Mikael Andreas Sætre

Climate change influences reproduction in Arctic breeding geese through altered predator-prey interactions

Master's thesis

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Abstract

Climate change is affecting Arctic herbivores both directly and indirectly via bottom-up mechanisms. However, recent evidence suggests that indirect effects of climate change may also occur through changes in abundance and behaviour of predators. It has been proposed that warming has benefitted the Arctic fox, the main predator on Arctic breeding geese, through an overall increase in prey and reindeer carcasses. Also, as sea-ice have contracted in parallel with climate change, polar bears have been forced to use alternative food sources in summer, particularly the eggs of ground-breeding birds. Previous observations across the Arctic indicate that polar bear predation may have devastating consequences for reproduction in geese. In this thesis, I aimed to quantify the effect of polar bear predation while accounting for other biotic and abiotic factors affecting population dynamics in a local population of barnacle geese that breed in Kongsfjorden, Svalbard. To achieve this, I used three decades of individual-based data and population count data in an integrated population model, extending previous population dynamical studies on the same population. The model estimated reproduction, survival, population sizes and effects of abiotic and biotic variables, including predation from Arctic foxes and polar bears. The results confirmed that (1) predation from Arctic fox had a strong negative effect on fledging rates, (2) advancing spring onset affected the number of goslings positively, (3) reproduction and survival was density dependent, and (4) warmer temperatures on the wintering grounds had a positive influence on survival. Most importantly however, I found that the marked increase in the number of bears visiting Kongsfjorden during the breeding period caused a strong tendency for a negative effect of polar bear predation on reproduction. The polar bear effect, acting through egg predation, was only evident in the second half of the study period. These findings add to the growing body of evidence suggesting that Arctic ecosystems are undergoing fundamental environmental changes. Changes which result in changing community dynamics, including indirect climate change effects operating through altered top-down dynamics due to shifts in predator abundances and behaviour.

Acknowledgements

Contents

1. Introduction

Globally, the climate is changing at an unparalleled rate in modern history. Rapidly increasing temperatures and spatiotemporal changes in precipitation patterns are leading to poleward shifts in climate zones and altered weather systems, with consequences for species distribution, behaviour and demography across the biosphere (Parmesan and Yohe 2003; Chen et al. 2011; IPCC 2014; Nolan et al. 2018; Dunn and Møller 2019; IPCC 2021). At the same time, habitat is being lost and fragmented at an alarming rate on a global scale, threatening biodiversity and ecosystem functioning (Powers and Jetz 2019). Such environmental changes can affect species and populations either directly or indirectly through other species in the form of changes in resource availability (bottom-up) or predator-prey dynamics (top-down) (Hunter and Price 1992; Menéndez et al. 2007; Blaustein et al. 2010; Morrissette et al. 2010; Nolan et al. 2018). While there are numerous examples of direct effects of environmental change (Bale et al. 2002; Robinet and Roques 2010; Stirling and Derocher 2012; Charmantier and Gienapp 2014; Hoegh-Guldberg et al. 2017), much less is known about the indirect effects occurring through changes in other species and trophic interactions, despite the fact that indirect biotic mechanisms are important in mediating climate change responses (Hansen et al. 2013; Ockendon et al. 2014).

In the Arctic, changes in climate have been especially pronounced, as surface temperatures have risen at more than twice the rate of the global mean and warming is anticipated to accelerate further in the region in the coming decades (Curry et al. 1995; Screen and Simmonds 2010; Serreze and Barry 2011; Cohen et al. 2014). Rapid warming along with changes in precipitation patterns have resulted in fundamental changes in abiotic conditions, most notably loss of sea-ice, changes in snow-cover and snow-pack characteristics, with consequences for species throughout the Arctic food web (Post et al. 2009; Clausen and Clausen 2013; Post et al. 2013; Bintanja and Andry 2017; Box et al. 2019).

For instance, one consequence of accelerated warming in the Arctic is a rapid advance in timing of snow melt and initiation of the growing season, also referred to as spring onset (Foster 1989; Clausen and Clausen 2013; Lameris et al. 2017; IPCC 2021). Consequently, the relatively short growing season in the Arctic has lengthened and plant production increased, leading to higher food availability for local and migratory herbivores (Gilg et al. 2012; Tveraa et al. 2013; Ernakovich et al. 2014; Fjelldal et al. 2020). Thus, climate change may have effects on condition through changes in access to forage (bottom-up), which has

consequences for survival and reproduction and therefore population dynamics (Post et al. 2009; Albon et al. 2017). In Arctic breeding birds, the population dynamical consequences of advance in timing of spring onset have been beneficial for many species but negative for some (Jensen et al. 2008; Saino et al. 2011; Descamps et al. 2019; Nolet et al. 2019). Also, at specific locations in the Arctic, changes in precipitation and temperature following climate change has contrasting effects on plant phenology in spring, highlighting heterogeneity in climate change effects across locations in the Arctic (Bjorkman et al. 2015).

Climate change can also affect herbivores indirectly through effects on predators (Gauthier et al. 2003; Forchhammer et al. 2008; Perkins et al. 2018). In eastern Greenland, climate change has been linked to a marked shift in the previously predictable cyclical dynamics between the four predator species of stoat *(Mustela erminea)*, Arctic fox *(Vulpes lagopus)*, snowy owl *(Bubo scandiacus)* and long-tailed skua (*Stercorarius longicaudus*) and their main prey, the lemmings (*Lemmus lemmus)* (Schmidt et al. 2008; Gilg et al. 2009). In Svalbard, the Arctic fox, which is one of the main predators on Arctic breeding birds, has increased in abundance as a likely consequence of climate change (Fuglei et al. 2003; Layton-Matthews et al. 2020). Furthermore, in Arctic Canada and in Svalbard, an unprecedented loss of sea-ice during the past few decades has altered predator-prey dynamics between polar bears (*Ursus maritimus*) and colonially breeding birds, with devastating consequences for reproduction in the latter in some instances (Smith et al. 2010; Iverson et al. 2014; Prop et al. 2015).

Thus, it is clear that the effects of climate change, operating either through direct or indirect mechanisms, can have major implications for the population dynamics of many Arctic species. Together, the net effect of climate change may act positively, negatively or have contrasting effects on population dynamics, depending on the direction and magnitude of the direct- and indirect climate effects (Jenouvrier et al. 2009; Morrissette et al. 2010; Jenouvrier 2013; Dunn and Møller 2019). However, the net effect of climate change can also be mediated by density-dependent effects, which can buffer against some of the negative and positive consequences of changes in climate on population dynamics (Reed et al. 2013; Gamelon et al. 2017; Hansen et al. 2019).

One group of species which has benefitted greatly from environmental changes in the form of changes in climate and land-use is Arctic breeding geese, which have rapidly expanded in both breeding ranges and population sizes over the past few decades (Fox et al. 2010; Fox and Madsen 2017; Hessen et al. 2017; Doyle et al. 2020). Arctic breeding geese are generally

long-distance migrants subject to different climates during their annual cycle, as they typically overwinter, stop-over and breed at different locations (Loonen et al. 1998; Black et al. 2014). In general, Arctic breeding geese are capital breeders that invest in considerable body stores at their overwinter and stopover sites (Jönsson 1997; Gauthier et al. 2003; Varpe et al. 2009). These body stores, along with local resources, are then later used for production of eggs at the breeding site (Hahn et al. 2011). Hence, Arctic breeding geese may be susceptible to carryover effects of weather from one seasonal site to another, emphasising the importance of taking all parts of the life cycle into account when analysing population dynamics in these species (Morrissette et al. 2010; Layton-Matthews et al. 2020).

The local population of barnacle geese (*Branta leucopsis*) that breed in Kongsfjorden can be considered one of the populations that have benefitted from environmental change along with changes in land-use and hunting policies, as it has increased threefold during the past three decades (Layton-Matthews et al. 2020). Layton-Matthews et al. (2019, 2020) found that climate change has contrasting effects on this population. At the breeding site, advancing spring onset had a positive influence on clutch size and increasing temperatures have improved hatching rates, whilst minimum temperature at the overwintering site (Solway Firth, Scotland) had a positive influence on survival rates. Furthermore, precipitation at the stopover site (Helgeland, Norway) during spring had a positive carryover effect on production of eggs at the breeding site. However, the Arctic fox, which is the main predator on goslings and adults, seem to have increased in local abundance in parallel with warming, leading to a decline in fledging rate (Layton-Matthews et al. 2020). Additionally, density regulation appeared to affect reproduction at the breeding site and survival at the overwintering grounds (Layton-Matthews et al. 2019; Layton-Matthews et al. 2020). Consequently, the net effect of climate change on population size appears neither negative nor positive.

However, more recently, a longer sea-ice free period following climate warming seem to have contributed to higher summer presence of polar bears in the fjords, and an apparent increase in polar bear predation on eggs of barnacle geese and other Arctic breeding birds in Kongsfjorden (Prop et al. 2015). Here, I aimed to assess the potential influence of polar bear predation on vital rates while accounting for other biotic and abiotic factors affecting population dynamics in the local population of barnacle geese that breed in Kongsfjorden, Svalbard.

Hence, the research questions I aimed to answer were:

What is the influence of egg predation by polar bears on reproduction of barnacle geese breeding in and around Ny-Ålesund?

To answer this, I revised and extended an integrated population model (IPM), based on the framework initially developed by Layton-Matthews et al. (2019). The IPM estimated annual age-class specific survival, reproductive rates and population sizes, along with parameterised effects of direct- and indirect climate variables. This framework allowed me to assess the direction and magnitude of direct- and indirect climate variables on respective vital rates. In other words, it provided an opportunity to put the polar bear effect into an updated, holistic context. Historically, similar integrated population models have proven useful in understanding the effects of environmental variation on populations, as integrated models can incorporate environmental as well as demographic uncertainty whilst jointly estimating parameters (Lande et al. 2003; Oppel et al. 2014; Nilsen and Strand 2018).

According to Layton-Matthews et al. (2019, 2020), I expected that temperature on the breeding grounds and date of spring onset would have positive effects on reproduction, and that survival was density-dependent and positively affected by temperature at the overwintering grounds. I also expected Arctic fox predation to have a strong negative influence on fledged success, hatching success to increase over the study period and density regulation to act primarily on reproduction. I predicted that predation from polar bears would have a negative influence on reproduction and number of polar bears visiting Kongsfjorden during the incubation period to have a positive trend, based on observations and findings at the same study location and in other analogous systems across the Arctic (Rockwell and Gormezano 2009; Smith et al. 2010; Stirling and Derocher 2012; Prop et al. 2015). However, as polar bears were mostly absent from Kongsfjorden during summer in the time period from 1990-2006, I predicted that I would not find any influence prior to 2006 (Prop et al. 2015).

2. Methods

2.1 Study population

Barnacle geese are migratory birds that breed in the Arctic and inhabit separate locations for overwintering and breeding. In addition, they utilise several stopover locations throughout their migration (Loonen et al. 1998; Layton-Matthews et al. 2020). The species is long-lived, monogamous and, if successful in reproduction, each pair produces a single clutch of 3 to 5 eggs in each breeding season (Black et al. 2014). Barnacle geese are capital breeders that invest in considerable body stores at their overwinter and stopover site. Resources which they later utilise, along with local resources, for production of eggs at the breeding site (Hahn et al. 2011). The local population investigated in this study, nest on the islands of Storholmen and Prins Heinrich in Kongsfjorden, Svalbard (Figure 1). They raise their goslings and fledglings in and around the town of Ny-Ålesund. The population overwinters at Solway Firth, Scotland and have stopover sites on their migration route along the north-western coast of Norway (Figure 2). On the islands, barnacle goose eggs are exposed to predation from polar bears, whilst in Ny-Ålesund goslings (and on rare occasions adults) are exposed to predation from Arctic foxes that frequently visit the village (Prop et al. 2015; Layton-Matthews et al. 2020). The findings of Prop et al. (2015) suggest that polar bears have been visiting Kongsfjorden and predating nests of barnacle geese more frequently over the past few decades, especially after 2006.
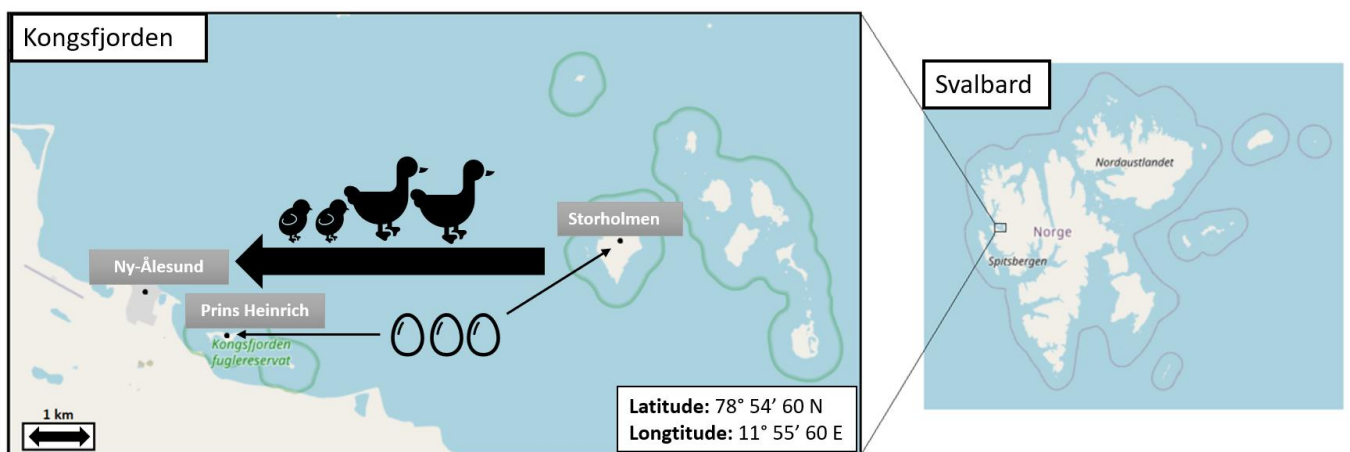
Figure 1: The study area in Kongsfjorden (left) on Svalbard (right). The local population that breeds in Kongsfjorden nest and incubate primarily on the islands of Storholmen and Prins Heinrich before breeding pairs depart for the area in and around the town of Ny-Ålesund to raise their goslings after the eggs have hatched.
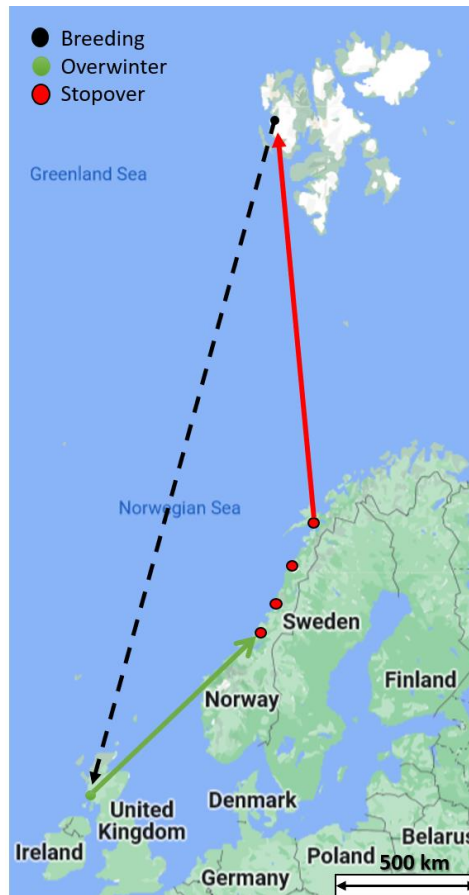
Figure 2: Migration route for the local population of barnacle geese breeding in Kongsfjorden. The population overwinters with the flyway population at Solway firth, Scotland (green) from September to March/April when they migrate to the stop-over sites along the north-western coast of Norway (red) before the local population arrives at their breeding grounds in Kongsfjorden, Svalbard (black) in May/June. In September, after breeding, they migrate back to Solway Firth (black arrow) (Google 2022).

2.2 Survival and reproduction data

Individual-based data on survival and reproduction was collected between 1990-2020 from barnacle geese in and around the village of Ny-Ålesund and on the islands of Storholmen and Prins Heinrich, Svalbard (see methods in Loonen et al. 1998 and Layton-Matthews 2020 for detailed descriptions on data collection). The data on reproduction included: nest ID, number of goslings and fledglings per identified breeding pair of barnacle geese. Nest ID and sightings was collected with 1-2 days interval on the nesting islands of Storholmen and Prins Heinrich during the incubation period, whilst number of goslings and fledglings was

collected daily in and around the town of Ny-Ålesund throughout the breeding season. It was assumed that a breeding pair observed without any goslings did not have any. Data on survival included individual-based mark-recapture data that was collected continuously throughout the field season from mid-May until mid-August on the islands of Storholmen and Prins Heinrich, and inside and in close proximity of the town of Ny-Ålesund from observations of ringed individuals of both sexes (Loonen et al. 1998). In this analysis, I included the reproductive stages: probability of having one or more goslings (H), number of goslings per female (G) and probability of fledging (F). I also included age-class (a) specific survival in fledglings (S_f) and adults (S_{ad}). Survival was analysed using mark-recapture data. H was analysed using individual-based data on whether as female was observed with one or more goslings, G using the total number of goslings per female and F using the total number of fledglings per female.

2.3 Covariates

Covariates included in the IPM were chosen primarily based on the findings of Layton Matthews et al. (2019, 2020) (Figure 3). The potential effect of polar bear predation was investigated on H, based on the findings of Prop et al. (2015) on barnacle goose nest predation and unpublished data from Ny-Ålesund on polar bear abundance and predation events (Loonen, M.J.J.E, Unpublished data 2022).

On survival (S_a), I included average minimum temperature ($T_{scotmin}$) and flyway population size at the overwintering site (N_{scot}) as covariates. I included number of days with polar bears in Kongsfjorden in the incubation period (beardays), regime period (Reg), average temperature in Ny-Ålesund from mid-June to mid-July ($T_{sval,JJ}$) and local adult population size ($N_{sval, ad}$) as covariates on H, the probability of having one or more goslings. On G, I included date of spring onset (Julian), proportion of active Arctic fox dens in Kongsfjorden (Fox) and $N_{sval, ad}$ as covariates. On F, I included Fox, sum of precipitation between mid-July to mid-August ($P_{sval,JA}$) and $N_{sval, ad}$ as covariates. Local adult population size on Svalbard ($N_{Sval, ad}$) was included on all reproductive stages to account for possible density-dependent effects (Layton-Matthews et al. 2019).

The final choice of covariates included on H resulted from an assessment of model candidates based on exploratory analyses of barnacle goose and polar bear data. In these analyses, I found that (1) the incubation period of barnacle geese advanced rather suddenly from ~2006 (2) there were almost no polar bears in Kongsfjorden during incubation before 2006 (See

Prop et al. 2015 and figure 14A) and (3) no major nest predation events by polar bears were observed prior to 2006 (Loonen, M.J.J.E, Unpublished data 2022). Consequently, I included the Reg variable as a covariate on H. Regime period 0 (Reg = 0) indicated the time period from 1990-2005 and regime period 1 (Reg = 1) from 2006-2020. I included an interaction between Reg and Beardays to test whether the effect of polar bear predation changed from the first half of the study period to the second.
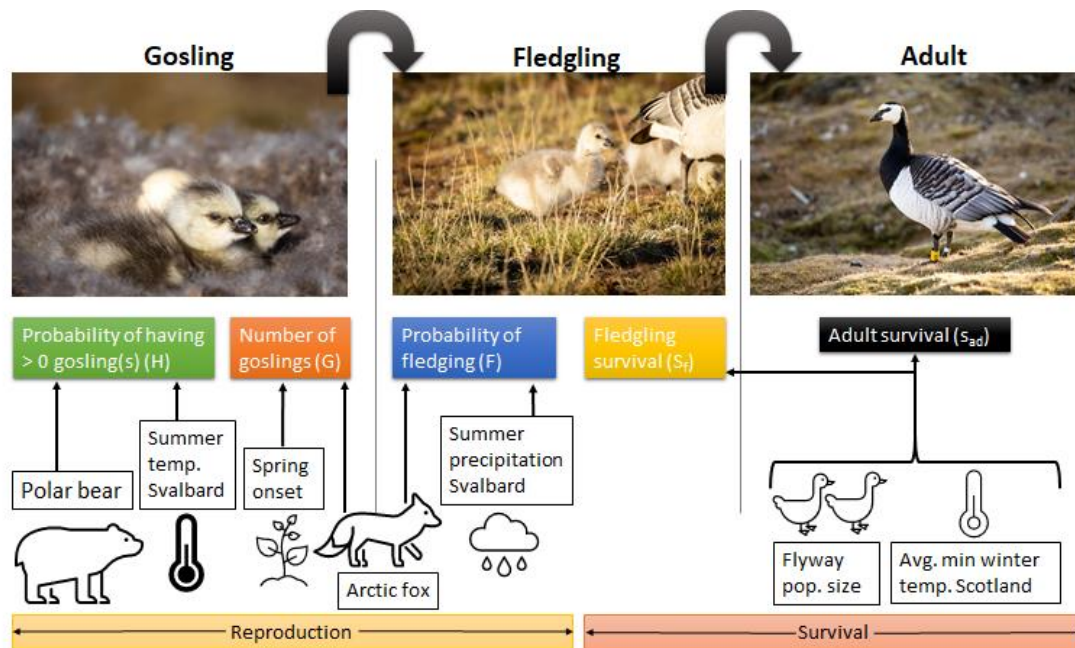
Figure 3: Schematic diagram showing each reproductive- and survival stage (coloured boxes) included in the analysis along with respective covariates (black and white boxes) included in each step. Local adult population size on Svalbard is not shown in the schematic but was included as a covariate on each stage of reproduction (H, G and F). The regime period variable which was included on H is also not shown in this schematic.

2.4 Collecting and sorting covariate data

I collected climate data on temperature and precipitation from the breeding grounds from the Norwegian Meteorological Institute (Meteorologisk Institutt 2021). I obtained data on average temperature from mid-June to mid-July ($T_{sval,JJ}$) and sum of precipitation between mid-July to mid-August ($P_{sval,JA}$) on the breeding grounds from the weather station at Ny-Ålesund. I collected data on average minimum temperature ($T_{scotmin}$) at the overwintering site from the UK Meteorological Office from the weather station at Eskdalemuir (UK Met Office 2021). I estimated flyway population size at the overwintering site (N_{scot}) in a logistic model

with observation error (Figure 4, Appendix 1) using census count data from the UK Waterbird Monitoring Programme (WWT 2021). I obtained data on proportion of active Arctic fox dens from the Environmental monitoring of Svalbard and Jan Mayen and used this as a proxy for predation, as it was likely to reflect annual variation in local fox abundance (MOSJ 2021). Counts of local population size ($N_{sval, ad}$) and number of days with polar bears in Kongsfjorden during summer was provided by Dr. Maarten J.J.E Loonen and the barnacle goose team from University of Groningen (RUG).

I calculated the number of days with polar bears in Kongsfjorden during the incubation period (beardays) for this population of barnacle geese. Beardays was used as a proxy for polar bear predation as it was assumed to indicate annual variation in local polar bear abundance. Two beardays indicated either one polar bear observed for two days, or one polar bear observed in a single day, comparable to the approach of Prop et al. (2015). From 1990-2005 the incubation period was defined from 15th of June until 10th of July and from 2006-2020 it was defined from 8th of June until 3rd of July (Loonen, M.J.J.E, Unpublished data 2022).

All covariates besides beardays were standardized to make it easier to compare the relative importance of the different covariates in explaining variation in vital rates. However, a box-cox transformation was applied to the beardays covariate to create a linear relationship between the number of beardays and H. This was done to account for a likely non-linear relationship between number of beardays and H, because I expected possible diminishing effects of number of beardays, as a single polar bear can have a major impact on a breeding colony (Prop et al. 2015). The transformed beardays was mean-centered to avoid problems with convergence and to ensure correct parameter estimates (Kéry 2010).
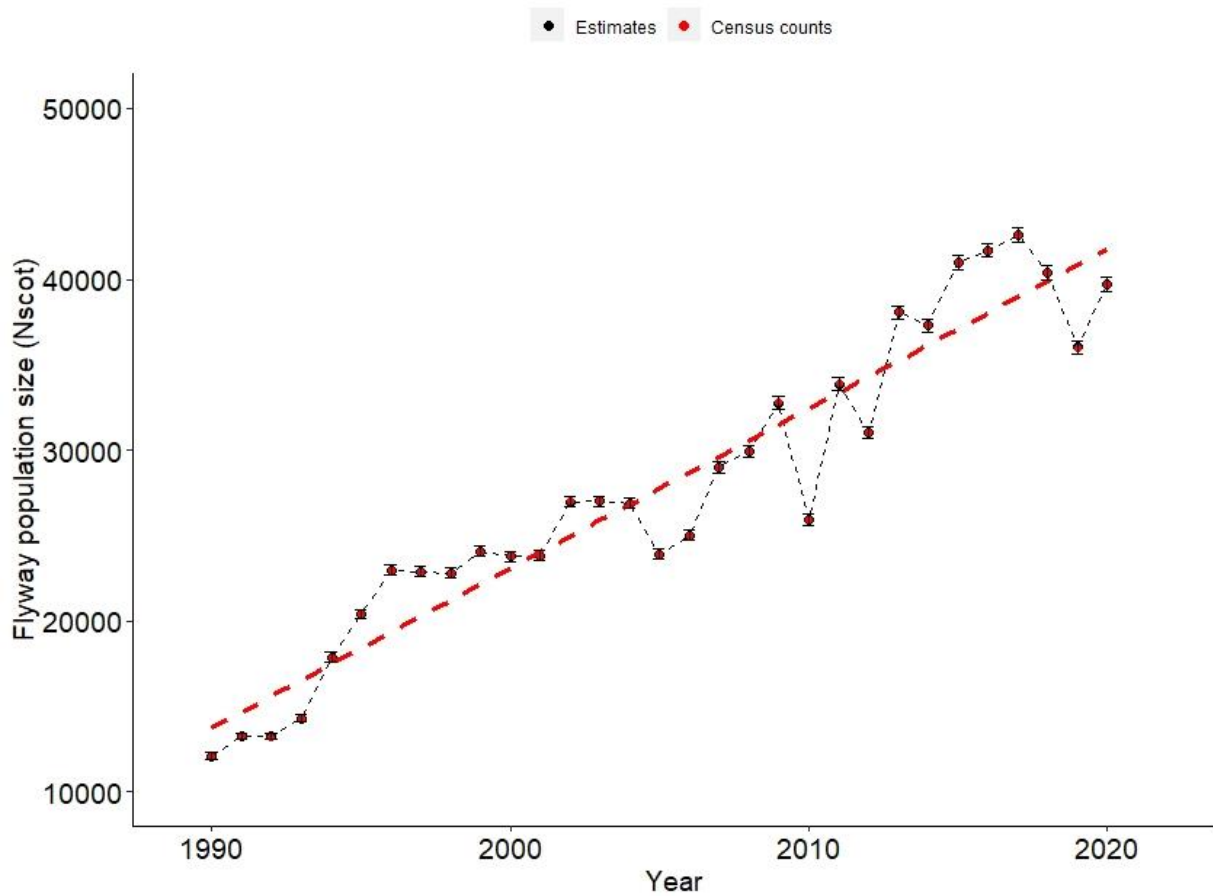
Figure 4: Model estimates (black dots) and census counts (red dots) of flyway population size (N_{scot}) at Solway Firth, Scotland from 1990-2020 with 95% credible intervals (black bars). Annual Estimates of N_{scot} were used as a covariate in the analyses. The dashed red line indicates the linear trend over the study period.

2.5 Model revision and extension

The IPM utilised in this analysis was constructed based on the framework initially developed by Layton-Matthews et al. (2019). However, I made major revisions. The IPM was extended and most of the components from the original model were reconstructed to fit the purposes of this thesis (Appendix 1). I included the fledgling and adult stages in the survival model and the gosling and fledgling stages in the reproductive model. I analysed the effect of all covariates, including the novel polar bear effect directly on each vital rate within the IPM (Appendix 1). Furthermore, I estimated flyway population size in Scotland using census count data from Solway Firth in a logistic population model with observation error inside the IPM (Appendix 1).

2.6 Integrated population model (IPM)

Population size was estimated using an integrated population model (IPM) framework comprised of three models: Survival (2.6.1) which was modelled using a Cormack-Jolly-Seber model (CJS), reproduction (2.6.2) modelled in a generalized linear mixed model (GLMM) and a state-space model that modelled the annual population counts (2.6.4-2.6.5) (Lebreton et al. 1992; Gimenez et al. 2007). The IPM was applied in a Bayesian framework, implemented in JAGS via the program JAGSUI using Markov Chain Monte Carlo simulations (MCMC) to produce posterior distributions of parameter estimates (Plummer 2003; Kellner 2016). Non-informative prior distributions were used for vital rates and effect sizes of covariates (Appendix 1).

2.6.1 Survival

Apparent survival (s) rates and detection probability was estimated by analysing mark-recapture data in the Cormack-Jolly-Seber (CJS) modelling framework (Appendix 1) (Lebreton et al. 1992; Oppel et al. 2014; Layton-Matthews et al. 2019). Apparent survival (s) and detection probability (p) was modelled using a multinomial distribution using logit link functions (equation I and II, Appendix 1). Survival was modelled as time (t) and age-specific (a) with two age classes: (1) Fledglings included all individuals under 1 year of age and (2) adults, which included all individuals of age 1-28 (maximum age observed). Fledgling survival (s_f) described survival in the first year of life whilst adult survival (s_{ad}) describes survival from the second year and beyond. Average minimum winter temperature between October and March at the overwintering grounds (T_{min}) and local population size (N_{scot}) was included as covariates on survival. By including N_{scot} as a covariate, I accounted for potential density regulation affecting survival at the overwintering site (Layton-Matthews et al. 2019).

$$\text{Logit}(s_{a, t+1}) = \mu_{s, a} + \beta_{Tminscot} \times T_{minscot, t} + \beta_{Nscot} \times N_{scot, t} + \varepsilon_{s, a, t+1} \tag{I}$$

Detection probability (p) was modelled as sex-specific (g), with a random year effect and p was used as a parameter for survival (Appendix 1, Equation II). Detection probability was modelled as sex-specific because previous studies indicate higher detection probability in females, which may be due to higher philopatry in this sex (Black et al. 2014).

$$\text{Logit}(p_{g, t+1}) = \mu_{p, g} + \varepsilon_{g, t+1} \tag{II}$$

2.6.2 Reproduction

Reproduction was modelled in three separate steps: (1) The probability of females having one or more goslings **(H)** was modelled using individual-based data on females observed with one or more whilst (2) number of goslings per female **(G)** was modelled using the total number of goslings per female and (3) the probability of fledging **(F)** was modelled using the total number of fledglings per female. All reproductive stages were modelled using generalized linear mixed models (GLMM) within a Bayesian modelling framework (Appendix 1). H and G was modelled using a zero-inflated Poisson model to account for a large number of zero values in the data on number of goslings per female, which were assumed to originate from two sources: (1) the Bernoulli process (failure) and (2) the Poisson (count) process (Zuur et al. 2009). The Bernoulli process described failure (no goslings) and the Poisson process described success (i.e., number of goslings for females that produced goslings) (Appendix 1):

1. Proportion of females with at least one gosling was assumed to follow a Bernoulli distribution, with parameter **H**, the probability of a female having one or more goslings. Variation in H was modelled using a logit link with the covariates regime (0 = 1990-2005, 1 = 2006-2020), number of days with polar bears in Kongsfjorden during the incubation period (beardays), an interaction between regime (reg) and beardays (Regbear), average temperature in Ny-Ålesund from mid-June to mid-July ($T_{sval,JJ}$) and local adult population size at the breeding grounds ($N_{Sval, ad}$) (equation III).

$$\text{Logit}(H_t) = \mu_H + \beta_{reg} \times Reg_t + \beta_{bear} \times \text{transformed}(beardays_t) + \beta_{Regbear} \times Reg_t \times beardays_t + \beta_{Tsval, JJ} \times T_{sval,JJ,t} + \beta_{Nsval\_H} \times N_{Sval, ad,t} + \varepsilon_{H,t} \qquad \textbf{(III)}$$

2. The observed number of goslings per female was assumed to follow a Poisson distribution with parameter G. Variation in G was modelled using a log link with the Arctic fox abundance proxy (Fox), date of spring onset (SO) and $N_{Sval, ad}$ as covariates (equation IV).

$$\text{Log}(G_t) = \mu_G + \beta_{Fox\_G} \times Fox_t + \beta_{SO} \times SO_t + \beta_{Nsval\_G} \times N_{Sval, ad,t} + \varepsilon_{G,t} \qquad \textbf{(IV)}$$

3. The observed number of fledglings was assumed to follow a binomial distribution with parameters number of goslings and probability (F). Variation in F was modelled using a logit link with sum of precipitation on the breeding grounds between mid-July to mid-August ($P_{Sval,JA}$) and Fox and $N_{Sval, ad}$ covariates (equation V).

$$\textbf{Logit(F}_t\textbf{)} = \boldsymbol{\mu_F} + \boldsymbol{\beta_{Psval}} \times \textbf{ P}_{\textbf{sval, JA, }t} + \boldsymbol{\beta_{Fox\_F}} \times \textbf{ Fox}_t + \boldsymbol{\beta_{Nsval\_F}} \times \textbf{N}_{\textbf{Sval, ad,}t} + \boldsymbol{\varepsilon_{F,t}} \qquad \textbf{(V)}$$

2.6.3 Accounting for correlated environmental effects

To account for potential dependencies among the vital rates, which was not accounted for by covariates included in the model, I included a multivariate, normally distributed random year effect term. To ensure consideration of possible correlated environmental effects of covariates, the variance in vital rates (survival, H, G and F) was modelled assuming that it was derived from a random process with mean equal to zero (De Valpine and Hastings 2002). In this framework, temporal residuals for each vital rate were a realisation from a multivariate normal distribution with mean equal to zero and a variance-covariance matrix (Z) that used the scaled Wishart distribution as a prior (Gelman and Hill 2006; Schaub et al. 2013).

2.6.4 State-space model

Annual population counts ($C_{a,t}$) were modelled in a state-space model, which combined a state-process model and an observation process model. The state-space model described the true state of the population, based on population counts and vital rates, whilst the observation process model described the observation process and hence the observation error (De Valpine and Hastings 2002). As population counts were not available for the fledglings, this was included as an estimated latent variable (Layton-Matthews et al. 2019). A log-normal distribution was assumed for the population count data. The population counts of fledglings (C_f) and adults (C_{ad}) were modelled by combining the state-process and observation process models where σ^2 represents the observation error:

$Log(C_{f, t}) \sim Normal(Log(N_{f, t}), \sigma_c2)$
$Log(C_{ad, t}) \sim Normal(Log(N_{a, t}), \sigma_c2)$

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2.6.5 State process model

The state process model used the underlying vital rates (survival and reproduction parameters) to estimate the expected number of individuals in each age class per year. Number of fledglings in year t ($N_{f, t}$) was modelled as a Poisson process assuming equal sex ratio (hence 0.5 of the population potentially reproducing) whilst the number of yearlings ($N_{y, t}$) and number of adults ($N_{ad, t}$) were modelled as binomial processes to include demographic stochasticity into the analysis:

$$N_{f, t} \sim Poisson(N_{ad, t} \times 0.5 \times H_{t-1} \times G_{t-1} \times F_{t-1})$$

$$N_{y, t} \sim Binomial(S_{f, t-1}, N_{f, t-1})$$

$$N_{ad, t} \sim Binomial(S_{ad, t-1}, N_{y, t-1}) + Binomial(S_{ad, t-1}, N_{ad, t-1})$$

Thus, the total number of adults and yearlings ($N_{ad}N_y$) and total number of individuals (N_{total}) could be calculated:

$$N_{ad}N_{y, t} = N_{y, t} + N_{ad, t}$$

$$N_{total, t} = N_{f, t} + N_{y, t} + N_{ad, t}$$

2.6.6 Model estimates and temporal trends

Using the IPM, I produced annual estimates of age class-specific survival (s_a), probability of having one or more goslings (H), number of goslings (G), probability of fledging (F) the product of the reproductive stages (i.e., number of fledglings per female, $H \times G \times F$) and local adult population size (Figure 5, 6 and 7).

2.7 Testing for temporal trends

To test whether there were significant temporal trends in vital rates, covariates and population sizes, I fitted regressions of annual covariate values, reproductive and survival estimates with year as an explanatory variable (Figure 4, 5, 6, 7, 14 and section 3.3-3.4). Temporal trends in all covariates and vital rates were investigated in linear models, except number of beardays, which exhibited a non-linear trend over the study period (Figure 13A).
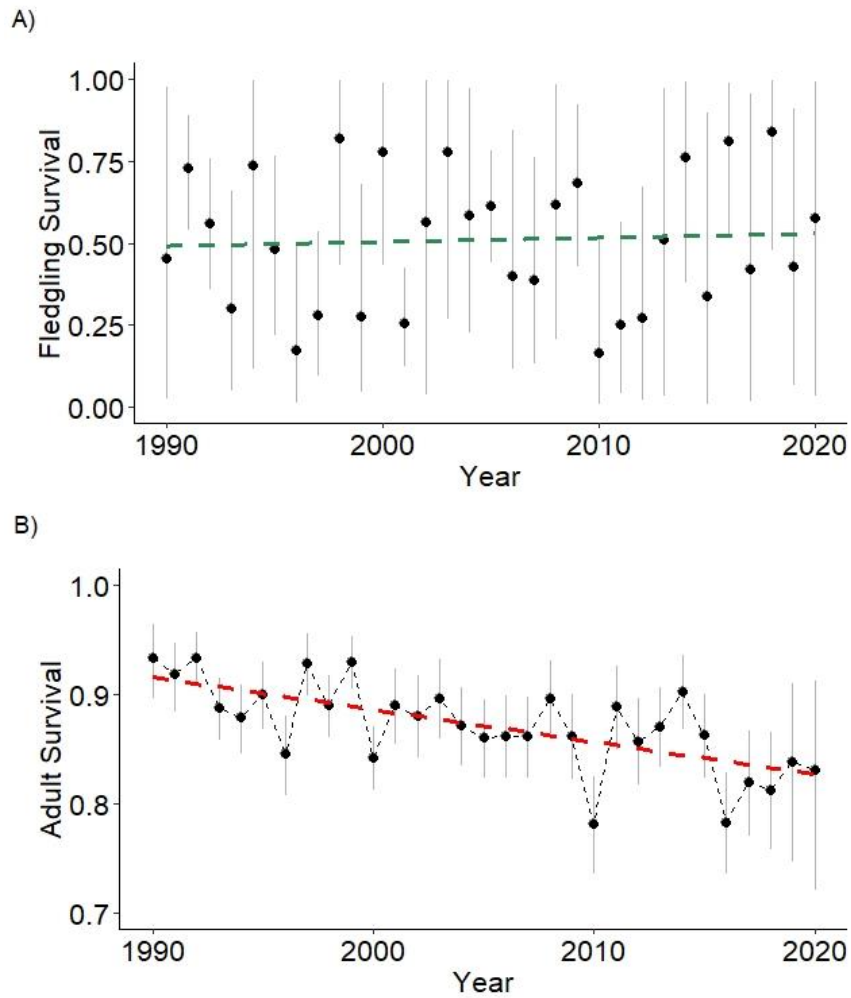
Figure 5: Annual estimates of survival rates in (black dots) fledglings (sf) and adults (sad) over the study period with 95% credible intervals (grey bars). Coloured dashed lines indicate the linear trend over the study period.
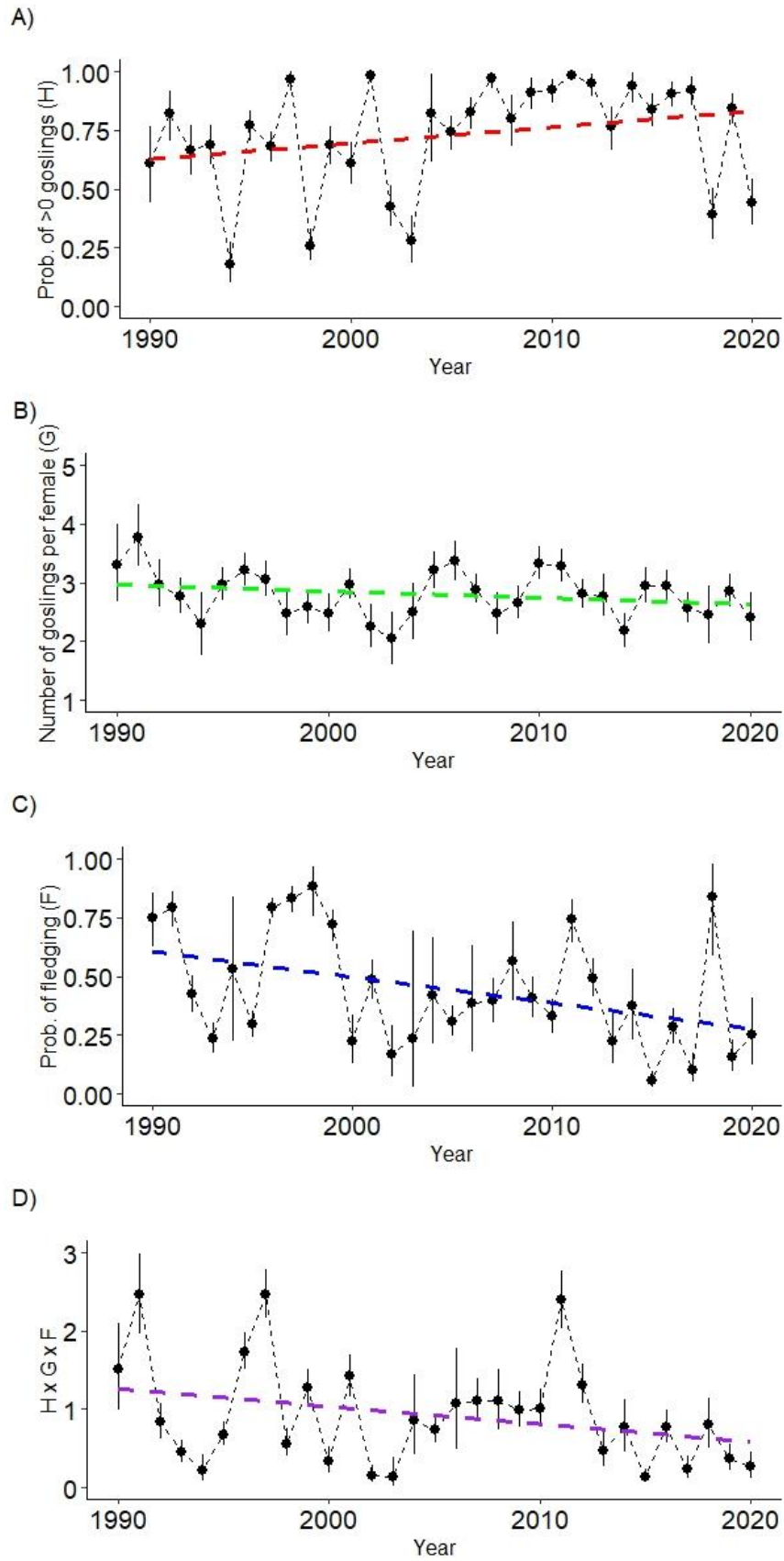
Figure 6: Annual estimates of reproductive rates (black dots) with 95% credible intervals (black bars). Coloured dashed lines indicate the linear trend over the study period.

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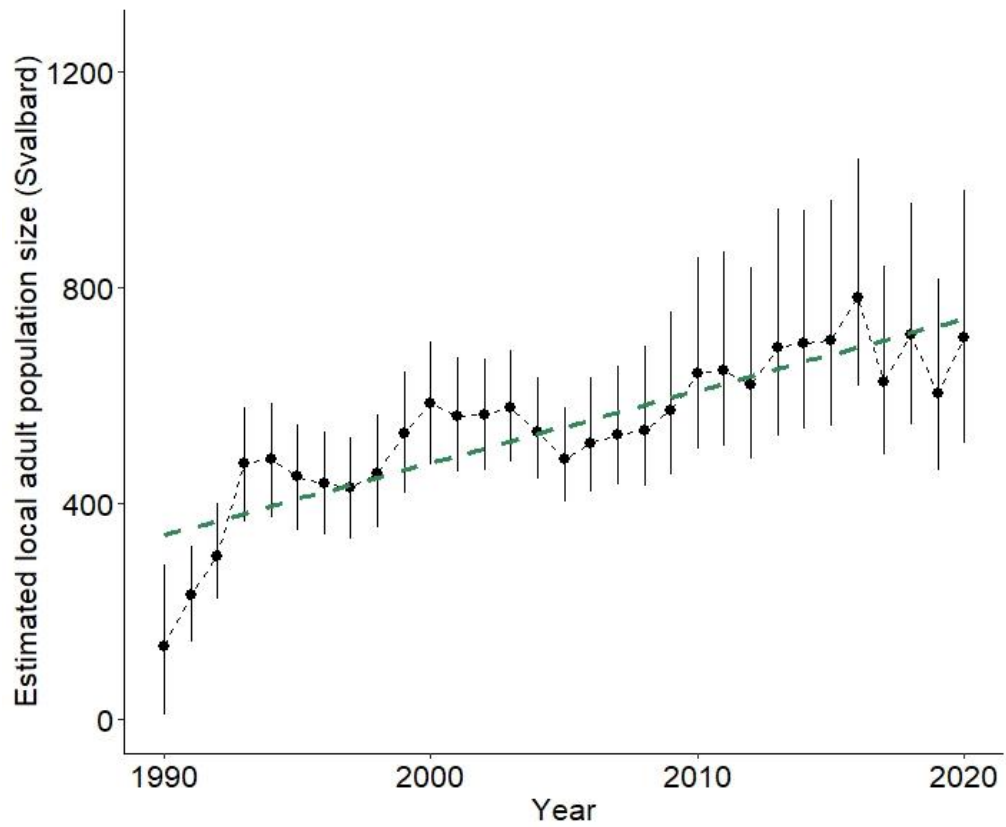
Figure 7: Annual estimates of local adult population size of barnacle geese breeding in Kongsfjorden and and Ny-Ålesund (black dots) with 95% credible intervals (black bars). The dashed green line indicates the linear trend over the study period.

3 Results

3.1 Climate and density at the overwinter grounds affecting survival

Adult and fledgling survival was positively influenced by minimum winter temperature ($T_{scotmin}$) at the overwintering grounds in Scotland (Figure 8 and 9), whilst flyway population size in Scotland (N_{scot}) had a marginal negative effect on survival (Table 1).
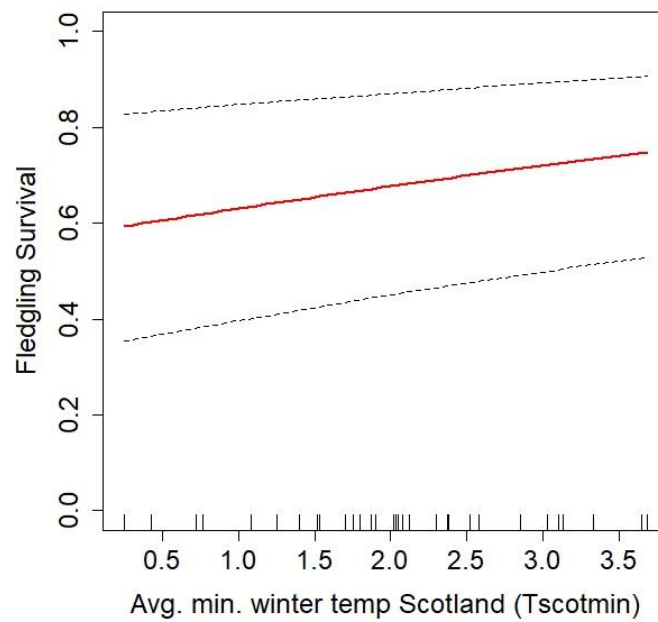
Figure 8: Predicted relationship between average minimum winter temperature at the overwintering grounds in Scotland ($T_{scotmin}$) and fledgling survival (S_{ad}) (red line) with 95% credible intervals (dashed lines). Distribution of $T_{scotmin}$ over the study period is included as rugs on the x-axis.
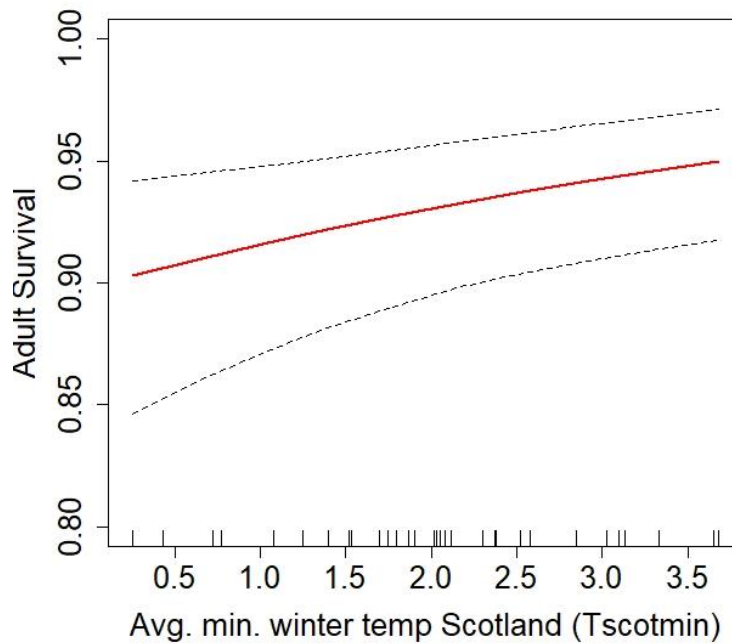
Figure 9: Predicted relationship between average minimum winter temperature at the overwintering grounds in Scotland ($T_{scotmin}$) and fledgling survival (S_{ad}) (red line) with 95% credible intervals (dashed lines). Distribution of $T_{scotmin}$ over the study period is included as rugs on the x-axis.

3.2 Climate, trophic interactions and density at the breeding grounds affecting reproduction

3.2.1 Probability of having one or more goslings (H)

The effect of number of days with polar bears in Kongsfjorden during the incubation period (beardays) on probability of a female having one or more goslings (H) appeared to be dependent on the regime period. The interaction between beardays and regime was close to statistically significant ($p = 0.06$) at a significance level of alpha = 0.05 (Table 1), when p was defined as the proportion of posterior distributions that was greater than zero. There was no clear effect of beardays in regime period 0 from 1990-2005 and a negative effect in regime period 1 from 2006-2020 (Table 1, Figure 10). Neither Average temperature from Mid-June to Mid-July in Kongsfjorden (T_{sval_JJ}) or local adult population size (N_{sval_ad}) had any clear effect on H (Table 1). Regime period had an effect size that was equal to zero on H (Table 1).

Years: 2005-2020
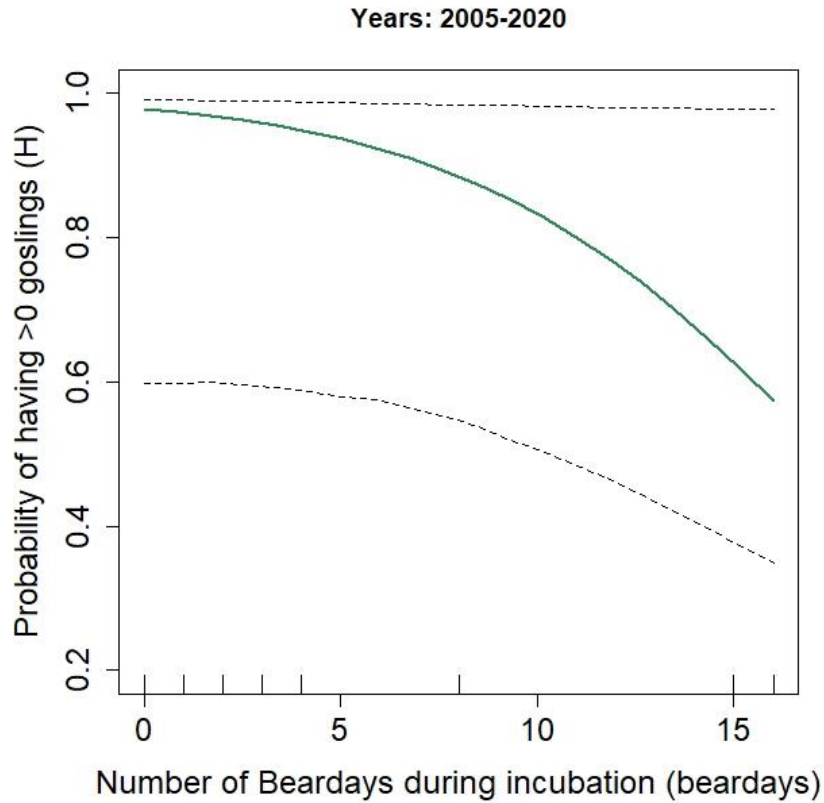
Figure 10: Predicted relationship between number of beardays in Kongsfjorden in the incubation period for barnacle geese and probability of having one or more goslings (H) in regime period 1 from 2006-2020. Dashed lines indicate the 95% credible intervals. Distribution of the beardays in the second regime period from 2006-2020 is included as rugs on the x-axis.

3.2.2 Number of goslings per female (G)

The Arctic fox abundance proxy (Fox) had no effect on number of goslings per female (G), whilst date of spring onset (SO) and local adult population size (N_{sval_ad}) had negative effects on G (Table 1, Figure 11 and 12).
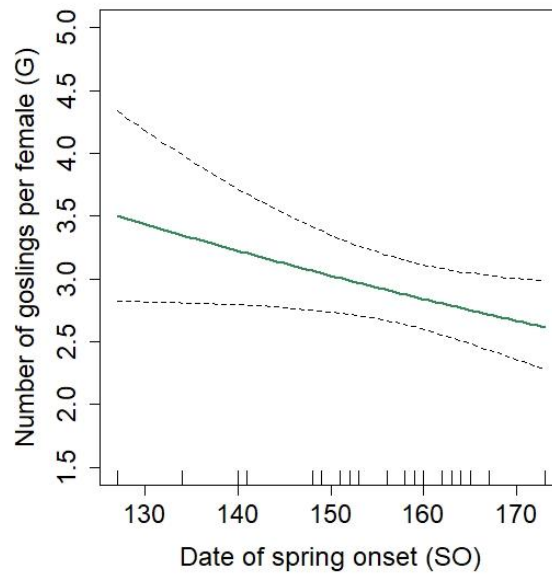
Figure 11: Predicted relationship between date of spring onset (SO) and number of goslings per female (G) (green line) with 95% credible intervals (dashed lines). Local adult population size (N_{sval_ad}) was kept at the mean value over the study period. Distribution of SO is included as rugs on the x-axis.
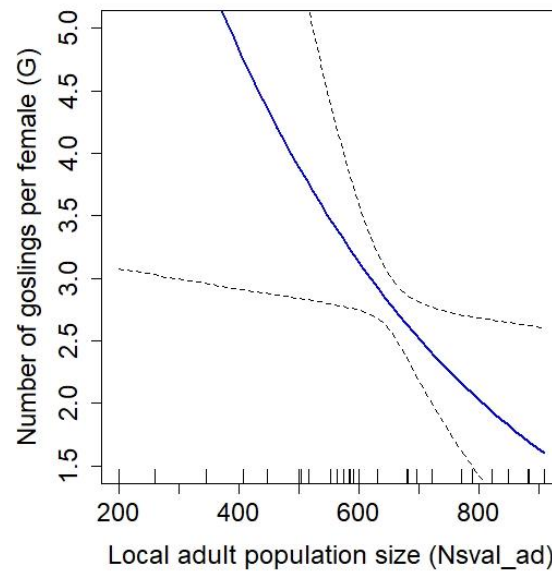
Figure 12: Predicted relationship between local adult population size ($N_{Sval, ad}$) and number of goslings per female (blue line) and 95% credible intervals (dashed lines). Date of spring onset (SO) was kept at the mean value over the study period. Distribution of $N_{Sval, ad}$ over the study period is included as rugs on the x-axis.

3.2.3   Probability of fledging (F)

Sum of precipitation from mid-July to mid-August (P_{sval}) and local adult population size (N_{sval_ad}) had no effects on probability of fledging (F) whilst the Arctic fox abundance proxy (Fox) had a strong negative effect on F (Table 1, Figure 13).
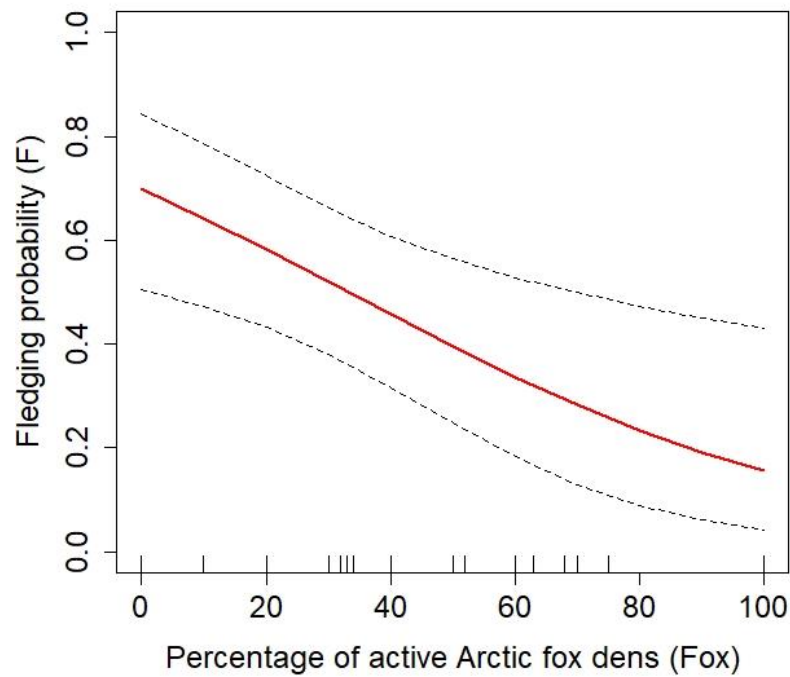
Figure 13: Predicted relationship between percentage of active Arctic fox dens in Kongsfjorden (Fox) and probability of fledging (F). Dashed lines indicate 95% credible intervals. Distribution of Fox over the study period is included as rugs on the x-axis.

Table 1: Mean effect sizes and 95% credible intervals (CRI) of covariates affecting vital rates. Covariates with a 95% CRI that did not overlap 0 is highlighted in bold text (equivalent to p<0.05). Covariates with an * after the abbreviation had a 95% CRI that had a minor overlap with zero (equivalent to 0.05<p<0.10).

Covariate	Abbreviation	Vital rate	Mean	2.50%	97.50%
Minimum winter temperature (°C), Scotland	**Tminscot**	**S**	**0.184**	**0.045**	**0.322**
Flyway population size, Scotland	**N$_{scot}$**	**S**	**-0.00002**	**-0.00004**	**-0.00001**
Regime (0 = 1990-2005, 1 = 2006-2020)	Reg	H	0.000	-2.772	2.195
Number of beardays in Kongsfjorden during incubation	Beardays	H	0.324	-0.169	0.932
Interaction between regime and beardays	**Reg×Bear***	**H**	**-0.455**	**-1.109**	**0.110**
Avg. temperature (°C) from Mid-June to Mid-July, Kongsfjorden	T$_{sval\_JJ}$	H	0.171	-0.464	0.810
Local adult population size, Kongsfjorden	N$_{sval\_ad\_H}$	H	0.880	-2.845	4.713
Proportion of active Arctic fox dens in Kongsfjorden	Fox_G	G	-0.009	-0.066	0.044
Date of spring onset (Julian)	**SO***	**G**	**-0.062**	**-0.125**	**0.000**
Local adult population size, Kongsfjorden	**N$_{sval\_ad\_G}$**	**G**	**-0.393**	**-0.809**	**-0.045**
Sum of precipitation from mid-July to mid-August (mm)	P$_{sval\_JA}$	F	-0.160	-0.631	0.295
Proportion of active fox dens in/around Kongsfjorden	**Fox_F**	**F**	**-0.625**	**-1.105**	**-0.165**
Local adult population size, Kongsfjorden	N$_{sval\_ad\_F}$	F	-1.434	-3.822	0.939

3.3 Temporal trends in population sizes and climate variables

Number of days with polar bear(s) in Kongsfjorden during the incubation period for barnacle geese increased non-linearly over the study period (Mean±SE = 1.37±1.04 beardays per year, p<<0.01, Figure 14A) whilst the Arctic fox abundance proxy did not exhibit a clear trend (0.04 ± 0.05 per year, p=0.42). Date of spring onset on Svalbard advanced over the study period (-0.63 ± 0.15 per year, p<<0.01, Figure 14B) and minimum winter temperature in Scotland had no significant trend (-0.02 ± 0.02 per year, p=0.31). Flyway population size in Scotland increased markedly (934 ± 55 individuals per year, p<<0.01, Figure 4) whilst estimated local adult population size on Svalbard had a positive trend (13.37 ± 1.47 individuals per year, p<<0.01) over the study period (Figure 7).
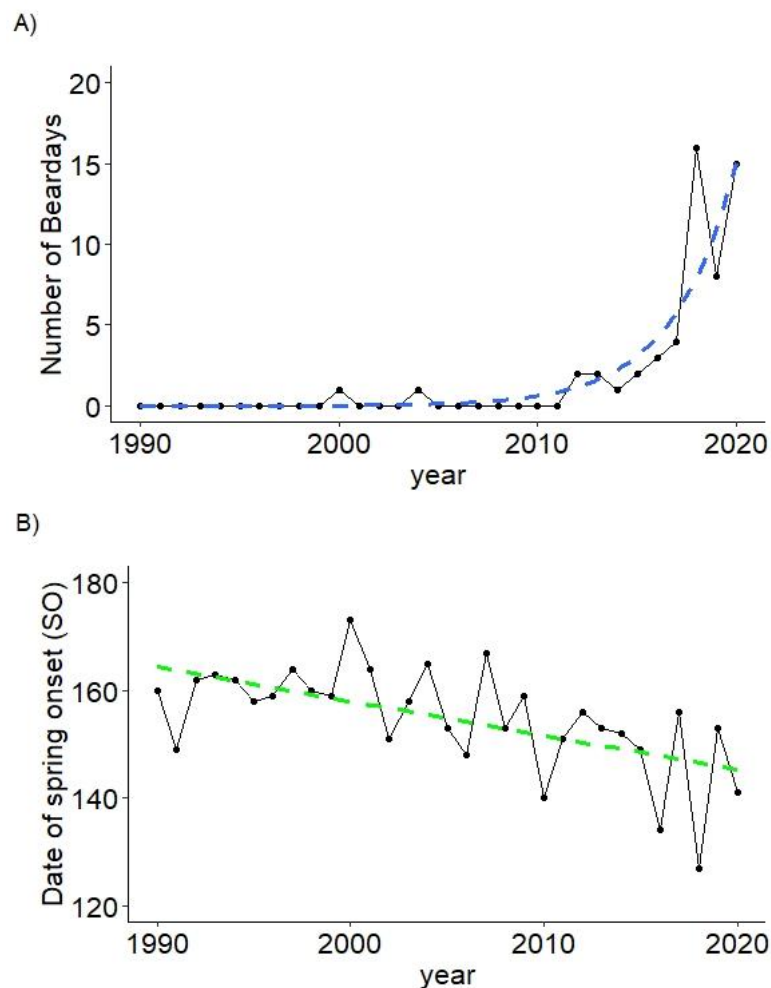

Figure 14: Timeseries (black dots) and linear trends (coloured dashed lines) of number of beardays during the incubation period (A) and date of spring onset (B) over the study period. Trend in SO was fitted using a linear model whilst trend in beardays was fitted in using a Poisson regression in a generalized linear model with a log link function.

3.4 Temporal trends in vital rates

There was a significant negative trend in adult survival (Mean = -0.0030 ± SE = 0.0006 per year, p<<0.01, Figure 5A) and no trend in fledgling survival (0.001 ± 0.004, p=0.77) over the study period (Figure 5B). No trend was found in probability of having one or more goslings (H) (0.007 ± 0.004, p=0.14, Figure 6A) or number of goslings per female (G) (-0.011 ± 0.008, p=0.17, Figure 6B) over the study period. Probability of fledging (F) had a marked negative trend (- 0.011 ± 0.005, p<0.05, Figure 6C), whilst number of fledglings per female (product of H*G*F) had a tendency for a negative trend (-0.023 ± 0.013, p=0.09) over the study period (Figure 6D).

4. Discussion

In this study, I have demonstrated how the influence of polar bear predation has changed over three decades in a local population of Arctic breeding geese. In agreement with my predictions, there was a strong tendency for a negative effect of polar bear predation in the second regime period from 2006-2020 (Figure 10) and no clear effect in the first from 1990-2005 (Table 1). I have also confirmed previous findings, notably that the timing of spring onset at the breeding grounds and temperature at the overwintering site had positive effects on reproduction and survival, respectively (Figure 8, 9 and 11). Additionally, I have verified that predation from Arctic foxes remain the strongest top-down mechanisms in this system, as it had a strong negative effect on fledging rates (Figure 13). Lastly, I confirmed that density regulation is acting through breeding population size on reproduction and through flyway population size on survival (Table 1, Figure 12).

The change in abundance and behaviour of polar bears, detected in Kongsfjorden in this study and at other locations in the Arctic in other studies, can have major implications for the Arctic breeding birds, as they are not likely to have anti-predatory responses to match the novel predators (Sih et al. 2010). Hence, it is not surprising that previous observations and findings from the same and other populations across the Arctic suggest that nest predation from polar bears on colonially breeding birds may be devastating for their reproduction. In the Canadian Arctic, polar bears have been predating bird colonies much more frequently in parallel with loss of sea-ice, and these events have been catastrophic for reproduction on some occasions (Smith et al. 2010; Iverson et al. 2014). Similar results have also been found on Svalbard, where Prop et al. (2015) found that up to 90% of barnacle goose nests were predated in some years when the polar bears arrived before or during the incubation period.

They also found that the arrival date of polar bears has progressively advanced over the past few decades, whilst the number of days with polar bears during summer have increased significantly. Hence, the tendency for a negative influence of polar bear predation on reproduction found in the second half of the study period was not surprising. The lack of effect during the first half of the study period was likely because there were almost no observations of polar bears in Kongsfjorden during the incubation period from 1990-2006 and no major predation events occurred during this time (Loonen, M.J.J.E, Unpublished data 2022). Earlier arrival combined with a positive trend in number of polar bears during summer in Kongsfjorden also explains why I found a significant positive trend in number beardays in the incubation period over the study period (Figure 14A).

Polar bears have already been known to sporadically predate eggs of colonially breeding birds since the early 1900s (Schaudinn 1900; Lønø 1970). What is new however, is that it is occurring at new locations and with increasing impacts on bird colonies throughout the Arctic, including the ones in Kongsfjorden (Rockwell and Gormezano 2009; Smith et al. 2010; Iverson et al. 2014; Prop et al. 2015). So, why then has an increasing number of polar bears expanded their ranges to Kongsfjorden and other new locations in the Arctic and why are they predating eggs of bird colonies? Most of the research that exists point towards behavioural adaptations as a consequence of loss of sea-ice, the main hunting habitat for polar bears during spring, where they accumulate most of their body stores to survive the rest of the year (Rockwell and Gormezano 2009; Stirling and Derocher 2012; Iverson et al. 2014; Prop et al. 2015; Rode et al. 2015). However, recolonization may also be part of the explanation at some locations where polar bears used to be more common before the introduction of humans (Lønø 1970; Prop et al. 2015). Also, a recent study in the southern Beaufort sea reveals that learning may be a component to predation on colonially breeding birds, as on-shore behaviour is, at least partly, learned from mother to cubs in polar bear (Lillie et al. 2018).

Although there were some uncertainty in the estimated influence of polar bear predation on reproduction in this study, it is likely that the polar bear will have an increasing impact on colonially breeding birds in the Arctic in general in the decades to come, as sea-ice, and thus their main hunting habitat is retracting in parallel with climate change (Stirling and Derocher 2012; Box et al. 2019; IPCC 2021). However, the future impact of polar bear predation appears to be dependent on a temporal overlap between the arrival of polar bears at the colonies and the incubation period of Arctic breeding birds (Rockwell and Gormezano 2009;

Prop et al. 2015). Hence, the future consequences of this trophic interaction is both dependent on the response of polar bears to retreating sea-ice and Arctic breeding birds' responses to environmental change. Also, as the barnacle goose, and other Arctic breeding goose species typically are long-lived species, the cost of single predation events in terms of lifetime reproductive success, and thus for long-term population dynamics, may not necessarily be that large, as they can reproduce again in later years (Black et al. 2014). Polar bear predation on eggs may also be a temporary phenomenon, as it is unlikely that the polar bear will survive as a species in the long-term, if the sea-ice disappears completely in the Arctic (Derocher et al. 2004; Stirling and Derocher 2012; Rode et al. 2015). The Arctic fox on the other hand, is a well-established predator on Arctic breeding birds throughout most of its distribution, including the study population in Kongsfjorden (Samelius and Alisauskas 2000; Fuglei et al. 2003; Layton-Matthews et al. 2020) Hence, it was not surprising to confirm that the Arctic fox had a strong negative effect on fledging rates in this population of barnacle geese (Figure 13). I did not find a clear trend in proportion of active fox dens in this study. However, previous studies indicate that the Arctic fox is increasing in abundance both in Kongsfjorden and elsewhere on Svalbard (Fuglei et al. 2003; Layton-Matthews et al. 2020).

The positive influence of temperature at the overwintering grounds on survival found in this study was not unexpected, given that Layton-Matthews et al. (2020) found the same relationship in the same study population, and the fact that a positive relationship between temperature and survival have also been found in barnacle geese on Greenland and pink-footed geese (*Answer brachyrhynchus*) on Svalbard (Kéry et al. 2006; Doyle et al. 2020). Consequently, the warming that is expected in the coming decades, as a result of climate change, may have a positive effect on survival, and thus on population dynamics, as long-lived species such as the barnacle geese is highly sensitive to changes in survival (Morris and Doak 2004; Sæther et al. 2013; IPCC 2021). Although there was a strong positive trend in in flyway population size in Scotland throughout the study period (Figure 4), the effect of density at the overwintering grounds on survival was most likely not particularly influential, as the effect size was marginal (Table 1). These results are to some extent consistent with the lack of evidence for density regulation affecting populations at the flyway level at overwintering grounds in goose species (Larsson and Forslund 1994; Fox and Madsen 2017). However, the effect size of density at the overwintering grounds found in this study should be interpreted with some caution as Layton-Matthews et al. 2020 found a stronger influence than the one identified in this thesis.

The negative trend in adult survival found in this study validates the results of Layton-Matthews et al. (2020). Nevertheless, it is worth mentioning that resighting heterogeneity, the fact that resighting rates differ among individuals, may in some instances cause apparent declines in survival in population dynamical studies that use long-term mark-recapture data (Lebreton 1995). Yet, the decline in adult survival was likely real, as I did account for resighting probability in the survival model. However, it is important to be aware that mortality may also be confounded by permanent emigration, when assuming an open population to be closed, highlighting the importance of caution when interpreting decline in survival in long-term studies (Kéry et al. 2006).

I also confirmed that an advancing timing of spring onset had a positive influence on reproduction, specifically on the number of goslings per female (Figure 11) (Layton-Matthews et al. 2020). A positive effect of advancing spring onset on the gosling stage is likely, given that growth rate varies considerably in goslings and is dependent on both the amount and quality of forage in barnacle geese (Loonen et al. 1997). Also, in general, plant phenology is essential in controlling both the timing and success of reproduction in Arctic breeding geese (Langvatn et al. 1996; Tveraa et al. 2013; Nolet et al. 2019). However, I found no clear trend in the number of goslings per female (G) over the study period (Figure 6B). A lack of trend in G could be explained by density dependence, which acted strongly on through adult breeding population size on G (Figure 11). This may be likely, as that the local adult population on Svalbard increased steadily over the study period (Figure 7). These results support the notion that density regulation acts primarily on reproductive stage before fledging in capital breeding duck- and goose species (Sedinger et al. 1998; Elmberg 2003; Prop and Quinn 2003). Thus, density-dependent effects may have functioned as a buffer against some of the changes in climate in this population (Reed et al. 2013; Hansen et al. 2019).

In contrast to Layton-Matthews et al. (2020), I found no clear effect of summer temperature or precipitation in Kongsfjorden on reproduction in this study nor any positive trend in H (Table 1). This discrepancy may have been caused by differences in methodology along with differences in type and amount of data analysed. In this study, I analysed the effect of all covariates using directly within an IPM, which yields joint parameter estimates and uncertainty, which may produce different results, especially when analysing more years of data and a unique combination of covariates, age classes and vital rates (Abadi et al. 2017; Weegman et al. 2017; Plard et al. 2019).

Future directions

Introduction of novel predators is a problem associated with climate change (Sih et al. 2010). Therefore, it is vital to gain a better understanding of the consequences for the prey species. Perhaps particularly so in Arctic communities, which often have few and strong trophic interactions (Gauthier et al. 2004; Hansen et al. 2013; Barrio et al. 2016; Fauteux et al. 2021). Firstly, there is a need for more quantitative studies investigating the consequences of novel predator-prey interactions resulting from indirect climate effects. Secondly, these findings should be put into context at the community level, to determine the likely consequences for Arctic ecosystems (Hansen et al. 2013). In the context of recent changes in behaviour and abundance of polar bears, there is a need for more research on both the underlying causes and consequences. It is likely that loss of sea-ice is the most important cause of polar bear predation on bird colonies in the Arctic. However, possible corroborating factors such as recolonization and learning should be investigated further (Prop et al. 2015; Lillie et al. 2018). Perhaps most importantly, there is a need to investigate whether terrestrial food resources can offset some of the resources that are lost for polar bears in relation to loss of sea-ice as a hunting habitat. This is crucial to determine whether this is a phenomenon that will continue in the foreseeable future and thus will have long-term consequences for population dynamics in Arctic breeding birds. The study of Rockwell and Gormeazano (2009) suggests that resources from colonially breeding birds could offset some of the lost resources related to loss of sea-ice, whilst the comprehensive reviews of Stirling and Derocher (2012) and Rode et al. (2015) reveal that this may not be the case.

Conclusion

In this study, I have confirmed many of the previous findings of climate change effects on this local population of breeding barnacle geese. An advancing spring onset had a positive effect on reproduction, temperature at the overwintering grounds had a positive effect on survival and the Arctic fox remains the most important predator in this system, with a strong negative effect on fledging rates. I have also confirmed that reproduction and survival is density regulated. Most importantly however, the findings of this study suggests that predation from polar bears may be starting to have a noticeable negative influence on reproduction, in this local population of barnacle geese. These findings add to the growing number of studies suggesting that similar predator invasions by polar bears are occurring at new locations throughout the Arctic, in parallel with loss of sea-ice related to ongoing climate

change. However, I have also revealed that there is a gap in our current understanding of the novel change in polar bear behaviour and abundance investigated in this thesis. Especially in quantifying the population dynamical consequences but also in identifying all of the underlying mechanisms. Our ability to predict future changes in Arctic ecosystems following climate change is dependent on gaining a better understanding of the indirect mechanisms at play.

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