the east and west Atlantic, with  
473 phenology more than a month later in the west. One potential explanation is that this may be

474 due to differences in the temperature of the currents passing each coast (southward flowing  
475 Labrador Current being cold in comparison with the warmer and northward flowing Gulf  
476 Stream) which leads to more pronounced seasonality in water temperature in the west for a  
477 given latitude (Mackas et al., 2012).

478

479 We also found no evidence for cross-species shared phenological responses for populations in  
480 the same breeding LMEs, and the same was true for most wintering LMEs (the exception being  
481 the North Sea). Primary productivity (Behrenfeld et al., 2006) and abundance of prey  
482 (Frederiksen et al., 2005) vary in their temporal availability at spatial scales smaller than the  
483 LME categorisation used in this study, such that although they occupy the same general ocean  
484 basin, the scale, magnitude and direction of any adjustment in timing of breeding in response  
485 to the environment may differ across sites within it. Furthermore, bathymetry, tides and  
486 currents are all important for prey distributions and aggregations, and thereby for seabird  
487 foraging (Amélineau, Grémillet, Bonnet, Bot, & Fort, 2016; Christensen-Dalsgaard, May, &  
488 Lorentsen, 2018; Vihtakari et al., 2018), and may vary considerably within small areas  
489 (Sankaranarayanan, 2007). At smaller spatial scales we found evidence for cross-species shared  
490 responses within about a third of small-scale regions and sites. Positive covariance in  
491 phenology at a local scale may be driven by several factors, such as local habitat or weather  
492 conditions (Porlier, Charmantier, Bourgault, Perret, & Blondel, 2012); abundance and  
493 phenology of prey (Frederiksen et al., 2005); inter- (Schoener, 1974) and intra-specific  
494 competition for food (Lewis, Sherratt, Hamer, & Wanless, 2001), social interaction – which  
495 has been implicated as an influence on intraspecific annual variation (Youngflesh et al. 2018),  
496 but might also arise between species – or a combination of effects. Small-scale physical  
497 features potentially cause subtle differences in conditions at each site despite site proximity,  
498 which could result in the observed differences in covariance between sites.

499

500 In terms of species effects, we detected significant positive covariance responses across  
501 populations of only one species, the black-legged kittiwake, with timing of breeding in  
502 populations from both sides of the Atlantic and spanning almost all of the breeding range  
503 tending to vary in tandem by  $\pm 6$  days. In the North Atlantic, the majority of kittiwakes from  
504 most populations winter in the Labrador Sea, and one explanation for the covariance in  
505 phenological response is that they experience similar conditions during this period (Bogdanova  
506 et al., 2017; Frederiksen et al., 2012). It is plausible that water temperature over the winter, via  
507 its effect on resources, may determine when kittiwakes return to waters around their colonies,  
508 with carry-over effects on timing of breeding. Although there was significant among-year  
509 covariance in laying dates of kittiwakes across breeding sites, this only explained an average  
510 of 27.1% of the total among-year variance experienced by each population (min. = 11.97%  
511 [Hornøya], max. = 78.18% [Prince Leopold Island]), and correlations in lay date decreased  
512 with distance between sites. As kittiwakes are restricted to foraging on the water's surface, this  
513 may make them more responsive to environmental effects on local conditions than other  
514 species that can dive (Furness & Tasker, 2000). It is evident that kittiwakes may therefore be  
515 sensitive to environmental conditions across multiple spatial scales (Frederiksen et al., 2004).

516

517 With the exception of the black-legged kittiwake, we found no shared variance across  
518 populations of the same species, which implies that they do not respond similarly to a spatially  
519 consistent driver. A consequence of the low amount of regional synchrony for all species other  
520 than the kittiwake is that species may be somewhat buffered by a spatial portfolio effect  
521 (Schindler, Armstrong, & Reed, 2015). For instance, if extreme weather negatively impacts a  
522 population at one stage of the breeding season, a population at a different stage of reproduction  
523 elsewhere may experience less severe effects, thereby promoting stability at higher aggregate

524 levels such as multiple populations of species at the regional or meta-population level  
525 (Schindler et al., 2015). This may benefit the resilience of North Atlantic seabird species  
526 (Bogdanova et al., 2017; Fayet et al., 2017) in the face of wide-scale perturbations (Schindler  
527 et al., 2015) expected under future climate scenarios (Stocker et al., 2013).

528

529 We found that residual variance for European shags (i.e., between-year variance in lay date  
530 within a population, after all other terms have been taken into account) greatly exceeded the  
531 levels estimated for other species in the analysis (Table 3). European shags are partial migratory  
532 whereby a proportion of the population remain resident at the breeding colonies throughout the  
533 year, and most migrant individuals make shorter-distance movements than the other study  
534 species (Grist et al., 2014; Moe et al. 2021), so may be more sensitive to local conditions, such  
535 as abundance of forage fish (Lorentsen, Anker-Nilssen, Erikstad, & Røv, 2015) and have an  
536 unusually high capacity to adjust laying dates accordingly. While auk populations in our  
537 analysis do remain in the North Atlantic over winter and spring, many migrate to a variety of  
538 different areas (Fayet et al., 2017; Frederiksen et al., 2016), although it should be noted that  
539 synchronised survival in Atlantic puffin has been attributed to an overlap in non-breeding  
540 grounds of some Norwegian populations used in this analysis (Reiertsen et al., 2021). This  
541 suggests that the conditions driving auk phenology are unlikely to be consistent for all  
542 populations. Finally, the tern species included in this analysis (common, roseate and Arctic)  
543 are all long-distance migrants, and individuals from the same or different breeding sites may  
544 take alternative migration routes, at different times, and to different destinations (Becker et al.,  
545 2016; Egevang et al., 2010; Mostello, Nisbet, Oswald, & Fox, 2014; Nisbet, Arnold, Oswald,  
546 Pyle, & Pattern, 2017), potentially experiencing different conditions. Further research  
547 comparing laying dates of tracked individuals known to have similar migration strategies



548 would therefore elucidate the extent to which phenology covaries between individuals within  
549 and across colonies (Grecian et al., 2016).

550

551 We restricted our analysis to include datasets of eight or more years in duration, but in some  
552 instances the time series overlap was low, reducing our ability to infer precise covariances. Our  
553 simulations (appendix 2) revealed that where time series are short and with limited overlap our  
554 power to detect a variance of 20 could fall below 0.8. Whilst the posterior median for year  
555 (co)variance was  $< 20$  for 29 of 33 terms in our core model (Table S2), in 22 of these cases the  
556 2.5% CI was removed from zero (i.e., variance was significant) or the upper 97.5% CI was  $<$   
557 20 (i.e., we can infer variance was low). Nonetheless there were cases where our CIs were  
558 broad and we anticipate that repeating these analyses in the future will improve precision  
559 thereby allowing additional insights to be gleaned. While our model structure did not allow for  
560 negative covariance between phenological time series, when we compared pairwise estimates  
561 of phenological correlations expected under our model to those obtained from raw data we  
562 found a good correspondence between the two (Figure S5). On this basis we infer that observed  
563 negative covariances are consistent with what one would expect to observe by chance when  
564 sample sizes are small, and the true covariance is close to zero. Finally, our analysis considered  
565 the effects of conditions at the breeding and main wintering grounds, but did not take into  
566 account pre-breeding, post-breeding, staging and migration routes. More detailed tracking  
567 information would allow future analyses to take this into account.

568

569 For many plant and animal taxa great strides have been made in identifying the aspects of the  
570 environment that give rise to temporal or spatial variation in phenology (e.g., Cohen et al. 2018;  
571 Thackeray et al. 2016), often finding that temperature in the two months or so preceding  
572 phenology has an important role. There may be other groups that are similar to seabirds in that

573 identification of drivers of phenology is more challenging, perhaps due to environmental  
574 drivers influencing condition over a much longer period – as appears to be the case in red deer  
575 (Stopher, Bento, Clutton-Brock, Pemberton, & Kruuk, 2014). In such cases and where data  
576 exist for multiple populations we anticipate our alternative approach will be useful. A second  
577 potential application of among year population phenology covariance estimation is to the study  
578 of communities. While many studies focus on individual species, a small number of studies  
579 have started to examine how phenological shifts influence synchrony and interactions at the  
580 level of the community (CaraDonna, Iler, & Inouye, 2014). We propose that the among  
581 population year covariance in phenology could be used to arrive at a measure of cohesiveness  
582 of the phenological response across a community that could be compared among sites or  
583 trophic levels. For instance, one measure of phenological cohesiveness at a site could be  
584 calculated as the *shared year variance* divided by *the mean of the total annual variances*  
585 *estimated across species (i.e., where total annual variance for a species = the shared year*  
586 *variance plus the annual variance unique to the species)*, giving a value that varies between 0  
587 = no cohesiveness and 1 = perfect cohesiveness. In the case of seabirds this value would tend  
588 to be very low, whereas if it were applied to the leaf out phenology of temperate trees we would  
589 expect to see a much higher value (Roberts, Tansey, Smithers, & Phillimore, 2015).

590

591 Phenology is widely used as a measure of species' response to environmental change, yet for  
592 higher trophic level species, particularly those that are highly mobile, the drivers are often  
593 poorly understood. We estimated covariance of average lay date across multiple populations  
594 of seabirds, to identify the scale at which drivers of phenology operate in this group of highly  
595 mobile top predators. For many populations, the majority of annual variance in breeding time  
596 was at the site level, highlighting the importance of local conditions in driving phenology for  
597 some species in this taxonomic group. Should broad-scale perturbations cause conditions to

598 deteriorate rapidly across a large region, we conclude that the near absence of regional  
599 phenological covariance, apart from black-legged kittiwakes, may allow for increased  
600 resilience at the meta-population scale via phenological portfolio effects. Further research  
601 combining individual tracking and phenology data could reveal drivers operating at additional  
602 spatial, temporal and biological scales, for example conditions experienced by individuals or  
603 populations on migration routes, stop-overs, or during autumn or spring periods. Identifying  
604 the multiple scales at which phenology is driven will allow us to further understand how  
605 organisms respond to fluctuating conditions, and how they may continue to do so in the future.

606

## 607 [Acknowledgements](#)

608 This work could not have been carried out without decades of data collection by field workers  
609 across all sites. Specific thanks to Thierry Boulinier, Karen McCoy, Torkild Tveraa, Aurore  
610 Pochon, Jérémy Tornos, Frédéric Angelier, Pierre Blévin, Céline Clément-Chastel, Geir Wing  
611 Gabrielsen, Aurélie Goutte, Solveig Nilsen, Kjetil Sagerup, Sabrina Tartu and several  
612 anonymous reviewers for comments that greatly improved the manuscript. Discussions with  
613 Bob Swann provided inspiration for the manuscript. The authors also thank funding sources:  
614 the Natural Environment Research Council (NERC; UK National Capability award number  
615 NE/R016429/1 as part of the UKSCaPE programme); Joint Nature Conservation Committee  
616 (JNCC); Environment and Climate Change Canada; Natural Resources Canada; New Bedford  
617 Harbor Trustee Council; The Norwegian Environment Agency (and its predecessors), the  
618 SEAPOP programme ([www.seapop.no](http://www.seapop.no)) and its key institutions: The Norwegian Institute for  
619 Nature Research, The Norwegian Polar Institute and Tromsø University Museum and the  
620 French Polar Institute. The authors declare no conflict of interest.

621

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