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). There was considerable interannual variation in both egg- and clutch sizes but no temporal trends. 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 two of the kittiwakes' most preferred prey species. Most of the variation was explained by the volumes of Atlantic Water 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 the kittiwake.

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Running page head: Kittiwake egg size

INTRODUCTION

36   Egg formation is demanding in terms of energy and resource requirements (Nager 2006).

37   Furthermore, egg production coincides with other costly processes, such as mate acquisition and

38   nest defence, that will exacerbate any effects of variable resource availability. These costs may be

39   met through an increase in uptake of protein and energy (reviewed in Williams 2005, Sorensen et al.

40   2009a).

41   Because a bird's breeding season is generally timed to coincide with a seasonal maximum

42   food availability during the chick-rearing period, an elevated energy expenditure early in the season,

43   i.e. during egg production, may be seriously limited by temporal variation in what is often a period of

44   low food and/or macro- and micronutrient availability (Williams 2005). Whereas the process of egg-

45   laying may be completed within a few days, the breeding season may be initiated many weeks before

46   any seasonal increase in food availability as parents undergo extensive physiological and behavioural

47   preparations (Williams 2005). The Atlantic puffin *Fratercula arctica*, for example, may prepare for the

48   nutritional demands of egg production by consuming a high trophic-level diet several months before

49   the breeding season (Kouwenberg et al. 2013).

50   Among seabirds, there are several examples of marine resource-related effects on egg

51   production with increasing or decreasing prey availabilities resulting in females laying respectively

52   larger or smaller eggs and clutches (Regehr & Montevecchi 1997, Tomita et al. 2009, Sorensen et al.

53   2009b, but see Hipfner 2012). Similarly, clutch and egg-size of the omnivorous yellow-legged gull

54   *Larus michahellis* decreased after closure of an open-air landfill that functioned as a ready food

55   source for the species (Steigerwald et al. 2015). Three longer-term studies of seabirds have also

56   shown that declines in a preferred food base early in the egg-production period may cause declines

57   in egg and/or clutch size over 3–9 decades (Mills et al. 2008, Blight 2011, Barrett et al. 2012).

58   The black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) is common in the North

59   Atlantic and North Pacific but has recently suffered widespread and severe population declines

60   throughout much of its range (Frederiksen 2010, Sandvik et al. 2014, Hamilton et al. 2016, Descamps

61   et al. 2017). After declines of 6–8% p.a. since the mid-1990s (Barrett et al. 2006) and forecasts of

62   local extinctions within the first 5–10 decades of the 21st century (Sandvik et al. 2014), Norwegian

63   kittiwakes are now red-listed as 'endangered' (Henriksen & Hilmo 2015). An accompanying decline in

64   breeding success at some Norwegian colonies has also been registered (Barrett 2007 & pers. obs.,

65   Anker-Nilssen et al. 2016). Being small surface-feeding gulls (Laridae) that work at or near their

66   energetic ceiling during periods of peak energy demands, kittiwakes are particularly sensitive to

67   changes in the marine environment (Furness & Tasker 2000, Welcker et al. 2010, Collins et al. 2016).

68   As a result, important breeding performance and demographic parameters have been shown to be

69   sensitive to changes in food supply (e.g. Aebischer et al. 1990, Regehr & Montevecchi 1997, Wanless

70   et al. 2007, Reiertsen et al. 2014). In Norway, breeding success of kittiwakes increased with food

71   availability near the colony (Barrett 2007), whereas adult survival responded positively to food

72   availability far at sea during the non-breeding season (Reiertsen et al. 2014). Furthermore,

73   population numbers responded negatively to ocean warming through declines in adult survival and

74   breeding success (Barrett 2007, Sandvik et al. 2014). Due to the precarious position of the kittiwake

75   population, there is an immediate need to explore all further possible causes of the decline in both

76   numbers and breeding success (Fauchald et al. 2015). Because egg and clutch sizes are positively

77   related to offspring quality (breeding date, hatching success, chick growth and survival) (Coulson &

78   Porter 1985, Williams 1994, Sorensen et al. 2009b, Krist 2011) and thus important components of

79   breeding success, it is important to address the initial investment during egg-laying (Hargitai et al.

80   2016).

81   A North Norwegian kittiwake egg weighs approximately 50 g (Runde & Barrett 1981), which

82   is equivalent to 12 % of the adult body mass (mean ca. 400 g, Barrett et al. 1985). Being income

83   breeders, gulls rely on adjustments of food intake during breeding rather than body stores to cover

84   extra costs (Ramírez et al. 2010 and refs. therein). With clutch sizes of 1–3 eggs (≡ 12–36 % of body

85   mass), the female kittiwake needs to allocate substantial resources to the eggs during the 2–3 week

86   laying period (Maunder & Threlfall 1972, Coulson 2011), resources that may also be needed for other

87   concurrent costly processes such as mate acquisition, nest building and site defence (Coulson 2011).

88   As such, egg and clutch size can be expected to vary in response to both female body condition and

89   the energy invested, both of which are affected by food availability prior to egg-laying (Nager 2006,

90   Ramirez et al. 2010, Vallarino et al. 2012). Such food availability is often highly dependent on a

91   complex marine ecosystem as in the Barents Sea where this study was conducted.

92   The Barents Sea is a shallow continental shelf area with an average depth of 230 m whose

93   climatic variability is determined mainly by the inflow of relatively warm and saline Atlantic Water

94   (AW) (Loeng 1991). AW dominates the southern region of the Barents Sea and the mean monthly

95   volume influx varies with a marked maximum in winter (Dalpadado et al. 2012, Ingvaldsen 2016,

96   Appendix Fig. A1). Changes in the inflow have profound effects on the ecosystem of the Barents Sea

97   and rates of biological production through all trophic levels from plankton to fish (Loeng 1989,

98   Eriksen et al. 2012, Johannesen et al. 2012). Any warming of the Barents Sea through an increase in

99   AW influx will result, for example, in distributional shifts of cold-water species northwards

100   (Dalpadado et al. 2012). Such shifts will likely cause changes in food abundance and availability for

101   top-predators. In this study, we investigated long-term variation in egg and clutch size of kittiwakes

102   in a colony in the southern Barents Sea to understand the proximate constraints of early breeding

103   investment. We address the hypothesis that environmental conditions (both prey abundance and

104   climate factors) prior to and during egg-production influence kittiwake egg-laying parameters and

105   predict that larger and more eggs would be laid in years of increased availability of preferred prey.

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MATERIAL AND METHODS

Field protocols

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111   This study was carried out at Hornøya (70° 22' N, 31° 08' E) on the eastern tip of the Varanger

112   Peninsula in NE Norway between 1980 and 2012. When the study started, an estimated 21 000 pairs

113   of kittiwakes bred on the island (Furness & Barrett 1985), but numbers steadily declined throughout

114   the study period to ca. 9 000 pairs in 2012 (pers. obs.). In addition to monitoring breeding numbers

115   nearly every year, egg- and clutch sizes of kittiwakes were measured using standardised protocols.

116   Clutch size was determined through a single visual inspection of a large sample of nests spread

117   throughout the colony on, or very soon after, the first day a newly-hatched chick was seen in the

118   colony in 1980-1983 and 1987-2012 (normally in early June, range 24 May – 19 June). The contents

119   of all well-constructed nests that showed signs of regular occupation were noted. Newly-hatched

120   chicks were included in the counts and considered as eggs in the clutch size determination.

121   Except in 1980–1982 when eggs of known laying sequence were measured during the laying

122   season, egg measurements were also made toward the end of the incubation period in 1987, 1988,

123   1990 and 1992–2012. Egg volume was determined from egg length and breadth measured with

124   Vernier calipers to the nearest 0.1 mm using the formula vol (ml) = k x length x breadth^2 (in cm)

125   where k = 0.4861 (for North Norwegian kittiwakes, Runde & Barrett 1981). An annual index of clutch

126   volume was modelled based on the volumes of eggs in 2-egg clutches, as they are the most

127   consistent in size among the three clutch sizes (Coulson 1963, Runde & Barrett 1981, Coulson 2011,

128   Hipfner 2012).

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Environmental covariates

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133   Many physical and biological covariates have been found to influence the seabirds breeding

134   on Hornøya, including estimates of stock sizes of important forage fish and other food items, and a

135   variety of oceanographic and meteorological parameters (e.g. Barrett 2007, Barrett et al. 2012,

136   Reiertsen et al. 2014, Sandvik et al. 2014). For kittiwakes, the most frequent food items identified

137   during the chick-rearing period for both adults and chicks include mature capelin *Mallotus villosus*, 1-

138   yr old Norwegian spring-spawning herring *Clupea harengus*, sandeels *Ammodytes* sp. and fry of

139   gadoids (Barrett 2007, Thorvaldsen et al. 2015). Outside the breeding season, capelin in the Barents

140   Sea and pteropods (Thecosomata) in the Grand Banks/Labrador Sea area where Hornøya kittiwakes

spend November-January (Frederiksen et al. 2012) have also been shown to affect their survival rate

(Reiertsen et al. 2014). Because no stock size data exist for sandeels nor 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 (Appendix 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 (Appendix 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 (SAS 2015). 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 the 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 (Appendix Fig. A1). 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 ΔAIC_C (Burnham &

Anderson 2002).

RESULTS

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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, Appendix 2). 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 volume of all eggs measured was 46.8 ml (SE = 0.06, N = 3986) and of eggs in 2-egg clutches was 46.7 ml (SE = 0.07, 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^{-1} in 1987 and a maximum of 2.15 in 1999 (Fig. 1, Appendix 3). 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 eggs clutch^{-1} (N = 24 293 nests, SE = 0.006). There was a large variation in the proportion of nests containing 3 eggs (Appendix 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).

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 year) and during spring (no lag). Adding herring and both herring and capelin to this model increased ΔAICc by 6.15 and 10.54 units respectively giving no support of any effect of these prey species (Table 1). Overall, the top rank model explained 0.39% of the variation in egg volume (Table 1).

Modelling the variance in clutch size over years gave much the same top rank model as for the egg volume including AW inflow during autumn and winter (with the lag of 1 year) and during spring (no lag). However, this model also included capelin. This top rank model had an explained variance of 48% (Table 1). Adding herring to this model increased ΔAICc 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 Appendix Fig. A2, which shows no apparent trend over time for these to potential prey species and the clutch size. The capelin stock collapsed three times since 1980 but with no evidence of a negative effect on clutch size.

The effect of AW influx during winter and autumn with 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 egg volume, the impacts of these three parameters were (partial correlation) 0.25, 0.19 and 0.14 for autumn, winter and spring respectively (Table 2, Appendix Fig. A3). The variance inflation factor (VIF) was close to 1 suggesting no collinearity among parameters. The sign of estimates of AW from the top rank model for clutch size

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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, 0,14 for AWwinter, capelin, AWautum and

AWspring respectively The inflation factor for the three parameters was also low (Table 2, Appendix

Fig. A3).

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 months previously and the preceding autumn followed 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 has been often highlighted as a key prey for kittiwakes (Barrett 2007, Barrett et

al. 2004, 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 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 this study of a statistically significant response to

the capelin proxy was thus unexpected. It may have been, however, 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 x 10^6 km^2, Loeng 1989)

whereas the kittiwake foraging area is much smaller (ca. 6 x 10^3 km^2 with a foraging range of ca. 50

km [Coulson 2011] and when excluding land) (Barrett 2007, Ponchon et al. 2014). This mismatch was,

however, 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).

245   In the absence of any direct biological explanation, the delayed but clear, negative response
246   to AW inflow infers an indirect effect of ocean climate on kittiwake egg volume and number. As the
247   main source of heat in the Barents Sea, the influx of AW has a crucial impact on the marine climate
248   and trophic dynamics of the region (Dalpadado et al. 2012). It has a maximum in winter (Appendix
249   Fig. A1, Ingvaldsen et al. 2004) such that variability at this time of year has potentially a larger impact
250   than changes at other times of the year, as found in this study. This climatic forcing may affect
251   kittiwakes along many paths, including through an increased predation pressure on the kittiwakes'
252   preferred food by predators such as northeast arctic cod *Gadus morhua* and herring, two species that
253   profit from warmer waters (Hjermann et al. 2004). Other possibilities are a reduction in growth or a
254   northward shift in distribution of the kittiwakes' preferred food items or, in turn, negative effects on
255   underlying trophic levels on which the preferred prey feed. Both would result in reduced food
256   availability prior to egg-laying.

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

274   But why then the larger, delayed and negative response to winter and autumn AW inflow by
275   kittiwakes at Hornøya? The timing of the study coincided with a period of an extraordinary (and
276   ongoing) climatic situation in the Barents Sea. Sea temperatures started to increase rapidly in 1980
277   and reached maxima (>1 ºC above normal) in 2006 and 2012, the former of which was accompanied
278   by an extreme AW winter inflow (Levitus et al. 2009, Walczowski et al. 2012, Ingvaldsen 2016). This
279   situation has put the Barents Sea into a state of considerable flux with trophic control alternating

280   between bottom-up, top-down and back to bottom-up (Johannesen et al. 2012). The AW is rich in

281   nutrients and zooplankton and inflow increases will have periodically favoured a growth in other

282   large fish stocks such as the cod and young herring, both of which are the most important predators

283   of the capelin stock (Hjermann et al. 2004, Gjøsæter et al. 2009). This predation effect may have

284   contributed to the lagged negative effect of AW inflow on kittiwake egg investment. Furthermore,

285   entry of new species from warmer areas with the AW inflow has led to an increased species diversity

286   in the Barents Sea (Johannesen et al. 2012). This, and a general northward displacement of cold-

287   water species such as capelin beyond the normal foraging range of breeding kittiwakes (as occurred

288   during the chick-rearing period in 2011 [Ponchon et al. 2014]) may have masked or even outweighed

289   the potential advantages of changes in capelin growth and spawning movements gained by Hornøya

290   kittiwakes during warm years. Our result that an overall increase in AW inflow results in smaller and

291   fewer kittiwake eggs challenges the suggestion of Dalpadado et al. (2012) that seabirds that depend

292   on capelin as prey in the SW Barents Sea may benefit from a current warming of the waters.

293   The lack of a temporal trend in kittiwake egg size in 1980–2012 at Hornøya was in sharp

294   contrast to the 2 % yr^{-1} decline in puffin egg size at the same colony (and at Røst, also in North

295   Norway) over the same period (Barrett et al. 2012). It was also in contrast with the 50–100 year

296   decline in egg investment among Glaucous-winged Gulls *L. glaucescens* in British Columbia, Canada,

297   which was interpreted to be a result of an accompanying impoverishment of the coastal ecosystem

298   (Blight 2011). Furthermore, during a 10-yr study of Herring Gulls *Larus argentatus* on the Isle of May,

299   Scotland, a cull of adults, which reduced the breeding population by ca. 75 % resulted in a 5 %

300   increase in egg size while the clutch size remained constant (2.7 eggs) (Coulson et al. 1982). This was

301   thought to be a reflect an improved condition of breeding birds from reduced competition for food

302   or reduced stress and aggression under lower nesting density (Coulson et al. 1982). Although the

303   kittiwake population at Hornøya declined by >50 % during our study period, no such density-

304   dependent response was evident. Furthermore, the lack of a long-term trend in egg or clutch size

305   rules out a possible decline in early investment as the main cause of a near halving of kittiwake chick

306   production registered on Hornøya since the turn of the millennium (Reiertsen 2013).

307   This study shows that there was negative impact of an increased influx of AW into the

308   Barents Sea on kittiwakes on egg investment that in turn may influence breeding success.Because

309   any further warming of the Barents Sea through climate change is thus likely to be detrimental for

310   this nationally endangered species, it is essential to better determine what prey is important as a

311   driver of early breeding investment by expanding the current monitoring of the species by including

312   studies of diet in the pre-laying and laying periods .

313

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475   Table 1. Summary of a forward selection of covariates using PROC GLMSELECT in SAS. The models are

476   run separately for egg volume and clutch size, which are highly correlated (Fig.1). The covariates entered

477   to the model were values of Atlantic water influx (AW) into the Barents Sea during winter, spring and

478   autumn without and with one year lag. Potential prey entered with no lags were the spawning

479   population of capelin (2–5 yr old) and 1-yr old herring from the Barents Sea. See text for details about

480   covariates.

481

a) Egg volume				
Step	Effects in	Model R^2	Adj R^2	AICc
0	0-model (Int.)			47.61
1	$AWautumn_{lag1}$	0.19	0.15	45.06
2	$AWwinter_{lag1}$	0.29	0.22	44.37
3	**AWspring**	**0.39**	**0.30**	**43.85***
4	$AWspring_{lag1}$	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				
0	0-model (Int.)			-58.46
1	$AWautumn_{lag1}$	0.20	0.17	-62.03
2	Capelin	0.31	0.24	-63.03
3	$AWwinter_{lag1}$	**0.39**	**0.32**	**-64.50**
4	**AWspring**	**0.48**	**0.39**	**-65.12***
5	$AWspring_{lag1}$	0.50	0.39	-62.95
6	Herring	0.51	0.37	-59.44
7	AWwinter	0.53	0.36	-55.98

482   *Optimal value of criterion

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487   Table 2. Estimated slopes, explained variance (partial and for the model) and variance inflation factor

488   (VIF) for the variables best explaining the annual variation in the yearly mean egg volumes of black-

489   legged kittiwakes at Hornøya for the period 1980–2012. Estimates are from the top ranked model in

490   Table 1. See text for details about covariates.

491

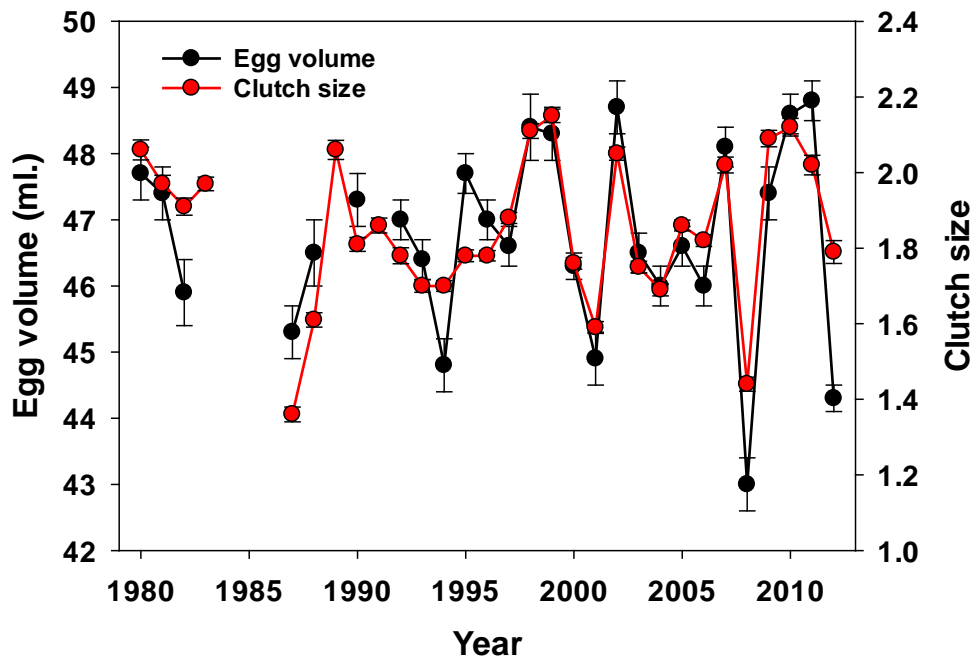| a) Egg volume						
Variable	Estimate (SE)	t-value	Pr>|t|	Partial R^2	Model R^2	VIF
Intercept	48.17 (0.74)					
$AWautumn_{lag1}$	-0.80 (0.30)	-2.64	0.01	0.25	0.39	1.09
$AWwinter_{lag1}$	-0.42 (0.19)	-2.20	0.03	0.19	0.39	1.05
AWspring	0.49 (0.27)	1.82	0.08	0.14	0.39	1.11
b) Clutch size						
Intercept	2.05 (0.10)					
$AWautumn_{lag1}$	-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
$AWwinter_{lag1}$	-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

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Figure 1. Mean (± 1 SE) volume of black-legged kittiwake eggs (in ml) in 2-egg clutches and mean (± 1
SE) clutch size (eggs/occupied nest) at Hornøya, NE Norway, 1980–2012. (r^2 = 0.61, P < 0.001, N = 28)
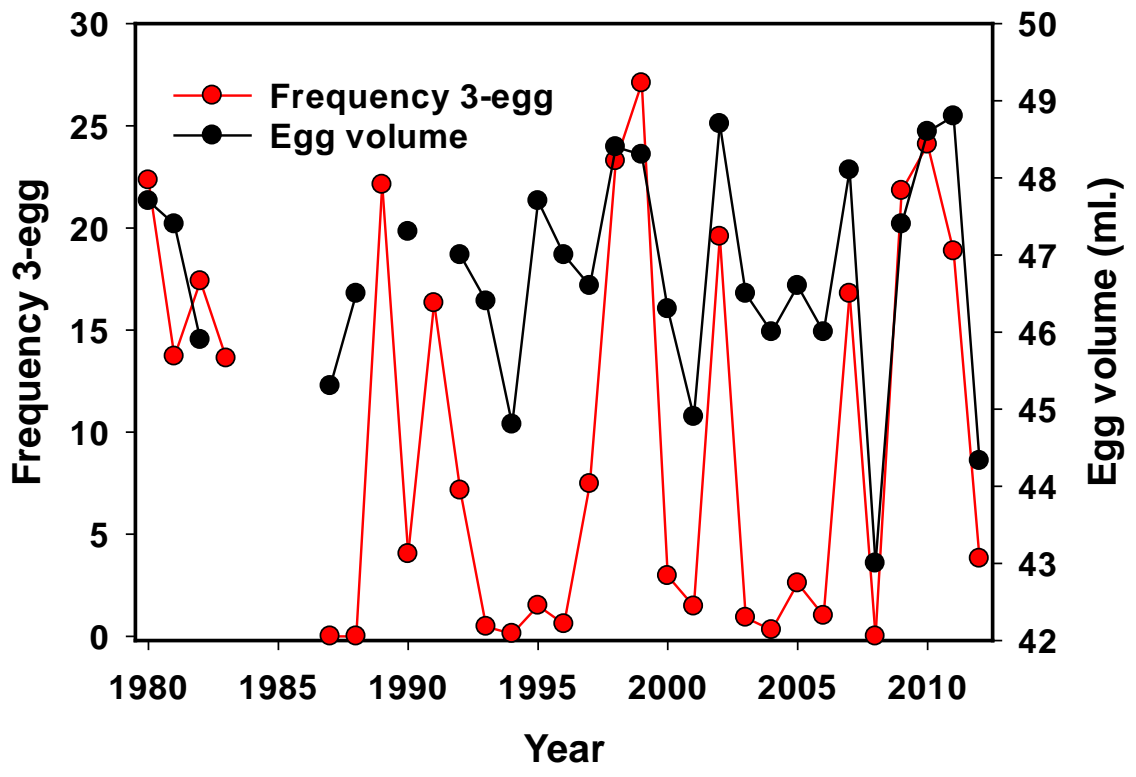

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504   Fig 2. The relationship between egg volume and the frequency of 3-egg clutches in the population
505   over years (r^2 = 0.51, P <0.001, N = 27)

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508

509 Fig. 3. Annual variation in mean egg volume (in ml) in 2-egg clutches (A) and clutch size (B) of black-
510 legged kittiwakes at Hornøya, NE Norway. The figure shows the observed values and the predicted
511 values (mean ± 1SE) from the top ranked model that best described the variation over time. For the
512 egg volume the top rank model explained 39 % and for clutch size 48 % of the variation over years
513 (See Tables 1 & 2 for details).
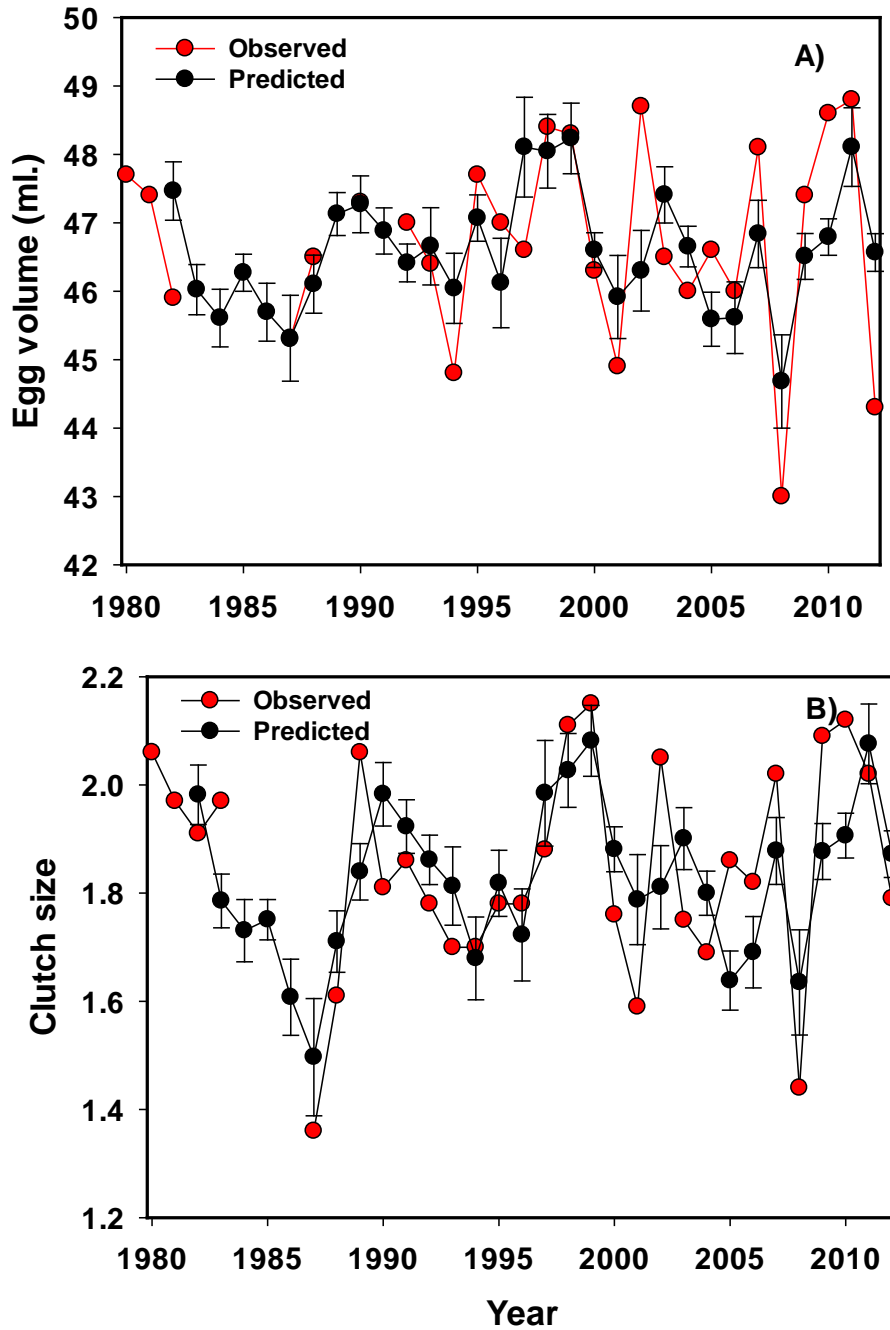
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515   **Appendix 1.** Overview of the covariates used in the regression models examining the variation in

516   black-legged kittiwake egg and clutch sizes at Hornøya, NE Norway, 1980–2012. Sources: ICES -

517   International Council for the Exploration of the SEAS, IMR - Norwegian Institute of Marine Research.

518

Covariate	Unit	Area	Time period	Source
Mature capelin	Stock size (3–5 yr old)	Barents Sea	October	ICES
Young herring	Stock size (1 yr old)	Barents Sea	January	ICES
Atlantic water inflow	Volume	Barents Sea	Dec-Feb, Mar-May, Sep-Nov	IMR

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520   Mature capelin. Estimates of stock in number by age group from acoustic and trawl survey data, from

521   Table 9.5 in ICES (2015a). Details of the indices are given in the report.

522   Young herring. Estimates of stock in number by age group from acoustic and trawl survey data, from

523   Tables 3.7.4.1 and 7.6.2.3.1 in ICES (2006) and ICES (2015b) respectively. Details of the indices are

524   given in the respective reports.

525   Atlantic water inflow. The climatic variability in the Barents Sea depends on the amount and

526   properties of the Atlantic water flowing in from the Norwegian Sea (see introduction and figure

527   below). The volume flux has been measured using current-meter moorings since 1997 (Ingvaldsen et

528   al. 2004) and modelled using the Regional Ocean Modelling System (ROMS, www.myroms.org)

529   (details in Myksvoll et al. 2013). For the analysis, the inflow was divided into three periods: winter

530   (Dec (in yr-1)-Feb), spring (Mar- May) and autumn (Sep-Nov).

531

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543   model predicts growth of top predator young. PloS ONE 8(11): e79225.
544   doi:10.1371/journal.pone.0079225

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546   Fig. A1. Monthly influx (in Sv) of Atlantic Water into the Barents Sea in 1980–2012 to illustrate the
547   especially large and variable inflow during in winter and the very low variation in summer.
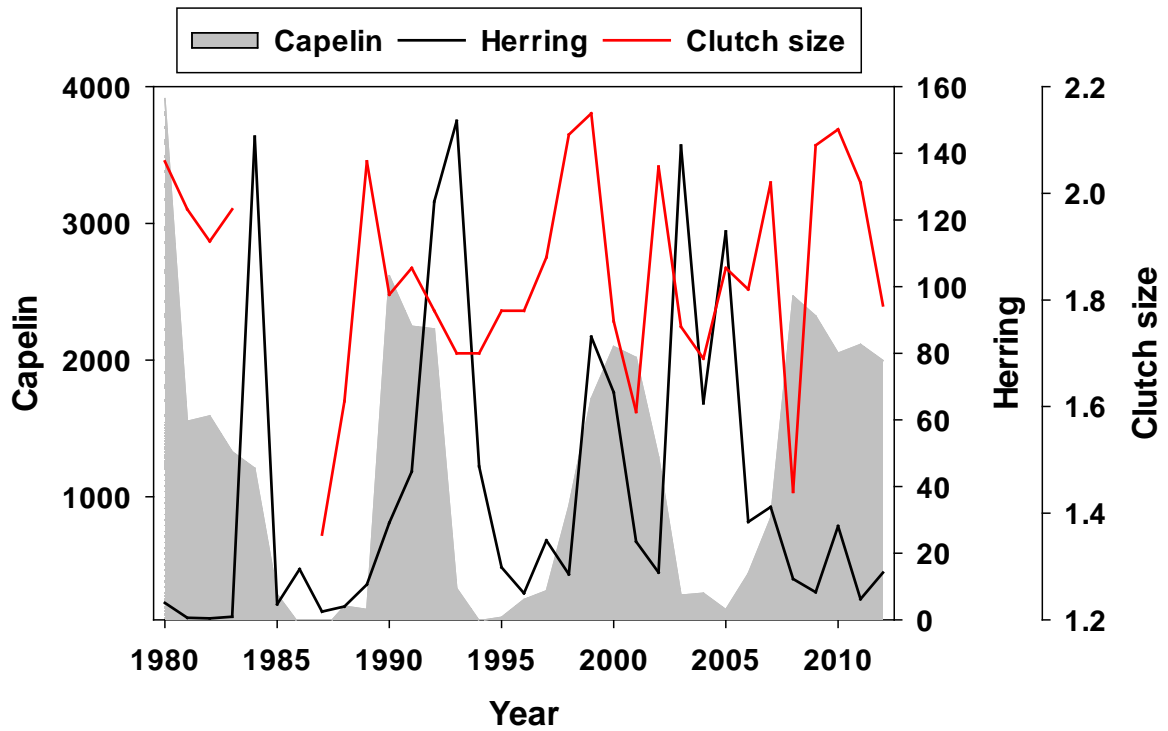
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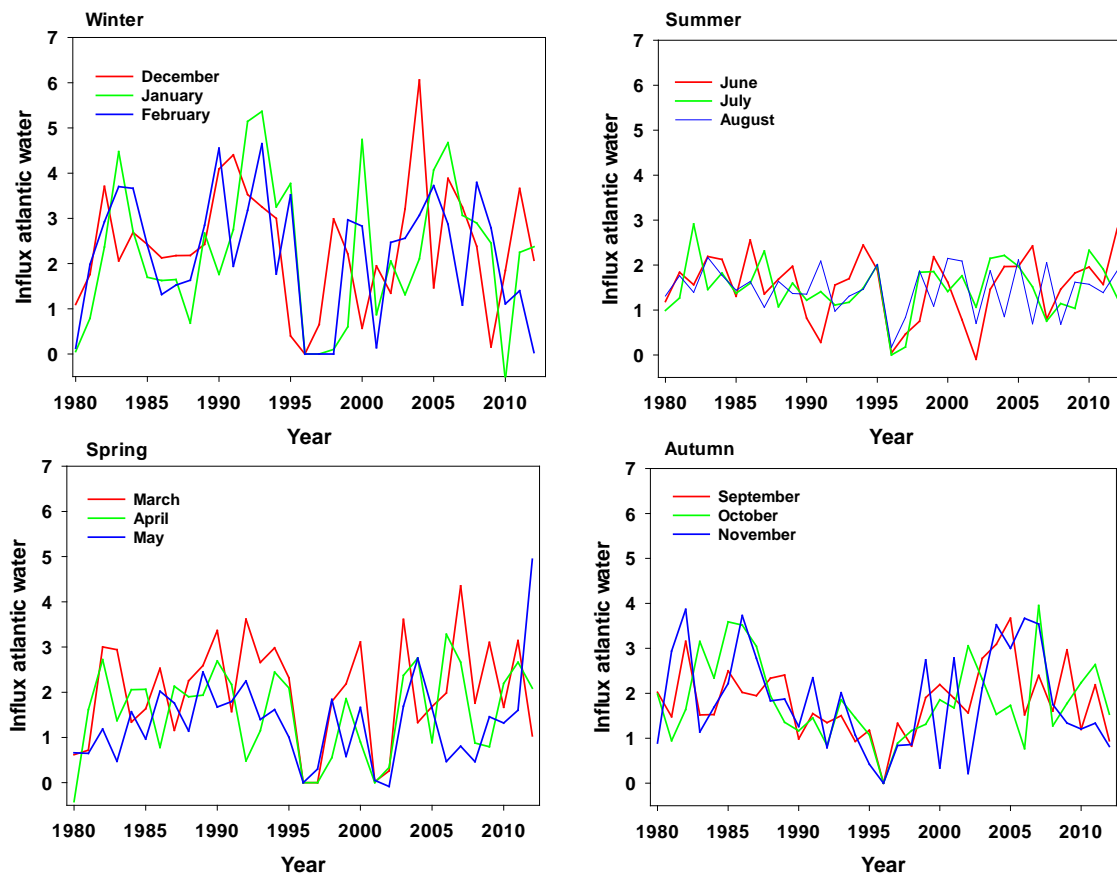
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553   Fig. A2. Interannual variation in black-legged kittiwake clutch sizes at Hornøya, NE Norway in relation
554   to estimates of stock size of mature capelin (no. x 10^9) and 1-yr old herring in the Barents Sea (no. x
555   19^9) (1980-2012).
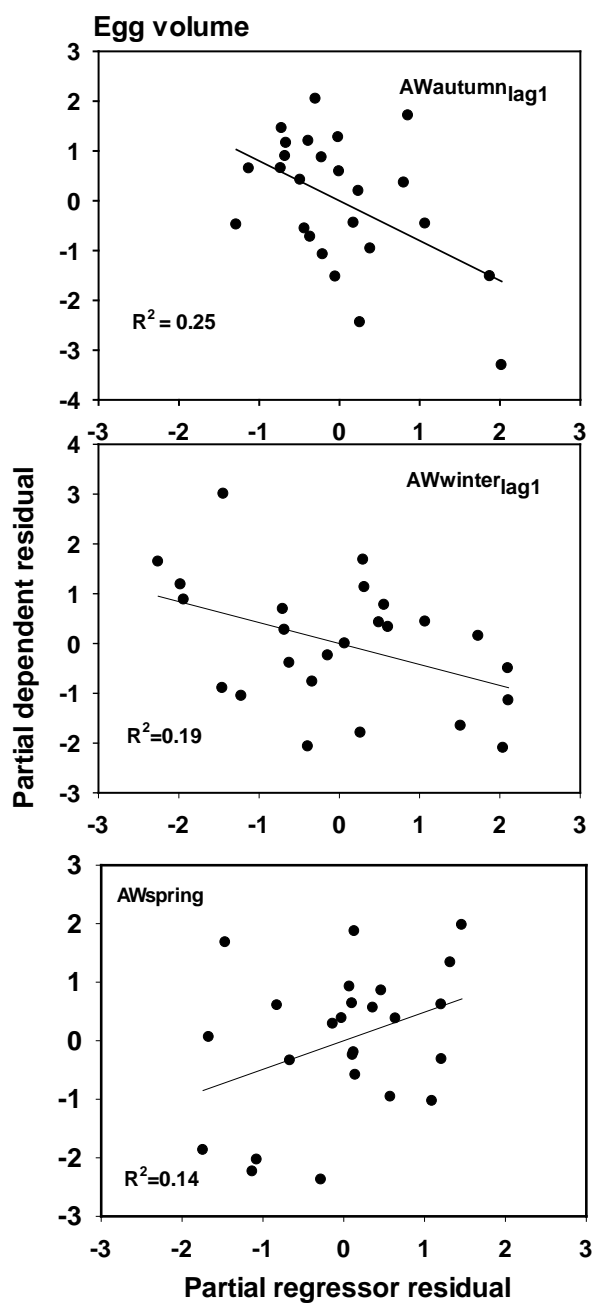
556
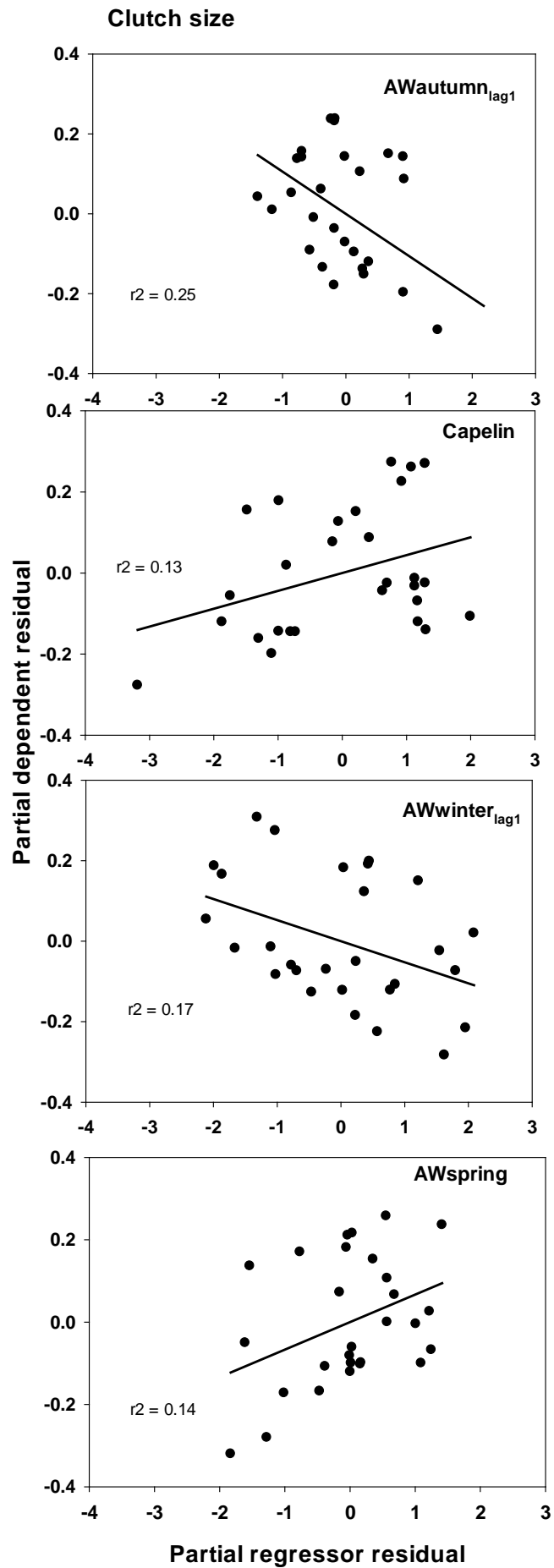
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Fig. A3. Partial plots for the impact of different parameters from the top rank model. See Tables 1

560 and 2 for details

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Clutch size

AWautumn$_{lag1}$

r2 = 0.25

Partial dependent residual

Capelin

r2 = 0.13

AWwinter$_{lag1}$

r2 = 0.17

AWspring

r2 = 0.14

Partial regressor residual

565　**Appendix 2**. Mean volume (ml) of black-legged kittiwake eggs laid in all clutches and in 2-egg
566　clutches at Hornøya, NE Norway, 1980–2012.

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		All clutches				2-egg clutches		
Year	N	Vol.	SD	SE	N	Vol.	SD	SE
1980	138	47.6	3.9	0.3	75	47.7	3.6	0.4
1981	136	46.8	3.9	0.3	82	47.4	4.0	0.4
1982	115	46.0	3.4	0.3	58	45.9	3.9	0.5
1987	112	45.4	3.1	0.3	68	45.3	2.9	0.4
1988	90	46.7	3.6	0.4	60	46.5	3.8	0.5
1990	111	47.0	3.5	0.3	90	47.3	3.6	0.4
1992	176	46.9	3.6	0.3	117	47.0	3.7	0.3
1993	150	46.6	3.8	0.3	136	46.4	3.8	0.3
1994	124	44.8	3.7	0.3	98	44.8	3.5	0.4
1995	164	47.4	4.0	0.3	144	47.7	3.5	0.3
1996	155	46.7	3.5	0.3	122	47.0	3.3	0.3
1997	130	46.8	3.4	0.3	100	46.6	3.2	0.3
1998	151	48.5	3.9	0.3	89	48.4	4.3	0.5
1999	170	48.1	4.0	0.3	100	48.3	3.8	0.4
2000	341	46.2	3.6	0.2	293	46.3	3.6	0.2
2001	97	44.3	3.5	0.4	72	44.9	3.3	0.4
2002	163	48.4	3.7	0.3	110	48.7	3.9	0.4
2003	104	46.4	3.3	0.3	86	46.5	3.1	0.3
2004	127	45.7	3.6	0.3	102	46.0	3.4	0.3
2005	95	46.5	3.2	0.3	90	46.6	3.2	0.3
2006	205	46.0	3.9	0.3	185	46.0	3.8	0.3
2007	183	48.0	3.7	0.3	114	48.1	3.7	0.3
2008	113	43.3	3.6	0.3	78	43.0	3.3	0.4
2009	109	47.1	3.4	0.3	82	47.4	3.6	0.4
2010	223	48.6	3.5	0.2	127	48.6	3.8	0.3
2011	152	48.4	3.1	0.2	99	48.8	2.9	0.3
2012	152	46.4	2.8	0.2	132	44.3	2.7	0.2

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588 **Appendix 3**. Counts of eggs and mean clutch size in black-legged kittiwake occupied nests at
589 Hornøya, NE Norway, 1980–2012.

Year	Date	0 egg	1 egg	2 eggs	3 eggs	4 eggs	N	Clutch size - all nests		Clutch size - excl. empty nests	
				Number of occupied nests with				Mean	SD	Mean	SD
1980	25–28 May	95	67	267	96	0	525	1.69	0.97	2.06	0.61
1981	3–13 June	55	87	360	71	0	573	1.78	0.78	1.97	0.55
1982	4–5 June	331	130	283	87	0	831	1.15	1.06	1.91	0.65
1983	9 June	106	150	598	118	1	973	1.75	0.81	1.97	0.56
1987	14 June	216	243	138	0	0	597	0.87	0.76	1.36	0.48
1988	12–13 June	157	195	306	0	0	658	1.23	0.81	1.61	0.49
1989	14 June	42	91	342	123	0	598	1.91	0.81	2.06	0.62
1990	15–18 June	92	136	435	24	0	687	1.57	0.76	1.81	0.48
1991	3 June	652	148	256	79	1	1136	0.79	1.02	1.86	0.67
1992	12–13 June	226	140	302	34	0	702	1.21	0.95	1.78	0.56
1993	19 June	141	199	441	3	0	784	1.39	0.78	1.70	0.47
1994	14 June	247	243	550	1	0	1041	1.29	0.83	1.70	0.46
1995	19 June	129	156	502	10	0	797	1.49	0.77	1.78	0.44
1996	13 June	156	188	645	5	0	994	1.50	0.76	1.78	0.43
1997	13 June	130	210	783	80	0	1203	1.68	0.75	1.88	0.50
1998	28 May	88	94	506	182	0	870	1.90	0.84	2.11	0.58
1999	27 May	112	134	649	291	0	1186	1.94	0.86	2.15	0.61
2000	3 June	176	224	595	25	0	1020	1.46	0.8	1.76	0.49
2001	8 June	586	230	307	8	0	1131	0.77	0.87	1.59	0.52
2002	23 May	319	117	516	154	0	1106	1.46	1.05	2.05	0.58
2003	20 June	185	168	486	6	0	845	1.37	0.83	1.75	0.45
2004	19 June	199	199	451	2	0	851	1.30	0.83	1.69	0.47
2005	20 June	94	120	591	19	0	824	1.65	0.71	1.86	0.41
2006	17 June	137	111	475	6	0	729	1.48	0.8	1.82	0.41
2007	26 May	209	88	382	95	1	775	1.47	1.02	2.02	0.58
2008	10 June	190	298	230	0	0	718	1.06	0.76	1.44	0.50
2009	2 June	165	70	360	120	0	715	1.61	1.02	2.09	0.58
2010	26 May	61	69	366	138	0	634	1.92	0.84	2.12	0.59
2011	24 May	71	75	295	86	0	527	1.75	0.89	2.02	0.59
2012	12 June	26	58	170	9	0	263	1.62	0.71	1.79	0.49

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