Forage fish abundance is a predictor of timing of breeding and hatching brood size in a coastal seabird

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ABSTRACT: Current and future climate alterations might impact ecological processes like timing of breeding. We used multivariate linear models to assess the importance of food availability and climate on timing of breeding and hatching brood size of European shags *Phalacrocorax aristotelis* in 2 colonies, Sklinna (65° N) and Røst (67° N), in the Norwegian Sea over 21 yr (1989 to 2009). Predictor variables were ICES abundance estimates of young saithe *Pollachius virens*, the staple food of shags in these colonies, the previous winter's North Atlantic Oscillation index (wNAO), and sea surface and air temperatures. Annual population size was included to control for density-dependent effects. The best model for hatching date explained 15% (Sklinna) and 70% (Røst) of the variation and showed that shags bred earlier when 1 yr old saithe were more abundant. The model for Røst also included 2 yr old saithe and wNAO. The best model for hatching brood size explained 40% (Sklinna) and 48% (Røst) and included a positive effect of population size at both sites. The model for Røst also included a positive effect of 1 yr old saithe. Our study demonstrates that abundance of 1 yr old saithe is a key factor for the breeding performance of shags in both colonies, whereas the climate variables were of less importance. Delayed breeding and low brood size were not associated with a high population of breeders, indicating breeding performance was density-independent and that the positive relationship between breeding numbers and saithe abundance mainly reflected variation in non-breeding among established breeders.

KEY WORDS: *Phalacrocorax aristotelis* · Norwegian Sea · Timing of breeding · Brood size · *Pollachius virens* · NAO

INTRODUCTION

Environmental changes caused by anthropogenic as well as natural climate alterations may have profound impacts on ecological processes and biodiversity (Walther et al. 2002, Edwards & Richardson 2004, Thomas et al. 2004). In marine ecosystems, strong effects of climate change on the timing of seasonal activities (i.e. phenology) have been demonstrated for all trophic levels, from primary producers (e.g. Edwards & Richardson 2004) to top predators like seabirds (e.g. Frederiksen et al. 2004, Wanless et al.

2009). For seabirds, one of the potential outcomes of climate change is seasonal mismatch between peak abundance of prey and critical periods of energy demand, such as chick rearing (e.g. Durant et al. 2007, Myksvoll et al. 2013), potentially leading to reduced breeding success and, eventually, decreasing populations (e.g. Cairns 1987).

Northern hemisphere sea surface temperature (SST) has increased by 0.71°C from 1850 to 2004 (Rayner et al. 2006) and is expected to increase further due to global warming (IPCC 2007). Thus, there is an urgent need to understand how temperature-

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induced changes in timing and productivity at lower trophic levels can influence food availability for seabirds and other top predators. In seasonal climates, production at the lowest trophic levels typically has a pronounced spring peak and many animals respond to environmental cues that may be predictors of the peak in food availability, and adjust the timing of their breeding accordingly; cf. the match/mismatch hypothesis (Cushing 1990, see also Durant et al. 2007). For seabirds, this hypothesis has been tested in a number of studies, of which many found a mismatch between predator and prey phenologies (e.g. Visser & Both 2005, Grémillet et al. 2006, Watanuki et al. 2009, Burthe et al. 2012, but see Durant et al. 2005). One general problem with the match/mismatch hypothesis, however, is that it ignores the level of food abundance, which can compensate for small mismatches in timing (cf. Durant et al. 2005). For marine top predators such as fish-eating seabirds, spring peaks at lower trophic levels might not be relevant cues as their main prey does not depend on phytoplankton but on secondary and higher level consumers (e.g. crustaceans such as copepods and krill), that might or might not display seasonal peaks. Thus, the numerical abundance of fish prey, which might vary considerably between years, may be the most important information for deciding if and when to breed and how many eggs to lay. Such mechanisms can operate if there is a threshold in the abundance of the prey required by the predator, and if prey is available for longer when above this threshold, enabling the predator to advance breeding. Advanced breeding is also often accompanied with an increase in the number of eggs laid (Monaghan et al. 1989, Moe et al. 2009, Shultz et al. 2009).

However, several studies have shown that seabird breeding phenology and success is associated with climate variables, such as large-scale climatic signals like the North Atlantic Oscillation (NAO, Hurrell et al. 2003) (e.g. Durant et al. 2004a, Sandvik et al. 2012, 2014), or local conditions like SST, spring air temperature, and wind conditions (e.g. Durant et al. 2004b and references therein). For instance, Frederiksen et al. (2004) demonstrated that the phenology of 2 dispersive species, the black-legged kittiwake *Rissa tridactyla* and the common guillemot *Uria aalge* were correlated with NAO, whereas the more resident species European shag *Phalacrocorax aristotelis* was more affected by local conditions reflected by SST around the colony. Furthermore, species and species groups may respond differently to climate change with timing of breeding being positively correlated with NAO in some species and at the same time neg-

atively correlated with climatic signals in other species (Wanless et al. 2009). Such effects may also vary across regions and are most often indirect through changes in the birds' food supply (e.g. Durant et al. 2004b, Burthe et al. 2012, Sydeman et al. 2012), although it is difficult to exclude any direct effects (e.g. Aebischer 1986, Daunt et al. 2006). Few studies, however, have been able to test the combined effects of climate variables and prey abundance on seabird breeding phenology and brood size.

Here, we explore the effects of climate and prey abundance in the Norwegian Sea on timing of breeding and hatching brood size of European shags *Phalacrocorax aristotelis* in Norway. Cook & Heath (2005) demonstrated a close positive correlation between recruitment, spawning-stock biomass and SST for saithe *Pollachius virens* in the North Sea. Although no such correlations have been published for the Northeast Arctic saithe in the Norwegian Sea, SSTs have been increasing there since 1990 (e.g. Ottersen 2010), and the size of the spawning stock of Northeast Arctic saithe (hereafter saithe) increased steeply until 2005 followed by a substantial decrease thereafter (ICES 2013, Mehl 2013). Young saithe of this stock is the most important forage fish for European shags (hereafter shag) breeding in colonies along the central Norwegian coast (e.g. Hillersøy & Lorentsen 2012, T. Anker-Nilssen unpubl. data). Concurrent with the stock increase of Northeast Arctic saithe during the 1990s and early 2000s, the Norwegian breeding population of shag also increased (Barrett et al. 2006), and Bustnes et al. (2013) demonstrated that the annual population growth rates of shags in 2 colonies in the Norwegian Sea were positively correlated with the abundance of 1 yr old saithe and negatively correlated with the lagged (1 yr) NAO winter index.

In this study we follow up on Bustnes et al. (2013) and explore the relationships between saithe abundance and 2 aspects of the shags' reproductive performance: the timing of their breeding and their brood size at hatching, and test how these parameters are affected by the abundance of young saithe and the size of the breeding population. When controlling for any density-dependent effects of shag population size, we expect that, in years with high abundance of saithe, hatching brood size will be higher than in years with low saithe abundance. Furthermore, as the shags from our study colonies (Sklinna and Røst) remain on the central Norwegian coast throughout the year (Bakken et al. 2003) and the adults often stay close to the colonies in winter (F. Daunt, T. Anker-Nilssen, S.-H. Lorentsen unpubl. data), we expect

that they are able to explore the abundance of 1 and 2 yr old saithe, as these are the only age-groups that are available in the vicinity of the colonies before the onset of breeding (see below). Thus, we expected that the shags breed earlier in years with high abundance of saithe. Moreover, as shags are exposed to both large-scale and local climatological factors we also wanted to explore how their reproductive performance and the availability of their staple food during the breeding season interact with these factors.

MATERIALS AND METHODS

Shag data

Annual data on shag population size and breeding performance (expressed by counts of nests and nest contents) were collected as part of the Norwegian monitoring programme for seabirds (e.g. Barrett et al. 2006, Lorentsen & Christensen-Dalsgaard 2009) and the seabird monitoring and mapping programme SEAPOP (e.g. Anker-Nilssen et al. 2006). We used data from 2 colonies: (1) Heimøya (65° 13′ N, 10° 58′ E), the largest shag colony in Sklinna, a small archipelago situated ~20 km off the mainland coast of Nord-Trøndelag in central Norway, and (2) the island of Ellefsnyken (67° 27′ N, 11° 55′ E), which holds the largest shag colony in Røst, the outermost municipality of the Lofoten Islands, situated 100 km west of the mainland coast in Nordland (Fig. 1) (see Bustnes et al. 2013 for details on population sizes and trends). The counts were aimed for consistent long-term monitoring of population size and unfortunately the field work at the 2 sites did not coincide in time. This prevented direct comparisons of nest contents and called for simple ways of estimating indices that reflect timing of breeding and brood size at the same time of season (peak of hatching) as detailed below.

We used data from the period 1989 to 2009, which includes all years with complete data sets from both colonies and parallel data on abundance of 1 and 2 yr old saithe. Population size in each colony was determined by nest counts in study plots in early June (Heimøya, hereafter Sklinna) and June–July (Ellefsnyken, hereafter Røst). At both sites the study plots covered the whole colony, and nest content (whenever visible) was registered for all nests concurrently with the monitoring of population size. At Sklinna,
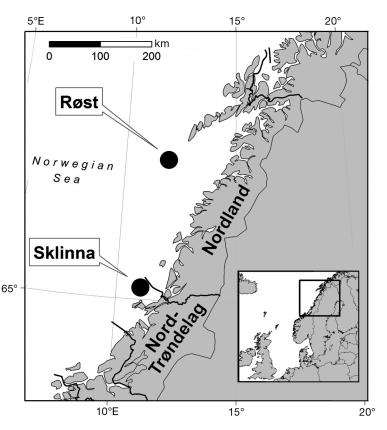

Fig. 1. Location of the study colonies, Sklinna and Røst

this usually took place during 1 to 2 consecutive days in the first 2 wk of June (range 28 May to 15 June, mean 7 to 8 June) when 0–60 % (mean 14 %) of the nests contained at least 1 chick (0 % had hatched in 2008 and 2009). The work at Røst started on average 13 d (range 0–27) later when hatching had occurred in 0–76 % (mean 35 %) of the nests (0 % in 1996), and the counts of the 9 different plots were spread over a longer period of time (mean 23 d, range 2–39). As annual proxies of timing of breeding and hatching brood size in our analysis, we used estimates of the median hatch date (i.e. when hatching had occurred in 50 % of the nests) and of the mean number of eggs plus chicks in all nests inspected (including empty nests) at the same date (hereafter termed 'hatching brood size'). Due to the different timing of the field work, slightly different approaches were used to calculate these parameters for the 2 colonies. For Sklinna, the mean progress of hatching in the years 2007 to 2012 ($x = 4.03 \times \ln(101.62 / y - 1) - 0.90$, where x = deviation from median hatching day and y = % hatched), calculated by a 3 parameter sigmoidal regression from annual subsamples of about 50 nests checked at 5 d intervals throughout most of the breeding season (S.-H. Lorentsen unpubl. data), was

used in all years to estimate the median hatch date for the nests in the population monitoring plots. Similarly, annual hatching brood size on these dates was estimated in the same way by using the corresponding mean rate of change in hatching brood size (−0.008 eggs or chicks d^{-1}) calculated for the same sub-samples of nests. At Røst, the field work covered the week of peak hatching in 14 of the 21 years, which enabled estimating the median hatch date more reliably from a linear regression between the observed proportions hatched in each study plot against the day of visit in the same year. The same approach was used to estimate annual hatching brood size in these years. For the other years, when hatching had already occurred in 70 to 76% of the nests before the first visit (6 years) or only 20% had hatched before the last visit (one extreme year, 1996), we extrapolated from these proportions by applying the mean regression rate of hatching (2.36% d^{-1}) in 17 other years (1989 to 2012) when field work covered the peak of hatching more adequately. Hatching brood size was then estimated using the mean rate of change in clutch size between median hatch date and the date of first visit (6 years, −0.012 to −0.011 eggs or chicks d^{-1}) or last visit (1 year, −0.006 eggs or chicks d^{-1}).

Climate variables

The winter NAO index (December to February) was used as a proxy for large-scale climate variation. Using NAO as a proxy is favourable since it has been demonstrated that large-scale climate indices often better predict variation in ecological processes than local climate parameters (Hurrell et al. 2003). Data on

the station-based winter NAO index (wNAO) for all relevant years were obtained from www.cgd.ucar. edu/staff/jhurrell/ and entered unlagged as a covariate in the analyses (Fig. 2).

Sea surface temperature (SST), averaged for February to April, was used as a proxy for the environmental conditions experienced by young saithe and other potential prey in the colony area during the pre-breeding period of the shags. The SST data, averaged over a 2° × 2° grid around each colony were obtained from http://iridl.ldeo.columbia.edu/SOURCES/. NOAA/.NCDC/.ERSST/.version3b/ (Smith et al. 2008) and entered as colony-specific covariates in the analyses (Fig. 2).

Winter air temperatures (wAT) from the meteorological stations at Sklinna and Røst were averaged for December to February and used as an additional proxy to NAO of the local environmental conditions experienced by wintering shags. The data were obtained from www.yr.no and entered as mean values for the 2 colonies in the analyses (Fig. 2).

Fish data

The Northeast Arctic saithe stock spawns in pelagic waters in the eastern part of the Norwegian Sea in late winter (peaks in February), and the young fish move into the kelp forest in shallow coastal waters along the Norwegian coast during their first summer where they stay until they recruit to the pelagic stock when 3 yr old (Mehl et al. 2011).

All data on the variation in abundance of young saithe were extracted from the latest report of the ICES Arctic Fisheries Working Group (ICES 2013) with permission from ICES. These data were
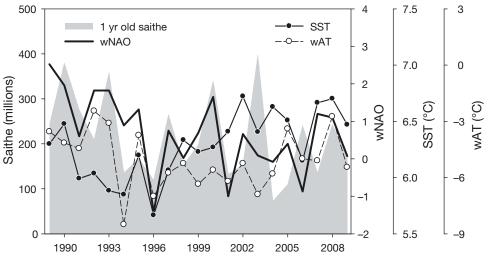

Fig. 2. Annual variation in abundance (individuals) of 3 yr old saithe *Pollachius virens* (back-lagged by 2 yr to indicate 1 yr old saithe), winter (December to March) North Atlantic Oscillation index (wNAO), mean sea surface temperature (SST) from February to April within a 2° × 2° block around the colony, and mean winter (December to February) air temperature (wAT) at the colony. For simplicity, SST and wAT are presented as the average of the values for Sklinna and Røst, which were strongly correlated (SST: $r^2 = 0.98$, p < 0.001; wAT: $r^2 = 0.59$, p < 0.001)

derived from the extended survivor's analysis (XSA) assessment of the Northeast Arctic saithe stock, which spawns along the Norwegian coast between 62 and 69° N (ICES 2013). The model is based on age-specific data on catch numbers, weight and maturity and a fixed natural mortality and is tuned by CPUE data from trawl fisheries and indices from an acoustic survey. We used the abundance estimates for saithe recruits at age 3 as indices of 1 yr old (Saithe[1]) and 2 yr old saithe (Saithe[2]) by backdating them by 2 and 1 years, respectively. As in our previous study (Bustnes et al. 2013), we had no data to account for possible inter-annual variation in mortality rates of the youngest age classes when lagging the data. All fish data were log-transformed prior to analysis to achieve linear relationships on a log scale.

Statistical analyses

All analyses were carried out in SAS v. 9.2 (SAS 2008). Before their use in further analyses, parameters with significant temporal trends were detrended by using the residuals from their linear relationship with year. Multivariate linear regression models (PROC REG) were then used to examine the associations between hatching brood size, hatching date and population size, and the various covariates. We used the command 'white' in PROC REG to obtain heteroscedastic-consistent standard errors when necessary, and applied autoregressive models (PROC AUTOREG) to test for any covariance in error structure over time. Models with different covariates were compared using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$), preferring models with the lowest ΔAIC$_c$ (and highest model likelihood; Burnham & Anderson 2002). Non-nested models within 2 ΔAIC$_c$ units of each other were considered to be equally well supported, whereas models nested within the top rank model were considered unsupported if they contained more parameters, even if their ΔAIC$_c$ was < 2.

As a final step, we ran autoregressive models (PROC AUTOREG) and used the ARCH test to explore if there were any 1 to 3 yr lagged autocorrelation in the error structure for the best models.

RESULTS

Long-term trends and bivariate correlations

Breeding population size of shags increased during the study period in both colonies (Table 1), and was highly correlated (r = 0.64, p < 0.01). Hatching date also increased in both colonies (Fig. 3, Table 1), but did not correlate between the colonies (r = 0.29, p > 0.05) or with population size (Sklinna r = −0.25, p > 0.05; Røst r = 0.16, p > 0.05). We did not detect any correlation in hatching brood size between the 2 colonies (r = 0.38, p > 0.05), although hatching brood size was correlated to population size at both colonies (Sklinna r = 0.63, p < 0.01; Røst r = 0.53, p < 0.05). In both cases, hatching brood size also correlated strongly with median hatch date (Sklinna r = −0.49, p < 0.05; Røst r = −0.62, p < 0.01).

SST increased significantly during the study period, whereas wNAO showed a similar decrease and wAT was stable (Table 1). As is typical for climate parameters, there was some autocorrelation between these variables in the study period (Table 2), but we considered it sufficiently moderate (all r^2 < 0.3) to justify that we entered them all into the same model. As only one of them (wNAO) ended up in a top rank model (see 'Results'), there is no reason to expect this biased the interpretation of our results.

There were no temporal trends in the populations of 1 and 2 yr old saithe during the study period (Table 1). Population size of 1 yr old saithe correlated positively with wNAO (r = 0.49, p < 0.05), but not with SST (r = 0.11, p > 0.05) or wAT (r = 0.24, p > 0.05). No such correlations were observed for 2 yr old saithe.

Table 1. Tests for yearly linear trends in parameters used to examine the relationship between median hatch date and the contemporary hatching brood size of shags *Phalacrocorax aristotelis* at 2 colonies (Sklinna and Røst, Norway) and various environmental factors. Sample size = 21 (number of years from 1989 to 2009) for all parameters. Parameters with temporal trends were normalised before analyses by using the residuals from a regression with year

Parameter	Slope (±SE)	r^2	p
Population size Sklinna	0.071 (0.0009)	0.75	<0.0001
Population size Røst	0.049 (0.012)	0.46	0.0008
Median hatch date Sklinna	0.673 (0.236)	0.56	<0.0001
Median hatch date Røst	1.711 (0.283)	0.66	<0.0001
Hatching brood size Sklinna	−0.035 (0.010)	0.39	0.002
Hatching brood size Røst	−0.020 (0.020)	0.06	0.29
1 yr old saithe	−0.037 (0.016)	0.22	0.03
2 yr old saithe	−0.014 (0.019)	0.03	0.47
SST (February to April)	0.027 (0.009)	0.35	0.005
wNAO (December to March)	−0.078 (0.033)	0.22	0.03
wAT (December to February)	−0.034 (0.056)	0.02	0.55

Fig. 3. Annual variation in median hatch date and the contemporary hatching brood size of shags *Phalacrocorax aristotelis* at 2 colonies (Sklinna and Røst, Norway) from 1989 to 2009. Data is presented as deviance from the overall mean (0 on the *y*-axis), and predicted values with 95% CI (grey shading) from the top-ranked model (see Tables 3−5)

Table 2. Correlation matrix for different parameters used to estimate the yearly variation in median hatch date and the contemporary hatching brood size in 2 shag *Phalacrocorax aristotelis* colonies (Sklinna and Røst, Norway). Sample size is 21 (number of years from 1989 to 2009) for all correlations. Parameters: winter NAO (wNAO), winter air temperature (wAT), sea surface temperature (SST), 1 yr old saithe (Saithe[1]) and 2 yr old saithe (Saithe[2]). *Significant ($p < 0.05$) correlations (in **bold**)

	Saithe[2]	SST	wAT	wNAO
Saithe[1]	−0.19	0.11	0.24	**0.49***
Saithe[2]		−0.03	−0.29	−0.14
SST			0.38	**0.49***
wAT				**0.54***

Multivariate models for timing of hatching

In both colonies, the best model for median hatch date included a negative effect of 1 yr old saithe (Table 3), i.e. hatching occurred earlier in years with high abundance of saithe. The model for Røst accounted for 70% of the variation in hatch date and also included equi-directional effects of 2 yr old saithe and wNAO, which explained 14% and 12%

respectively, while the model for Sklinna explained only 15% and contained no additional covariates (Table 4). The second best model for Sklinna included also wNAO and had an AIC_c value 0.88 units higher than the top-ranked model (Table 3), whereas the second best model for Røst included 4 covariates (1 and 2 yr old saithe, wNAO and wAT), and had a 1.3 units higher AIC_c than the top ranked model. These models are also less plausible as they contain one parameter more and were nested within the top ranked models.

The total AIC weight for all models of hatching dates including 1 yr old saithe was 0.65 and 0.95 for Sklinna and Røst, respectively. At both colonies, wNAO and wAT contributed to models within 2 AIC_c units of the top-ranked model, as did SST at Røst.

Multivariate models for brood size

For both colonies, the best model for hatching brood size included a positive effect of population size (Table 5), i.e. the brood size was larger in years with large population sizes. The model for Sklinna explained 40% of the variation and included no other
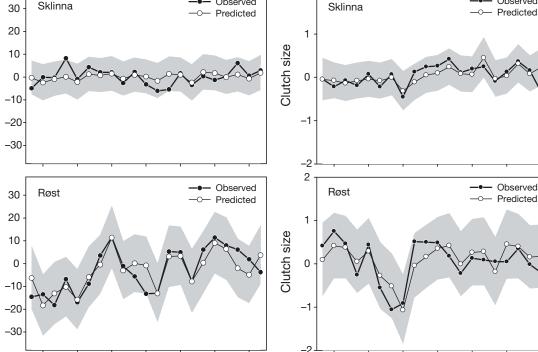
Table 3. Comparison of candidate models describing the annual variation in median hatch date of shags *Phalacrocorax aristotelis* breeding at 2 colonies (Sklinna and Røst, Norway) from 1989 to 2009. Parameters: winter NAO (wNAO), winter air temperature (wAT), sea surface temperature (SST), population size (Pop.size), 1 yr old saithe (Saithe[1]) and 2 yr old saithe (Saithe[2]). Models are ranked by ΔAIC_c, but model likelihood (ML), AIC weight (AICwt) and r^2 are also given. Only models with $\Delta AIC_c < 5$ are shown

Rank	Colony/model	AIC_c	ΔAIC_c	ML	AICwt	r^2
	Sklinna					
1	Saithe[1]	54.44	0.00	1.00	0.11	0.15
2	Saithe[1] + wNAO	55.32	0.88	0.64	0.07	0.21
3	Saithe[1] + Saithe[2]	55.74	1.30	0.52	0.06	0.20
4	Pop.size	55.98	1.54	0.46	0.05	0.09
5	Saithe[1] + wAT	56.12	1.68	0.43	0.05	0.18
6	Saithe[2]	56.25	1.82	0.40	0.04	0.08
7	Saithe[1] + Pop.size	56.61	2.17	0.34	0.04	0.16
8	Saithe[1] + Saithe[2] + wNAO	56.72	2.29	0.32	0.03	0.26
9	Saithe[1] + Saithe[2] + wAT	56.77	2.33	0.31	0.03	0.26
10	Saithe[1] + SST	56.83	2.39	0.30	0.03	0.15
11	Saithe[1] + wNAO + SST	56.87	2.43	0.30	0.03	0.26
12	Saithe[2] + Pop.size	57.66	3.22	0.20	0.02	0.12
13	SST	57.68	3.24	0.20	0.02	0.01
14	wAT	57.78	3.34	0.19	0.02	0.01
15	Pop.size + wAT	57.81	3.37	0.19	0.02	0.11
16	Saithe[1] + Pop.size + wNAO	57.89	3.45	0.18	0.02	0.22
17	wNAO	57.89	3.45	0.18	0.02	0.00
18	Saithe[2] + wAT	57.99	3.55	0.17	0.02	0.11
19	Saithe[1] + wNAO + wAT	58.00	3.57	0.17	0.02	0.22
20	Saithe[1] + SST + wAT	58.13	3.70	0.16	0.02	0.21
21	Saithe[1] + Saithe[2] + SST + wAT	58.24	3.80	0.15	0.02	0.32
22	Pop.size + wNAO	58.29	3.85	0.15	0.02	0.09
23	Saithe[1] + Pop.size + wAT	58.35	3.91	0.14	0.01	0.20
24	Pop.size + SST	58.36	3.92	0.14	0.01	0.09
25	Saithe[1] + Saithe[2] + SST	58.41	3.97	0.14	0.01	0.20
26	Saithe[1] + Saithe[2] + wNAO + SST	58.41	3.97	0.14	0.01	0.31
27	Saithe[1] + Saithe[2] + Pop.size	58.44	4.00	0.14	0.01	0.20
28	Saithe[2] + SST	58.47	4.04	0.13	0.01	0.09
29	Saithe[2] + wNAO	58.64	4.20	0.12	0.01	0.08
30	Saithe[2] + Pop.size + wAT	59.24	4.80	0.09	0.01	0.17
31	Saithe[2] + SST + wAT	59.25	4.82	0.09	0.01	0.17
32	Saithe[1] + Pop.size + SST	59.31	4.88	0.09	0.01	0.17
33	Saithe[1] + Saithe[2] + wNAO + wAT	59.32	4.89	0.09	0.01	0.28
	Røst					
1	Saithe[1] + Saithe[2] + wNAO	78.70	0.00	1.00	0.31	0.70
2	Saithe[1] + Saithe[2] + wNAO + wAT	80.00	1.30	0.52	0.16	0.72
3	Saithe[1] + Saithe[2] + wNAO + SST	80.57	1.87	0.39	0.12	0.72
4	Saithe[1] + Saithe[2] + Pop.size + wNAO	81.07	2.37	0.31	0.10	0.71
5	Saithe[1] + Saithe[2] + wNAO + SST + wAT	82.03	3.32	0.19	0.06	0.75
6	Saithe[1] + Saithe[2]	83.08	4.38	0.11	0.04	0.57
7	Saithe[1] + Saithe[2] + Pop.size + wNAO + wAT	83.11	4.41	0.11	0.03	0.73

covariates, whereas that for Røst explained 48% and also included an equally important positive effect of 1 yr old saithe abundance (Table 6). The second best model for Sklinna explained no more of the variation than the best model, but included abundance of 2 yr old saithe in addition to population size, while the second best model for Røst included the abundance of both 1 and 2 yr old saithe as well as wAT (Table 3). However, not only did these models have higher AIC_c values (2.34 and 1.24 units for Sklinna and Røst, respectively), but they were also considered less plausible because they had 1 parameter more and were nested within the top-ranked models.

The total AIC weight values for all models including 1 yr old saithe was 0.17 and 0.84 for Sklinna and Røst, respectively. None of the climate variables contributed to models within 2 AIC_c units of the top-ranked model at Sklinna, and only wAT contributed at Røst.

For median hatch date there was no autocorrelation in the error structure for the best models (all p > 0.36), but hatching brood size at both colonies could be best fitted to an AR1 model (Sklinna $t = -1.99$, p = 0.06; Røst $t = -2.17$, p = 0.04). Correcting for this autocorrelation increased the predictive power of the models from 40% to 53% for Sklinna and from 48% to 57% for Røst.

DISCUSSION

Due to huge inter-annual variation in the onset of breeding, the field work did not cover the peak of hatching in all years. For 18 yr at Sklinna and 7 yr at Røst, we therefore estimated the date of 50% hatched by applying the average rate of hatching in years when field work was better timed. For the

Table 4. Estimated slopes, explained variance (partial and for the model) and variance inflation factor (VIF) for the variables best explaining the annual variation in mean hatching dates of shags *Phalacrocorax aristotelis* at 2 colonies (Sklinna and Røst, Norway) from 1989 to 2009. Estimates are from the top rank model in Table 3. Parameters: winter NAO (wNAO), 1 yr old saithe (Saithe[1]) and 2 yr old saithe (Saithe[2]). Standard errors (SE) and p-values are adjusted for heteroscedasticity (not constant variance over time)

Colony/ variable	Estimate (SE)	t	Pr > |t|	Partial r^2	Model r^2	VIF
Sklinna						
Intercept	0.3744 (0.7709)	0.49	0.6327			
Saithe[1]	−0.00002 (0.000008)	−1.85	0.0804	0.15	0.15	
Røst						
Intercept	1.2573 (1.0452)	1.2	0.2455			
Saithe[1]	−0.00005 (0.00001)	−4.85	0.0001	0.44	0.44	1.34
Saithe[2]	−0.00004 (0.00001)	−3.54	0.0025	0.14	0.58	1.04
wNAO	−3.8221 (1.0651)	−3.59	0.0023	0.12	0.70	1.32

other 14 yr at Røst, the estimation could be made more reliably because the longer period of field work covered the peak of hatching and allowed use of the hatching rate from the same year. Consequently, we expect the estimates for Sklinna to be more biased than those for Røst, which may well explain why the best model for this colony only explained 21% of the variation in timing, whereas that for Røst accounted for as much as 70%. A similar difference was not evident for hatching brood size.

Our study indicates that shags in the Norwegian Sea only depend to a minor degree on climatic cues for timing of their breeding (e.g. Burthe et al. 2012, but see Frederiksen et al. 2004, Wanless et al. 2009), but phenological relationships may be masked by high abundance and/or broad peaks of seasonal prey (Durant et al. 2005). More importantly, we demonstrate that the shags' timing of breeding as well as their hatching brood size is closely correlated with stock abundance estimates of the available age groups of saithe also found in their diet. These results strongly support previous assumptions that saithe is a key prey species for shags breeding in the Norwegian Sea (e.g. Anker-Nilssen 2005, Hillersøy & Lorentsen 2012, Bustnes et al. 2013). In a recent study based on fish otoliths in pellets regurgitated by adults (Hillersøy & Lorentsen 2012, S.-H. Lorentsen unpubl. data), it was found that saithe comprised between 27% and 89% (mean 68%) of the diet biomass of shags at Sklinna during the breeding seasons 2007 to 2012. Saithe is also the most common prey of shags breeding at Røst (Anker-Nilssen 2005, T. Anker-Nilssen unpubl. data). Although Bustnes et al. (2013) demonstrated that population size in the previous year negatively affected the annual rate of population change in our study colonies, in this study we show that a high population size did not delay breeding or reduce brood size. This is an important finding because it strongly indicates that the population increase in years of peak prey abundance mainly reflects reduced nonbreeding among experienced breeders and is not caused by increased recruitment of young birds that would tend to lay late and smaller clutches (e.g. Sæther 1990, Oro et al. 2014). Additional support for this hypothesis comes from Sklinna in 2009, when the size of the breeding population temporarily

Table 5. Comparison of candidate models describing the annual variation in hatching brood size of shags *Phalacrocorax aristotelis* breeding at 2 colonies (Sklinna and Røst, Norway) from 1989 to 2009. Parameters: winter NAO (wNAO), winter air temperature (wAT), sea surface temperature (SST), population size (Pop.size), 1 yr old saithe (Saithe[1]) and 2 yr old saithe (Saithe[2]). Models are ranked by ΔAIC$_c$, but model likelihood (ML), AIC weight (AICwt) and r^2 are also given. Only models with ΔAIC$_c$ <5 are shown

Rank	Colony/model	AIC$_c$	ΔAIC$_c$	ML	AICwt	r^2
	Sklinna					
1	Pop.size	−62.92	0.00	1.00	0.29	0.40
2	Saithe[2] + Pop.size	−60.58	2.34	0.31	0.09	0.40
3	Pop.size + wAT	−60.53	2.38	0.30	0.09	0.40
4	Pop.size + wNAO	−60.42	2.50	0.29	0.08	0.40
5	Saithe[1] + Pop.size	−60.41	2.51	0.29	0.08	0.40
6	Pop.size + SST	−60.40	2.51	0.28	0.08	0.40
7	Saithe[2] + Pop.size + wAT	−57.98	4.93	0.08	0.02	0.41
	Røst					
1	Saithe[1] + Pop.size	−39.64	0.00	1.00	0.24	0.48
2	Saithe[1] + Pop.size + wAT	−38.40	1.24	0.54	0.13	0.52
3	Saithe[1] + Saithe[2] + Pop.size	−37.88	1.76	0.42	0.10	0.51
4	Saithe[1] + Pop.size + SST	−37.42	2.22	0.33	0.08	0.49
5	Saithe[1] + Pop.size + wNAO	−36.84	2.81	0.25	0.06	0.48
6	Saithe[1] + Pop.size + SST + wAT	−36.08	3.57	0.17	0.04	0.54
7	Saithe[1] + Saithe[2] + Pop.size + wAT	−35.98	3.66	0.16	0.04	0.54
8	Saithe[1] + Pop.size + wNAO + wAT	−35.77	3.87	0.14	0.03	0.53
9	Pop.size	−35.27	4.37	0.11	0.03	0.28
10	Saithe[1] + Saithe[2] + Pop.size + SST	−35.14	4.50	0.11	0.03	0.52

Table 6. Estimated slopes, explained variance (partial and for the model) and variance inflation factor (VIF) for the variables best explaining the annual variation in hatching brood size of shags *Phalacrocorax aristotelis* at 2 colonies (Sklinna and Røst, Norway) from 1989 to 2009. Estimates are from the top-ranked model in Table 5. Parameters: population size (Pop.size) and 1 yr old saithe (Saithe[1]). Standard errors (SE) and p-values are adjusted for hetero-scedasticity (not constant variance over time)

Colony/variable	Estimate (SE)	t	Pr > |t|	Partial r^2	Model r^2	VIF
Sklinna						
Intercept	−0.0268 (0.0428)	−0.63	0.5387			
Pop.size	0.0004 (0.0001)	3.44	0.0027	0.40	0.40	
Røst						
Intercept	−0.0216 (0.0765)	−0.28	0.7812			
Saithe[1]	0.000002 (0.0000007)	3.24	0.0046	0.24	0.24	1.01
Pop.size	0.0015 (0.0004)	3.68	0.0017	0.24	0.48	1.01

dropped to only 60 to 71% of that in the adjacent years and the biomass of 1 yr old saithe in the shag diet (24%) was nearly one third of the average (61%) for the other years in the period 2007 to 2012 (S.-H. Lorentsen unpubl. data).

In our study, median hatch dates and wNAO did not correlate at Sklinna, but for Røst the correlation was significant and negative indicating earlier breeding after winters with high NAO indices. Moreover, the abundance of 1 yr old saithe was positively correlated with wNAO and in both colonies the shags bred earlier when more 1 yr old saithe were available. Saithe in the North Sea has responded positively to increasing SSTs (Cook & Heath 2005), and an earlier spawning has also been observed for saithe in Faroese waters (Homrum et al. 2012). There were no correlations between SSTs and the abundance indices of young saithe in our analysis (Table 2), nor when we back-lagged the saithe data an extra year to account for possible effects on first-year fish (r = 0.08, p = 0.736). We did however use SSTs sampled around the colonies, whereas the Northeast Arctic saithe spawns further offshore along the shelf edge where the warmer Atlantic Current has more influence.

In both colonies the timing of breeding was strongly related to the abundance of 1 yr old saithe, but the ecological links with climate and lower trophic levels are still unclear, especially since climate expressed as SST or wAT did not contribute significantly to the best models, and wNAO only explained 12% of the variation at one colony (Røst). Although the Norwegian Sea, where both colonies are situated, comprises a seasonal environment, both shags (cf. Bakken et al. 2003) and young saithe are resident in the same ecosystem throughout the year.

Thus, the shags should always be able to track the abundance of young saithe of different age classes. Daunt et al. (2006, 2014) showed that shorter individual foraging times in late winter, an indication of good food availability, were associated with earlier and more successful breeding. Thus pre-breeding intrinsic foraging ability was critical in determining breeding phenology, and our study suggests that this is also the case for shags breeding at Sklinna and Røst.

At both study sites the shags' hatching brood size increased with their population size, probably reflecting that more adults achieve the condition to breed and lay a bigger clutch when breeding conditions are favourable (e.g. Chastel et al. 1995, Svagelj & Quintana 2011, Svagelj et al. 2012). There were no correlations between hatching brood size at Sklinna and climate parameters, but at both colonies hatching broods were smaller when breeding was late. This corresponds with the findings of Frederiksen et al. (2004) who demonstrated lower breeding success of shags in late years. There are at least 2 possible explanations for this pattern: (1) Late breeding and small hatching broods might, through their association with low wNAO reflecting colder weather conditions, indicate lower body conditions or increased mortality of adults before the onset of breeding. It has, at least, been shown that young shags may suffer increased mortality during harsh weather conditions (Frederiksen et al. 2008). Whether cold weather conditions during winters with negative wNAO make foraging more difficult (cf. Finney et al. 1999) and, thereby, reduce pre-breeding body conditions and delay the onset of breeding, is still unknown. However, shags, like all cormorants, need to dry off on land after each feeding bout (e.g. Grémillet et al. 2005) and may therefore be more susceptible to cold weather conditions in winter. (2) Poor feeding conditions in years of late breeding, as indicated by the negative relationships between abundance of 1 yr old saithe and median hatch date, may reflect that the shags delayed their breeding when abundance of 1 yr old saithe was low. As 0-group (first-year) saithe are probably not available in the shags' feeding areas early in the breeding season and do not appear as an important component of the shag diet until early July (S.-H. Lorentsen unpubl. data), it might be expected that the shags in such years could instead switch to 2 yr old saithe, if available. How-

ever, at Sklinna this age-group normally constitutes less than 10% of the total biomass of saithe in the shag diet (Hillersøy & Lorentsen 2012, S.-H. Lorentsen unpubl. data), perhaps because 2 yr old saithe is >240 mm long and possibly too large or fast-swimming to be an easy prey (cf. Hillersøy & Lorentsen 2012). The relative importance of these hypotheses is still unknown.

In a longer perspective than that covered by our study, SST and wNAO are positively correlated in the Northeast Atlantic (Visbeck et al. 2001). Although there was a significant increase in SST at both Sklinna and Røst over the study period, wNAO showed an opposite trend, and wAT was variable with no overall trend. Concurrently, hatching was progressively delayed at both colonies, in contrast to many other studies documenting that earlier breeding is a common response of seabirds to a warming climate (e.g. Moe et al. 2009, Reed et al. 2009, Votier et al. 2009, Wanless et al. 2009, Watanuki et al. 2009). Delayed breeding parallel to increasing temperatures has, however, also been demonstrated for some seabird populations in both the northern (Frederiksen et al. 2004, Wanless et al. 2008, Moe et al. 2009, Shultz et al. 2009, Wanless et al. 2009) and southern hemisphere (e.g. Barbraud & Weimerskirch 2006, Surman et al. 2012) and has sometimes been explained by a parallel decrease in food availability. Given the decadal-scale regime shifts typical for ocean climate at high latitudes (e.g. Stenseth et al. 2004), such contrasting effects are not unexpected: both prey and predator populations will respond negatively when ambient temperatures move outside (i.e. either warmer or colder) of the optimal range for the individuals' reproduction and/or survival (Irons et al. 2008). Direct physiological effects of temperature changes may also affect the predator and prey differently, especially when one spends most of the time in open air and the other lives in the sea.

The main functional responses between food abundance and different components of seabird breeding parameters need to be fully understood before implementing seabirds as indicators (Cairns 1987, Piatt et al. 2007). However, the close relationships between the breeding performance and diet of shags and the abundance of young saithe can very likely be developed into cost-efficient, early warning indicators of major shifts in saithe stock recruitment and other important changes in the coastal ecosystem of the Norwegian Sea (e.g. Barrett 1991, Anker-Nilsen 2005, Hillersøy & Lorentsen 2012). In this context, our study adds important options for refinements by including more parameters to the equation besides

the annual change in breeding numbers (Bustnes et al. 2013), although we suggest that the shags' diet should be explored in more detail. The apparent lack of density-dependent effects on median hatch date and hatching brood size acts to increase the potential value of these variables as indicators, but we emphasize the importance of collecting data during the peak of hatching to secure the most adequate estimates. The first step, standardising and continuing the monitoring effort at Sklinna and Røst, has been undertaken. The next step should be to explore if the seasonal abundance and age structure of saithe in the diet of these shags underpin the relationships already demonstrated.

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