

# Changes in the Norwegian breeding population of European shag correlate with forage fish and climate

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**ABSTRACT:** While many seabird species in the North Atlantic have declined over the last decades, the Norwegian population of the European shag *Phalacrocorax aristotelis* has increased. In the present study, we assessed the impact of food availability and climate on the shag population by analysing 25 years of data (1985 to 2009) on breeding numbers in 3 large colonies: 2 in the Norwegian Sea (65°N and 67°N) and 1 in the Barents Sea (70°N). Predictor variables were ICES abundance estimates of young saithe *Pollacius virens*, the most important forage fish for shags in the Norwegian Sea, and for the Barents Sea colony also total stock size estimates of Barents Sea capelin *Mallotus villosus*. As proxies for climate variation, we used the North Atlantic Oscillation index (NAO) for the last and the preceding winter (lagged by 1 yr). Finally, the annual population size of the study colonies in the preceding year was included in the models to control for potential density-dependent effects. The predictor variables explained 46 to 67% of the variation in annual growth rate in the colonies. In the Barents Sea colony, the shag population growth rate was only associated with capelin abundance, whereas for the Norwegian Sea colonies, there were strong positive relationships with 1 yr old saithe and a negative effect of the lagged NAO winter index. The latter effect may be a result of unfavourable weather conditions with high winds and precipitation in winter increasing mortality among non-breeding age classes of shag. Our study is the first to demonstrate a close correlation between stock estimates of the primary forage fish for European shags and shag breeding numbers. This suggests that the population growth rate and diet of shags may be used as cost-efficient and reliable indicators of major shifts in saithe stock recruitment.

**KEY WORDS:** *Phalacrocorax aristotelis* · Norwegian Sea · Barents Sea · NAO · Saithe · Breeding numbers

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## INTRODUCTION

Population growth rates of fish-eating seabirds are likely to be affected by the abundance and/or availability of forage fish near their colonies at the onset of breeding. However, documenting relationships be-

tween the growth rates of seabird breeding populations and forage fish abundance is not always straightforward. For example, measuring fish abundance on a scale at which seabirds actually forage may prove difficult as many fish species are patchily distributed and show great variations in population

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sizes (e.g. Godø 2003, Gjørseter et al. 2009, Olsen et al. 2010). In addition, the knowledge of the composition of and seasonal variation in their diet may be limited and obscured by the fact that the parents might feed their chicks different kinds of fish than those eaten by the adults (e.g. Bugge et al. 2011, Erikstad et al. 2013). Thus, studies of regulation of seabird breeding populations often use proxies for local fish abundance, such as large-scale stock estimates (e.g. Bunce 2004, Barrett et al. 2012, Jennings et al. 2012) or industrial catch data (Rindorf et al. 2000, Bertrand et al. 2012), when assessing the impact of variation in food availability. Moreover, many studies have found that variation in local climate predicts fluctuations in reproductive performance, survival and recruitment in seabird populations (e.g. Durant et al. 2003, 2004b, 2006, Gjerdrum et al. 2003, Frederiksen et al. 2004, Bustnes et al. 2010, Reiertsen et al. 2012, Sandvik et al. 2012). However, local meteorological and oceanographic factors are strongly influenced by large-scale phenomena; i.e. interactions between the ocean and atmosphere result in dynamic systems with complex patterns of variation. This variation may profoundly influence ecological processes, both in marine and terrestrial ecosystems (Ottersen et al. 2001). For example, the North Atlantic Oscillation (NAO) (Hurrell et al. 2003) has been found to predict variation in a range of population parameters in seabirds, such as return date to colonies (Harris et al. 2006), timing of breeding (Durant et al. 2004a, Frederiksen et al. 2004), body condition (Lehikoinen et al. 2006), juvenile survival (Lehikoinen et al. 2006) and adult survival (Grosbois & Thompson 2005, Harris et al. 2005, Sandvik et al. 2005, Votier et al. 2005, Sandvik & Erikstad 2008). Hence, large-scale measurements of forage fish abundance and climate systems may be combined to develop prediction models for fluctuations in seabird populations.

Breeding populations of many cormorant species (Phalacrocoracidae) fluctuate greatly, often as a result of events in the non-breeding season; e.g. a higher proportion of European shags *Phalacrocorax aristotelis* (hereafter shag) than of other seabird species may die during inclement weather events in winter (Frederiksen et al. 2008). One reason for this is probably that the plumage of cormorants is less waterproof than that of other diving birds, an adaptation to efficient underwater feeding (Grémillet et al. 2005, Frederiksen et al. 2008).

The Norwegian coast is an important breeding area for shag, with an estimated population of 24 000 pairs (or >30% of the NE Atlantic population), and over the last 2 decades, several colonies have

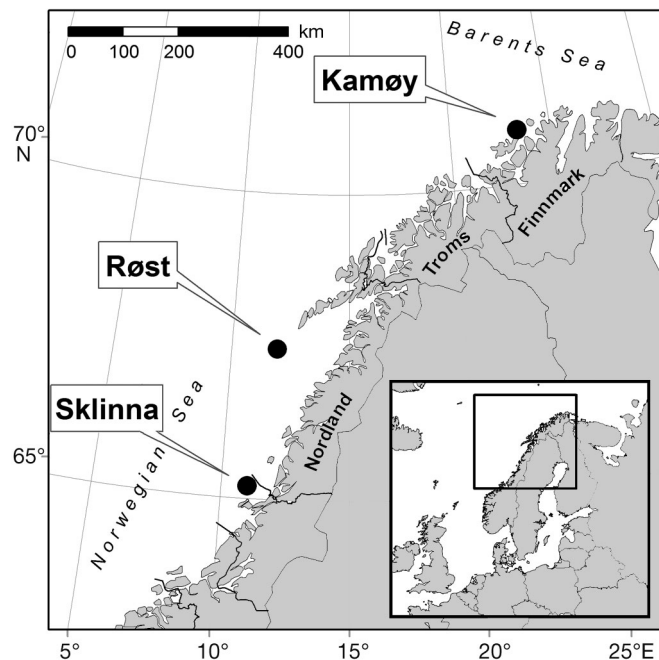


Fig. 1. Study colonies in the Norwegian Sea (Sklinna and Røst) and in the Barents Sea (Kamøy)

increased considerably in size (Barrett et al. 2006). However, except for the study by Anker-Nilssen (2005), who found that the yearly growth rate of the shag population at Røst (67°N) was negatively correlated to the NAO lagged by 1 yr, no analyses have explored potential factors influencing population growth rates in this region. In Norway, shags may feed on various species of fish, including sandeel (*Ammodytidae*) and occasionally on capelin *Mallotus villosus* in the northernmost colonies (Barrett et al. 1990, Barrett 1991, R. T. Barrett unpubl. data). However, in the colonies along the Norwegian Sea, gadoids (*Gadidae*) seem to be the most important forage fish for breeding shags, especially young age classes of saithe *Pollachius virens* which may comprise up to 90% of the diet in the reproductive season in some years (Barrett et al. 1990, Barrett 1991, Anker-Nilssen 2010, Hillersøy & Lorentsen 2012).

To document potential mechanisms behind fluctuations in shag populations on the Norwegian coast, we studied population growth rate in 3 large breeding colonies (Fig. 1) over a 25 yr period (1985 to 2009): Lille Kamøy (70°N) in the Barents Sea and Røst (67°N) and Sklinna (65°N) in the Norwegian Sea (Fig. 1). The primary objective was to assess the utility of large-scale measurements of forage fish and climate to predict annual colony growth rate. As predictor variables, we used the annual stock estimates for 2 age classes (1 and 2 yr old) of saithe. For the

northernmost colony, we also tested the relationship to annual stock size estimates for capelin since this species is known to be a driver in the Barents Sea food web (Gjørseter et al. 2009). Unfortunately, no data on the variation in sandeel abundance have been collected in this area. The shags from our study colonies remain on the Norwegian coast throughout the year, although the winter dispersal might differ between colonies (Bakken et al. 2003).

## MATERIALS AND METHODS

The data series used in the present study were collected within the framework of the Norwegian monitoring programme for seabirds (Lorentsen & Christensen-Dalsgaard 2009) and the seabird monitoring and assessment programme SEAPOP (Anker-Nilssen et al. 2006). Nest counts were carried out in monitoring plots in each of the colonies (Fig. 1) annually between 1985 and 2009, with only 2 missing years for one of the colonies (Lille Kamøy in 1990 and 2001).

Lille Kamøy (70° 51' N, 23° 03' E; hereafter Kamøy) is a rocky island situated in Hasvik, Finnmark (Fig. 1). The total population of shag in this colony is ~2000 pairs, of which the 2 to 4 monitoring plots that were counted once each year contained up to 800 pairs. Røst (ca. 67° 30' N, 12° 00' E) is a 20 km long archipelago situated 100 km west of the mainland coast in Nordland and is the outermost municipality of the Lofoten Islands (Fig. 1). The total population of shag in this colony was ~1700 pairs in 2008 (Anker-Nilssen 2009). About 25% of the shags breed on the 450 m long and 92 m high island of Ellefsnyken (67° 27' N, 11° 55' E), on which all shag nests and (if possible) their contents were counted once each year by manual inspection in late June to early July. Sklinna (65° 13' N, 10° 58' E) is a small archipelago situated ~20 km off the mainland coast of Nord-Trøndelag in central Norway (Fig. 1). The total population of shags in this colony was at its highest in 2006, with 3200 breeding pairs (Lorentsen 2006). All shag nests, and their contents, were counted once each year in early June. It is, however, possible that a few counts may have slightly underestimated the population size at some colonies, if the peak of breeding activity was missed in years of extraordinary late breeding.

## Climate variables

Climate variation is reflected by a multitude of physical measurements (e.g. air pressure, air and sea temperature, wind, precipitation, etc.) that are usually highly seasonal in nature. As covariates in studies of longer-term ecological processes, such variables are therefore best averaged across short-term periods, e.g. months or seasons, based on a *priori* assumptions of what mechanisms may be in action (Burnham & Anderson 2002). Moreover, 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). The NAO can be indexed by the sea-level pressure variability between the Azores and Iceland and, especially the winter index, summarizes, on a large scale, a number of climate variables along the Norwegian coast, including temperature and precipitation (Hurrell et al. 2003). Data on the winter NAO index (December to February) for all relevant years were obtained from [www.cgd.ucar.edu/cas/jhurrell/indices.html](http://www.cgd.ucar.edu/cas/jhurrell/indices.html) and entered unlagged (wNAO) or with a 1 yr lag (wNAO<sub>lag1</sub>) as a covariate in the analyses (Fig. 2).

## Fish data

All data on fish stock variation were extracted from ICES/Arctic Fisheries Working Group (ICES 2011) with permission from ICES. The data series for saithe was derived from the extended survivors analysis (XSA) assessment of the Northeast Arctic saithe

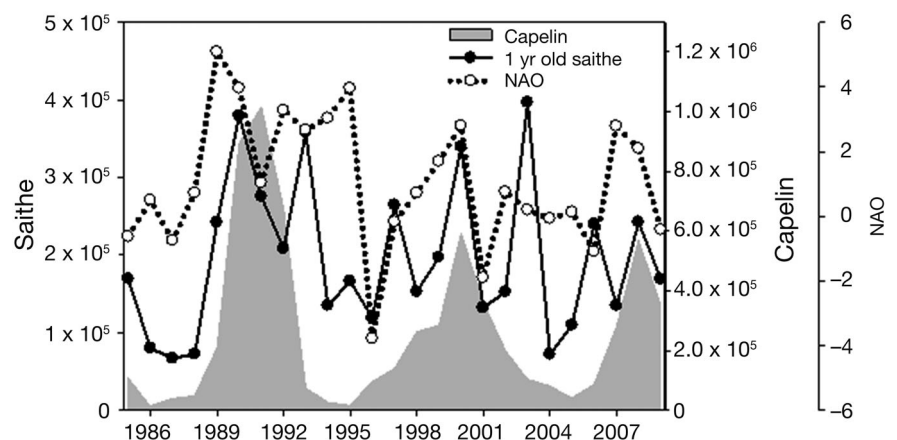


Fig. 2. Annual variation in the winter North Atlantic Oscillation (NAO) index (December to March) and in fish stock-size indices (abundance estimates, individuals) of capelin and 1 yr old saithe, known as important prey species for shags breeding in the study area

stock, which spawns along the Norwegian coast between 62 and 69°N. 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 2 yr old saithe and 1 yr old saithe by backdating them by 1 and 2 yr respectively. These age classes are the most prevalent in the shag diet (Hillersøy & Lorentsen 2012). As all attempts at establishing year class strength at Ages 0 to 2 for the Northeast Arctic saithe stock have so far failed (ICES 2011), we were not able to account for possible inter-annual variation in mortality rates of the youngest age classes when lagging the data. For capelin, we used the total number of 1 to 2 yr old fish in the Barents Sea in autumn as estimated by acoustic and trawl surveys. All fish data were log-transformed prior to analysis to achieve a linear relationship on a log scale.

### Statistical analyses

All analyses were carried out in SAS version 9.2 (SAS Institute 2008). To get a complete time series for Kamøy, we estimated population size in the 2 missing years using the expand procedure (PROC EXPAND) in SAS. To estimate yearly variation in growth rate, we used the change in the number of birds in each census ( $N$ , log scaled) from one year to the next. In the time interval  $t_i - t_{i+1}$ , this variation is defined as follows:

$$\log N_{i+1} - \log N_i = \log (N_{i+1}/N_i) = \log \lambda_i \quad (1)$$

As the first step, we tested for any temporal linear trends in population size, population growth rate and the different covariates. Population size increased significantly in all 3 colonies, but neither the population growth rate nor data on fish showed any trend over the years (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m489p235\\_supp.pdf](http://www.int-res.com/articles/suppl/m489p235_supp.pdf)). Multivariate linear regression models (PROC REG) were then used to examine the population growth rate in relation to estimates of fish abundances (acoustic and trawl surveys) and NAO. We confined the regression analyses to consider only the abundances of 1 and 2 yr old saithe for Røst and Sklinna but also added the total stock size of capelin in the analysis for Kamøy. We also tested for density-dependent effects by entering population size as a covariate. We used the command 'white' in PROC REG to obtain heteroscedastic-consistent standard errors when necessary and applied

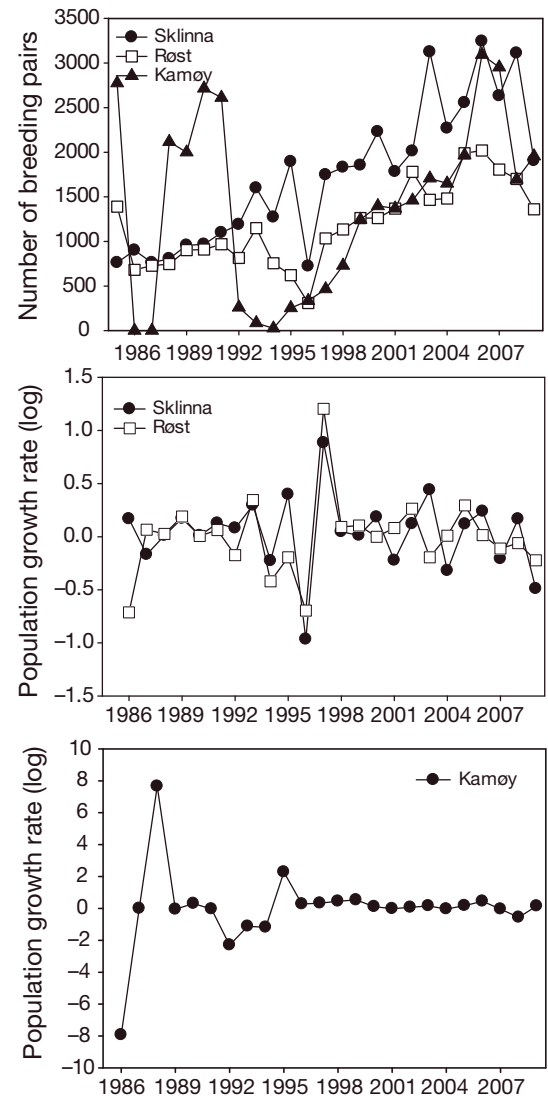


Fig. 3. Annual variation in (A) approximate breeding population size (number of breeding pairs in selected monitoring plots) and in population growth rate of shags at (B) Sklinna and Røst and (C) Kamøy during the years 1985 to 2009. Note the different growth rate scale for the Kamøy plot

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  $AIC_C$  (and highest model likelihood; Burnham & Anderson 2002). Non-nested models within 2  $AIC_C$  of each other were considered equally well supported. We examined residual plots and used GAM models to test for non-linear alternatives. However, none of these models significantly increased the fit of the models (results not shown).

## RESULTS

### Population trends and synchrony between colonies

The number of breeding pairs increased in all 3 colonies between 1985 and 2009 (Fig. 3, Table S1 in the Supplement). Tests of slopes (interaction terms in PROC GLM) show an overall difference between the 3 colonies ( $p = 0.05$ ). The Kamøy population had the steepest increase (Fig. 3, Table S1). However, comparisons of slopes between single colonies showed only small differences (Kamøy vs. Røst,  $p = 0.06$ ; Kamøy vs. Sklinna,  $p = 0.12$ ; Sklinna vs. Røst,  $p = 0.08$ ). Whereas Røst and Sklinna showed a relatively constant increase, the fluctuations at Kamøy were much larger; e.g. in 1986, 1987 and 1994, hardly any shags laid eggs in this colony (Fig. 3).

There was a strong synchrony between Sklinna and Røst in terms of yearly population growth rate ( $r = 0.62$ ,  $p = 0.001$ ; Pearson's correlation coefficient), whereas Kamøy deviated from the other colonies (Kamøy vs. Røst,  $r = 0.30$ ,  $p = 0.15$ ; Kamøy vs. Sklinna,  $r = -0.02$ ,  $p = 0.91$ ).

### Colony growth rates in relation to fish abundance and climate

The best model for Kamøy (Table 1) included only a positive effect of capelin (accounting for 17% of the variation) when controlling for population size and no effect of saithe and/or NAO (Tables 1 & 2). The second-best model for Kamøy included capelin, population size and 2 yr old saithe and had a  $\Delta\text{AICc}$  only 0.66 units higher than the top-ranked model. However, this model is questionable as it has 1 parameter more and is nested within the top-ranked model.

In contrast, the best models for Røst and Sklinna included a strong positive effect of 1 yr old saithe (Table 1), explaining 20% and 38% of the variation in growth rate, respectively, in addition to population size (Table 2). Moreover, in both colonies, there was no impact of wNAO, but  $w\text{NAO}_{\text{lag}1}$  had a negative effect, accounting for 19% of the variation at Røst and 14% at Sklinna (Table 2). The second-best

model for Sklinna included population size, wNAO,  $w\text{NAO}_{\text{lag}1}$  and 1 yr old saithe and had a  $\Delta\text{AICc}$  1.07 units higher than the top-ranked model. However, this model is considered less plausible as it has 1 parameter more and is nested within the top-ranked model. A list of all models tested is shown in Table S2.

To further test if the  $w\text{NAO}_{\text{lag}1}$  effect was caused by impacts of climate on saithe in an earlier year, we tested the relationship between these parameters. There was a significant negative relationship ( $r^2 = 0.16$ ) between 2 yr old saithe and  $w\text{NAO}_{\text{lag}1}$ , but not for 1 yr old saithe (Table 3).

As a final step, we ran autoregressive models (PROC AUTOREG) and used the ARCH test to explore any lagged autocorrelation in the error structure for the best models. For Kamøy and Røst, there was no such autocorrelation (Kamøy AR1,  $t = -1.52$ ,  $p = 0.14$ ; Røst, AR1,  $t = 1.89$ ,  $p = 0.14$ ). However, the growth rate of Sklinna could best be fitted to an AR1 model (AR1,  $t = 3.79$ ,  $p = 0.001$ ). Correcting for this autocorrelation increased the predictive power of the model from 67% (Tables 1 & 2) to 80% (see Fig. 4).

Table 1. Comparison of candidate models describing the variance in yearly population growth rate of 3 shag colonies (Sklinna, Røst and Kamøy) along the Norwegian coast from 1986 to 2009. The covariates entered are winter NAO (wNAO), winter NAO lagged by 1 yr ( $w\text{NAO}_{\text{lag}1}$ ), shag population size (Pop.size), 1 yr old saithe (Saithe[1]) and 2 yr old saithe (Saithe[2]). For the Kamøy population, the total capelin stock in the Barents Sea was also entered (Capelin). Models are ranked by  $\Delta\text{AICc}$ . For each model, we also give the model likelihood ( $\text{ML} = \exp(-0.5 \times \Delta\text{AICc})$ ) and  $r^2$ . Only the 5 best models are shown. For a list of all models, see Table S2 in the Supplement

Model	AICc	$\Delta\text{AICc}$	ML	$r^2$
<b>Sklinna</b>				
Pop.size + $w\text{NAO}_{\text{lag}1}$ + Saithe[1]	-72.82	0	1	0.67
Pop.size + wNAO + $w\text{NAO}_{\text{lag}1}$ + Saithe[1]	-71.75	1.07	0.59	0.70
Pop.size + $w\text{NAO}_{\text{lag}1}$ + Saithe[1] + Saithe[2]	-70.44	2.38	0.30	0.68
Pop.size + wNAO + $w\text{NAO}_{\text{lag}1}$ + Saithe[1] + Saithe[2]	-69.09	3.73	0.15	0.70
$w\text{NAO}$ + $w\text{NAO}_{\text{lag}1}$ + Saithe[1]	-68.29	4.53	0.10	0.61
<b>Røst</b>				
Pop.size + $w\text{NAO}_{\text{lag}1}$ + Saithe[1]	-59.46	0	1	0.56
Pop.size + wNAO + $w\text{NAO}_{\text{lag}1}$ + Saithe[1]	-56.61	2.85	0.24	0.56
Pop.size + $w\text{NAO}_{\text{lag}1}$ + Saithe[1] + Saithe[2]	-56.55	2.91	0.23	0.56
$w\text{NAO}_{\text{lag}1}$ + Saithe[1]	-55.08	4.38	0.11	0.41
Pop.size + NAO + $\text{NAO}_{\text{lag}1}$ + Saithe[1] + Saithe[2]	-53.39	6.07	0.05	0.56
<b>Kamøy</b>				
Pop.size + Capelin	33.64	0	1	0.46
Pop.size + Capelin + Saithe[2]	34.29	0.66	0.72	0.50
$w\text{NAO}_{\text{lag}1}$ + Pop.size + Capelin	35.90	2.27	0.32	0.46
Pop.size + Capelin + Saithe[1]	36.05	2.42	0.30	0.46
$w\text{NAO}$ + Pop.size + Capelin	36.23	2.60	0.27	0.46



Table 2. Estimated slopes, explained variance (partial and for the model) and variance inflation factor (VIF) for the variables best explaining the annual variation in the population growth rate for 3 shag colonies (Sklinna, Røst and Kamøy) in 1986 to 2009. Estimates are from the top-ranked model in Table 1

Variable	Estimate (SE)	<i>t</i>	Pr >   <i>t</i>	Partial <i>r</i> <sup>2</sup>	Model <i>r</i> <sup>2</sup>	VIF
<b>Sklinna</b>						
Intercept	-3.30 (0.83)					
Pop.size <sub>lag1</sub>	-0.23 (0.06)	-3.63	0.0007	0.15	0.15	1.0
wNAO <sub>lag1</sub>	-0.10 (0.02)	-4.16	0.0004	0.14	0.29	1.11
Saithe[1]	0.43 (0.06)	6.76	<0.0001	0.38	0.67	1.11
<b>Røst</b>						
Intercept	-1.75 (1.53)					
Pop.size <sub>lag1</sub>	-0.32 (0.11)	-3.12	0.005	0.18	0.18	1.0
wNAO <sub>lag1</sub>	-0.10 (0.02)	-4.19	0.0005	0.19	0.37	1.11
Saithe[1]	0.32 (0.11)	2.85	0.01	0.20	0.57	1.11
<b>Kamøy</b>						
Intercept	-6.0 (4.0)					
Pop.size <sub>lag1</sub>	-0.84 (0.20)	-4.17	0.0004	0.29	0.29	1.38
Capelin	0.95 (0.37)	2.53	0.02	0.17	0.46	1.38

Table 3. Correlation matrix for the different covariates used to estimate the yearly variation in population growth in 3 shag colonies along the Norwegian coast (1985 to 2009). See Table 1 for covariate definitions. \**p* < 0.05, \*\**p* < 0.01

	wNAO	wNAO <sub>lag1</sub>	Saithe[1]	Saithe[2]	Capelin
wNAO	1	0.14	0.41*	0.38	0.17
wNAO <sub>lag1</sub>		1	0.31	0.40*	0.25
Saithe[1]			1	0.14	0.55**
Saithe[2]				1	0.38

## DISCUSSION

Interpreting results from analyses of breeding numbers in seabird colonies is complicated since such numbers are results of different components. First, the long-term increase in colony sizes may come about through increased survival among local breeders or natal recruitment following years of high production. Alternatively, good feeding conditions in one area may attract shags from other areas (Martínez-Abraín et al. 2001), although this seems to be relatively rare in this species (Aebischer 1995). Non-breeding, however, seems to be very common (Aebischer & Wanless 1992), and the great annual fluctuations, especially at Kamøy between 1986/87 and 1988 (Fig. 3), cannot be explained by recruitment and very unlikely by mass mortality. However, the Kamøy population may have been affected by heavy mortality between 1993 and 1994, given that the population only increased gradually in the following years (Fig. 3).

There was a high co-variation in breeding numbers between the 2 Norwegian Sea colonies Sklinna and Røst (*r* = 0.62), implying that they belong to the same marine ecosystem with similar environmental conditions, i.e. conditions for the juvenile saithe. Moreover, many of the birds from the colonies may winter in the same area at the coast of Central Norway (~62 to 65° N) (Bakken et al. 2003), suggesting that they are exposed to the same winter climate and feeding conditions. Thus, poor conditions in the wintering areas may have a similar effect on survival and potential recruitment for the colonies within the Norwegian Sea. In contrast, the population changes at Kamøy were largely uncorrelated to those of the other colonies, possibly because the birds tend to winter further north than the Røst and Sklinna birds (Bakken et al. 2003), where climate and feeding conditions are different. However, ring recoveries are dominated by birds found in their first winter, and tracking of adult shag movements from 2 Norwegian colonies using geolocators indicates many adult shags stay relatively close to the breeding area throughout the year (F. Daunt et al. pers. comm.).

Over its distribution range, shag has been found to feed on different fish species, probably depending on their availability (reviewed by Hillersøy & Lorentsen 2012). Saithe is a very common pelagic fish along the whole Norwegian coast, where shallow near-shore waters serve as nursery grounds for the young from when they leave the pelagic zone in their first summer until they recruit to the pelagic stock at 3 yr of age (Olsen et al. 2010). In a recent study from Sklinna, Hillersøy & Lorentsen (2012) found that saithe comprised between 62% and 88% of the diet biomass of shags in the breeding seasons between 2007 and 2010. In addition, other gadoids made up much of the remaining diet, whereas species known to be important in other areas, such as sandeel (Rindorf et al. 2000), were of little importance. The diet of shag in other Norwegian colonies is less well studied, but gadoid prey (probably mainly saithe) is also the staple food item in their summer diet at Røst (Anker-Nilssen 2010, T. Anker-Nilssen et al. unpubl. data). We have no dietary information from Kamøy, but the diet of shags breeding on Hornøya 300 km farther east in the Barents Sea seems to be domi-

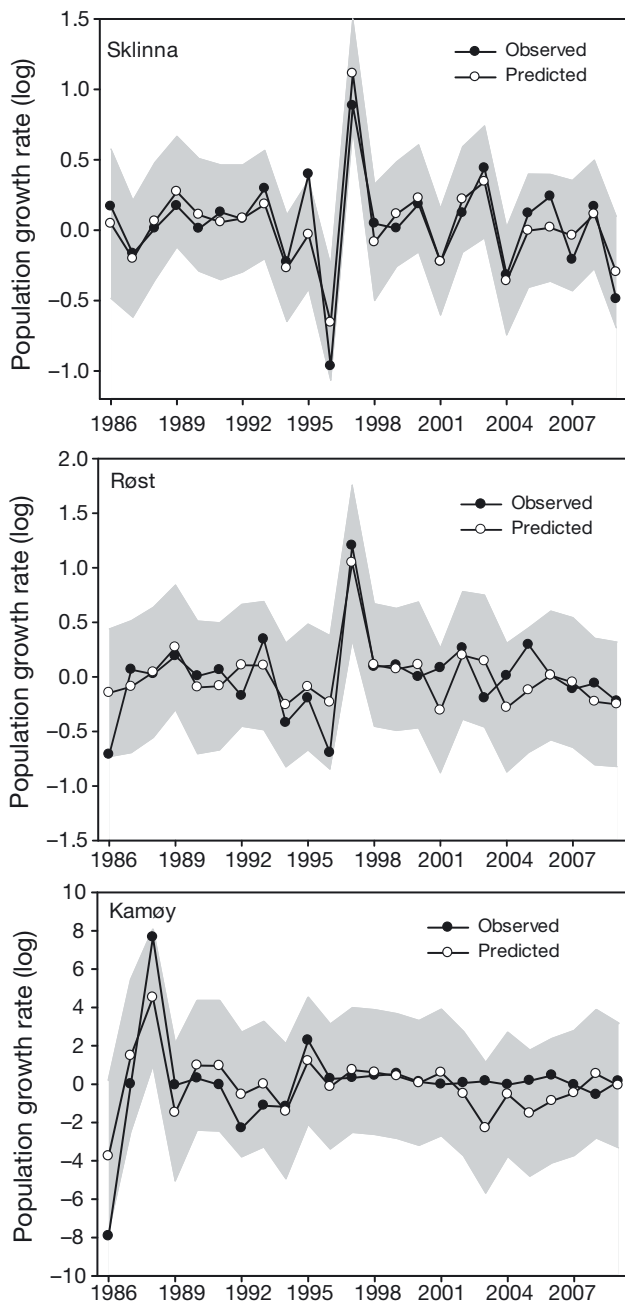


Fig. 4. Annual population growth rate of shags in 3 study colonies (Sklinna, Røst and Kamøy) and fitted values with 95% CI from the top-ranked model (see Tables 1 & 2) that best describes the population growth rate for the whole time period

nated by sandeel and gadoids, and perhaps capelin occasionally (Barrett et al. 1990, Barrett & Erikstad 2010, R. T. Barrett unpubl. data). Typically, the capelin stock also fluctuates greatly in numbers (Hjermann et al. 2004, Gjørseter et al. 2009), and in this context, it is interesting to note that the 3 years

when the shags at Kamøy did not even try to reproduce (1986, 1987 and 1994; Fig. 2) were all years with very low capelin stocks (ICES 2011). The capelin collapse in 2003 was not reflected in low breeding numbers of the shag or other seabird species in the Barents Sea (Fig. 2). However, in marked contrast to the former capelin crashes, stocks of several other forage fish species in the area, such as young cod *Gadus morhua* and herring *Clupea harengus*, were not depleted in that year (ICES 2011, Erikstad et al. 2013). Nevertheless, it is possible that young saithe is an important prey for shags also at Kamøy, but the local saithe availability at Kamøy may be less well reflected in the national stock estimates compared to the other colonies.

Local meteorological and oceanographic factors are strongly influenced by large-scale phenomena; i.e. interactions between the ocean and atmosphere result in dynamic systems with complex patterns of variation. This variation may profoundly influence ecological processes, both in marine and terrestrial ecosystems (Ottersen et al. 2001). As such, the NAO index is a well-known and commonly applied large-scale representation of the winter climate on the coast of Norway (Ottersen et al. 2001, Stenseth et al. 2004). However, the mechanisms of climate impacts on the shag populations are to be found locally and might work through impacts on fish stocks (e.g. via temperatures) or by direct effects on the birds themselves (e.g. stormy weather and precipitation). Previous studies have shown that the shag and other Phalacrocoracidae are vulnerable to inclement weather conditions, especially strong winds and wet conditions (Aebischer 1993, Frederiksen et al. 2008, Sherley et al. 2012). Since a high NAO is associated with strong onshore winds and high rainfall in the North-east Atlantic (Hurrell et al. 2003), we hypothesised that there would be a negative correlation between yearly population growth rate and the NAO index in the last winter, due to increased mortality in years of harsh weather (Frederiksen et al. 2008). However, the breeding numbers at both Sklinna and Røst were unrelated to the last winter NAO index ( $wNAO$ ) but were associated with the NAO in the winter 1 yr earlier ( $wNAO_{lag1}$ ). This suggests that established breeders were not very vulnerable to the winter weather they experienced within the climate range of our study period. However, shag may start breeding at the age of 2 (Daunt et al. 2007), and Frederiksen et al. (2008) showed that young shags may suffer increased mortality under adverse weather conditions. The lagged NAO effect may thus be a result of increased mortality among potential recruits already

in their first winter. An alternative explanation, i.e. that the recruitment of saithe in years with a high NAO was reduced, leading to smaller stocks of the 1 yr age class and fewer birds breeding, was not supported. However, it is important to keep in mind that the indices we used for 1 yr saithe were simply lagged (with no further adjustments) from estimates of 3 yr old pelagic fish, which may not reflect the true relationship between NAO and young saithe in near-shore waters.

The present study is the first to demonstrate the close correlation between stock estimates of the primary forage fish for shags and shag breeding numbers. As such, the current stock size estimate of juvenile saithe in the Northeast Arctic is a good predictor of population trends of shag in the Norwegian Sea, explaining 20 to 40% of the variation. Our results thus strongly support previous assumptions that saithe is a key species for shags in the Norwegian Sea (Anker-Nilssen 2005, Hillersøy & Lorentsen 2012). In addition, they suggest that there is a lagged effect of climate, as reflected by the wNAO index. The causal relationship here is more difficult to interpret than that of the saithe effect, but it is possible that bad weather leads to increased mortality among shag recruits in their first winter. The fact that the northernmost colony showed a different pattern may not be surprising given the fact that it belongs to a different marine ecosystem. To improve the understanding of shag population ecology on the Norwegian coast, we encourage the collection of more data on the survival and reproductive output of the populations, in addition to striving for better understanding of the diet in different regions. Such knowledge may also prove valuable for fisheries management in the Norwegian Sea given that saithe is Norway's fourth largest fishery and there is currently a lack of more immediate indicators of saithe year-class strength than the number of recruits to the pelagic stock at 3 yr of age. As also pointed out by Barrett (1991), Anker-Nilssen (2005) and Hillersøy & Lorentsen (2012), the population growth rate and diet of shags may potentially be developed as cost-efficient early warning indicators of major shifts in saithe stock recruitment and other important changes in these coastal ecosystems.

*Acknowledgements.* The present study was carried out as part of the SEAPOP programme ([www.seapop.no](http://www.seapop.no)), which is financed by the Norwegian Ministry of Environment via the Directorate for Nature Management (DN), the Norwegian Ministry of Petroleum and Energy and the Norwegian Oil and Gas Association. The field work was part of the National

monitoring programme for seabirds, which is funded by DN. We thank the large number of field workers who helped collect the data at the study sites, in particular P. Anker-Nilssen, K. Einvik, T. Nygård, N. Røv and T. Aarvak, who assisted in many years. We also thank H. Sandvik and 3 anonymous referees for valuable comments to the manuscript. Access to the colonies was granted by permissions from the Røst municipality administration and the county governors of Nord-Trøndelag, Nordland, and Finnmark. We are also indebted to the Norwegian Coastal Administration for allowing us to use the Sklinna lighthouse as a field station.

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*Editorial responsibility: Rory Wilson,  
Swansea, UK*

*Submitted: February 22, 2013; Accepted: June 10, 2013  
Proofs received from author(s): August 19, 2013*