Prevailing weather conditions and diet composition affect chick growth and survival in the black-legged kittiwake

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ABSTRACT: To identify priorities for management of seabirds during the breeding season, it is important to understand the ecological mechanisms driving chick growth and survival. In this study, we examined the effects of diet and prevailing weather on the growth and survival of chicks of black-legged kittiwakes *Rissa tridactyla* over a 10 yr period at Anda, a seabird colony in northern Norway. We show that across all years, there was a significant effect of diet composition delivered to chicks on their growth and survival. A higher proportion of sandeel *Ammodytes* spp. in the chick diet was associated with an increase in daily growth rates, a pattern that was especially pronounced for the youngest chick in 2-chick broods. A high proportion of mesopelagic fish in the chick diet was associated with a decrease in survival, again, especially for the youngest chick in 2-chick broods. Periods of strong southerly winds also led to reduced survival, probably linked to nests being washed down from the colony. Growth rates of kittiwake chicks were negatively affected by wind speed, likely due to adults having to work more in the exposed habitats in strong winds, causing a reduction in the amount of food supplied to the chicks. Our results emphasise the importance of conservation of specific marine habitats shown to be important foraging areas in ensuring the reproductive success of seabirds. This might prove increasingly important if future climate regimes make ecological conditions more challenging for seabirds.

KEY WORDS: Foraging effort · Mesopelagic fish · Nestling development · Prey availability · *Rissa tridactyla* · Sandeel · Wind conditions

INTRODUCTION

Seabird populations have declined worldwide during the last decades, increasing the conservation concern for this species group (Croxall et al. 2012, Lewison et al. 2012, Lescroël et al. 2016). There is thus an urgent need to identify and understand the ecological mechanisms leading to reduced performance of seabirds. Population change is a function of all life history traits. Therefore, an important question in life history theory as well as for conservation measures is the relative importance of environmental influences on adult survival, offspring production and recruitment (Stearns 1992, Weimerskirch et al. 2003, Sandvik et al. 2012). The general pattern for long-lived species with delayed reproduction like seabirds is that adult survival has high, and fecundity low, elasticity (importance for the population growth rate) (Sæther & Bakke 2000). This is also evident from demographic analyses indicating that population growth rates of long-lived species will be more sensitive to changes in post-fledging juvenile or adult sur-

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vival than breeding success (Doherty et al. 2004, Stahl & Oli 2006, Finkelstein et al. 2010). However, recent research has also shown that poor breeding success can be an important driver of the population decline observed in seabirds (Sandvik et al. 2012, Reiertsen 2013). We therefore need to understand the environmental factors causing the changes in breeding success and thus also breeding numbers observed in many seabird populations. In this context, both offspring survival rate and condition are important to consider, since breeding success, chick growth and chick body condition can have long-term consequences on recruitment rates and future fitness of recruits (Cam et al. 2003, Cam & Aubry 2011, Monticelli & Ramos 2012).

During the breeding season, seabirds must balance their resource allocation between maintaining their own body condition and the needs of their offspring (Erikstad et al. 1998). Being long-lived animals, they are expected to prioritize their future residual reproductive value over current reproduction (Stearns 1992). A decrease in prey availability or increase in external pressures during the breeding season is therefore expected to be passed over to the offspring, leading to reduced offspring growth and, ultimately, survival (Stearns 1992, Rishworth & Pistorius 2015).

One seabird species of conservation concern is the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake), a small pelagic surface-feeding gull with a Holarctic distribution, breeding in the Arctic and boreal zones throughout the Northern Hemisphere. The global population is large and estimated to be more than 9 million adults (Coulson 2011), but many colonies in the Atlantic Ocean are in rapid decline (Frederiksen 2010, Descamps et al. 2017), with the species being listed as Vulnerable in the global Red List of the IUCN (BirdLife International 2017) and as Endangered in the Norwegian Red List (Henriksen & Hilmo 2015). Kittiwakes feed predominantly on fish and marine invertebrates (Coulson 2011), and rely on prey being available near the ocean surface (Furness & Tasker 2000). Furthermore, kittiwakes appear to operate at their energetic ceiling during the breeding season (Welcker et al. 2010), hence exacerbating their sensitivity to ecological changes in the marine ecosystem (Monaghan 1996, Furness & Tasker 2000). The foraging behaviour and breeding success of kittiwakes can be affected by prevailing weather conditions (Lloyd 1985, Elliott et al. 2014, Christensen-Dalsgaard et al. 2018), highlighting the importance of understanding how weather patterns predicted for the next centuries might impact the reproductive output of kittiwakes (Christensen-Dalsgaard et al. 2018).

Kittiwakes lay between 1 and 3 eggs, with a modal clutch size of 2 eggs (Coulson 2011). In multi-egg clutches, the eggs usually hatch asynchronously at 1–2 d intervals (Hatch et al. 2009). Chicks that hatch first (hereafter 'α-chick') usually have a higher growth and survival rate than the second (hereafter 'β-chick') or third hatchling, especially under conditions of low food availability (Gill et al. 2002, White et al. 2010, Young et al. 2017). Kittiwakes can, however, raise 2 or even 3 offspring to fledging if food conditions are favourable. The chicks are not homeothermic until around 16 d post hatching (Gabrielsen et al. 1992), and when prey availability allows for it, they are always attended by 1 adult in the first days of their life (Coulson 2011).

The kittiwake has been a focal species in numerous studies examining responses to environmental stressors during the breeding season, including variation in food availability (Gill et al. 2002, Young et al. 2017), prey composition (Barrett 2007) and wind conditions (Elliott et al. 2014). In our study, we included the different environmental stressors to examine the relative importance of intrinsic and extrinsic determinants of kittiwake chick growth rate and survival during the nestling period. The study was carried out at the island of Anda, northern Norway. We used a long-term monitoring dataset from breeding kittiwakes to test 3 main *a priori* hypotheses regarding factors affecting chick growth and survival: (1) chick status, including singletons (in 1-chick broods), α- and β-chicks (in 2-chick broods), (2) chick diet composition and (3) prevailing weather conditions.

Based on previous research (Coulson & Porter 1985, Gill et al. 2002, Jodice et al. 2008, Elliott et al. 2014, Young et al. 2017), we predicted that (1) prey composition would affect growth and survival of chicks, but (2) that this is related to the age of chicks and their hatching order, with all small chicks, and in addition all age-classes of β-chicks being most influenced by diet composition. Last, we predicted that (3) prevailing weather conditions would affect (1) growth indirectly through reduced amount of food supplied to the chicks or (2) survival directly through exposure and cooling of the chicks.

MATERIALS AND METHODS

Study system

Fieldwork was conducted in June and July during the 10 yr period of 2007−2016 at the island of Anda (69° 03′ N, 15° 10′ E) in the northern Norwegian Sea.

Anda is one of few sites in Norway (excluding Svalbard) where population numbers of kittiwakes have remained stable over the last decade (Anker-Nilssen et al. 2017). Here, the birds rely on nearby feeding habitats within ca. 60 km of the colony both offshore along the continental shelf break and in inshore areas (Christensen-Dalsgaard et al. 2018). During the study period, a mean of 898 pairs (range 719–957) of kittiwakes nested in the colony.

Data collection

Data on chick growth and survival were collected from randomly selected study nests (n = 13–50 nests yr^{-1}; total nest-years included in study = 296). We monitored breeding birds at the same ledges in the colony in all years (as defined by reachable nests). Kittiwake nests were situated on steep cliffs, and sampling was done either by accessing nests from a ledge on the cliff or by rappelling from above. To reduce possible adverse impacts of disturbance, nests were only monitored approximately every 5 d throughout the chick-rearing period. The nests included in the study were individually numbered each year, but specific nest ID was not kept between years. Nests with 3 eggs or chicks were excluded from the analysis because they were rare (annual average 8.3%; range = 0.0–30.8%) and the sample size was therefore too small to allow for proper statistical analysis. At each 5 d monitoring event of the nests, the age of a chick (precision ±2 d) hatched since the last visit was determined based on knowledge of the status of the egg during the previous visit (intact, pipped or starred), combined with wetness of the plumage or measurements of total head length (head and bill; using a slide calliper to the nearest 0.01 mm). The status of chick(s) (singleton, α or β in 2-chick nests) was determined by monitoring of hatching time of the eggs or relative body size of chicks if both eggs had hatched within the same 5 d monitoring period. Chicks in each nest were individually marked by either colouring them on the top for the head with permanent markers or using plastic colour rings for identification. At each nest visit, the status of the chicks was recorded as alive, dead or disappeared, and body mass was measured with a spring balance (Pesola, ±1 g). As the laying dates of the eggs were usually unknown, we were unable to predict the expected hatching dates of eggs and, thus, could not determine the survival rates of chicks between hatching date and our first visit to the nest after hatching (age 0–5 d). Further,

kittiwake chicks do not fledge until an age of ~40 d (Coulson 2011), but they become mobile at around 30 d. To avoid the risk of premature fledging, we did not visit nests in the 10 d period before the predicted fledging date. Moreover, we could not determine whether a 30–40 d old chick that had disappeared was dead or had fledged. Thus, we restricted our analysis to chicks aged 5–28 d in the study.

Diet was determined from samples of crop and stomach contents collected from chicks and chick-rearing adults when birds regurgitated during handling. Each diet sample was categorized as being considered complete (the adult had just returned from a foraging trip) or partly consumed. Diet samples were grouped within the same 5 d periods as the nest monitoring (n = 713 diet samples; average per 5 d period = 12.3; range per 5 d period = 4–25; for more information, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m604p237_supp.pdf). Each sample was collected in a separate plastic bag and was stored at −20°C. In the laboratory, the samples were thawed and weighed to the nearest 0.1 g, and the contents were sorted and identified to the lowest possible taxon. The samples were then further digested in a saturated solution of biological washing powder (Biotex) at 50°C for at least 24 h. Diet composition was determined by identification of prey remains, comparing residual bones, scales and other hard parts to reference collections described by Breiby (1985), Härkönen (1986), Watt et al. (1997) and a personal reference collection (R. T. Barrett unpubl. data). To identify in which foraging areas the different prey species were caught, diet samples were collected from breeding birds instrumented with GPS loggers when they returned from foraging trips (n = 46; logger type: i-gotU GT-120 GPS-loggers from MobileAction disassembled from their outer casing and refitted with a smaller battery to reduce weight). Tracking methods are described by Christensen-Dalsgaard et al. (2018). The foraging trip conducted prior to capture was used to assign prey type to foraging habitats based on where the location furthest away from the colony was situated. The foraging habitats were separated in 2 categories; 'oceanic', representing zones of upwelling around the edge of the continental shelf, and 'coastal', representing feeding areas along the coast and into the fjords. The distinction was based on visual inspection of whether the birds travelled into the fjords or to the shelf break.

Prey types were generally easy to distinguish visually in the food samples, and their proportions were estimated before digestion in the laboratory. The taxonomic composition of each sample was deter-

mined as the proportion of the diet by mass in the individual loads, separated into the following 4 main diet categories: sandeels *Ammodytes* spp.; meso-pelagic fishes (glacier lantern fish *Benthosema gla-ciale*, spotted barracudina *Arctozenus risso* and sil-very lightfish *Maurolicus muelleri*); gadids (cod, haddock and related species); and herring *Clupea harengus*. In addition, the diet samples contained miscellaneous prey (other fish species, crustaceans, offal). These were not included in the analysis due to low sample size. For each period between 2 subse-quent visits, the proportion of each diet category was calculated as the mean proportion of all diet samples collected within that period.

Weather data were obtained from the Norwe-gian Meteorological Institute (www.eklima.no). Wind speed and temperature were obtained at hourly intervals from the weather station at Andøya (46 km northeast of Anda), whereas daily precipitation was obtained from both Andøya and Sortland (41 km south of Anda). We used 2 sites to account for the pat-terns of precipitation at Anda, which is affected by conditions both inland (represented by Sortland) and on the coast (represented by Andøya). Average values of precipitation from these 2 sites were calcu-lated. An index of effective temperature (chill factor in °C) was calculated with the following function (www.nws.noaa.gov):

$$T_{effective} = 13.12 + 0.6215 \times T_a - 11.37 \times V^{0.16} + 0.3965 \times T_a \times V^{0.16} \quad (1)$$

where T_a is the ambient temperature (°C) and V is the wind velocity (km h^{-1}).

Mean values of wind speed and effective tempera-ture for each period between 2 visits were calculated. The wind direction, obtained hourly, was divided into 3 groups, i.e. north-easterly (NE, 0–120°), southerly (S, 120–240°) and north-westerly (NW, 240–360°) based on the prevailing wind directions during for-aging trips (see Christensen-Dalsgaard et al. 2018). Subsequently, the prevailing wind direction in each 5 d period was defined as the direction with >50% of the prevalence. If there was no prevailing wind direction under this definition, the wind direction was defined as 'mixed'. For analysis of precipitation, we used the day with the highest amount of precipi-tation in each 5 d period as a measure of greatest exposure. To standardize coefficients to a common scale for comparison, binary and continuous vari-ables were subsequently scaled by subtracting the mean and dividing by 2 SD (Gelman 2008). To con-trol for variation in hatching dates between years, the hatching dates were scaled separately for each year.

Growth of kittiwake chicks

Daily growth rates of the individual kittiwake chicks were calculated as the change in mass be-tween 2 consecutive visits divided by the number of days between the visits. During the data exploration prior to fitting the models, we identified non-linearity of growth rate as a function of chick age. Chick growth was thus modelled with a restricted cubic spline with 3 knots in all models (Harrell 2001). Daily growth rate as a function of the explanatory covariates was then analysed using linear mixed-effects models. Analysis was carried out using the R package 'lme4' (Bates et al. 2015), with bird ID nested within nest ID, nested within year included as random intercept to account for non-independent observations.

Survival of kittiwake chicks

We calculated survival rates of individual kittiwake chicks with staggered entry Kaplan-Meier models using the R (R Core Team, 2017) package 'survival' (Therneau 2015). Data from chicks with estimated ages 5–28 d were included in the model, and en-counter histories were created based on each period between 2 subsequent visits.

To incorporate time-varying covariates, left-cen-sored data and irregular check intervals in our analy-sis, we analysed our survival data with the Andersen-Gill model (Andersen & Gill 1982, Johnson et al. 2004, Winder et al. 2018). In the Andersen-Gill mo-del, encounter histories were coded separately for each visit, such that each chick contributed 1–5 encounters to the model with 5 d intervals between Days 5 and 28 after hatching. Kittiwakes are cliff-nesting seabirds with chicks confined to narrow ledges without the possibility to move far away from the nest, and we considered a missing chick age <29 d to be dead. Each encounter record consisted of age at entry, age at exit, the chick's fate at the end of the observation interval (1 = dead or disappeared, 0 = present and alive) and the environmental covariates for the preceding 5 d period. Initial entry into the model was defined as the first time the chick was registered or when the chick was ≥5 d of age. To account for a lack of independence between chicks from the same nest, nest ID was included as a ran-dom effect with the cluster function. The Andersen-Gill formulation of the Cox proportional hazards model was then fit using the 'surv' and 'coxph' func-tions of the R package 'survival' (Therneau 2015). We tested the proportional hazards assumption of the

models using the 'cox.zph' function to check the fit of Schoenfield residuals for our global model and individual predictor variables (Therneau 2015). Last, hazard functions were calculated using smoothing spline functions with the R package 'gss' to examine the age-specific patterns of mortality in chicks aged 5–28 d caused by the variables in the model best fitting the data (Gu 2014).

Model selection

We developed subsets of models according to our 3 hypothesized factors affecting chick growth and survival: (1) chick status, (2) diet composition and (3) weather conditions. 'Chick status' included number of chicks in the nest, hatching order and status of the sibling; 'diet composition' consisted of the proportion of the 4 most common species or species groups of prey brought back to the chicks (i.e. not the total diet); and 'weather conditions' included wind strength, prevailing wind direction, precipitation and effective temperature (chill factor) in 5 d windows. We included interacting effects when this was in accordance with our hypotheses, but restricted it to 2-way interactions to reduce the number of parameters to be estimated (for all models included, see Tables S2 & S3 in the Supplement). Support for different candidate models was assessed using Akaike's information criterion adjusted for small sample size (AIC_c, Burnham et al. 2011). The model with the lowest AIC_c value was considered best supported. Models were considered to be equally parsimonious if they differed from the best

model by less than 2 AIC_c units (Burnham & Anderson 2002).

RESULTS

Mean clutch size, growth rate, survival and fledging success in the study nests varied among years in our 10 yr study (Table 1). Years 2008, 2012 and 2013 had the lowest survival rates and 2012 had the lowest growth rate, whereas 2007, 2015 and 2016 stood out as years with overall high growth rate and survival.

The proportions of different prey groups in the diet varied during the study period, with sandeel and mesopelagic fishes being the main part of the diet, followed by gadids, herring and other prey (Fig. 1, Table S1). Analysis of diet obtained from the GPS-instrumented birds showed that 89% of the diet samples containing mesopelagic fish were obtained in the oceanic habitat (n = 9, Fig. 2). The remaining sample containing mesopelagic fish originated from a bird that had taken a foraging trip including both coastal and oceanic habitat. Of diet samples containing respectively herring (n = 8), sandeel (n = 20) and gadids (n = 4), 87, 95 and 100% were obtained from the coastal areas (Fig. 2). The amount of sandeel and mesopelagic fish in the diet were negatively correlated (Pearson's product moment correlation, r = −0.58, p < 0.001), but pairwise comparisons of the other diet categories were not correlated. When considering only the complete diet samples, diet samples containing coastal species (mean ± SE weight: 24.7 ± 0.69 g, n = 379) were on average heavier than those containing oceanic species (19.49 ± 1.05 g, n = 91).

Table 1. Annual variation in numbers of nests monitored, number of chick 5 d monitoring periods, hatching rate, daily growth rates, and 28 d survival of kittiwake chicks and diet composition of the 2 main prey groups at Anda, Norway, 2007–2016. Summary statistics are based on nests with 1 or 2 chicks. Values are given as mean ± SE

| Year	No. of nests	No. of 5 d periods	No. of chicks hatched nest^{-1}	Growth rate (g d^{-1})	Survival to Day 28 (proportion)	Diet composition Sandeel (%)	Mesopelagic fish (%)
2007	24	110	1.63 ± 0.10	15.47 ± 0.34	0.79 ± 0.08[a]	35.4 ± 11.38	0.0 ± 0.00
2008	29	143	1.59 ± 0.09	14.55 ± 0.44	0.44 ± 0.08	40. 2 ± 7.94	24.5 ± 5.04
2009	15	66	1.64 ± 0.13	15.04 ± 0.67	0.69 ± 0.10[b]	59.6 ± 12.90	23.8 ± 9.90
2010	13	59	1.61 ± 0.14	15.17 ± 0.57	0.63 ± 0.16	46.4 ± 7.52	28.7 ± 4.48
2011	17	73	1.65 ± 0.12	14.33 ± 0.62	0.54 ± 0.12	65.3 ± 12.06	13.9 ± 1.63
2012	34	146	1.58 ± 0.10	11.19 ± 0.58	0.33 ± 0.07	15.7 ± 4.54	46.1 ± 12.06
2013	40	164	1.45 ± 0.08	14.13 ± 0.41	0.38 ± 0.07	52.9 ± 7.35	18.4 ± 3.63
2014	18	87	1.50 ± 0.08	14.82 ± 0.62	0.72 ± 0.09[b]	36.6 ± 11.14	16.3 ± 4.04
2015	52	295	1.52 ± 0.07	15.69 ± 0.33	0.76 ± 0.05	59.9 ± 11.14	16.7 ± 9.11
2016	50	340	1.66 ± 0.07	15.58 ± 0.26	0.88 ± 0.05	46.1 ± 7.24	3.8 ± 3.41

[a]Up to Day 21, [b]Up to Day 17
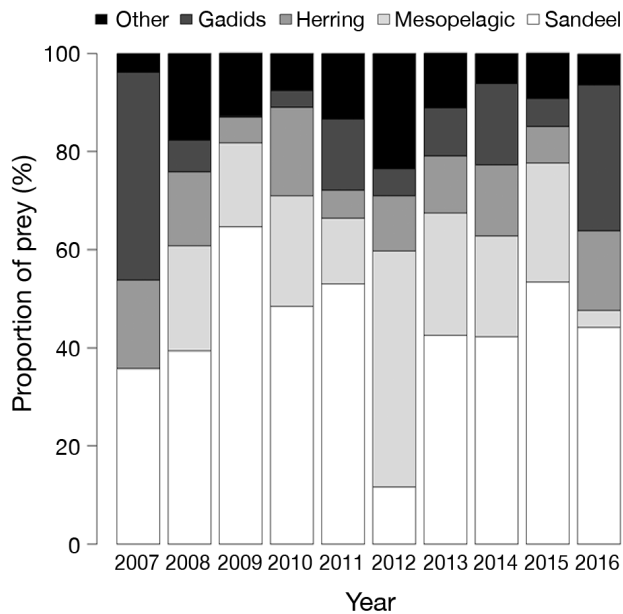
Fig. 1. Annual means of different prey classes in the kitti-wake diet during the study period at Anda, northern Norway, 2007 to 2016

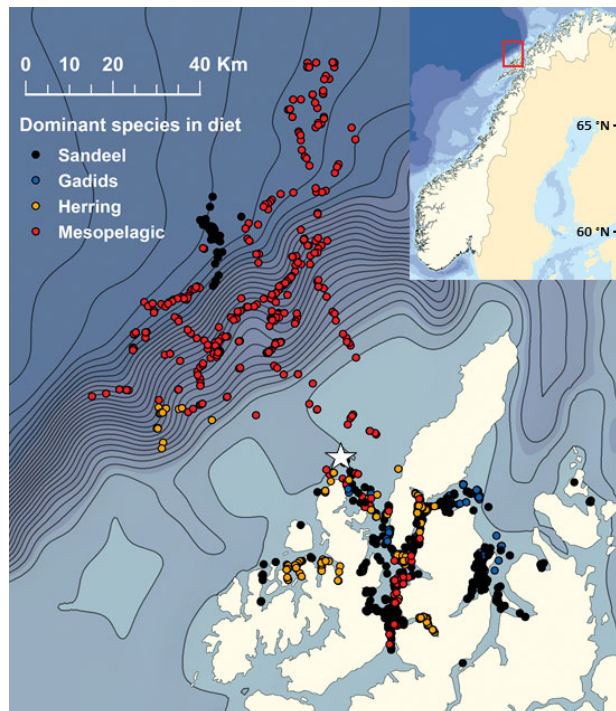
Fig. 2. Kittiwake colony on Anda (marked with a star) and distribution of foraging locations of GPS-instrumented kittiwakes (coloured dots, n = 46). Samples of stomach contents were collected from regurgitating birds after return to the colony. Dot colours represent the dominant species targeted during each trip. Black lines are 100 m depth contours. Inset shows the location of the colony in northern Norway

Chick growth

For chick growth rate related to intrinsic factors, 3 models had considerable support (Table 2). The highest ranked model described growth as a function of number of chicks in the nest, with 2-chick nests having a lower daily growth rate than chicks in 1-chick nests ($\beta = -0.89$, 95% CI = -1.45 to -0.33). The second-best model included growth rate in relation to change in sibling status (i.e. after the loss of a sibling). To evaluate the results from this model, the variables in the model were re-ordered to compare what happened when the sibling of respectively α- and β-chicks disappeared, and the remaining chick thus became a singleton. Both α- and β-chicks increased in growth rate after the death of a sibling, but neither increase was significant ($\beta_{\alpha\text{-chick}} = 0.75$, 95% CI = -0.10 to 1.57; $\beta_{\beta\text{-chick}} = 0.75$, 95% CI = -0.77 to 2.25). The third model showed that β-chicks had a lower daily growth rate than α-chicks ($\beta = -0.77$, 95% CI = -1.38 to -0.16), whereas there was no difference in growth rate between singletons and α-chicks ($\beta = 0.28$, 95% CI = -0.47 to 1.03).

The most strongly supported model explaining growth as a function of diet showed that growth rate was positively related to the proportion of sandeel in the diet ($\beta = 1.99$, 95% CI = $1.32–2.67$). Expanding this model with the intrinsic effect of hatching order of chicks and their interaction further improved model fit ($\Delta AIC_c = -9.51$). The results of this model showed that growth rates of both β-chicks and singletons were more positively related to the proportion of sandeel than among α-chicks (respectively $\beta_{\beta\text{-chick}} = 1.20$, 95% CI = -0.01 to 2.41 and $\beta_{singleton} = 1.85$, 95% CI = $0.41–3.28$, Fig. 3).

For effects of prevailing weather on the growth rate, a model including the effective temperature (wind chill) performed best, with a positive relationship between growth rate and effective temperature ($\beta = 1.86$, 95% CI = $1.18–2.55$).

The best model describing the growth rate in relation to wind strength and diet included proportion of sandeel, wind strength and their interaction. Growth was positively affected by an increase in the proportion of sandeel in the diet ($\beta = 1.93$, 95% CI = $1.26–2.59$) but negatively by an increase in wind speed ($\beta = -1.08$, 95% CI = -1.70 to -0.46). The interaction revealed that under conditions of strong wind, growth is especially dependent on the proportion of sandeel in the diet ($\beta = 1.79$, 95% CI = $0.53–3.04$, Fig. 4). When considering all models explaining growth of chicks, there was strong evidence of proportion of sandeel in the diet being the most important variable (Table 2).

Table 2. Model selection results for growth of kittiwake chicks (displayed are selected models with $\Delta AIC_c < 5$, and null model including only the effect of age on growth; all other models with $AIC_c > 5$ have been culled for space. See the Supplement for all models.). Results are shown for models grouped by 3 hypothesized factors affecting chick growth and survival (1: chick status; 2: diet composition; 3: weather conditions) and when comparing all models. The models with the lowest ΔAIC_c and highest AIC_c weight in each group are shown in **bold**. rcs: restricted cubic spline (see growth analysis in 'Materials and methods'). Model notations: no. of chicks = 1 vs. 2, sibling status = sibling alive vs. dead, hatching order = α vs. β, sandeel diet = % in diet, chill = effective temperature (°C), wind speed = mean wind speed (km h^{-1})

| Model	Hypothesis	df	Hypothesis groupings			All models together	
			ΔAIC_c	ΔAIC_c	AIC_c wt	ΔAIC_c	AIC_c wt
rcs(age, 3)		7	7910.0			41.7	0.00
rcs(age, 3) + no. of chicks	1	8	7711.9	**0.0**	0.55	33.6	0.00
rcs(age, 3) + sibling status	1	11	7713.2	1.3	0.29	34.9	0.00
rcs(age, 3) + hatching order	1	9	7714.4	2.5	0.16	36.1	0.00
rcs(age, 3) + sandeel diet	2	8	7689.0	**0.0**	**1.00**	10.6	0.00
rcs(age, 3) + sandeel diet × hatching order	1, 2	12	7679.5	**0.0**	**0.78**	1.1	0.33
rcs(age, 3) + sandeel diet × no. of chicks	1, 2	10	7682.0	2.5	0.22	3.7	0.09
rcs(age, 3) + chill	3	8	7692.9	**0.0**	**0.85**	14.6	0.00
rcs(age, 3) + wind direction × chill	3	14	7696.5	3.6	0.14	18.1	0.00
rcs(age, 3) + sandeel diet × wind speed	2, 3	10	7678.3	**0.0**	**0.99**	**0.0**	**0.57**
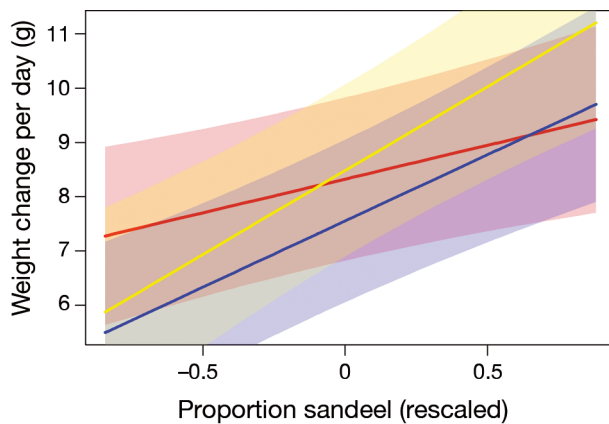
Fig. 3. Predicted probabilities from the best model describing the growth of kittiwake chicks as a linear function of diet and hatching order. The red line represents α-chicks, blue line β-chicks and yellow line singletons, with shaded values showing the 95% confidence intervals for each group. The values on the *x*-axis are rescaled values of the proportion of sandeel in the diet
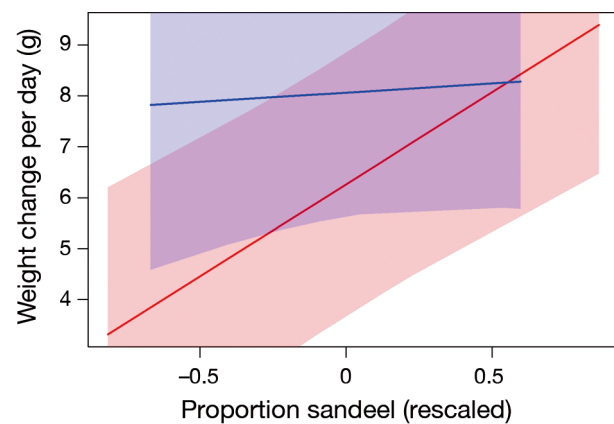

Fig. 4. Predicted probabilities from the best model describing the growth of kittiwake chicks as a function of diet and wind strength. The blue line represents low wind (calculated as mean wind − 1 SD) and red line strong wind (calculated as mean wind + 1 SD), with shaded values showing the 95% confidence intervals for each group. The values on the *x*-axis are rescaled values of the proportion of sandeel in the diet

Chick survival

For the effect of intrinsic factors on survival, 2 models had $\Delta AIC_c < 2$, one representing hatching order of chicks ($w_i = 0.65$) and another representing fate of the sibling ($w_i = 0.32$, Table 3). The model with the lowest AIC_c showed that for all study years combined, survival during the 23 d period from chick age 5 to 28 d was significantly higher for α-chicks (0.69 ± 0.04 SE; hazard ratio = 1.78, 95% CI = 1.35–2.35, $z = 4.07$, p < 0.001) than for β-chicks (0.51 ± 0.05 SE), but not significantly different between α-chicks and singletons (0.58 ± 0.06 SE; hazard ratio = 1.32, 95% CI = 0.85–2.06, $z = 1.25$, p = 0.21). The hazard functions showed an overall low and quite stable mortality risk for α-chicks with a small increase at ~15–20 d after hatching, and β-chicks had a higher mortality risk than α-chicks peaking at ~11 d, around the onset of thermoregulation. For singletons, the risk of mortality increased with age, with a slight peak at ~18 d (Fig. 5). The second best model included fate of the sibling, i.e. whether the sibling in 2-chick nests was dead or alive. This model showed that there was no significant effect

Table 3. Model selection results for survival of kittiwake chicks (displayed are selected models with $\Delta AIC_c < 5$, and null model; all other models with $AIC_c > 5$ have been culled for space. See the Supplement for all models.). Results are shown for models grouped by 3 hypothesized factors affecting chick growth and survival (1: chick status; 2: diet composition; 3: weather conditions) and when comparing all models. The models with the lowest ΔAIC_c and highest AIC_c weight in each group are shown in **bold**. Model notations: sibling status = sibling alive vs. dead, hatching order = α vs. β, mesopelagic diet = % in diet, precipitation = day with the highest amount of precipitation in each 5 d period, wind speed = mean wind speed (km h^{-1}). K: number of estimable parameters

	Hypothesis	K	Hypothesis groupings			All models together	
			AIC_c	ΔAIC_c	AIC_c wt	ΔAIC_c	AIC_c wt
Hatching order	1	2	1724.0	**0.0**	**0.65**	23.3	0.00
Sibling status	1	4	1725.4	1.4	0.32	24.6	0.00
Mesopelagic diet	2	1	1708.4	**0.0**	**0.92**	7.6	0.01
Gadid diet	2	1	1713.3	5.0	0.08	12.6	0.00
Mesopelagic diet × hatching order	1, 2	5	1704.9	0.0	0.92	4.1	0.07
Wind direction : wind speed	3	4	1708.8	**0.0**	**0.82**	8.1	0.01
Wind direction : precipitation	3	8	1712.0	3.1	0.17	11.2	0.00
Mesopelagic diet × wind speed	2, 3	3	1700.8	**0.0**	**0.60**	**0.0**	**0.54**
Mesopelagic diet + wind speed	2, 3	2	1701.6	0.9	0.39	0.9	0.35

on survival for α- or β-chicks of the sibling dying (p = 0.21 and p = 0.32, respectively).

The best fit model explaining survival as a function of diet included the proportion of mesopelagic fish in the diet, with survival probability of chicks decreasing with an increase in the proportion of mesopelagic fish in the diet (hazard ratio = 2.05 ± 0.14 SE, 95% CI = 1.57–2.68, z = 5.25, p < 0.001). Expanding the diet model with the hatching order of chicks and their interaction improved model fit (ΔAIC_c = −3.49), showing the same tendency of a decrease in mesopelagic fish in the diet leading to a higher survival probability (hazard ratio = 1.74 ± 0.24 SE, 95% CI = 1.16–2.62, z = 2.67, p = 0.008), and β-chicks having lower survival than α-chicks (hazard ratio = 1.79 ± 0.19 SE, 95% CI = 1.33–2.40, z = 3.85, p < 0.001).
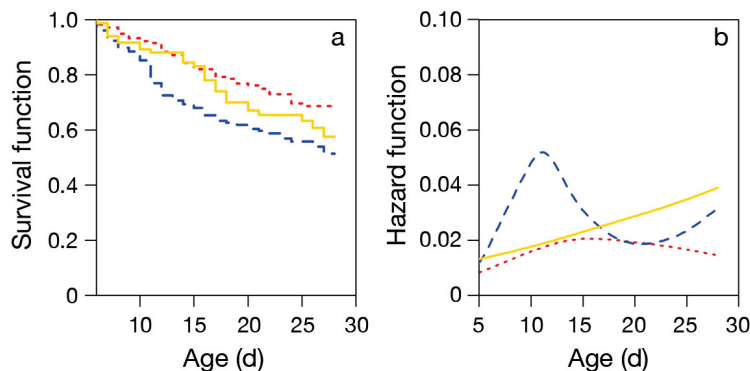

Fig. 5. (a) Kaplan-Meier plots of the cumulative survival and (b) hazard functions of kittiwake chicks 5–28 d of age as a function of hatching order. Red dotted line represents α-chicks, blue dashed line β-chicks and yellow solid line singletons

There was no interaction between the 2 covariates (p = 0.17).

When considering the prevailing weather conditions, a model including the interaction between wind direction and wind strength within the 5 d windows performed best in the survival analysis. The probability of survival was reduced with increasing wind strength from NW (hazard ratio = 3.43 ± 0.45 SE, 95% CI = 1.54–7.63, z = 3.02, p = 0.002) and S (hazard ratio = 5.99 ± 0.33 SE, 95% CI = 3.45–10.39, z = 6.36, p < 0.001) directions.

Furthermore, the survival probability was negatively associated with both an increase in the proportion of mesopelagic fish in the diet (hazard ratio = 2.18 ± 0.14 SE, 95% CI = 1.65–2.89, z = 5.42, p < 0.001) and in wind strength in the 5 d windows (hazard ratio = 1.60 ± 0.16 SE, 95% CI = 1.13–2.27, z = 2.63, p = 0.008). Strong winds were associated with decreased survival probability independent of diet, but the interaction of the 2 variables showed that a high proportion of mesopelagic fish in the diet and strong winds were associated with reduced survival probability throughout the whole chick period (Fig. 6).

When comparing all the models included in the analysis of survival, the proportion of mesopelagic fish in the diet overall had the strongest impact on survival of kittiwake chicks (Table 3). An increase in mesopelagic diet was associated with significant reduction in survival probability, especially in interaction with wind speed
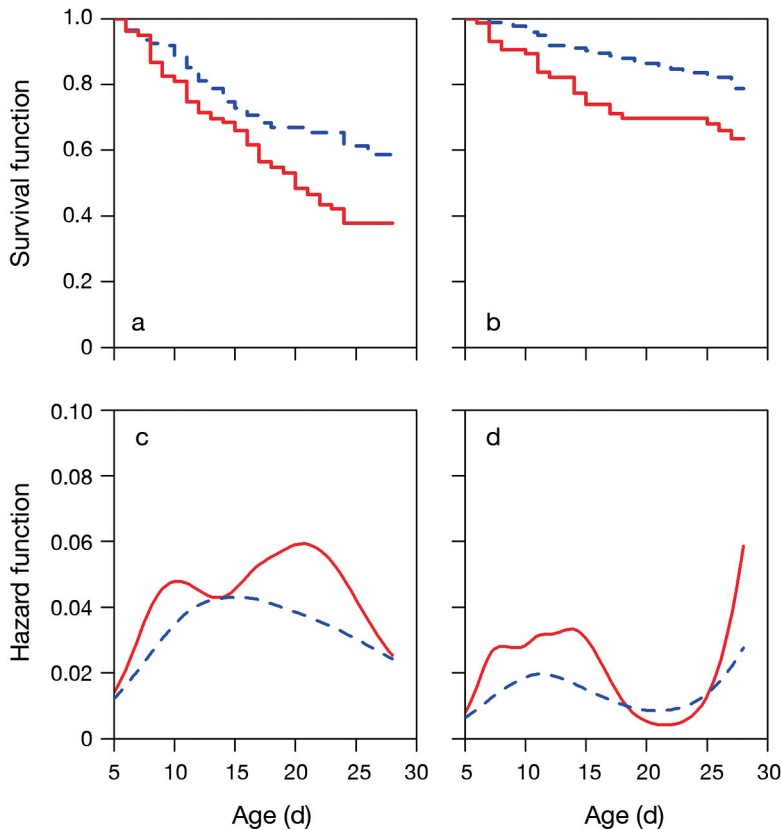
Fig. 6. (a,b) Kaplan-Meier plots of the cumulative survival and (c,d) hazard functions of kittiwake chicks 5–28 days of age as a function of proportion of mesopelagic fish in the diet (high proportion: a and c; low proportion: b and d) and wind strength (strong: red solid line; weak: blue dashed line)

(AIC$_c$ weight = 0.83) or the hatching order of the chicks (AIC$_c$ weight = 0.11).

DISCUSSION

Reproductive performance can be influenced by multiple factors including adult body condition (Lorentsen 1996), prey availability (Frederiksen et al. 2008), prey composition (Barrett 2007), predation risk (Peery & Henry 2010, Ekanayake et al. 2016) and meteorological conditions (Dunn 1975, Descamps et al. 2015). As an adaption to unpredictable feeding conditions, seabird chicks can temporarily arrest growth when insufficient amounts of food are available, enhancing the probability of survival until fledging (Schew & Ricklefs 1998). Nutritional deficits experienced during early development can, however, propagate into pervasive detrimental permanent effects on the adult individual (Metcalfe & Monaghan 2001, Cam et al. 2003, Kitaysky et al. 2006, Vincenzi & Mangel 2013).

In this study, we tested the relative importance of weather parameters and diet in combination with brood size (1 vs. 2 chicks) and chick age on kittiwake chick growth rate and survival. Overall, we found effects of brood size and hatching order, different prey types and weather conditions on both parameters. The effects of brood size and hatching order on growth and survival in kittiwake chicks are well known (Barrett & Runde 1980, Gill et al. 2002). Thus, we have extended this knowledge by identifying interactions with important environmental variables.

Effects of diet on chick growth and survival

The composition of diets fed to kittiwake chicks affected both their survival and growth. However, different prey species that represented different foraging areas for adults proved to be most important in explaining the 2 parameters. The proportion of sandeel in the diet was positively related to daily growth rate of chicks. Sandeel is a small schooling fish with high lipid content and is an important prey species for many marine predators such as predatory fish and seabirds, including kittiwakes (Monaghan 1992, Frederiksen et al. 2008). However, the probability of survival in kittiwake chicks was negatively related to the proportion of mesopelagic fish in the diet. Mesopelagic fish occur offshore at depths of several hundred metres during the day (Gjøsæter 1973), migrating to the upper 100 m of the water column at night (Kristoffersen 1999). The availability of mesopelagic fish at the surface to kittiwakes in northern Norway is likely made possible by strong upwelling currents along the edge of the continental shelf break near Anda (Barrett 1996, see also Paredes et al. 2014). The mesopelagic fish species are energy-rich food items (Pedersen & Hislop 2001, Spitz et al. 2010) and have previously been shown to be important prey for kittiwakes (Barrett 1996, Paredes et al. 2014). Kittiwakes from Anda appear to be alternating between foraging sites, using the oceanic habitat consistently between years in a fine-tuned pattern, primarily dictated by the diurnal patterns of prey availability in the different habitats (Christensen-Dalsgaard et al.

2018). However, Christensen-Dalsgaard et al. (2018) showed that kittiwakes at Anda on average conducted trips of longer duration and with longer path lengths when foraging in the oceanic habitat. In addition, across all years the average mass of the diet delivered to the kittiwake chicks on Anda was higher when the adults foraged in the coastal habitat compared to the oceanic habitat. Hence, it appears that the increase in trip distance and duration associated with foraging for mesopelagic prey species was not compensated by the amount of prey obtained from the offshore foraging areas. Thus, for kittiwakes breeding on Anda, reliance on mesopelagic fish species had a negative influence on chick performance. Interestingly, these findings contrast with results from the Pacific where mesopelagic fish species are important prey for kittiwakes (Lance & Roby 2000, Paredes et al. 2012). With foraging trip lengths and mass of diet at Anda being comparable with that of kittiwakes on the Pribilof Islands (Paredes et al. 2012, Christensen-Dalsgaard et al. 2018), the apparent different effect of mesopelagic diet on chick growth and survival is puzzling. One hypothesis is that this discrepancy might be explained by different life history strategies between the North-Atlantic and Pacific kittiwakes, with kittiwakes on average having smaller clutch sizes in the Pacific (Frederiksen et al. 2005).

Indeed, the growth and survival of α-chicks did not respond as strongly to an increase in sandeel or mesopelagic fish as that of β-chicks or singletons. Our results could signify that, irrespective of the overall prey availability around Anda in the study period, α-chicks were sufficiently fed regardless of the type of prey in their diet, and thus, the foraging habitat of the adults. In contrast, growth of β-chicks and singletons was dependent on the amount of sandeel in the diet. It is surprising that this effect was apparent for singletons, as we had expected them to be comparable to α-chicks in growth. Coulson & Porter (1985) showed that large clutches were laid by higher-quality individuals. This could indicate that the parental quality of individuals with 1- and 2-chick clutches might differ, which could explain some of the difference. For β-chicks, our results corroborate previous findings that the nest is a competitive environment, where β-chicks are more sensitive to changes in food supply than α-chicks (Gill et al. 2002, Young et al. 2017). In species with asynchronous hatching, parents preferentially allocate resources to older, larger chicks, which are of higher value to them than younger offspring that are less likely to survive until fledging (Parker et al. 2002).

Avian predation can be an important source of breeding failure in colonies of cliff-nesting seabirds (Clode 1993). However, we were unable to model the effects of predation on survival rates of chicks, although predation was likely important at our field site. We observed incidental predation of chicks at Anda by peregrine falcons *Falco peregrinus*, but the highest level of predation was by hooded crow *Corvus cornix* and common raven *Corvus corax* taking eggs while the birds were incubating (S. Christensen-Dalsgaard pers. obs.). Predation could be acting as a reinforcing effect if low prey availability led to reduced adult attendance at nests with chicks (Barrett & Runde 1980, Wanless & Harris 1989). Christensen-Dalsgaard et al. (2018) showed that adults were on average 1 h longer away from the nest when foraging on mesopelagic fish compared to the coastal species. However, it has not been documented if increased amounts of mesopelagic fish in the diet lead to reduced adult attendance of kittiwakes on Anda. It is thus unclear if predation may have been a mechanism underlying the negative relationship between the proportion of mesopelagic fish in the diet and survival of kittiwake young.

Effects of prevailing weather conditions on chick growth and survival

Prevailing weather conditions may affect demographic rates such as growth and survival directly (Moreno & Møller 2011) or indirectly by influencing the birds' ability to forage and/or the accessibility of their prey (Weimerskirch et al. 2012, Lewis et al. 2015). Contrary to Elliott et al. (2014), who showed that kittiwakes adjusted their foraging behaviour to compensate for poor weather, we found a negative relationship between wind speed and chick growth. We also found that wind speed and proportion of sandeel in the diet had an interactive effect on growth of kittiwake chicks. When parents fed on sandeel and foraged in sheltered fjords, the wind speed did not affect growth rate. However, when foraging for mesopelagic species in the open ocean, an increased wind strength negatively affected chick growth. Furthermore, strong winds caused a decrease in chick survival probability when they were fed predominantly on mesopelagic species. The interaction suggests that the negative effect of wind speed on kittiwake chick growth and survival is linked to adults having to work more in the exposed habitats when prevailing winds are strong, leading to a reduction in the amount of food sup-

plied to the chicks, and thereby reducing growth rates.

Strong southerly winds had a negative effect on survival of kittiwake chicks. This is likely associated with the location of the study colony. Part of the colony is situated in a small bay facing south. This locality is sheltered from the prevailing northerly wind directions, but exposed to strong southerly winds that build up large waves in the bay, increasing the risk of the nests being washed down (S. Christensen-Dalsgaard pers. obs.).

Predictions of weather patterns for the next century suggest an increase in mean and maximum wind speed in Northern Europe (McInnes et al. 2011) and an increase in precipitation intensity (Semmler & Jacob 2004, Sorteberg & Andersen 2008). Our results suggest that the weather patterns forecasted for the next century are likely to have a negative effect on the reproductive performance of kittiwakes on Anda. The mechanisms revealed might also apply to other seabird species with similar traits as the kittiwake.

CONCLUSION

In our study, we have shown complex effects of prey species composition in combination with adverse weather conditions on both growth and survival of kittiwake chicks. Whilst foraging on energy-rich prey items in both the oceanic habitat and the fjords, a diet dominated by sandeel resulted in higher growth and survival of chicks compared to a diet consisting of mesopelagic fish. The effects of diet composition were further enhanced by adverse wind conditions, evidently making it worse to forage in the exposed oceanic habitat compared to the sheltered fjords when experiencing strong winds. Our results emphasise the importance of conservation of specific marine habitats shown to be important foraging areas in order to ensure the reproductive success of seabirds. From a management perspective, it is also important to consider the interactions among environmental factors, as these may be especially important in a future of changing climate regimes (Descamps et al. 2015).

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