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Effects of Climate on Chick Growth in the Black-legged Kittiwake (*Rissa tridactyla*)

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MSc in Biology

Submission date: December 2015

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PREFACE

This master's thesis has been written at the Department of Biology at the Norwegian University of Science and Technology (NTNU) in collaboration with the Norwegian Institute for Nature Research (NINA).

To my supervisors Svein-Håkon and Claus, thank you for sharing your knowledge, for your guidance, and for all the invaluable feedback throughout the process of writing this thesis. And to Signe, thank you for all the help with the data and for functioning as a co-supervisor, especially during the last months. I also want to thank Rob Barrett for analysing the diet samples, and also for teaching me so much about seabirds through all his work.

I've spent four summers in the field together with some great people. I want to extend my biggest thanks to Magdalene; thank you for everything you've taught me, all of the laughs, the loud singing, and all the Anda cookies. Also to Vegard, it's been so much fun having you there every year. To my "field family", Kyrre, Ingrid and Anne, whom always provided a safe haven for us on Stø, thank you.

This thesis would never have seen the light of day without the statistical insight provided by my friends Friederike, Bart, Christoffer, Torgeir and Knut Andreas. Thank you guys so much.

To all my friends: thank you for proof reading, for all the fun distractions, for always keeping my spirits up, and for being the amazing people you are. Ingrid, thank you for being the best roommate I could wish for. Didrik, Sophie, my parents, and all the rest of my family: thank you for taking interest in my work, the progress, and for all your love and encouragement.

Trondheim, December 2015

Rakel Jansen Alvestad

ABSTRACT

Seabirds are declining worldwide as a result of anthropogenic influences, primarily through climate change affecting the food availability. One of the declining species is the black-legged kittiwake (*Rissa tridactyla*), whose breeding populations in Norway have declined by 60-80 % since the 1980's.

Chick growth is a good indicator of the environmental conditions as it reflects food availability during the rearing period, and affects post-fledging survival and population recruitment. The present study investigated the impact of various climatic variables on the growth rate of kittiwake chicks. This was done by using data on individual chick growth rates obtained during the breeding seasons of 2007 through 2015 from the island Anda, in northern Norway. The growth of 179 kittiwake chicks was assessed against the North Atlantic Oscillation winter index (NAO_w), sea-surface temperatures of the pre-breeding and breeding season, precipitation, wind, and air temperature using a non-linear mixed effects model. Precipitation and NAO_w were both shown to negatively affect the growth rate of the chicks. Precipitation presumably affects chick growth rates directly through increasing their energy budgets. The NAO_w is assumed to affect chick growth through food availability, although no significant results were found between diets and the NAO_w index.

As chick growth is likely to affect post-fledging survival, increased knowledge on which climatic parameters affect the growth, and to what extent, is useful for distinguishing the effects of climate from other factors influencing the populations. This is important in order to direct management efforts towards all factors influencing the population development.

SAMANDRAG

Det er observert ein global nedgang i sjøfuglbestandar grunna menneskeleg påverknad, då i all hovudsak gjennom klimaendringane si verknad på tilgangen til mat. Ein av dei minskande artane er Krykkja (*Rissa tridactyla*), som har ein hekkande bestand i Noreg som har hatt ein nedgang på 60-80 % sidan 1980-talet.

Ungevekst er ein god indikator på miljøforholda då det speglar tilgangen på mat, og påverkar overlevnaden til ungene etter at dei forlét reiret og slik seinare rekruttering til bestanden. Denne studia undersøkte verknaden av ulike klimavariablar på vekstraten hjå Krykkje-ungar. Dette vart gjort ved å nytte data på individuelle vekstratar frå Krykkje-ungar, samla inn i løpet av hekkesesongane i 2007 til og med 2015 på øya Anda i Vesterålen, Noreg. Veksten til 179 ungar vart testa mot NAO vinter indeksen (NAO_w), havoverflatetemperaturar før- og under hekkesesongen, nedbør, vind og lufttemperatur ved å nytte ein ikkje-lineær «mixed effects» modell. Nedbør og NAO_w viste baa negative effektar på vekstraten til ungene. Nedbør har truleg ein direkte negativ effekt på vekstratane ved at det aukar energibruken deira. NAO_w påverkar truleg veksten indirekte igjennom å påverke tilgangen på mat, sjølv om ingen signifikante resultat vart funne mellom gjennomsnittlege diettverdiar og NAO_w -indeksen.

Då ungevekst har noko å seie for overlevnaden etter at ungene forlét reiret vil auka kunnskap om kva klimaparametere som påverkar veksten, og i kva omfang, vera nyttig for å skilje effektane av klima frå andre faktorar som påverkar bestandane. Dette er viktig for å kunne rette forvaltningsinnsats mot faktorane som påvirker bestandsutviklinga.

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1 INTRODUCTION

1.1. Background

The marine environment is changing due to anthropogenic influences such as over-harvesting, pollution, habitat modifications, and global climate change (e.g. Halpern et al. 2008, Stocker et al. 2013). In the North Atlantic many seabird species have experienced large reductions in population size and breeding success during the last decades. This most likely results from reduced prey abundance, as a consequence of climate change and overfishing (e.g. Frederiksen et al. 2004, 2007, Barrett et al. 2006).

In seabirds, the effect of climate has also been demonstrated for a number of life-history parameters such as timing of breeding (Moe et al. 2009), breeding-success (Golet et al. 2000, Moe et al. 2009), chick diet (Romano et al. 2006, Hatch 2013), chick growth (Vincenzi & Mangel 2013), and adult survival (Kitaysky et al. 2006, Sandvik et al. 2012, Vincenzi & Mangel 2013).

1.2 Climate

In the Northern Hemisphere, seabird responses to climate are commonly described using climate proxies such as sea-surface temperature (SST), wind, precipitation or air temperature, or a combination of these partly expressed in indices like the North Atlantic Oscillation (NAO) (e.g. Moe et al. 2009, Bustnes et al. 2013, Breton & Diamond 2014, Hovinen et al. 2014, but see Mesquita et al. 2015).

The NAO refers to a redistribution of atmospheric air masses between the Arctic and the subtropical Atlantic and is one of the most prominent and recurrent patterns of variation in atmospheric circulation, particularly during winter. Monthly NAO indices are based on the difference in normalized sea-level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Hurrell et al. 2003). The NAO index has been shown to affect terrestrial vegetation (Post et al. 2001), herbivores and carnivores (Post et al. 1997, Stenseth et al. 1999), and marine life and fish stocks (Stenseth et al. 2004, Sandvik et al. 2005, 2012, Breton & Diamond 2014) through both direct and indirect patterns (see Mysterud et al. (2003) for a full review on NAOs effect on terrestrial ecosystems). Through the effect on wind

speed and direction, air temperatures, heat and moisture transports, and precipitation, the NAO is able to exert strong forces on the ocean, affecting the temperature of the water, the salinity, vertical mixing, and ice-formation in the northernmost parts (Visbeck et al. 2003). The indirect biological effect of the NAO is mediated through local variations in physical and chemical water characteristics, with varying physical responses across the North Atlantic (Drinkwater et al. 2003).

Sea-surface temperatures are driven by changes in the surface wind and air-sea heat-exchanges that are associated with NAO variations (Hurrell et al. 2003). In the Barents Sea a positive NAO phase increases the flux of warm water from the southwest, along with increasing cloud cover, air- and water temperatures, both directly and indirectly influencing fish growth and survival (Ottersen & Stenseth 2001).

While harsh weather conditions can have a direct effect on seabird mortality, large-scale climate variations can indirectly affect their survival through changes in prey abundance (Sandvik et al. 2005). For example, variations in SST is suggested to indirectly affect both the adult survival (Breton & Diamond 2014) and the breeding success of Atlantic puffins (*Fratercula arctica*) through the availability of first-year herring (*Clupea harengus*) (Anker-Nilssen 1992, Durant et al. 2003).

1.3 Chick growth

With the on-going changes in climate, it is of increasing importance to identify the effects of climate on seabirds. In this context, better knowledge of how the growth and survival of chicks respond to varying climate during the breeding season could help predict future population trajectories. Thus, to predict how the changes in climate will affect future populations, targeted monitoring of life-history parameters is essential. In this context, chick growth, provisioning rate, and fledging weight are suggested to be more sensitive indicators of environmental conditions in seabirds than the number of fledged young. This is due to their influence on post-fledging survival and hence the recruitment to the population (Croxall & Rothery 1991, Cam et al. 2003).

To optimize growth under unpredictable feeding conditions, seabird nestlings have the ability to temporarily arrest growth when insufficient amounts of food are available, enhancing the probability of survival until fledging (Schew & Ricklefs 1998). Several studies, on various bird species, show a positive correlation between chick fledging mass and post-fledging survival (e.g. Tinbergen & Boerlijst 1990, Ringsby et al. 1998, Coulson 2011). This suggests that, even though temporarily arresting growth can enhance the probability of fledging, lighter chicks have a higher mortality post-fledging. Hence, the nutritional deficit experienced at the chick stage can affect populations through a lower subsequent recruitment (Metcalf & Monaghan 2001). For instance, Kitaysky et al. (2006) demonstrated that a temporary nutritional deficit of lipids in red-legged kittiwake (*Rissa brevirostris*) chicks affected cognitive abilities later in life. This could in turn account for low recruitment of young, raised in years of poor availability of high-lipid fish.

The amount of food supplied to the chicks also affects within-clutch aggression levels in facultative siblicidal species, e.g. the black-legged kittiwake (*Rissa tridactyla*) (White et al. 2010). Hence, in years of insufficient food availability there will be increased competition for food, leading to an adjustment of the brood size through either starvation or siblicide (e.g. Lack 1947, 1954).

1.4 Aim and hypotheses

The aim of the present study was to explore the influence of varying climatic parameters expressed through NAO_w, SST, air temperature, wind, and precipitation on chick growth in the black-legged kittiwake, using data on chick growth, diet and fledging success, collected during a 9-year period at a colony in northern Norway.

The study is based on the following hypotheses:

- There will be a negative correlation between NAO_w indices and chick growth rates. In years of high, positive NAO_w indices, creating low-pressure areas with heavy wind and precipitation, low chick growth rates are expected due to low feeding efficiency, expressed through lower food load masses, and changes in chick diet.
- Lower chick growth experienced in years with high NAO_w indices will cause higher chick mortality compared to years with low NAO_w indices.

2 METHODS AND MATERIALS

2.1 The study species

With a total population of nearly 9 million adults, and an estimated similar number of juveniles, the black-legged kittiwake (hereafter kittiwake) is by far the world's most numerous gull species (Birdlife International 2015). Kittiwakes have a circumpolar distribution, breeding in the arctic and boreal zone throughout the Northern Hemisphere including the Norwegian coast (Cramp & Simmons 1983).

Both sexes incubate the eggs (clutch size range 1-3 eggs, normally 2 eggs) during the 24-28 day incubation period (del Hoyo et al. 1996). In clutches with more than one egg, the eggs usually hatch with 1-2 days intervals (Hatch et al. 2009).

The chick that hatches first (hereafter the α -chick) grows faster than the second hatchling (hereafter the β -chick), and is often the only one to survive to fledging, at 5-6 weeks of age. After 2-3 years the juveniles return to the nesting area, usually not breeding until the subsequent year (Wooller & Coulson 1977). Its wide range and large numbers make the kittiwake an extensively studied species. Also, being top predators in the marine ecosystems, kittiwakes function as indicators of marine productivity and biotic interactions (Montevecchi 1993, Wanless et al. 2006, Piatt et al. 2007).

Kittiwakes are pelagic surface feeders, feeding up to 120 km from the colony (but see e.g. Thaxter et al. 2012, Ponchon et al. 2014) on small fish (usually < 100 mm) such as sandeel (*Ammodytidae* spp.), herring, and capelin (*Mallotus villosus*) found in the upper 1-2 metres of the sea. Factors preventing their prey from entering the top metres of the sea, such as severe storms, are likely to greatly affect their food availability (Baird 1990).

Starting in the 1980's, the kittiwake, along with many other seabirds, has undergone a global decline in population size (Croxall et al. 2012). In Norway there has been a massive decline in the overall breeding population (

Fig. 1), and most colonies are now only 20-40 % of their size in the early 1980's (Fauchald et al. 2015).

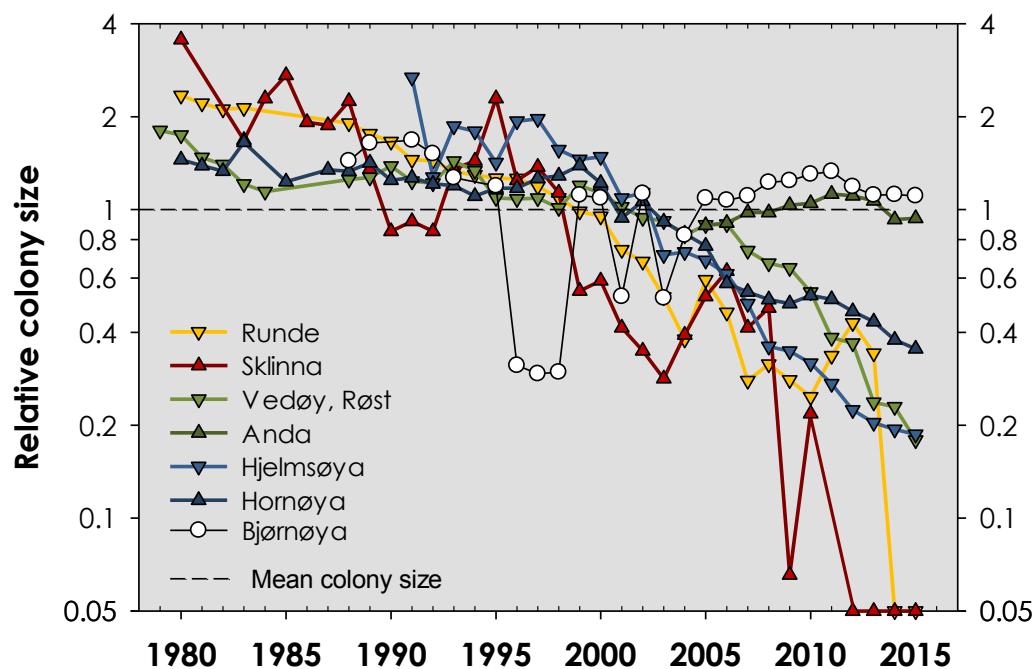


Fig. 1. Relative changes in number of kittiwakes in seven colonies in Norway and Svalbard 1980-2015 (From: The Norwegian monitoring programme for seabirds/SEAPOP).

In the Norwegian list of endangered species of 2015, the kittiwake was listed in the “endangered” category, with introduced species, competition for food with fisheries, and climatic changes listed as the main threats (Henriksen & Hilmo 2015).

2.2 Study area

This study was performed on the island of Anda (69°04'N 15°10'E) in Øksnes municipality, Nordland County, Norway (Fig. 2). Anda is a small island (ca 0.5 km²) that, due to its value as a breeding site for seabirds, is designated both as a nature reserve, and a protected wetland Ramsar-site.

The kittiwake population at Anda has not experienced the drastic decline most other Norwegian colonies have, counting 755 pairs at the first count in 2005 and 795 pairs in 2015 (+5 %). The kittiwakes breeding at Anda normally utilize two main feeding areas; they can either fly into the fjords and straits southeast of Anda to feed on sandeel, herring and gadids (*Gadidae* spp.), or they can fly northwest to the continental shelf to feed on mesopelagic prey living in the productive front systems (Christensen-Dalsgaard & Lorentsen unpubl.).

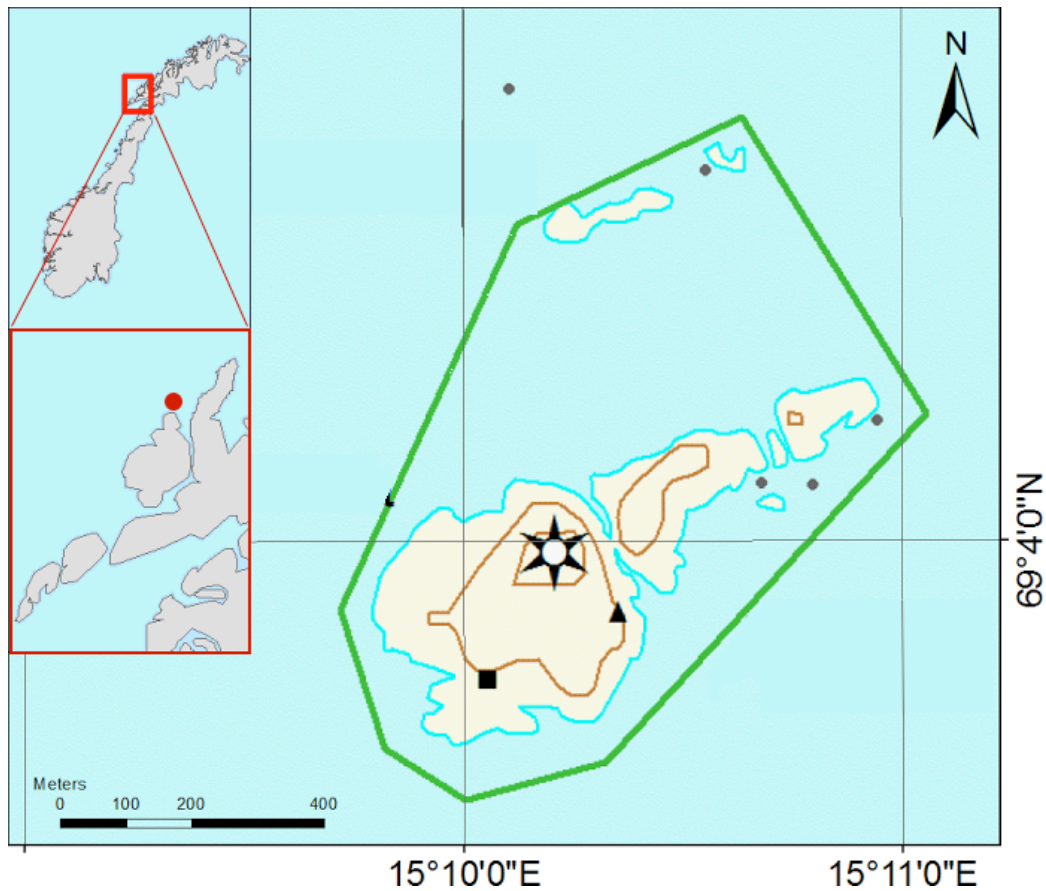


Fig. 2. Map of Anda marking the borders of the nature reserve. A map of Norway (top left) marks the area in which Anda is located, and the exact location is shown in the bottom left panel.

2.3 Fieldwork

Data on kittiwake chick growth and breeding success were collected during 2007-2015. Chick growth data were collected from 15-66 (mean = 37) nests established in the mid- to late incubation period. The nests were individually numbered and their content was checked every fifth day until breeding failure (defined as being the disappearance or death of the egg(s) or chick(s)), chick fledging, or until the end of the period of fieldwork. On each visit, the chicks were weighed using Pesola spring balances (accuracy of ± 2 g for 100 g, and ± 5 g for 500 g balances).

On average the chick hatches within 3.3 days after the first cracks in the eggshell are visible (2.3 days from first cracks to pipped, and 1 day from pipped egg to emerged chick; Hatch 2009). Consequently, the condition of the egg on the visit prior to appearance of the chick and/or the wetness of the chicks' plumage was used to estimate the hatching date.

To be able to identify individual chicks from one visit to another, permanent markers were used in 2007-2013 to colour the plumage of siblings, whereas plastic (darvic) colour bands were used in 2014 and 2015. The colour bands were removed when the chicks were banded with metal bands before fledging.

Spontaneous (non-provoked) regurgitations from chicks (during handling) together with regurgitations from adults caught when returning to their nests were collected during the study period. To ensure independence between diet samples, samples were not collected from adults and chicks of the same nest.

2.4 Data treatment

2.4.1 Chick growth

Growth of each individual chick was calculated as the mean daily increase in body mass (g) during the linear section of the growth curve (5-25 days of age; Hatch 2009). To maximize the number of growth curves to be included in the study, 19 days was set as the minimum age to calculate the linear growth. Growth phases shorter than 19 days were excluded. Throughout the years there were three nests with three chicks; these were excluded from the model due to the low sample-size.

2.4.2 Diet

Diet samples were stored frozen until being analysed at Tromsø University Museum. Each sample was thawed and weighed to the nearest 0.1 g, after which the remains of the diet were classified to the lowest possible taxon and the composition was expressed as frequency of occurrence.

For the analysis of load mass, only samples from adults were included. Since the adults were caught when returning to the nest from feeding trips it was assumed that the load mass represented the amount of food available to the chicks. Both adult and chick samples were used when expressing the diet composition. As sandeel is the main prey species of the kittiwakes on Anda, the diet samples were categorised into those consisting of sandeel and those consisting of other prey species. The other prey species included herring, glacier

lanternfish (*Benthoosema glaciale*), gadids, silvery lightfish (*Maurolicus muelleri*), spotted barracudina (*Arctozenus risso*), offal from fisheries, and crustaceans. Unidentified fish were excluded from the analysis.

2.4.3 Breeding success

Apparently occupied nests (AON), defined as “well-built nests capable of containing eggs with at least one adult present” (Walsh et al. 1995), were counted at the beginning of the breeding season. Clutch size was calculated as the average number of eggs in the nests surveyed for chick growth. Only selected study plots were counted in 2012, in all other years the entire colony was counted. Breeding success was calculated as the number of large chicks (> 12 days) at the end of the season divided by the number of AONs in the beginning of the season.

2.4.4 NAO

Winter NAO-indices (NAO_w) for December through February was used as a large-scale indicator of winter-conditions. These were obtained from the National Center for Atmospheric Research (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based>).

In a positive phase, surface pressures that are higher than normal south of 55° N combine with a broad region of particularly low pressures throughout the Arctic to enhance the climatological southern pressure gradient. The shift from one phase to another results in large changes in the mean wind speed and direction over the Atlantic Ocean and the neighbouring continents. Positive winter indices are associated with strong winter storms crossing the Atlantic across northerly tracks resulting in warmer, wetter, and windier winters. Negative indices are correlated with colder drier winters (Hurrell et al. 2003).

2.4.5 SST

The average SST for March-May and June-August each year was calculated, representing the pre-breeding and breeding environmental conditions, respectively. Monthly averages of the SSTs, at 5 metres depth over a 2° x 2° grid, were obtained from the IRI/LDEO Climate Data Library (<http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.version3b/>).

2.4.6 Local weather

The average daily air temperature, wind and precipitation experienced by each individual from the date of hatching until 19 days of age were used as measurements of local weather conditions during the breeding season. Daily weather data (air temperature (°C), wind speed (m/sec) and precipitation (mm)) were obtained from The Norwegian Meteorological Institute (www.eklima.met.no), from the Andøy weather station 46.5 km northeast of Anda.

2.5 Statistical analyses

2.5.1 Chick growth

All data was analysed using the software R, version 3.0.2 (<http://www.r-project.org/>).

To investigate interannual variations in chick growth an analysis of variance (ANOVA) was used. Chick growth data was analysed using the “Nonlinear Mixed-Effects Models” (nlme) package (Pinheiro et al. 2015), allowing the nest and the year chicks originated from to be plotted as nested random effects. Chick growth was set as the response variable, with hatching order (singleton, α - or β -chick), NAO_w , SST for pre-breeding, and breeding season, and the number of days with precipitation, average daily precipitation amount, temperature, and wind, experienced by each chick as explanatory variables. The interaction between NAO and the SST's was also included. To investigate the effects between the different levels of hatching order, the factors were re-ordered so that the hatching level specified was first.

The “Multi-model Inference” (MuMIn; Barto'n 2015) packages' “dredge” function was used to perform automated model selection, based on Akaike's Information Criterion (AIC), accounting for small sample sizes by applying AICc. $\Delta AICc$ values were reported relative to the null model. If two or more nested models deviated by less than 2 AICc units the most parsimonious model, the one requiring the fewest parameters, was preferred.

Models including correlated ($r > 0.60$) parameters simultaneously were excluded. This excluded models that included temperature and wind (-0.64), days and amount of precipitation (0.69), NAO_w and precipitation days (-0.69), spring SST and amount of precipitation (-0.79) or the two SST values (0.77) simultaneously (Table S1 in the supplement).

2.5.2 Diet

As 16% of the diets consisted of both sandeel and other prey types these diet samples were excluded from the food load mass model. Load mass was used as the response variable in a nlme, against proportion of sandeel, NAO_w, SST for pre-breeding and breeding season, and year was set as a random factor. The interaction effect between NAO_w and SSTs was included. To normalize the residuals the load mass was square rooted. To be able to compare diets with chick growth yearly average growth rates were set as the response variable against average load mass, proportions of sandeel, and NAO_w in a linear model.

2.5.3 Breeding success

To compare breeding success between years a “test of equal given proportions” (prop.test) was used, testing the null-hypothesis that the proportions (probabilities of success) in several years are the same. A test for correlation between paired samples (cor.test) was used for investigating possible correlations between breeding success and chick growth, and breeding success and clutch size.

3 RESULTS

3.1 Chick growth

The results were based on growth data from 179 chicks, of which 82 were α -chicks, 55 β -chicks, and 42 singletons. There was a lower number of β - than α -chicks as not all β -chicks fulfilled the criteria of being at least 19 days old at when the last measurements were obtained.

A significant inter-annual difference in daily chick growth rate was found ($F_{1,8} = 6.0394$, $p < 0.001$; Fig. 3). The highest average daily growth rate (16.7 g/day) was in 2010, closely followed by 2015 (16.3 g/day) whereas the lowest average daily growth rate was in 2012 (11.9 g/day).

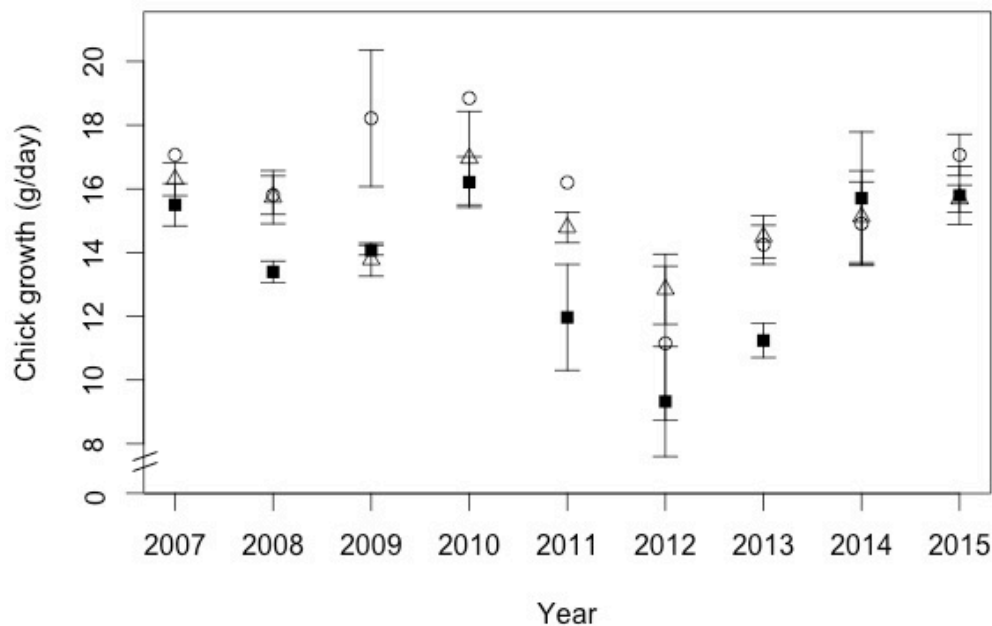


Fig. 3. Annual chick growth rates (mean with standard deviation) during 2007-2015 for singletons, α - and β -chicks, represented by circles, triangles and squares, respectively.

Excluding the correlating parameters, the model selection gave two models with $\Delta AICc$ less than 2 (Table 1). The first model was the most parsimonious, with more than 50 % of the AICc weights, making it the preferred model, even though parameter values are only marginally different from the second model. In the second model, the negative effect of air temperature

was not significant, and further did not improve the estimates of the other covariates compared to the first model.

Table 1. The models ranked and presented with the parameter estimates, standard error (SE), t- and p-value (significant p-values in bold) in addition to the $\Delta AICc$ and AICc values and weights.

Model rank	Parameter	Estimate	$\pm SE$	t-value	p-value	AICc	$\Delta AICc$	AICc weights
1	(Intercept)	17.429	0.802	21.721	0.000	870.3	0	0.72
	Sibling: α	-0.749	0.518	-1.447	0.155			
	β	-1.756	0.552	-3.182	0.003			
	Precipitation	-1.051	0.377	-2.792	0.008			
	NAO _w	-0.666	0.333	-2.001	0.085			
2	(Intercept)	18.363	2.556	7.184	0.000	872.1	1.89	0.28
	Sibling: α	-0.751	0.519	-1.447	0.155			
	β	-1.749	0.553	-3.162	0.003			
	Precipitation	-1.054	0.385	-2.735	0.009			
	NAO _w	-0.672	0.344	-1.956	0.091			
	Temperature	-0.090	0.230	-0.392	0.697			

Having a sibling reduced the daily growth rate; β -chicks had a 10 % lower daily growth rate, whereas α -chicks had a 4 % lower weight increment compared to singletons (both excluding standard errors). Re-ordering the levels of hatching order in the model, to see the effect when compared to α -chicks, showed a significantly lower growth rate (-6 %) for β -chicks compared to α -chicks, with no significant difference found between α -chicks and singletons.

For every additional millimetre of rain per day, daily growth was reduced by 6 %, 6.3 %, and 6.7 % for singletons α -chicks, and β -chicks respectively (Fig.4.).

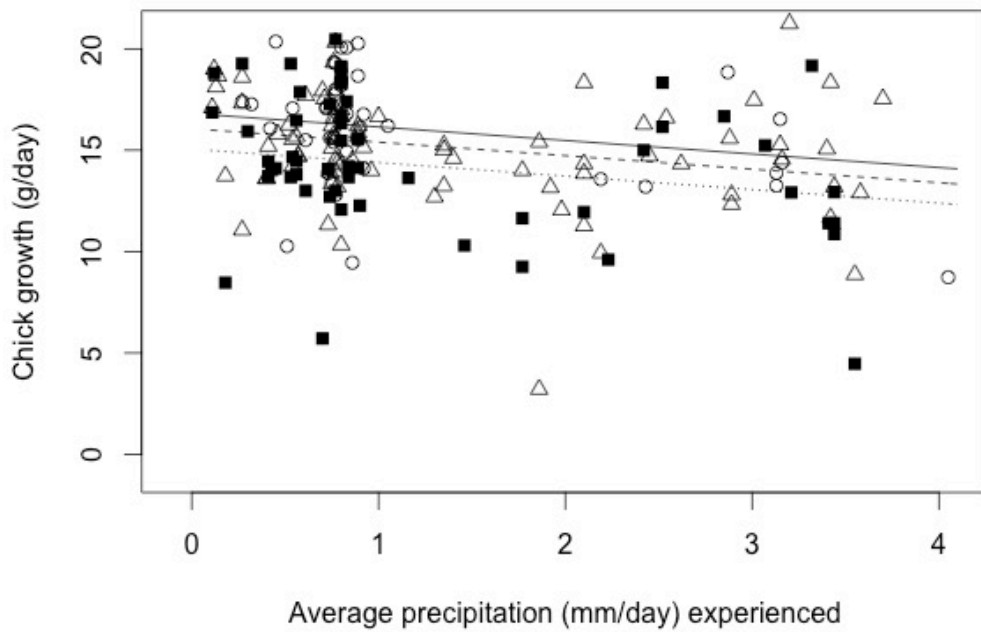


Fig. 4. Chick growth rate (g/day) as a function of the amount of rain (mm/day) that the chicks experienced from hatching until 19 days of age. Circles, triangles, and squares represent data points for singletons, α - and β -chicks, respectively. Solid, dashed, and dotted regression lines represent singletons, α - and β -chicks, respectively.

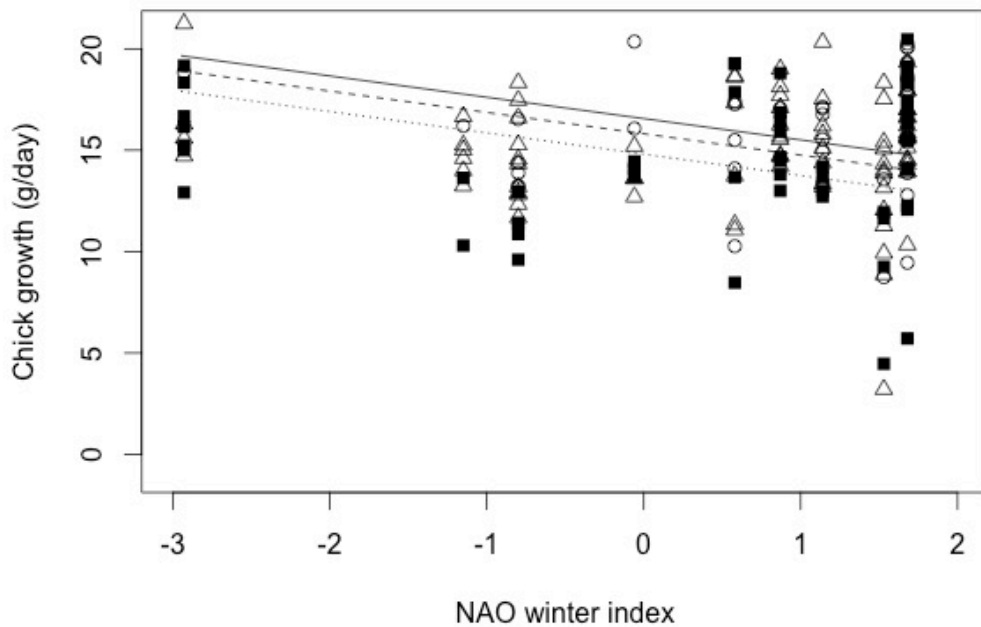


Fig. 5. Chick growth rate (g/day) as a function of the NAO winter index (December through February). Data points for singletons, α - and β -chicks are represented by circles, triangles, and squares, respectively. Solid, dashed, and dotted regression lines represent singletons, α - and β -chicks, respectively.

NAO_w showed marginally non-significant effects on chick growth (Fig. 5). There was a significant negative correlation between NAO_w and precipitation ($r = -0.54$, $df = 177$, $p < 0.001$), and excluding NAO_w from model 1 removed the significant relationship between precipitation and chick growth.

Possible two-way interactions between the different levels of the hatching order variable (singleton, α -, and β -chicks) and either one of the covariates (precipitation, NAO_w, and air temperature) were investigated, but none were found to be significant (results not shown).

3.2 Diet

For 2007-2015 a total of 630 diet samples were collected and analysed, 468 of which were from adult birds. Overall, there was slightly more of the other prey (51.4 %) than sandeel (48.6 %) in the diets. Sandeel was by far the dominating species of prey, followed by glacier lantern fish (17.8 %) and herring (11.9 %; Table S2 in the supplement).

The diet samples from 2012 had the lowest amounts of sandeel, with diets consisting of on average only 18 % sandeel prey on average, and a total of 82 % other prey. The average food load mass across all years was 22.3 g. The largest food loads were found in 2008, with average loads of 28.0 g, whereas 2011 and 2012 had the lowest average load masses, with 16.2 and 15.7 g, respectively (Table 2).

Table 2. Annual average of adult load masses together with number of diet samples (upper panel), and annual proportions of sandeel versus all other prey types in the diets of chicks and adults, together with number of diet samples (lower panel), during the years 2007-2015.

Year	2007	2008	2009	2010	2011	2012	2013	2014	2015
Load mass (g)	26.0	28.0	24.5	25.1	16.2	15.7	20.0	25.4	20.3
n	50	63	62	47	28	40	74	66	38
Other prey	0.67	0.59	0.23	0.56	0.46	0.82	0.51	0.50	0.29
Sandeel	0.33	0.41	0.77	0.44	0.54	0.18	0.49	0.50	0.71
n	62	68	65	50	41	59	105	84	96

The prey types, NAO_w , or the SSTs did not have any significant effects on the food load mass (Table S3 in the supplement). For the model using yearly averages, no significant relationships were found between chick growth and load mass, NAO_w or the proportion of sandeel in the diets. However when removing NAO_w from the model, food load mass had a marginally non-significant relationship on chick growth ($p = 0.082$).

3.3 Breeding success

There was a significant ($p < 0.001$) difference in breeding success between years (Fig. 6). The highest breeding success was recorded in 2007 with 0.99 chicks/nest, and the lowest in 2011 and 2014 with 0.30 and 0.32 chicks/nest, respectively. Chick growth and breeding success were positively correlated ($r = 0.20$, $df = 177$, $p = 0.006$; Fig. 6). Clutch size was positively correlated with breeding success ($r = 0.48$, $df = 177$, $p < 0.001$), but there was no significant correlation with the growth rates of chicks. The largest average clutch size was found in 2010 with an average of 2.07 eggs/nest, whereas average clutch size was smallest in 2014 with 1.53 eggs/nest (Table S4 in the supplement).

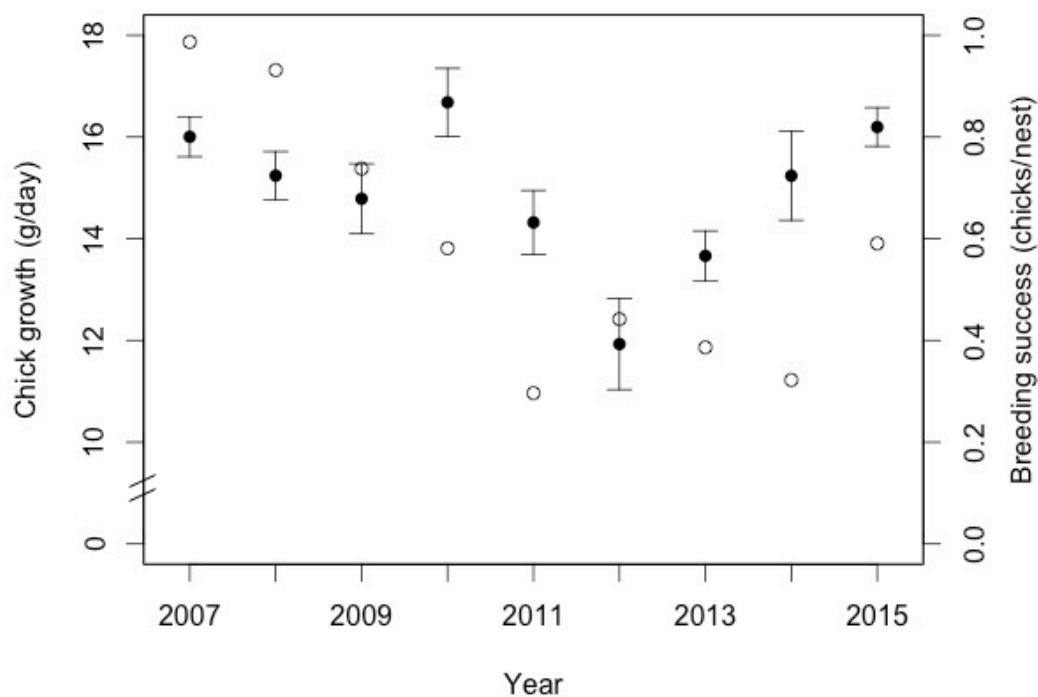


Fig. 6. Chick growth (solid circles with bars representing standard errors), and breeding success, (open circles), during the 2007–2015 breeding seasons.

4 DISCUSSION

4.1 General findings

This study found that chick growth showed a significant negative relationship with the amount of precipitation and the NAO_w . Hatching order also negatively affected the growth rate of individual chicks. Being a singleton was the most advantageous, followed by being the first-hatched out of two chicks. Sea surface temperatures, air temperature, and the number of days with precipitation did not show any significant effects on the growth rate of chicks. The clutch size was positively correlated with breeding success, which in turn was positively correlated with chick growth. No significant relationships were found between the large scale climate parameters (NAO_w and SSTs) and food load mass, and only a weak relationship between the food load mass and chick growth rate was found. No relationship was found between chick growth rate and the annual proportion of sandeel in the diet.

4.2 Chick growth and breeding success

The positive correlation between clutch size and breeding success found in this study was expected, as more eggs per nest lead to more chicks, which, as long as the feeding conditions during chick growth are not deteriorating (e.g. Ponchon et al. 2014), is likely to increase the number of surviving chicks per nest. A negative correlation between clutch size and chick growth could also have been expected through increased sibling competition when food was scarce (Braun & Hunt 1983). Such a correlation was however not found, indicating that other factors than food alone was more important for explaining the survival of the chicks in this study. Also, as clutch sizes are based on counts in the mid to late incubation period, egg predation, particularly by corvids (Christensen-Dalsgaard & Langset unpubl.), can have adjusted the clutch size prior to the counts.

The tendency of a positive effect of the average food load mass per year on the average growth rate of chicks, although weak, was expected, as chicks are able to maximize their growth rates when sufficient amounts of food are provided (Vincenzi & Mangel 2013). The lack of a stronger and significant correlation was unexpected, but might be caused by a number of possible explanations. First, due to the structure of the data, only a linear model

could be run, based on averages per year, masking individual variation in foraging performance between adults, and variation in foraging performance between adults with one or two chicks. For instance, adult kittiwakes with two chicks might have better body condition and be more experienced than parents with one chick (Coulson & White 1958). Second, it was expected that if the adult kittiwakes have to search longer for food then the return load mass should increase (e.g. Charnov 1976). The travelling distance to the fjords (where they catch their preferred prey type, sandeels) is about the same as the distance travelled to the edge of the continental shelf (where they mainly feed on mesopelagic fish). However, on the oceanic trips the birds fly further (Christensen-Dalsgaard & Lorentsen, unpubl.), indicating that they use more time to search for food along the continental shelf. Thus, it would be expected that individual load masses should be higher in years with more oceanic trips. Consequently, in years of high sandeel abundance, they could increase the number of trips, and their feeding efficiency. This would mask the effect of load mass on chick growth, as the birds may have a higher number of trips to the fjords, but provide smaller loads on each trip. There was however no effect of the proportion of sandeel in the diet on average chick growth, suggesting that the effect of food loads on chick growth might be mediated through an overall climatic effect on prey availability.

During 2011-2013, low chick growth rates coincided with low breeding success. This is in accordance with life-history theory that predicts a trade-off between cost of current reproduction and future survival (Stearns 1992). Hence, in order to minimize the impact of poor environmental conditions, adult seabirds may implement a “bet-hedging” strategy, in which they attempt to reduce the impact of poor environmental conditions on their own survival by sacrificing reproduction (e.g. Jenouvrier et al. 2005). The low chick growth rates and breeding success could be an indication of unfavourable conditions, forcing the parents to reduce their breeding efforts.

Other factors than food availability and climate might however also affect the breeding success of kittiwakes, predation being one such factor. For example, from 2009 and onwards, predation by ravens (*Corvus corax*) and crows (*Corvus cornix*) on kittiwake-eggs was frequently registered, although predation most likely also occurred in 2007 and 2008. In addition, predation on eggs and chicks by gulls (*Larus argentatus* and *L. marinus*) and sea

eagles (*Haliaeetus albicilla*) breeding near the kittiwake colony was observed (Christensen-Dalsgaard & Langset unpubl.). Furthermore, as demonstrated by Regehr and Montevecchi (1997), when *Larus* gulls in Newfoundland, Canada, experienced extreme food stress, due to a delayed availability of capelin and elimination of fisheries offal, they turned to kittiwake eggs and chicks as an alternate food source. If this holds true for other locations as well, it could imply that kittiwakes on Anda could experience an increased predation pressure by *Larus* gulls, when these gulls experience shortages in their own preferred prey.

Predation is likely to override any advantage in chick growth experienced due to hatching order and/or egg- or brood size, particularly in smaller colonies (Barrett & Runde 1980). Predation might also affect the feeding rate by forcing the parents to exert anti-predator behaviour instead of searching for food. However in periods of very poor feeding conditions adults might reduce chick guarding in order for both parents to search for food (Barrett & Runde 1980, Wanless & Harris 1989, Cadiou & Monnat 1996). As a result of this chicks might be left unattended, and will thus be more prone to predation, or falling out of their nest. Hence, if years of low food availability coincide with years of high predation pressure this could have detrimental effects on the number and condition of fledglings.

4.3 Direct effects of climate

In years with more precipitation during the linear growth phase chicks had lower growth rates. Rain increases heat loss through increased convective heat transfer, and as the plumage of the chicks is not yet fully waterproof, rain further increases the heat loss and hence energy expenditure (Gabrielsen et al. 1992). During the first 10-15 days, chicks are guarded by at least one of the parents. However, as the chicks grow older the activity of the parents at the nest changes and parents spend increasingly more time away from the nests, leaving the chicks more exposed (Gabrielsen et al. 1992, Roberts & Hatch 1993). In the years 2010, 2012 and 2013, the chicks experienced the most rain during their linear growth phase (Fig. S1 in the supplement), averaging more than 2.4 mm per day. Especially in 2012 and 2013 this might serve as one explanation for the low growth rates and breeding success observed.

In 2010, despite the large amounts of rain that the chicks experienced, this was the year with

the highest average chick growth and the largest average clutch size. This might indicate that other factors, such as sufficient food availability, might be more important factors than the amount of rain alone. For instance, a high food abundance in the wintering areas can increase the survival of adults (Reiertsen et al. 2014), and if the adults are in better body condition at the onset of the breeding season, an increased feeding efficiency to their chicks could be expected (Kitaysky et al. 2001). Furthermore, if the environmental conditions for primary and secondary trophic levels were advantageous prior to the breeding season, this could lead to an increased food abundance for the kittiwakes (Arnott & Ruxton 2002), and thus influence chick growth positively. It is expected that this higher food abundance might compensate for the effects of increased precipitation and energy budgets.

4.4 Indirect effects of climate

In years of high positive NAO_w anomalies, associated with low-pressure areas with heavy wind and precipitation (discussed above), the growth rates of chicks were lower than in years of negative indices. However, it is not only through these direct weather effects that the NAO_w might impact on chick growth. Through its effect on wind, air temperatures, heat and moisture transports and precipitation, the NAO_w exerts strong forces on the physiochemical properties of the ocean (Drinkwater et al. 2003). In turn, this affects the lower trophic levels that represent the food for the fish supplied to the chicks, and thereby also chick growth (e.g. Sandvik et al. 2005).

For the lesser sandeel (*Ammodytes marinus*) in the North Sea a negative relationship was observed between recruitment and the NAO_w , which affects sea temperatures during their egg and larval period (Arnott & Ruxton 2002). Sea temperatures, together with wind, also affects the interannual variation in abundance of the phyto- and zooplankton (i.e. *Calanus* sp.; Colebrook 1982). The abundance of sandeel is positively correlated with *Calanus* copepod abundance when the sandeel larvae hatch, indicating that it is an important prey species for the newly hatched sandeel larvae (Arnott & Ruxton 2002). Higher sea temperatures also increased the metabolic cost of wintering sandeels, reducing their growth rate, fecundity, and survival (Arnott & Ruxton 2002). This further lowered their nutritional value as prey for seabirds (Wanless et al. 2005). Hence, in years of high NAO_w anomalies, increased SSTs could

lower kittiwake chick growth through either lower recruitment of sandeel or by reduced nutritional values of the sandeel. With the current changes in climate, changes in life history events on the lower trophic levels can lead to mismatches in the timing of food peaks, resulting in possible collapses, not only for kittiwakes and other top predators, but for several levels of the food chain (Burthe et al. 2012).

Very little is known about the population dynamics of sandeel along the Norwegian coast. The sandeel population in the Gavlfjord South-east of Anda is however invaluable as a food source for the kittiwake (Bergstad et al. 2013). Having both the fjords and the oceanic sources of food probably explains why the kittiwakes at Anda has not experienced the same population decline as other Norwegian colonies (The Norwegian monitoring programme for seabirds, SEAPOP). Thus, the extremely low proportion of sandeel in the diets of 2012 (11.6 %), was compensated for by a fourfold increase in the amount of glacier lantern fish (43.0 %; Table S2 in the supplement). This further coincided with the lowest chick growth rates measured, and low breeding success. Data from GPS-loggers, deployed on breeding kittiwakes at Anda (during 2011-2014; Christensen-Dalsgaard & Lorentsen unpubl.; Fig. S2 in the supplement), support the observed dietary shift. In 2012 a more than twofold increase in oceanic feeding trips, 73 %; compared to inland/fjord trips, was observed in comparison to 22 %, 24 %, and 37 % in 2011, 2013 or 2014 respectively (Christensen-Dalsgaard & Lorentsen unpubl.). The distance to the continental shelf is similar to the distance to the fjords, but the total distances travelled during the oceanic trips are longer. The reason for this is probably that the kittiwakes are searching for food over a larger area, implying that the oceanic trips are more energetically costly for adults. Hence, when sandeel abundance is low, the adult kittiwakes have no option but to take the more energetically costly alternative, and search for food along the edge of the continental shelf.

Even though the NAO is a widely used proxy for “climate”, Mesquita et al. (2015) point out that it does not always explain the patterns in the variation of the populations examined. Rather, they found that point correlation maps, comparing variables at a particular point on a map with every other point on the map, could sometimes be more helpful for identifying significant explanatory indices related to climate. Their main conclusion being that solely using NAO as a proxy for climate, without looking for other climatic clues, might lead to the

erroneous conclusion that there is no correlation between certain ecological processes and climate only because no relationship with the NAO was found.

5 CONCLUSIONS

During the last three decades a shift from mostly negative to mostly positive NAO_w indices has been observed (Visbeck et al. 2001), with a magnitude that is unprecedented in the record (Hurrell 1995). The effects of this shift are hard to predict. Nevertheless, the force the NAO exerts on local weather and SST affects the timing of life history events for many trophic levels. This can in turn lead to a mismatch between the timing of food availability and food demands during the chick rearing period for kittiwakes. Although the effects of climate on seabirds may be direct, through physiological effects, or indirect, through an influence on prey availability, the relationship between the birds and climate is significantly affected by climatic influences on lower trophic levels.

Due to the changing climate, the patterns of precipitation have also been altered. In Northern Europe, Semmler and Jacob (2004) proposed a 50 % increase in precipitation for the period 2070-2100 compared to the period 1960-1990. The warm air masses, resulting from a warmer climate, are able to hold more vapour. As a result dry areas will become drier, and wet areas wetter (e.g. Semmler & Jacob 2004, Kundzewicz et al. 2006, Marvel & Bonfils 2013). Therefore, more rainfall is expected in the current study area (and the rest of coastal Norway). This may negatively affect chick growth rates and the condition of fledglings, and consequently future population recruitment.

The present study showed that an increase in the average daily amounts of rain reduced the growth of kittiwake chicks. Future predicted increases in the intensity of rainfall (Semmler & Jacob 2004) has the potential to significantly affect chick growth to an extent where juvenile survival, and thus future recruitment to the adult population, is impacted. The negative effect of precipitation could be related to the observed effect of the climate expressed through the NAO_w. However its main effect on chick growth is assumed mediated through the lower levels of the kittiwakes' food chain. Still, this study did not show statistically significant effects of NAO_w on the diets alone. The observed shift over the last three decades, where the NAO has shifted from mostly negative to mostly positive indices, increases the concern not only for the kittiwake but for lower trophic levels as well.

Knowledge about the effect of varying weather parameters on life history events,

incorporated into expected future weather scenarios, might help predict future kittiwake population trajectories. Being top predators, their response to climate and food availability could serve as a good indicator of the effect of climate on the whole food web.

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SUPPLEMENT

Table S1. Correlation matrix for the climate parameters used in the chick growth model.

	Prec.days	Ind.prec	Ind.temp	Ind.wind	SST.mam	SST.jja	NAO _w
Prec.days	1	0.69	0.06	-0.04	-0.45	-0.03	-0.69
Ind.prec	0.69	1	0.04	-0.24	-0.79	-0.50	-0.54
Ind.temp	0.06	0.04	1	-0.64	0.17	0.06	-0.23
Ind.wind	-0.04	-0.24	-0.64	1	0.31	0.43	0.01
SST.mam	-0.45	-0.79	0.17	0.31	1	0.77	0.26
SST.jja	-0.03	-0.50	0.06	0.43	0.77	1	-0.02
NAO _w	-0.69	-0.54	-0.23	0.01	0.26	-0.02	1

Key:

Prec.days: Number of days with precipitation during the linear growth phase of the chick

Ind.prec: Daily amount of precipitation during the linear growth phase of the chick

Ind.wind: Daily strength of wind during the linear growth phase of the chick

Ind.temp: Daily air temperature during the linear growth phase of the chick

SST.mam: Average sea surface temperatures for March-May

SST.jja: Average sea surface temperatures for June-August

NAO_w: North Atlantic Oscillation winter index for December-February

Table S2. Composition of the kittiwake diets for adults and chicks on Anda during 2007-2015.

Year	% of diets							
	Sandeel	Herring	Lantern fish	Gadids	Silvery lightfish	Spotted barracudina	Offal	Crustacea
2007	35.8	18.0	0.0	42.3	0	0	1.5	0.0
2008	38.9	14.8	20.8	6.5	0.3	0	0.0	6.5
2009	64.7	5.3	16.5	0.3	0.5	0	4.1	3.2
2010	48.5	18.0	14.1	3.4	8.4	0	4.3	1.4
2011	53.0	5.7	11.1	14.5	2.3	0	6.5	3.2
2012	11.6	11.3	43.0	5.5	0.4	4.7	0.8	15.1
2013	42.5	11.7	21.1	9.8	1	2.8	3.5	5.4
2014	42.3	14.5	16.2	16.6	1.6	2.7	1.9	2.0
2015	53.4	7.5	17.8	5.7	0.9	5.5	1.4	5.5
Avg	43.4	11.9	17.8	11.6	1.7	1.7	2.7	5.3

Table S3. The model parameters for the model with food load mass set as response variable, with the proportion of sandeel, NAO_w , SSTs as explanatory variables. Load mass was square rooted.

Parameter	Estimate	\pm SE	t-value	p-value
(Intercept)	-1563.974	1212.856	-1.290	0.198
Proportion Sandeel	-0.045	0.138	-0.329	0.742
NAO_w	1950.180	1625.166	1.2	0.442
SST.mam	247.755	190.618	1.3	0.418
SST.jja	145.326	112.514	1.291	0.419
NAO_w :SST.mam	-316.361	267.312	-1.183	0.447
NAO_w :SST.jja	-180.929	149.277	-1.212	0.439
SST.mam:SST.jja	-22.963	17.652	-1.301	0.417
NAO_w :SST.mam:SST.jja	29.345	24.54	1.196	0.443

Key, see Table S1.

Table S4. The number of singleton, α - and β -chicks per year, used to calculate chick growth. Average clutch size, breeding success and chick growth for 2007-2015.

Year	n singleton	n α	n β	Clutch size	Breeding success	Chick growth
2007	1	10	8	1.8	0.99	16.00
2008	6	8	4	1.8	0.93	14.79
2009	2	4	4	1.74	0.74	14.79
2010	1	4	7	2.07	0.58	16.68
2011	1	6	2	1.67	0.30	14.32
2012	2	13	4	1.74	0.44	11.93
2013	5	11	5	1.67	0.39	13.66
2014	5	6	5	1.53	0.32	15.24
2015	19	20	16	1.68	0.59	16.29

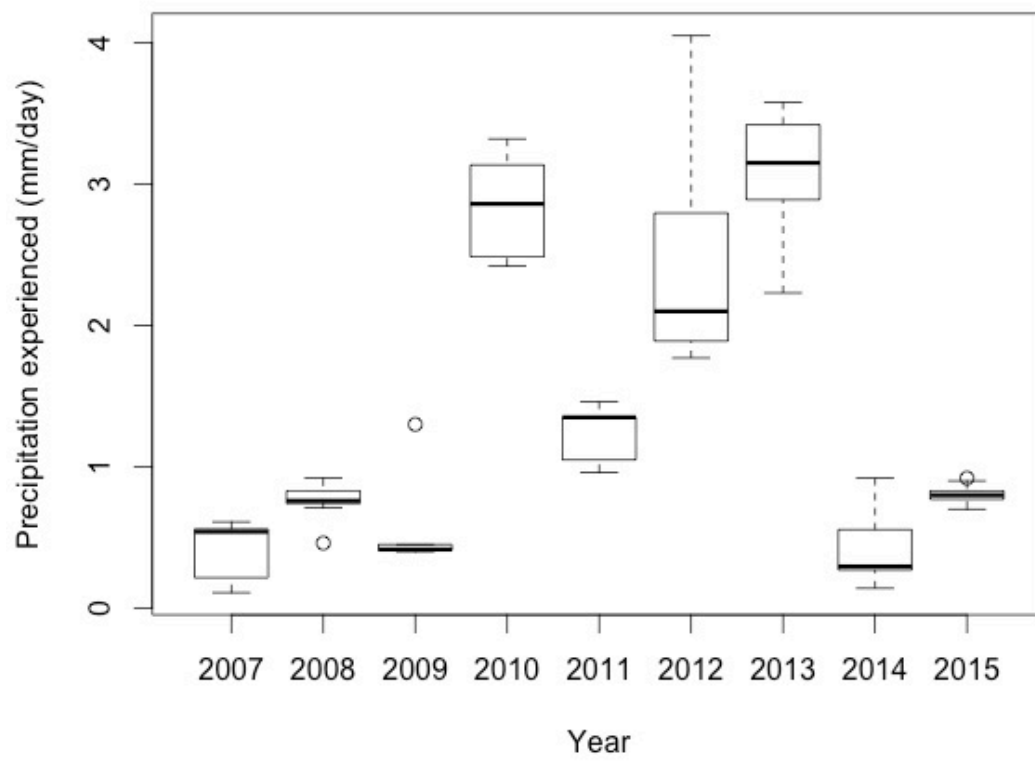


Fig. S1. The amount of precipitation chicks experienced during their linear growth phase during the breeding season 2007-2015 (mean values with boxes representing upper and lower quantiles, bars represent standard deviation).

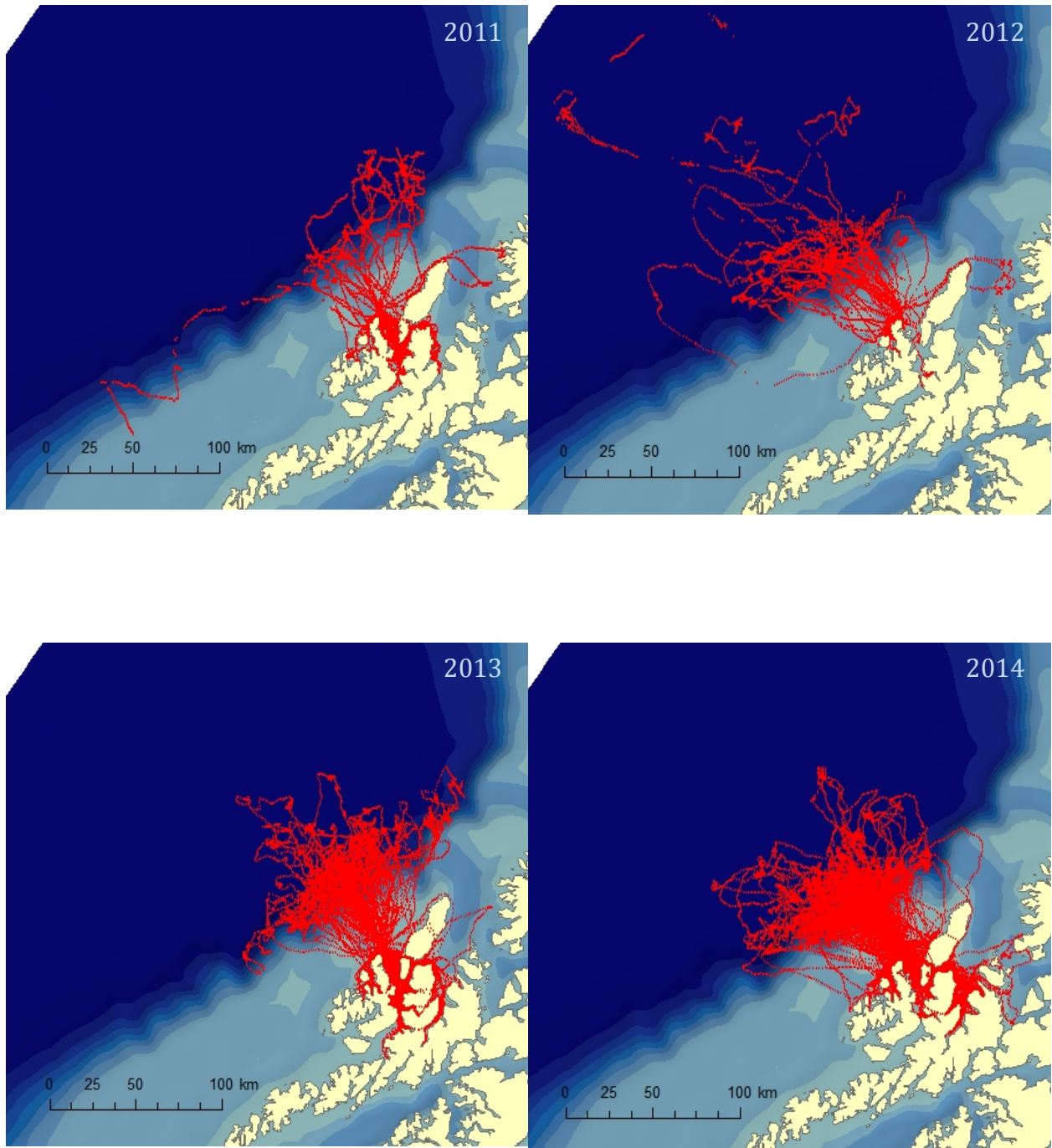


Fig. S2. Feeding trips by breeding kittiwakes collected from GPS loggers during 2011-2014.