

# Ocean climate and egg investment in the black-legged kittiwake *Rissa tridactyla*

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**ABSTRACT:** Birds allocate substantial resources to their eggs during the laying period, resources also needed for other concurrent costly processes such as mate acquisition, nest building and site defence. Egg and clutch sizes may thus vary in response to food availability prior to egg laying. We investigated the variation in egg and clutch size of black-legged kittiwakes *Rissa tridactyla* in a North Norwegian colony over a 33 yr period (1980–2012). Considerable interannual variation was evident in both egg and clutch sizes, but no temporal trends were observed. To identify environmental conditions explaining the variation, we modelled egg size and number in relation to the influx of warm Atlantic Water (AW) into the Barents Sea and to the abundance of 2 of the kittiwakes' most preferred prey species. Most of the variation was explained by the volumes of AW that flowed into the Barents Sea in winter and autumn. Both had a negative effect on egg investment. There was also a smaller, positive effect on egg investment of AW inflow (and capelin numbers for clutch size) immediately prior to egg laying. The negative impact of an increased influx of AW on kittiwakes may be partly due to the resulting warming of the waters, forcing a more northerly distribution of capelin beyond the foraging range of the kittiwakes at the colony or to changes at different trophic levels that are detrimental to kittiwake forage fish ecology. A further warming of the Barents Sea through climate change is thus forecast to be detrimental for kittiwakes.

**KEY WORDS:** Egg volume · Clutch size · Black-legged kittiwake · *Rissa tridactyla* · Ocean climate

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## INTRODUCTION

Egg formation is demanding in terms of energy and resource requirements (Nager 2006). Furthermore, egg production coincides with other costly processes, such as mate acquisition and nest defence, that will exacerbate any effects of variable resource availability. These costs may be met through an increase in uptake of protein and energy (reviewed by Williams 2005, Sorensen et al. 2010).

Because a bird's breeding season is generally timed to coincide with a seasonal maximum food availability during the chick-rearing period, an elevated energy expenditure early in the season,

i.e. during egg production, may be seriously limited by temporal variation in what is often a period of low food and/or macro- and micronutrient availability (Williams 2005). Whereas the process of egg laying may be completed within a few days, the breeding season may be initiated many weeks before any seasonal increase in food availability as parents undergo extensive physiological and behavioural preparations (Williams 2005). The Atlantic puffin *Fratercula arctica*, for example, may prepare for the nutritional demands of egg production by consuming a high trophic-level diet several months before the breeding season (Kouwenberg et al. 2013).

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Among seabirds, there are several examples of marine resource-related effects on egg production with increasing or decreasing prey availabilities resulting in females laying respectively larger or smaller eggs and clutches (Regehr & Montevecchi 1997, Sorensen et al. 2009, Tomita et al. 2009, but see Hipfner 2012). Similarly, clutch and egg size of the omnivorous yellow-legged gull *Larus michahellis* decreased after closure of an open-air landfill that functioned as a ready food source for the species (Steigerwald et al. 2015). Three longer-term studies of seabirds have also shown that declines in a preferred food base early in the egg-production period may cause declines in egg and/or clutch size over 3 to 9 decades (Mills et al. 2008, Blight 2011, Barrett et al. 2012).

The black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) is common in the North Atlantic and North Pacific but has recently suffered widespread and severe population declines throughout much of its range (Frederiksen 2010, Sandvik et al. 2014, Hamilton et al. 2016, Descamps et al. 2017). After declines of 6–8% yr<sup>-1</sup> since the mid-1990s (Barrett et al. 2006) and forecasts of local extinctions within the first 5 to 10 decades of the 21st century (Sandvik et al. 2014), kittiwakes are now categorised as ‘endangered’ in the Norwegian red-list of threatened species (Henriksen & Hilmo 2015). An accompanying decline in breeding success at some Norwegian colonies has also been registered (Barrett 2007, Anker-Nilssen et al. 2016, R. Barrett pers. obs.). Being small surface-feeding gulls (Laridae) that work at or near their energetic ceiling during periods of peak energy demands, kittiwakes are particularly sensitive to changes in the marine environment (Furness & Tasker 2000, Welcker et al. 2010, Collins et al. 2016). As a result, important breeding performance and demographic parameters are sensitive to changes in food supply (e.g. Aebischer et al. 1990, Regehr & Montevecchi 1997, Wanless et al. 2007, Reiertsen et al. 2014). In Norway, breeding success of kittiwakes increased with food availability near the colony (Barrett 2007), whereas adult survival responded positively to food availability far at sea during the non-breeding season (Reiertsen et al. 2014). Furthermore, population numbers responded negatively to ocean warming through declines in adult survival and breeding success (Barrett 2007, Sandvik et al. 2014). Due to the precarious position of the kittiwake population, there is an immediate need to explore all further possible causes of the decline in both numbers and breeding success (Fauchald et al. 2015). Because egg and clutch sizes are positively related to offspring quality (breeding date, hatching success, chick growth and survival; Coulson & Porter

1985, Williams 1994, Sorensen et al. 2009, Krist 2011) and thus important components of breeding success, it is important to address the initial investment during egg laying (Hargitai et al. 2016).

A North Norwegian kittiwake egg weighs approximately 50 g (Runde & Barrett 1981), which is equivalent to 12% of the adult body mass (mean ca. 400 g, Barrett et al. 1985). Being income breeders, gulls rely on adjustments of food intake during breeding rather than body stores to cover extra costs (Ramírez et al. 2010 and references therein). With clutch sizes of 1 to 3 eggs ( $\equiv$  12–36% of body mass), the female kittiwake needs to allocate substantial resources to the eggs during the 2–3 wk laying period (Maunder & Threlfall 1972, Coulson 2011), resources that may also be needed for other concurrent costly processes such as mate acquisition, nest building and site defence (Coulson 2011). As such, egg and clutch size can be expected to vary in response to both female body condition and the energy invested, both of which are affected by food availability prior to egg laying (Nager 2006, Ramirez et al. 2010, Vallarino et al. 2012). Such food availability is often highly dependent on a complex marine ecosystem as in the Barents Sea where this study was conducted.

The Barents Sea is a shallow continental shelf area with an average depth of 230 m whose climatic variability is determined mainly by the inflow of relatively warm and saline Atlantic Water (AW) (Loeng 1991). AW dominates the southern region of the Barents Sea and the mean monthly volume influx varies with a marked maximum in winter (Dalpadado et al. 2012, Ingvaldsen 2016; see Fig. S1 in Supplement 1 at [www.int-res.com/articles/suppl/m579p129\\_supp.pdf](http://www.int-res.com/articles/suppl/m579p129_supp.pdf)). Changes in the inflow have profound effects on the ecosystem of the Barents Sea and rates of biological production through all trophic levels from plankton to fish (Loeng 1989, Eriksen et al. 2012, Johannesen et al. 2012). Any warming of the Barents Sea through an increase in AW influx will result, for example, in distributional shifts of cold-water species northwards (Dalpadado et al. 2012). Such shifts will likely cause changes in food abundance and availability for top predators. In this study, we investigated long-term variation in egg and clutch size of kittiwakes in a colony in the southern Barents Sea to understand the proximate constraints of early breeding investment. We address the hypothesis that environmental conditions (both prey abundance and climate factors) prior to and during egg production influence kittiwake egg-laying parameters and predict that larger and more eggs would be laid in years of increased availability of preferred prey.

## MATERIALS AND METHODS

### Field protocols

This study was carried out at Hornøya (70°22' N, 31°08' E) on the eastern tip of the Varanger Peninsula in NE Norway between 1980 and 2012. When the study started, an estimated 21 000 pairs of kittiwakes bred on the island (Furness & Barrett 1985), but numbers steadily declined throughout the study period to ca. 9000 pairs in 2012 (R. T. Barrett pers. obs.). In addition to monitoring breeding numbers nearly every year, egg and clutch sizes of kittiwakes were measured using standardised protocols. Clutch size was determined through a single visual inspection of a large sample of nests spread throughout the colony on, or very soon after, the first day a newly hatched chick was seen in the colony in 1980–1983 and 1987–2012 (normally in early June, range 24 May to 19 June). The contents of all well-constructed nests that showed signs of regular occupation were noted. Newly hatched chicks were included in the counts and considered as eggs in the clutch size determination.

Except in 1980–1982, when eggs of known laying sequence were measured during the laying season, egg measurements were also made toward the end of the incubation period in 1987, 1988, 1990 and 1992–2012. Egg volume was determined from egg length and breadth measured with Vernier callipers to the nearest 0.1 mm using the formula:  $\text{Vol (ml)} = k \times \text{length} \times \text{breadth}^2$  (in cm), where  $k = 0.4861$  (for North Norwegian kittiwakes, Runde & Barrett 1981). An annual index of clutch volume was modelled based on the volumes of eggs in 2-egg clutches, as they are the most consistent in size among the 3 clutch sizes (Coulson 1963, 2011, Runde & Barrett 1981, Hipfner 2012).

### Environmental covariates

Many physical and biological covariates have been found to influence the seabirds breeding on Hornøya, including estimates of stock sizes of important forage fish and other food items, and a variety of oceanographic and meteorological parameters (e.g. Barrett 2007, Barrett et al. 2012, Reiertsen et al. 2014, Sandvik et al. 2014). For kittiwakes, the most frequent food items identified during the chick-rearing period for both adults and chicks include mature capelin *Mallotus villosus*, 1 yr old Norwegian spring-spawning herring *Clupea harengus*, sandeels *Ammodytes* sp. and fry of gadoids (Barrett 2007, Thor-

valdsen et al. 2015). Outside the breeding season, capelin in the Barents Sea and pteropods (Thecosomata) in the Grand Banks/Labrador Sea area where Hornøya kittiwakes spend November to January (Frederiksen et al. 2012) also affect their survival rate (Reiertsen et al. 2014). Because no stock size data exist for sandeels or for pteropods before 1992, and because gadoid fry do not enter the waters around Hornøya until well into the incubation and chick-rearing periods (late June and July) (Myksvoll et al. 2013), only capelin and 1 yr old herring were included in the models used to examine the variation in egg and clutch size (Supplement 1).

Rather than assuming that proxies such as the North Atlantic Oscillation index (Hurrell et al. 2003) or Barents Oscillation index (Chen et al. 2013) are adequate descriptions of regional climate, we chose a directly measured parameter that has been identified as an important driver of the Barents Sea ecosystem. This is the inflow of AW into the Barents Sea, which is the most important climatological process in the region and has been measured directly over many decades (Hjermann et al. 2004, Spielhagen et al. 2011, Walczowski et al. 2012, Ingvaldsen 2016). As a covariate, seasonal totals were modelled with 0 and 1 yr lags (Supplement 1), while capelin and herring abundances were modelled without any lags.

### Data analysis

Analyses of variation in egg and clutch sizes were carried out in Minitab® 15 and 17. Analyses of the relationship between egg volume and environmental factors were carried out in SAS version 9.4. Before use in further analyses, parameters were checked for temporal trends. We used a forward selection procedure using PROC GLMSELECT in SAS, entering all covariates to find the best candidate models. The covariates entered were mean values of the AW influx into the Barents Sea, during winter (mean of December, January and February), spring (mean of March, April and May) and autumn (mean of August, September and October). We excluded the summer time, since the influx of AW is very low and has low yearly variation (Fig. S1 in Supplement 1). We also entered abundances of mature capelin and 1 yr herring. As a second step, we examined the parameter estimates from the best model using the 'rsquare' option in PROC REG. We also used the command 'white' in PROC REG to obtain heteroscedastic-consistent error structure (change in error structure over time) and corrected standard errors and p-values

when necessary. We also considered the variance inflation factor of the parameters in the model to account for any collinearity amongst the covariates. Models with different covariates were compared using Akaike's information criterion corrected for small sample sizes ( $AIC_C$ ), preferring models with the lowest  $\Delta AIC_C$  (Burnham & Anderson 2002).

## RESULTS

Mean egg volumes in all clutches varied greatly from year to year ( $F_{26,3985} = 17.7$ ,  $p < 0.001$ ) as they also did in 2-egg clutches ( $F_{26,2918} = 16.0$ ,  $p < 0.0001$ ; Fig. 1, and see Supplement 2 at [www.int-res.com/articles/suppl/m579p129\\_supp.pdf](http://www.int-res.com/articles/suppl/m579p129_supp.pdf)). There was no evidence of a trend over time in egg volume in either group ( $r^2 < 0.01$ ,  $F_{1,25} = 0.02$ – $0.10$ ,  $p > 0.8$ ). The overall mean  $\pm$  SE volume of all eggs measured was  $46.8 \pm 0.06$  ml ( $N = 3986$ ) and that of eggs in 2-egg clutches was  $46.7 \pm 0.07$  ml ( $N = 2919$ ).

There was also significant variation ( $F_{29,24263} = 81.3$ ,  $p < 0.001$ ) in the mean clutch size (excluding empty nests) of kittiwakes between 1980 and 2012, with a minimum of 1.36 eggs clutch<sup>-1</sup> in 1987 and a maximum of 2.15 in 1999 (Fig. 1, see Supplement 3 at [www.int-res.com/articles/suppl/m579p129\\_supp.pdf](http://www.int-res.com/articles/suppl/m579p129_supp.pdf)). There was no evidence of a trend in clutch size during the same period ( $r^2 = 0.003$ ,  $F_{1,28} = 0.08$ ,  $p = 0.78$ ). The overall mean clutch size was  $1.45 \pm 0.006$  eggs clutch<sup>-1</sup> ( $N = 24293$  nests). There was a large variation in the proportion of nests containing 3 eggs (Supplement 3), but again with no evidence of a trend over time during the study period ( $r^2 = 0.001$ ,  $F_{1,28} = 0.01$ ,  $p > 0.5$ ).

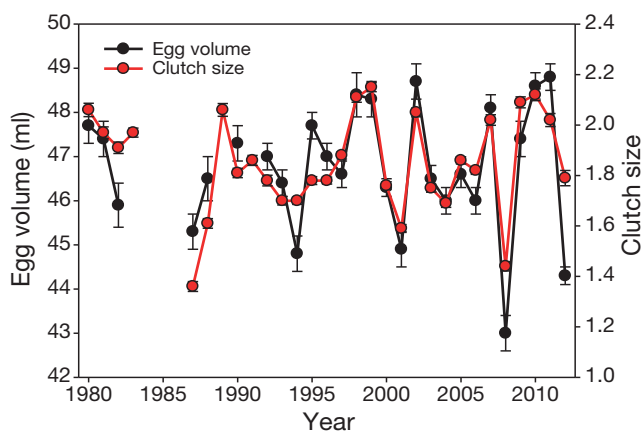


Fig. 1. Mean ( $\pm$  SE) volume (ml) of black-legged kittiwake *Rissa tridactyla* eggs in 2-egg clutches and mean ( $\pm$  SE) clutch size (eggs per occupied nest), at Hornøya, NE Norway, 1980–2012 ( $r^2 = 0.61$ ,  $p < 0.001$ ,  $N = 28$ )

Yearly variations in mean egg volume (in 2-egg clutches) correlated strongly and positively with both clutch size of the year (Fig. 1,  $r^2 = 0.62$ ,  $p < 0.001$ ) and the frequency of 3-egg clutches in the population (Fig. 2,  $r^2 = 0.51$ ,  $p < 0.001$ ).

The forward selection procedure showed that the parameters that best described the variance in egg volume were AW inflow during autumn and winter (with the lag of 1 yr) and during spring (no lag). Adding herring and both herring and capelin to this model increased  $\Delta AIC_C$  by 6.15 and 10.54 units, respectively, giving no support of any effect of these prey species (Table 1). Overall, the top-ranked model explained 0.39% of the variation in egg volume (Table 1, Fig. 3A).

Modelling the variance in clutch size over years gave much the same top-ranked model as for the egg volume including AW inflow during autumn and winter (with a 1 yr lag) and during spring (no lag). However, this model also included capelin. This top-ranked model had an explained variance of 48% (Table 1, Fig. 3B). Adding herring to this model increased  $\Delta AIC_C$  by 6.26 units, providing no support for the addition of that variable. The apparent lack of influence of capelin and herring in the models can also be seen in Fig. S2 in Supplement 1, which shows no apparent trend over time for these 2 potential prey species and the clutch size. The capelin stock has collapsed 3 times since 1980 but with no evidence of a negative effect on clutch size.

The effect of AW inflow during winter and autumn with a 1 yr lag was negative on the yearly variation in egg volume, while the influx of AW in the current spring had a positive effect both for egg volume and clutch size. The effect of capelin was positive. For

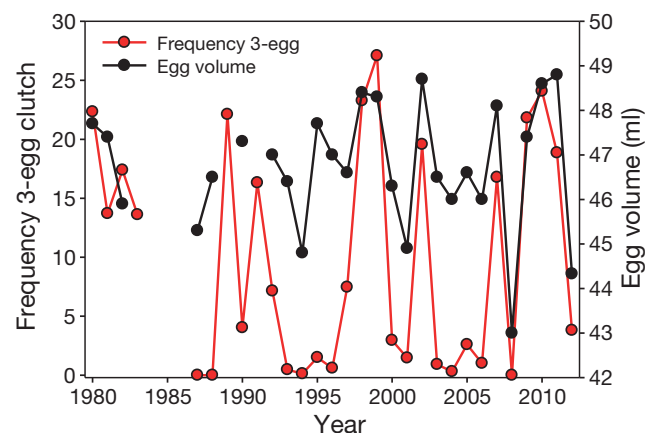


Fig. 2. Relationship between egg volume and the frequency of 3-egg clutches of black-legged kittiwake *Rissa tridactyla* in the population over years ( $r^2 = 0.51$ ,  $p < 0.001$ ,  $N = 27$ )

Table 1. Summary of a forward selection of covariates using PROC GLMSELECT in SAS. The models were run separately for egg volume and clutch size in black-legged kittiwakes *Rissa tridactyla*, which are highly correlated (Fig. 1). The covariates entered into the model were values of Atlantic water influx (AW) into the Barents Sea during winter, spring and autumn without and with a 1 yr lag. Potential prey entered with no lags were the spawning population of capelin (2–5 yr old) and 1 yr old herring from the Barents Sea. See 'Materials and methods' for details about covariates. AICc: Akaike's information criterion corrected for small sample size. **Bold**: lowest AICc values and hence best model

| Step               | Effects in               | Model R <sup>2</sup> | Adj R <sup>2</sup> | AICc                      |
|--------------------|--------------------------|----------------------|--------------------|---------------------------|
| <b>Egg volume</b>  |                          |                      |                    |                           |
| 0                  | 0-model (Intercept)      |                      |                    | 47.61                     |
| 1                  | AWautumn <sub>lag1</sub> | 0.19                 | 0.15               | 45.06                     |
| 2                  | AWwinter <sub>lag1</sub> | 0.29                 | 0.22               | 44.37                     |
| 3                  | <b>AWspring</b>          | <b>0.39</b>          | <b>0.30</b>        | <b>43.85<sup>a</sup></b>  |
| 4                  | AWspring <sub>lag1</sub> | 0.42                 | 0.30               | 46.18                     |
| 5                  | Capelin                  | 0.42                 | 0.27               | 50.00                     |
| 6                  | AWwinter                 | 0.42                 | 0.23               | 54.34                     |
| 7                  | Herring                  | 0.42                 | 0.18               | 59.33                     |
| <b>Clutch size</b> |                          |                      |                    |                           |
| 0                  | 0-model (Intercept)      |                      |                    | -58.46                    |
| 1                  | AWautumn <sub>lag1</sub> | 0.20                 | 0.17               | -62.03                    |
| 2                  | Capelin                  | 0.31                 | 0.24               | -63.03                    |
| 3                  | AWwinter <sub>lag1</sub> | 0.39                 | 0.32               | -64.50                    |
| 4                  | <b>AWspring</b>          | <b>0.48</b>          | <b>0.39</b>        | <b>-65.12<sup>a</sup></b> |
| 5                  | AWspring <sub>lag1</sub> | 0.50                 | 0.39               | -62.95                    |
| 6                  | Herring                  | 0.51                 | 0.37               | -59.44                    |
| 7                  | AWwinter                 | 0.53                 | 0.36               | -55.98                    |

<sup>a</sup>Optimal value of criterion

egg volume, the impacts of these 3 parameters were (partial correlation) 0.25, 0.19 and 0.14 for autumn, winter and spring, respectively (Table 2, Fig. S3 in Supplement 1). The variance inflation factor was close to 1, suggesting no collinearity among parameters. The sign of estimates of AW from the top-ranked model for clutch size was the same as for egg volume, and the estimate of capelin was positive. The impact of 4 parameters (partial correlation) was 0.25, 0.13, 0.17, and 0.14 for AWwinter, capelin, AWautum and AWspring, respectively. The inflation factor for the 3 parameters was also low (Table 2, Fig. S3 in Supplement 1).

## DISCUSSION

Between 1980 and 2012, kittiwake egg and clutch sizes at Hornøya changed considerably from year to year, with a strong negative response to variations in inflow of AW into the Barents Sea during the winter 18 mo previously and the preceding autumn, followed

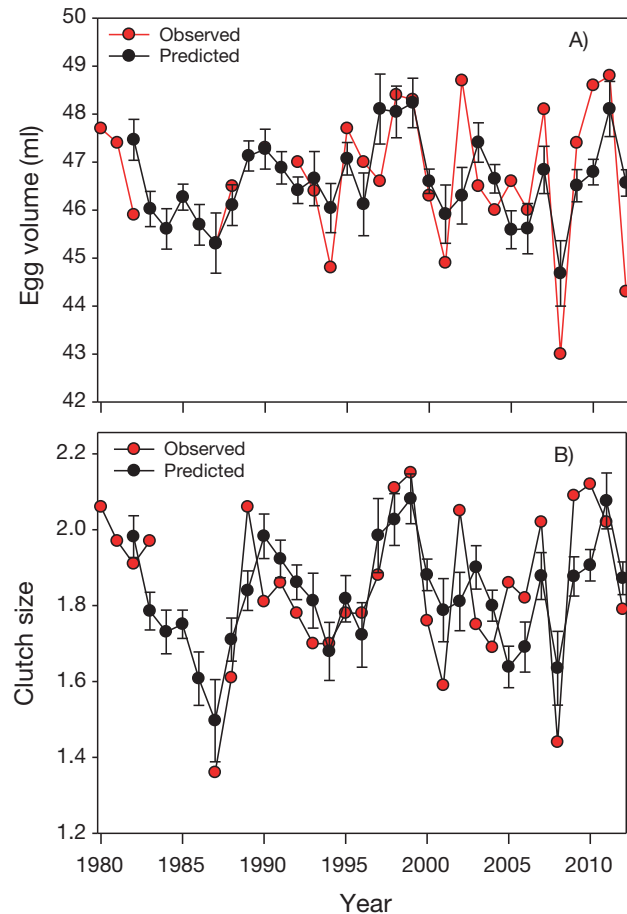


Fig. 3. Annual variation in (A) mean egg volume (ml) in 2-egg clutches and (B) clutch size of black-legged kittiwakes *Rissa tridactyla* at Hornøya, NE Norway. The figure shows the observed values and the predicted values (mean  $\pm$  1 SE) from the top-ranked model that best described the variation over time. For the egg volume, the top-ranked model explained 39%, and for clutch size 48%, of the variation over years (see Tables 1 & 2 for details)

by a positive response to AW inflow immediately prior to egg laying. Direct responses to biological covariates were all but absent, although there was a hint that amounts of mature capelin in the Barents Sea may affect investment in eggs. While an increase in AW per se will have no direct influence on kittiwake egg size, it does lead to an increase in water temperature, which in turn is a major driver of the Barents Sea macroecology. As such, it affects abundance, quality and/or availability of organisms at all trophic levels, including kittiwake prey (Hjermann et al. 2004, Eriksen et al. 2012, Johannesen et al. 2012).

Capelin comprises the largest stock of forage fish in the Barents Sea and plays a major role as an intermediary between plankton and predatory fish, seabirds and marine mammals (Gjøsæter 1998). At Hornøya, it

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 yearly mean egg volumes of black-legged kittiwakes *Rissa tridactyla* at Hornøya for the period 1980–2012. Estimates are from the top-ranked model in Table 1. See 'Materials and methods' for details about covariates

| Variable                 | Estimate (SE) | <i>t</i> | Pr>  <i>t</i> | Partial R <sup>2</sup> | Model R <sup>2</sup> | VIF  |
|--------------------------|---------------|----------|---------------|------------------------|----------------------|------|
| Egg volume               |               |          |               |                        |                      |      |
| Intercept                | 48.17 (0.74)  |          |               |                        |                      |      |
| AWautumn <sub>lag1</sub> | -0.80 (0.30)  | -2.64    | 0.01          | 0.25                   | 0.39                 | 1.09 |
| AWwinter <sub>lag1</sub> | -0.42 (0.19)  | -2.20    | 0.03          | 0.19                   | 0.39                 | 1.05 |
| AWspring                 | 0.49 (0.27)   | 1.82     | 0.08          | 0.14                   | 0.39                 | 1.11 |
| Clutch size              |               |          |               |                        |                      |      |
| Intercept                | 2.05 (0.10)   |          |               |                        |                      |      |
| AWautumn <sub>lag1</sub> | -0.11 (0.04)  | -2.82    | 0.009         | 0.25                   | 0.48                 | 1.12 |
| Capelin                  | -0.04 (0.02)  | 2.0      | 0.06          | 0.13                   | 0.48                 | 1.05 |
| AWwinter <sub>lag1</sub> | -0.05 (0.04)  | -2.73    | 0.01          | 0.17                   | 0.48                 | 1.06 |
| AWspring                 | 0.07 (0.03)   | 1.92     | 0.06          | 0.14                   | 0.48                 | 1.12 |

has been often highlighted as a key prey for kittiwakes (Barrett et al. 2004, Barrett 2007, Ponchon et al. 2014, Reiertsen et al. 2014), and earlier studies of the kittiwake (and other seabirds) at Hornøya have documented clear associations between the amount of capelin (and I-group herring) in the Barents Sea and other breeding parameters such as chick diet and breeding success (Barrett 2007, Fauchald et al. 2011). The absence in our study of a statistically significant response to the capelin proxy was thus unexpected; however, it may have been due to a large spatial mismatch between the stock assessment of mature capelin and the foraging range of kittiwakes. The capelin stock assessment area covers much of the Barents Sea (total area  $\approx 1.4 \times 10^6$  km<sup>2</sup>, Loeng 1989), whereas the kittiwake foraging area is much smaller (ca.  $6 \times 10^3$  km<sup>2</sup> with a foraging range of ca. 50 km [Coulson 2011] and when excluding land) (Barrett 2007, Ponchon et al. 2014). However, this mismatch was considerably reduced by restricting the covariate to the mature part of the fish stock that becomes concentrated along the Finnmark coast when spawning and therefore much closer to the kittiwake colony in spring. Despite this, there is still considerable variation in where spawning occurs in response to changes in sea temperature (Gjøsæter 1998, see below).

In the absence of any direct biological explanation, the delayed, but clear, negative response to AW inflow infers an indirect effect of ocean climate on kittiwake egg volume and number. As the main source of heat in the Barents Sea, the influx of AW has a crucial impact on the marine climate and trophic dynamics of the region (Dalpadado et al. 2012). It has a maximum in winter (Fig. S1 in Supple-

ment 1, Ingvaldsen et al. 2004) such that variability at this time of year potentially has a larger impact than changes at other times of the year, as found in this study. This climatic forcing may affect kittiwakes along many paths, including through an increased predation pressure on the kittiwakes' preferred food by predators such as northeast arctic cod *Gadus morhua* and herring, 2 species that profit from warmer waters (Hjermann et al. 2004). Other possibilities are a reduction in growth or a northward shift in distribution of the kittiwakes' preferred food items or, in turn, negative effects on underlying trophic levels on which the preferred

prey feed. Both would result in reduced food availability prior to egg laying.

The winter negative forcing seems to be partly counteracted by a shorter-term positive response by kittiwakes to increases in the inflow of AW in spring (March–April). This is precisely the period when conditions are thought to be the most important for determining zooplankton density in the southern Barents Sea (Dalpadado et al. 2012), and an increased inflow will create favourable conditions for kittiwake prey, including capelin (Gjøsæter & Loeng 1987) in this critical period. Furthermore, a strong spring inflow of AW into the Barents Sea results in an eastward shift along the Finnmark coast of the main spawning grounds of capelin, which is also favourable for birds breeding at Hornøya. The capelin stock remains in the Barents Sea through all life stages, but the mature fish perform extensive seasonal migrations towards the spawning grounds along the coast of North Norway and Russia in winter and early spring. These movements concentrate mature individuals close to the colony during the kittiwake pre-breeding season (Luka & Ponomarenko 1983). In years of weak inflow of AW, spawning may occur along the whole coast of North Norway, sometimes as far southwest as 69°N, whereas in years of strong AW inflow, this movement is displaced eastwards with spawning along the coast of East Finnmark and the Kola Peninsula (Luka & Ponomarenko 1983, Gjøsæter 1998). As such, during years of a strong AW inflow in March and April, energy-rich, gravid capelin become more available to Hornøya kittiwakes early in the breeding season when kittiwakes are forming and laying eggs.

But why then the larger, delayed and negative response to winter and autumn AW inflow by kittiwakes at Hornøya? The timing of the study coincided with a period of an extraordinary (and ongoing) climatic situation in the Barents Sea. Sea temperatures started to increase rapidly in 1980 and reached maxima ( $>1^{\circ}\text{C}$  above normal) in 2006 and 2012, the former of which was accompanied by an extreme AW winter inflow (Levitus et al. 2009, Walczowski et al. 2012, Ingvaldsen 2016). This situation has put the Barents Sea into a state of considerable flux with trophic control alternating between bottom-up, top-down and back to bottom-up (Johannesen et al. 2012). The AW is rich in nutrients and zooplankton, and inflow increases will have periodically favoured a growth in other large fish stocks such as cod and young herring, both of which are the most important predators of the capelin stock (Hjermann et al. 2004, Gjørseter et al. 2009). This predation effect may have contributed to the lagged negative effect of AW inflow on kittiwake egg investment. Furthermore, entry of new species from warmer areas with the AW inflow has led to increased species diversity in the Barents Sea (Johannesen et al. 2012). This, and a general northward displacement of cold-water species such as capelin beyond the normal foraging range of breeding kittiwakes (as occurred during the chick-rearing period in 2011, Ponchon et al. 2014) may have masked or even outweighed the potential advantages of changes in capelin growth and spawning movements gained by Hornøya kittiwakes during warm years. Our result that an overall increase in AW inflow results in smaller and fewer kittiwake eggs challenges the suggestion of Dalpadado et al. (2012) that seabirds that depend on capelin as prey in the SW Barents Sea may benefit from a current warming of the waters.

The lack of a temporal trend in kittiwake egg size in 1980–2012 at Hornøya was in sharp contrast to the  $2\% \text{ yr}^{-1}$  decline in puffin egg size at the same colony (and at Røst, also in North Norway) over the same period (Barrett et al. 2012). It was also in contrast with the 50–100 yr decline in egg investment among glaucous-winged gulls *Larus glaucescens* in British Columbia, Canada, which was interpreted to be a result of an accompanying impoverishment of the coastal ecosystem (Blight 2011). Furthermore, during a 10 yr study of herring gulls *L. argentatus* on the Isle of May, Scotland, a cull of adults, which reduced the breeding population by ca. 75%, resulted in a 5% increase in egg size while the clutch size remained constant (2.7 eggs; Coulson et al. 1982). This was thought to be a reflection of an improved condition of

breeding birds from reduced competition for food or reduced stress and aggression under lower nesting density (Coulson et al. 1982). Although the kittiwake population at Hornøya declined by  $>50\%$  during our study period, no such density-dependent response was evident. Furthermore, the lack of a long-term trend in egg or clutch size rules out a possible decline in early investment as the main cause of a near halving of kittiwake chick production registered on Hornøya since the turn of the millennium (Reiertsen 2013).

This study shows that there was a negative impact of an increased influx of AW into the Barents Sea on egg investment in kittiwakes that in turn may influence breeding success. Because any further warming of the Barents Sea through climate change is thus likely to be detrimental for this nationally endangered species, it is essential to better determine what prey is important as a driver of early breeding investment by expanding the current monitoring of the species by including studies of diet in the pre-laying and laying periods.

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