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Demographic consequences of rapid climate change and density dependence in migratory Arctic geese

Doctoral thesis

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Thesis for the Degree of
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Trondheim, May 2020

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…

Meanwhile the wild geese, high in the clean blue air,

are heading home again.

Whoever you are, no matter how lonely,

the world offers itself to your imagination,

calls to you like the wild geese, harsh and exciting –

over and over announcing your place

in the family of things.

Mary Oliver, **Wild Geese**

A barnacle goose family feeding on the tundra at
Ny-Ålesund, Svalbard (©Jasper Doest).

Acknowledgements

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List of papers

I. Layton-Matthews K, Loonen MJJE, Hansen BB, Coste FD, Sæther B-E, Grøtan V (2019) Density-dependent population dynamics of a high Arctic capital breeder, the barnacle goose. *Journal of Animal Ecology*. doi: 10.1111/1365-2656.13001

II. Layton-Matthews K, Hansen BB, Grøtan V, Fuglei E, Loonen MJJE (2019) Contrasting consequences of climate change for migratory geese: predation, density dependence and carryover effects offset benefits of high-arctic warming. *Global Change Biology*. doi: 10.1111/gcb.14773

III. Fjelldal MA*, Layton-Matthews K*, Lee AM, Grøtan V, Loonen MJJE, Hansen BB (2020) High-arctic family planning: earlier spring onset advances age at first reproduction in barnacle geese. *In press, Biology Letters*. doi: 10.1098/rsbl.2020.0075

IV. Layton-Matthews K, Grøtan V, Hansen BB, Loonen MJJE, Fuglei E, Childs DZ. Environmental change reduces body mass, but not population growth, in an Arctic herbivore. *Manuscript.*

Declaration of contributions

Paper I: KLM, BBH and VG designed the study. MJJEL collected goose data. KLM analysed the data with input from VG and CFDC. KLM wrote the manuscript, which was reviewed and commented on by BES, BBH, MJJEL and VG.

Paper II: KLM designed the study with input from MJJEL, BBH and VG. MJJEL provided goose data and EF provided fox data. KLM analysed the data with input from BBH, MJJEL and VG. KLM wrote the manuscript, which was reviewed and commented on by all co-authors.

Paper III: KLM, BBH and VG designed the study. MJJEL provided the data. MAF analysed the data, with input from AML and KLM. KLM and MAF wrote the manuscript, which was reviewed and commented on by all co-authors. MAF and KLM contributed equally to the study and are both co-first authors (*).

Paper IV: KLM and DZC designed the study, with input from BBH and VG. MJJEL provided goose data and EF provided fox data. KLM analysed the data, with input from DZC. KLM wrote the manuscript, which was reviewed and commented by all co-authors.

1 | Summary

Climate change effects are being felt across ecological levels and most strongly in the Arctic. Scaling up from effects on demographic rates to the population-level, and even community-level, is a daunting task. This is particularly the case for migratory species that experience different climate and density regimes over their annual cycle. However, increasingly sophisticated statistical tools provide us with the means to do so. In this thesis, I used state-of-the-art analytical approaches to provide a mechanistic and holistic understanding of the impacts of climate change and density dependence on the population dynamics of a migratory Arctic herbivore, the barnacle goose (*Branta leucopsis*). The study population of barnacle geese breeds in high-arctic Svalbard but spends the winter at Solway Firth, UK, with a spring stopover on mainland Norway. I investigated the dynamics of a local population breeding on western Svalbard, close to the settlement of Ny-Ålesund, using 28 years of individual-based data. In **paper I**, I used an integrated population model to quantify density-dependent effects on vital rates in this population, following their colonisation of new breeding grounds in a period of overall population increase. Local density regulation at the breeding grounds reduced population growth through negative effects on reproduction. This led to density-dependent changes in vital rate contributions to the population growth rate. These results provided empirical evidence that the population dynamics of capital breeders may be more reproduction driven. In **paper II**, I disentangled climate, density and trophic-interaction effects on population dynamics, considering the annual cycle of barnacle geese, i.e., breeding and non-breeding season effects on vital rates. Climate change in Svalbard positively affected egg production and hatching success through rapid advancement of spring onset. However, this was offset by reduced pre-fledging survival due to increasing predation by Arctic foxes, an indirect consequence of climate change linked with changes in abundance of overwintering herbivores. In this way, climate effects on one population can cascade throughout a community. Climate and density also influenced reproduction and survival during the non-breeding season, via carryover effects. Overall, counteracting density, carryover and (direct and indirect) climate effects stabilised breeding population size. In **paper III**, I analysed variation in an important life-history trait: age at first reproduction (AFR). As established in **paper II**, advancing spring onset increased the probability of females producing goslings in general, but importantly, this effect was stronger for first-time than experienced breeders. The two-week advance in spring phenology led to an earlier AFR, by more than doubling the proportion of two-year-olds reproducing (one-year-olds do not reproduce). How the effects of environmental change on such demographic rates are coupled to traits reflecting body condition is important to understand and predict population growth. Body mass is a key fitness-related trait for herbivores and fluctuates with resources, which are highly variable in the Arctic. Consequently, coupled trait-demography responses may be important in Arctic herbivores, particularly geese, where body mass has declined in response to habitat degradation. In **paper IV**, I quantified population-dynamic consequences of changes in body mass in barnacle geese. Despite a 10% decline in body mass, and positive effects of mass on survival and reproduction, this did not translate into trait-mediated effects on

population growth. Consequently, the population dynamics of Arctic geese, and possibly other Arctic herbivores, may be more resilient to changing body condition than expected. In this thesis, I highlight the sensitivity, but also resilience, of an Arctic herbivore population to climate change, and other sources of environmental change, and the complex mechanisms by which effects of climate change are translated into changes in population dynamics and abundance. The dynamics of this population were predominantly driven by variation in reproduction, which is the demographic rate most affected by climate change, directly and indirectly.

However, mechanisms buffering population dynamics against environmental variation were also evident, such as the lack of demographic effects of declining body condition on the population growth rate. Overall, this work illustrates that a holistic approach, jointly modelling vital rates and the mechanisms for how they influence population dynamics, are necessary to understand effects of e.g. climate change.

2 | Introduction

Arctic climate change

Global warming is occurring at an unprecedented rate, with severe and diverse effects around the world (Easterling *et al.* 2000; IPCC 2014). Global mean temperatures are estimated to rise by 2.6–4.8°C by the end of the century (compared to 1986–2005), under current emissions scenarios (Collins *et al.* 2013). The consequences are hard to ignore, with increasing frequencies of extreme events and dramatic shifts in weather systems (Rahmstorf & Coumou 2011). Warming is occurring most rapidly at the poles, as a result of Arctic amplification (Curry *et al.* 1995; Serreze & Barry 2011). Consequently, Arctic species are particularly at risk from climate change, and the effects are already disrupting biotic and abiotic processes (Post *et al.* 2009; Høye *et al.* 2013). Arctic migrants also have the additional challenge that climate change is occurring at different speeds across their flyway (Robinson *et al.* 2009), and they may not be able to adjust their migratory cues to track climate change (Both & Visser 2001).

The timing of snowmelt has advanced substantially and is considered a prevailing indicator of climate change in the Arctic (Foster 1989). This has serious, and complex, consequences for Arctic herbivores, who are strongly dependent on the short snow-free season for their survival and reproduction. Advancing spring onset may be beneficial for some herbivores, through earlier vegetation growth onset, i.e., food availability (Karlsen *et al.* 2014). However, it can also lead to problems of mismatched food-web interactions, i.e., if they cannot align their phenology to match the phenology of their food source (Lameris *et al.* 2018; Nolet *et al.* 2019). Evidence suggests that Arctic warming is potentially increasing vegetation productivity, although a general cross-species consensus is lacking (Elmendorf *et al.* 2012; Piao *et al.* 2019). Increased food availability in summer should benefit herbivores by increasing their body condition, which is fundamental for successful reproduction and survival (Festa-Bianchet *et al.* 1997; 1998; Post & Stenseth 1999). The capital-income breeding dichotomy separates species relying on body stores accumulated earlier in the annual cycle to initiate reproduction (capital breeders), from species investing in offspring using resources directly at the breeding grounds (income breeders) (Drent & Daan 1980; Stearns 1992; Jönsson 1997). Capital breeding is a strategy to cope with unpredictable conditions, allowing some independence from environmental variation and is therefore a common strategy at high latitudes (Jönsson 1997; Varpe *et al.* 2009). Consequently, capital breeding is characteristic of several Arctic herbivores (greater snow goose, *Chen c. atlantica*, Gauthier *et al.* 2003; e.g., muskox, *Ovibos moschatus*, Kerby & Post 2013). Capital breeding is therefore an important consideration when studying the effects of climate change, since not only environmental conditions during the breeding season are relevant for breeding success.

Signatures of climate change are clearly apparent in the Arctic; for instance, diminishing sea ice extent (Post *et al.* 2013), changes in snowpack characteristics (Peeters *et al.* 2019), vegetation productivity and phenology (Elmendorf *et al.* 2012) as well as increasing frequencies of extreme events (Fischer & Knutti 2015; Diffenbaugh *et al.* 2017). A comprehensive assessment of its implications for the persistence of Arctic populations is fundamental to understand their sensitivity to future warming. This is relevant for vulnerable

(e.g., reindeer, polar bear), but also thriving (e.g., Arctic geese), species, to inform both conservation and management decisions (IUCN, 2019).

Population responses to climate change

A complete understanding of demographic responses to climate change is necessary to predict population persistence into the future (Jenouvrier *et al.* 2009; Paniw *et al.* 2019). Population dynamics are influenced by density-dependent and environmental processes, which affect species' reproduction and survival (Turchin 1995; Lande *et al.* 2003). Assessing population responses to environmental factors requires an understanding of intrinsic processes, i.e., density regulation, life history and age structure (Benton *et al.* 2006; Vindenes *et al.* 2011; Abadi *et al.* 2012). In fact, not accounting for the structure and intrinsic properties of a population can lead to false inferences about underlying processes affecting fluctuations in population size (Stenseth 1999; Lande *et al.* 2006).

Demographic analyses aim to identify relationships between the environment and vital rates, which determine (variation in) population size. Across Arctic species, effects of climate change on reproduction and survival are, in several cases, well-documented (Forchhammer *et al.* 2008; Post *et al.* 2009). A warming Arctic can benefit reproduction, through earlier sea ice retreat (Gaston *et al.* 2005), snow melt (Cooper *et al.* 2011) and an advanced, longer growing season in terrestrial (Karlsen *et al.* 2014) and marine (Søreide *et al.* 2010) systems. However, negative effects of trophic mismatch on reproduction have also been documented, where species cannot advance their reproductive timing enough to follow advancing food peaks (Søreide *et al.* 2010; Jensen *et al.* 2014). Furthermore, retreating sea ice has had negative implications for reproduction and survival of marine predators such as polar bears (Molnár *et al.* 2010), and terrestrial herbivores may suffer from increased frequency of winter icing events (Hansen *et al.* 2019).

There are several pathways by which climate change can lead to population-dynamic consequences, not only through direct effects on demographic rates. Carryover effects occur when conditions in one season affect individual fitness in a later season (Norris 2005). Carryover effects on reproduction and survival are particularly relevant for migratory species, which utilise several locations over their annual cycle (Norris 2005; Inger *et al.* 2010; Sedinger *et al.* 2011). However, modelling climate effects on reproduction and survival, over an entire annual cycle, presents a challenge (Sedinger & Alisauskas 2014). Furthermore, populations are connected by interspecific interactions. Consequently, climate change can affect entire communities through these interactions, across trophic levels (Dunne *et al.* 2002; Ims & Fuglei 2005). Trophic interactions play an important role in Arctic systems (Gauthier *et al.* 2004; Morrissette *et al.* 2010; Ims *et al.* 2013b) and present a mechanism by which ecosystem responses to climate change can occur. Furthermore, Arctic trophic systems have been more severely, and rapidly, perturbed than in other ecosystems (Ims & Fuglei 2005; Post *et al.* 2009). Changes in bottom-up producers affect higher levels in the food chain, while changes in predation pressure act as 'top-down' controls (Ims *et al.* 2013b; Legagneux *et al.* 2014). Ignoring these trophic interactions can lead to false conclusions, when predicting population, and also community, persistence under future climate change (Gunn & Skogland 1997; Ims & Fuglei 2005). Climate change is also affecting

phenotypic trait distributions (e.g. Parmesan 2006; Jiguet *et al.* 2007). Fitness-related traits are closely associated with individual reproduction and survival. Therefore, changes in life-history traits and fitness-related phenotypic traits can ultimately scale up to influence population size (Ozgul *et al.* 2009; 2010).

However, determining the mechanisms behind population-dynamic responses requires an understanding of demography-trait associations and how they, in turn, are influenced by climate change (Pelletier *et al.* 2007; McLean *et al.* 2020).

3 | Thesis objectives

In this thesis, I aim to improve our understanding of how climate change has, through different mechanisms, affected the population dynamics of a migratory Arctic herbivore. This required disentangling the complex mechanisms behind, potentially age- and vital rate-specific, demographic responses, such as density dependence, direct and indirect effects of climate change, food-web interactions, and changes in trait dynamics. I studied the population dynamics of barnacle geese (*Branta leucopsis*), breeding in high Arctic Svalbard, using almost 30 years of individual-based data.

I had three overarching questions, which I answered with four papers:

1. How do density-dependent processes impact the dynamics and trajectories of a colonising population (**papers I**, **II**, **III**)?

Population size fluctuations are influenced by density-dependent and -independent processes (Lande *et al.* 2003). Density regulation may be a particularly relevant process in rapidly increasing (e.g., colonising) populations as vital rates can change substantially as population sizes grow towards (and often overshoot) the carrying capacity. However, density dependence can take several forms, depending on which, potentially age-specific, vital rates are affected, and can differ according to species' life history (Fowler 1987; Lande *et al.* 2002). In **paper I**, I aimed to explore how density-dependent processes acted to regulate the size of this study population and to what extent observed patterns of density regulation could be explained by the life history characteristics of barnacle geese. In **paper II**, I looked more in-depth into the life-history stages

of barnacle geese, to tease apart different density-dependent versus density-independent processes. By knowing at what stage these effects occur, I aimed to gain a more mechanistic understanding of how they affect demographic rates. In **paper III**, I asked whether density-dependent processes not only influence vital rates directly, but also important life-history traits such as the age at first reproduction in barnacle geese.

2. How has climate change directly or indirectly influenced population dynamics, and through which vital rates (**paper II**)?

Quantifying effects of climate change on demographic rates is key to predicting population persistence in the future (Jenouvrier 2013). In **paper II,** I explored the potential mechanisms by which rapid climate change in the Arctic is affecting the population dynamics of arctic geese. Specifically, I asked how weather, population density and trophic interactions influence reproduction and survival in the study population. I looked across the annual cycle, including both the breeding and non-breeding season, since environmental processes in one season can have carry-over effects on later seasons (Inger *et al.* 2010; Sedinger *et al.* 2011).

3. To what extent have key fitness-related traits been affected by climate/environmental change, and how do they contribute to variation in the population growth rate (**papers III**, **IV**)?

Not only climate change but also other sources of environmental change have altered phenotypic trait distributions, as well as the dynamics of natural populations (Parmesan 2006; Jenouvrier

et al. 2009). In **paper III**, I investigated how advancing spring onset at the arctic breeding grounds influences age at first reproduction. Coupled changes in traits and demographic rates can occur when both respond to variation in weather or density (Parmesan 2006; Ozgul *et al.* 2010).

Body mass is an important fitness-related trait in Arctic herbivores, and, across Arctic goose species, has been undergoing a decline due to habitat degradation. In **paper IV**, I aimed to quantify the importance of body mass-mediated effects on the dynamics of the study population and therefore how much the decline in body mass has influenced their population growth.

4 | Methods

Study system

Barnacle geese (Figure 1) are long-lived (up to 28 years) migratory birds, utilising distinct areas for breeding and overwintering, often with multiple stopovers during their seasonal migration. They are monogamous and are sexually mature from two years of age, laying one clutch per season with 3–5 eggs on average (Black *et al.* 2014). Barnacle geese are partial capital breeders, investing 23–88% of body stores acquired further south in egg production (Hahn et al., 2011).

Figure 1. A gaggle of geese waiting to receive leg rings for later re-identification (Ronald Cornelissen).

Arctic barnacle geese exist in three geographically distinct breeding populations; the Greenland, Russian and Svalbard populations. Numbers were severely depleted in the 1950s, due to excessive hunting pressure. The combined alleviation from hunting since the 1950s and the transition to agricultural lands at overwintering grounds has led to a dramatic, and sustained, increase (Fox & Abraham 2017; Fox & Madsen 2017). By the 1980s, the total number across the three flyways was approximately 112,000 (Madsen 1991), and by 2010 had reached over one million individuals (Fox & Leafloor 2018, BirdLife International 2004). The Svalbard population alone had an estimated population size of 40,400 in 2018. The population overwinters at Solway Firth, Scotland (UK; 55°N, 3.30°W), before flying to Svalbard for breeding in summer, with a spring stopover along the coast of mainland Norway (Figure 2).

Svalbard (76–81°N, 10–34°E) is located in the high-Arctic, between the Barents Sea and Greenland Sea. The extent of recent warming on Svalbard has been dramatic: since 1964 average temperatures have risen substantially (Hanssen-Bauer *et al.* 2019). Climate change is severely altering the entire Svalbard community, at all trophic levels (Post *et al.* 2009; Ims *et al.* 2013a). Arctic-breeding geese, such as barnacle geese, represent important species in this system. Geese play a 'bottom-up' trophic role as prey to Arctic foxes, *Vulpes lagopus* (goslings and occasionally adults, Fuglei *et al.* 2003), to other birds e.g., glaucous gulls, *Larus hyperboreus*, (eggs, Prop *et al* 1985) and more recently to polar bears, *Ursus maritimus* (Prop *et al.* 2015). They also play a key 'top-down' role as herbivores, providing nutrient transfer between temperate and Arctic ecosystems (Hahn *et al.* 2011; Hessen *et al.* 2017).
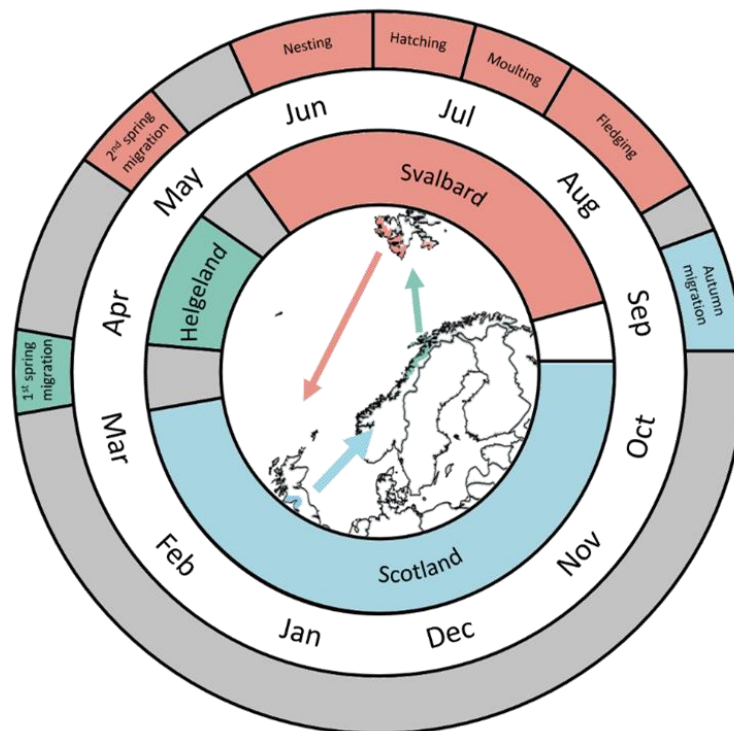
Figure 2. Migration route and timing of key life-history events for Svalbard barnacle geese. Barnacle geese overwinter at Solway Firth, UK (blue), before travelling to western Svalbard for breeding (pink) via a stopover on the coast of mainland Norway (green). The timing of migrations and reproductive events are shown in the outer circle.

Data collection

The work in this thesis is largely based on 28 years of individual-based data (1990-2017) from a population of Svalbard barnacle geese, breeding in Kongsfjorden (Figure 3), which forages around the settlement of Ny-Ålesund (78°55′ N, 11°56′ E). Individuals arrive at Kongsfjorden in late May and attempt to nest on islands in the fjord to avoid predation. Their offspring hatch around 1st July (range: 19th June – 19th July). During this time, the two main nesting islands; Storholmen and Prins Heinrichsøya were visited by researchers at one- to two-day intervals. Since 1990, 3,290 nests have been monitored, and individual IDs are recorded along with the clutch size. Immediately after hatching, parents leave the islands with their newly hatched goslings to forage along the coast on tundra vegetation. In general, adult geese begin moulting in July, although the timing depends on breeding status. Goslings fledge towards the end of August (Loonen *et al.* 1997a). During the moulting period, flightless individuals are caught around Ny-Ålesund and ringed with unique, engraved colour and metal rings. During a catch, an individual's sex is determined by cloacal inspection and body measurements are taken, e.g., weight. Re-sightings of marked individuals are recorded during twice-daily counts around Ny-Ålesund. All individuals leave Svalbard in October and return to Scotland (Owen & Black 1989).
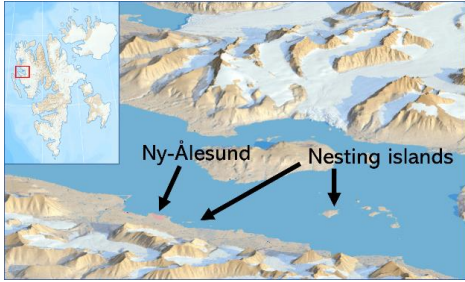
Figure 3. The study system at Kongsfjorden, western Svalbard. Arrows indicate the location of Ny-Ålesund and the two monitored nesting islands.

Integrated population models

Integrated population models (IPoMs) provide a framework to analyse demographic and count data in a unified way. IPoMs combine multiple data sources in one model, allowing for information flow among demographic processes (Schaub & Abadi 2011; Abadi *et al.* 2012). Combining demographic and count data, allows us to account for multiple sources of uncertainty, improve the accuracy of parameter estimation and estimate unknown parameters. IPoMs are generally implemented in a Bayesian framework, which inherently provides an efficient way to link process and observation models. In **paper I**, we constructed an IPoM, to estimate age class-specific demographic rates and numbers. The model estimated the number of individuals (N) at year $t+1$ in three age classes, by jointly estimating; survival (ϕ) of the fledgling (f), yearling (y) and adult classes (ad), the probability of a female producing fledglings (R) and fledged brood size (fec), at year t.

$$N_{f_{t+1}} \sim \text{Poisson}(R_{t+1}\, fec_{t+1}(N_{y_t}\phi_{y_t} + N_{ad_t}\phi_{ad_t})/2)$$

$$N_{y_{t+1}} \sim \text{Binomial}(\phi_{f_t}, N_{f_t})$$

$$N_{ad_{t+1}} \sim \text{Binomial}(\phi_{y_t}, N_{y_t}) + \text{Binomial}(\phi_{ad_t}, N_{ad_t})$$

Path analysis

Path analysis is a statistical approach to test multivariate hypotheses of associations among variables (Shipley 2000). Confirmatory path

analyses are extensions of structural equation modelling, which allow for hierarchical structures in the data, e.g., random effects (Shipley 2009). In **paper II**, we performed such an analysis to identify the main environmental effects of several reproductive stages in barnacle geese. We constructed a path diagram to test for links between covariates and responses variables, and dependencies among responses. Proposed independence relationships were tested using d-separation tests. Each test gives the necessary conditions for two variables to be independent, conditional on another set variables. The overall fit of the path diagram was confirmed using a Fisher's C test (Shipley 2009).

E-SURGE

The multi-event program E-SURGE (Multi-Event SURvival Generalized Estimation) incorporates uncertainties in both state (e.g., breeding status, sex, age) and detection uncertainty (Choquet *et al.* 2009), by considering them as a hidden Markov process. In **paper III**, we used this framework to estimate probabilities of reproducing for the first time. Multi-event models separate *states*, representing the 'true' reproductive status of an individual in a given year, which are not necessarily observable, and *events*, i.e., the observed state of an individual. We modelled four *states*; pre-breeder, non-breeder, breeder and dead. 'Pre-breeder' was any individual breeding at year t that had never bred previously (i.e., first-time breeders), 'non-breeder' was an individual not breeding at t but that had bred in a previous year, 'breeder' was a female that produced at least one gosling at t and which had previously bred, and 'dead' includes both dead and permanently emigrated individuals. Three *events* were considered: 'not seen, 'seen as breeder' and 'seen but not breeding', which were associated with certain *states*.

Integral projection models

Integral projection models (IPrMs) provide a framework to study coupled trait-population-dynamic responses to environmental change (Ellner *et al.* 2016). In **paper IV**, we constructed an IPrM, structured by age class and body mass, combining information on variation in mass and vital rates and their respective environmental- or density- dependencies, underpinned by time-varying regression parameters (Rees & Ellner 2009). We constructed a density-independent, stochastic IPrM (Rees & Ellner 2009; Ellner *et al.* 2016) describing the temporal dynamics of population size and the distribution of body mass (z) of fledglings (fl) and adults (ad). $F_{ad}^{(t)}(z', z)$ is the fecundity kernel describing production of mass z' fledglings by females of mass z, based on adult (ad) survival (φ) and reproductive (R, fec) rates:

$$F_{ad}(z', z) = \varphi^{(t)}(z, ad)R^{(t+1)}(z)fec^{(t+1)}C_0^{t+1}(z')/2.$$

$P_{fl,ad}^{(t)}$ are survival-growth kernels describing how individuals of mass z at time t, survive (φ) and grow (G) to reach mass z' at time $t+1$:

$$P_a^{(t)}(z', z) = \varphi^{(t)}(z, a)G^{(t)}(z', z).$$

The structure of the IPrM was, where U and L were the upper and lower integration limits, respectively:

$$n_{fl}(z', t+1) = \int_L^U F_{ad}^{(t)}(z', z)n_{ad}(z, t)dz$$

$$n_{ad}(z', t+1) = \int_L^U P_{ad}^{(t)}(z', z)n_{ad}(z, t)dz +$$

$$\int_L^U P_{fl}^{(t)}(z', z)n_{fl}(z, t)dz.$$

Matrix population analysis

Population projection matrices are a common tool to analyse population dynamics, providing useful metrics such as the population growth rate (λ) and sensitivities of λ to changes in underlying demographic rates (Caswell 2000, 2001). Prospective perturbation analysis measures the absolute (sensitivity) or proportional (elasticity) change in the population growth rate, given a change in a matrix element or vital rate (Caswell 2000). Retrospective perturbation analyses, commonly known as life-table response experiments (LTRE), can be used to calculate the 'realised' contribution of a vital rate to λ, accounting for realised variation in that vital rate as well as the sensitivity (Caswell 1989). Populations are constantly being perturbed by short-term, temporal variation in the environment (Bierzychudek 1999; Clutton–Brock & Coulson 2002) however. Transient population dynamics are therefore being used increasingly frequently to capture the consequences of this short-term variation in population dynamics (Hastings 2004; Koons *et al.* 2005; Ezard *et al.* 2010). Transient-LTREs partition variance in the realised population growth rate, λ_t, into contributions from demographic rates. In doing so, it allows us to incorporate effects of transient variation in the population structure or trait distributions (Rees & Ellner 2009). In **paper I**, we calculated elasticities (prospective) and contributions (retrospective) of a density-dependent matrix, comparing both asymptotic and transient LTRE analyses, based on Koons *et al.* (2016) and Caswell (2007). In **paper II**, we quantified the contributions of climate, density and trophic interactions to the asymptotic population growth rate using an LTRE. In **paper IV**, we applied a transient-LTRE to the IPrM, structured by age class and body mass, to partition variance in the realised population growth rate into direct and delayed (i.e., changes in the body mass distribution or age structure) parameter contributions (Maldonado-Chaparro *et al.* 2018).

5 | Results and discussion

1. How do density-dependent processes impact the dynamics and trajectories of a colonising population (**papers I, II, III**)?

In **paper I**, we showed that local density regulation at the breeding grounds reduced population growth through negative effects on reproduction but did not explain substantial temporal variation in fledgling or adult overwinter survival. Elasticities to vital rates changed as the population size approached carrying capacity: the influence of reproductive rates and early-life survival on the population growth rate declined, while the influence of adult survival on λ increased. The pattern of density dependence in this population of barnacle geese differed from that of income-breeding birds, where density regulation mainly occurs through effects on early-life survival (Sæther *et al.* 2016). This highlighted how the population dynamics of capital breeders such as barnacle geese may be more reproduction-driven than in income breeders. This was supported by later papers (**II** and **IV**), that despite adult survival being highly influential on the population size, in reality, variation in reproduction was by far the largest contributor to fluctuations in population size. This is a commonly observed pattern in long-lived species, where vital rates that are influential on the population growth rate generally exhibit less variability, i.e., demographic buffering hypothesis (Gaillard & Yoccoz 2003; Koons *et al.* 2014). I then wanted to tease apart in more detail, the underlying causes of variation in vital rates and the contributions to population dynamics. For further mechanistic insights into the density-dependent processes (**paper II**), reproduction was separated into several stages, indicating that pre-fledging brood size was the reproductive stage affected the most by density-

dependent processes, i.e., most affected by competition for food resources (Larsson & Forslund 1994; Loonen *et al.* 1997b). However, we found evidence for density-dependent effects across the annual cycle: total flyway population size negatively affected survival and egg production, via carryover effects. Particularly in the case of long-lived species, reproductive success can be age-dependent, as has been shown in barnacle geese (Forslund & Larsson 1992). Although reproductive success *per se* was not found to be age-dependent here, in **paper III**, we found that younger, more inexperienced adults were more affected by density-dependent processes, regarding when they produced goslings for the first time. Age and body size are both determinants of social status in barnacle geese (Stahl *et al.* 2001). Therefore, at high densities (i.e., greater competition) younger individuals of lower social status are forced to utilise nest-sites of poorer quality, with less food available (Prop & Deerenberg 1991; Stahl *et al.* 2001).

2. How has climate change directly or indirectly influenced population dynamics, and through which vital rates (**paper II**)?

Accounting for density-dependent processes, we showed in **paper II**, that recent climate change in Svalbard enhanced egg production and hatching success through positive effects of advanced spring onset (snow melt) and warmer summers (i.e. earlier vegetation green-up) respectively. However, there was a strong temporal decline over the course of the study in fledging probability due to increased local abundance of the Arctic fox, the main predator. Increasing Arctic fox abundance is in part an indirect result of climate change. Svalbard reindeer abundance

fluctuates dramatically in accordance with winter-icing events, which are associated with climate warming (Hansen *et al.* 2019). Both increased reindeer overall abundance and population crashes can boost carcass availability for Arctic foxes, improving their reproduction and, possibly, winter survival (Fuglei *et al.* 2003; Hansen *et al.* 2013), with negative consequences for goose reproduction. This highlights how climate change effects can influence a population's demographic rates through top-down food-web interactions. The Svalbard system is, however, largely bottom-up regulated (Ims *et al.* 2013c). Consequently, changes in vegetation have important consequences for the reproduction and survival of Arctic herbivores, such as reindeer and geese. On the other hand, grazing by Arctic herbivores has, in turn, altered vegetation communities (Van der Wal *et al.* 2001; 2006; Hansen *et al.* 2007). Therefore, climate change effects on one species can occur by both bottom-up and top-down trophic interactions, potentially affecting an entire Arctic community (Post *et al.* 2009). However, it is not only processes during the breeding season that influence migratory species, like barnacle geese (Kery *et al.* 2006; Marra *et al.* 2015). Barnacle geese can also be affected by conditions at lower latitudes. We found that weather during the non-breeding season (UK and mainland Norway) influenced population growth, through positive effects of winter temperature on adult survival and carryover effects of spring rainfall (stopover site) on egg production. Overall, this combination of density-dependent processes, direct and indirect climate change effects, and carryover effects appeared to stabilise local population size.

Although dramatic warming of the Arctic, specifically advancing spring onset, has the potential to benefit the reproductive success of arctic-breeding geese, we have shown that counteracting effects have ultimately led to the breeding population size neither increasing nor decreasing. Furthermore, geese can only benefit from advancing onset if they can adjust their migration phenology sufficiently, and some studies have indicated that this is not the case in other populations of barnacle geese (Lameris *et al.* 2018; Nolet *et al.* 2019). Importantly, our results also highlight the influence of environmental conditions during the non-breeding season. Although there was no positive trend in winter temperature over the study period, even a small warming trend in the future would benefit survival, although the positive consequences for population trajectories could, in turn, be curbed by density regulation at the overwintering grounds. This work therefore emphasises how gaining a mechanistic understanding of the different processes influencing a population's vital rates is fundamental to accurately predicting future population sizes, and therefore implementing appropriate management strategies.

3. To what extent have key fitness-related traits been affected by climate/environmental change, and how do they contribute to variation in the population growth rate (**papers III**, **IV**)?

In **paper III**, we identified climate and density effects on the probability of producing goslings for the first time. Delayed spring onset negatively affected reproduction probability overall but influenced first-time breeders more strongly than experienced breeders. These results demonstrate the importance of using multi-event models to estimate uncertain states, since a far larger

proportion of 2-year-olds were estimated to have produced goslings in the population than were actually observed. Spring onset has advanced by two weeks over the study period as a consequence of climate change, leading to a doubling in the proportion of 2-year-olds reproducing and thereby likely an earlier age at first reproduction. This highlights how Arctic climate change can strongly influence important life-history traits, with potentially positive implications for the population dynamics of barnacle geese. However, reproducing at an earlier age may also induce costs later in life since age at first reproduction represents a trade-off between current reproductive investment versus future reproduction or survival (Stearns 1989).

To understand mechanistically how changes in environmental conditions can ultimately affect population size, it is important to consider potential trait-mediated pathways. Such mechanisms can occur when both traits and vital rates respond to environmental fluctuations (Parmesan 2006; Ozgul *et al.* 2009; 2010). In **paper IV**, the goal was therefore to assess changes in body mass over time, and the importance of body mass-mediated effects for the population dynamics and population growth of my barnacle goose study population. Density-dependent processes influenced first-year body mass, particularly at high Arctic fox abundance, likely restricting the ability of the geese to utilise all available foraging areas (Loonen *et al.* 1998). Fledgling body mass had, in turn, a strong positive effect on first-year survival, but body mass in adults had little effect on survival. Body mass has declined dramatically in several Arctic goose species and across populations (Cooke *et al.* 1995; Loonen *et al.* 1997b; Larsson *et al.* 1998). Population expansion has led to widespread degradation of Arctic breeding grounds, reducing food availability and, consequently, body mass. Despite a 10% decline in cohort body mass (1980-2017) in this study population, and positive effects of body mass on reproduction and survival, changes in body mass had negligible effects on the population growth rate (λ). This can be explained by the fact that, achieving body mass-mediated effects on λ requires three conditions to be met. Namely, (1) body mass must fluctuate in the relevant age-specific life-history stage, (2) the demographic rate must be sensitive to body mass changes and (3) population growth must be sensitive to the varying demographic rate. Since all three conditions were not met for any of the age-specific demographic rates - e.g., (1) body mass of fledglings varied inter-annually, (2) fledgling survival is positively affected by body mass, but (3) λ was insensitive to fledgling survival. The demographic buffering hypothesis states that variation in λ reduces fitness (Tuljapurkar 1982), which should, therefore, result in selection for reduced variation in population size (Gaillard & Yoccoz 2003; Jongejans *et al.* 2010). Similarly, the population growth rate may also be buffered against variation in important fitness-related traits such as body condition. **Paper IV** (as well as **paper I**) highlights the reproduction-driven dynamics of arctic geese, and that reproduction is the demographic rate where climate change is having the most impact. While these results support **papers II** and **III**, in that advancing spring onset benefits reproduction, in **paper III** we also show that heavier individuals were more likely to produce fledglings than lighter ones, but only under poor spring breeding conditions (i.e., delayed spring onset). Accumulating fat reserves is beneficial under harsh conditions, but as spring advances with climate change, we could expect relaxed selection on body mass if individuals gain a survival advantage by requiring fewer fat

reserves for migration (Davies *et al.* 1988; Larsson *et al.* 1998). Overall, the results from **papers III** and **IV**, illustrate the importance of studying life-history and fitness-related traits, as pathways by which climate change can influence population dynamics. In doing so, we have identified mechanisms by which this population is buffered against variation in such traits.

This has implications for the resilience of Arctic geese, and possibly other Arctic herbivores, to environmental change, as changes in body condition, and other fitness-related traits, may have more limited population-dynamic consequences than we might expect (McLean *et al.* 2020).
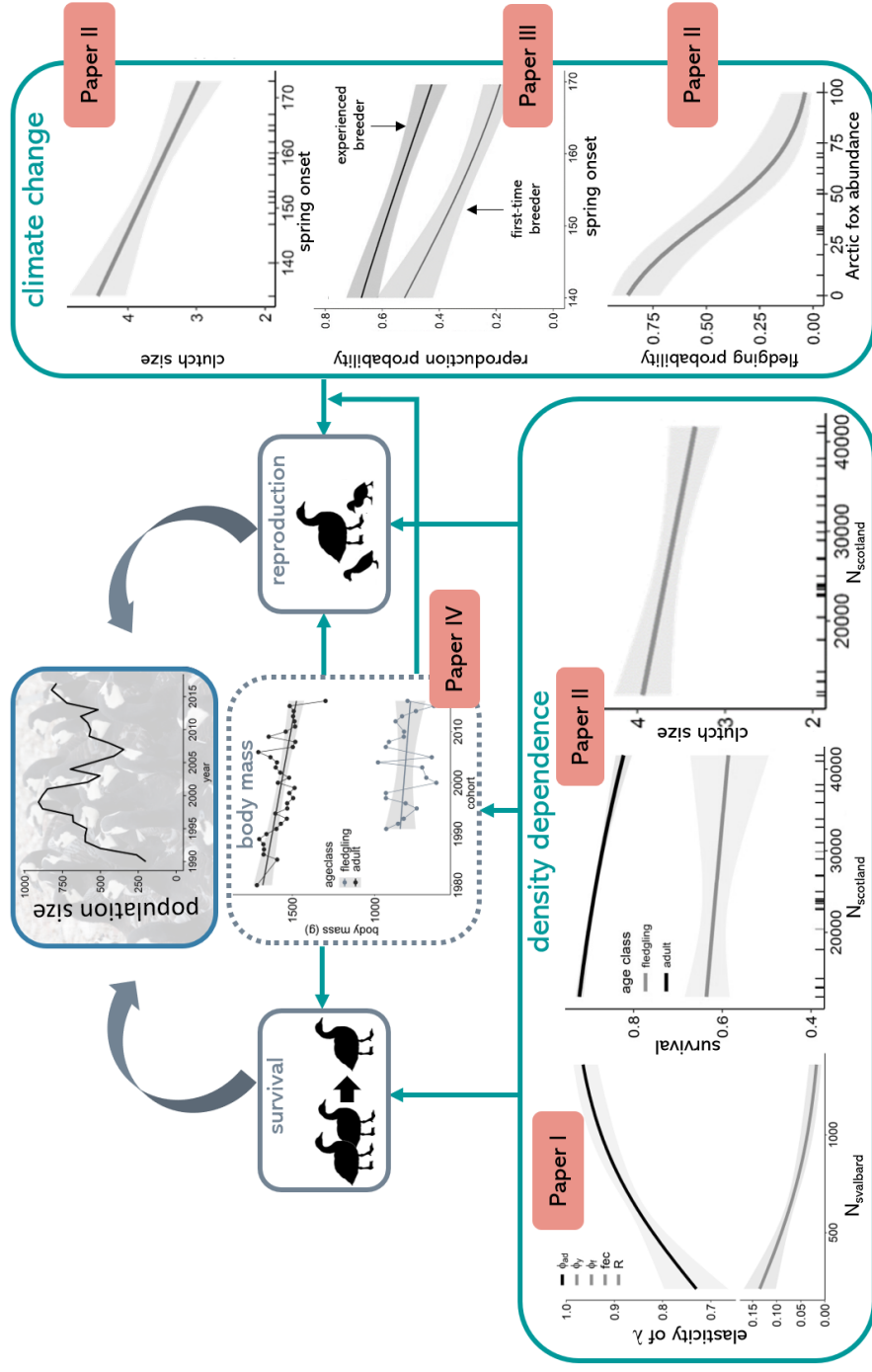
Figure 4. Summary of the main findings. Using figures from the four papers, I show how I have captured the effects of climate change: as effects of (1) the date of spring onset (ordinal day) on clutch size and the (reproduction) probability of producing goslings and (2) of Arctic fox abundance on the probability of fledging (increasing Arctic fox abundance is an indirect climate change effect). I have also captured effects of density dependence, both at the overwintering grounds ($N_{scotland}$) on clutch size and survival, and at the breeding grounds ($N_{svalbard}$) on the population growth rate (through effects on gosling brood size). This figure also illustrates the results that body mass affects survival and reproduction – and also how climate change influences reproduction - but effects of declining body mass did not scale up to influence the population growth rate.

6| Conclusions and prospects

By accounting for important trophic interactions, this thesis has disentangled the mechanisms by which climate change and density dependence affect the population dynamics of a key Arctic migrant, the barnacle goose. This work emphasises the importance of taking holistic approaches to demographic modelling, to study the consequences of climate change. Only by considering all the components of a population's dynamics; density dependence, temporal (co)variation in vital rates, indirect climate effects as well as important trophic interactions, can we paint an accurate picture of how populations are responding to climate change and, importantly, their persistence into the future (Reed *et al.* 2013). Furthermore, I show that considering the spatial heterogeneity in climate change, demographic models of migratory species need to consider their entire annual cycle. Although climate change is occurring most rapidly in the Arctic, and its effects have largely been on breeding success, I have shown that future changes in winter temperature in the UK could increase their overwinter survival, with potentially substantial population-dynamic consequences.

Overall, these results document the sensitivity of barnacle goose population dynamics to recent climate change, largely through effects on their reproduction. However, this work has also stressed the capacity of Arctic geese to cope with rapid environmental change, e.g., the buffering of effects of changes in body condition. While climate warming may pose some benefits for this species, and potentially other Arctic herbivores, by capturing the impacts of key trophic interactions, we showed that these benefits are offset by counteracting effects. Furthermore, the extent to which positive climate change effects could be offset by a mismatch between the timing of the geese arriving/breeding and the onset of the plant growing season, in the future remains uncertain. Different breeding populations of barnacle geese may not all react in the same way either (Lameris *et al.* 2017) and, hence, the consequences of trophic mismatch on reproduction success may differ among populations (Nolet *et al.* 2019). Although my approaches were applied on a particularly high-quality, long-term dataset, with access to local time-series on environmental variables and key interacting species, similar data series do exist for other breeding populations of barnacle geese as well, and also for other Arctic goose species. The combination of state-of-the-art analytical methods used in this thesis could serve as a framework for assessing, for example, the importance of spatial heterogeneity in responses to climate change, and its net impacts.

While environmental/climate change may not have had substantial, negative consequences for this population, as of yet, accurately predicting Arctic goose persistence is still extremely pressing right now. Management of Arctic geese is currently a topic of major interest, with large-scale hunting already re-started in some populations of barnacle, and other goose, species (Jensen *et al.* 2018). This holistic understanding of how climate change is affecting the population dynamics of barnacle geese should be incorporated in management planning, to prevent the risk of overharvesting in a species that is sensitive to climate change and has previously reached critically low numbers. Some of the results from this thesis have already been included into management recommendations for barnacle geese (Huysentruyt *et al.* 2020) and a report on climate change impacts on Arctic ecosystems, through food-web interactions (Pedersen *et al.* 2019). This demonstrates that

such demographic, mechanistically founded work is critical both to ensure that populations are managed sustainably and with regard to future climate, and environmental, change. With this thesis, I have also highlighted the importance of taking a community perspective when predicting the consequences of climate change for Arctic populations, accounting for key species interactions. The entire Arctic community is now undergoing extremely rapid change, as a result of strong warming, and more emphasis should be placed on multi-species analysis to understand how climate change is affecting entire communities in concert (Ims *et al.* 2013a).

7 | References

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Paper I

RESEARCH ARTICLE

Journal of Animal Ecology — BRITISH ECOLOGICAL SOCIETY

Density-dependent population dynamics of a high Arctic capital breeder, the barnacle goose

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Abstract

1. Density regulation of the population growth rate occurs through negative feedbacks on underlying vital rates, in response to increasing population size. Here, we examine in a capital breeder how vital rates of different life-history stages, their elasticities and population growth rates are affected by changes in population size.

2. We developed an integrated population model for a local population of Svalbard barnacle geese, *Branta leucopsis*, using counts, reproductive data and individual-based mark–recapture data (1990–2017) to model age class-specific survival, reproduction and number of individuals. Based on these estimates, we quantified the changes in demographic structure and the effect of population size on age class-specific vital rates and elasticities, as well as the population growth rate.

3. Local density regulation at the breeding grounds acted to reduce population growth through negative effects on reproduction; however, population size could not explain substantial variation in survival rates, although there was some support for density-dependent first-year survival.

4. With the use of prospective perturbation analysis of the density-dependent projection matrix, we show that the elasticities to different vital rates changed as population size increased. As population size approached carrying capacity, the influence of reproductive rates and early-life survival on the population growth rate was reduced, whereas the influence of adult survival increased. A retrospective perturbation analysis revealed that density dependence resulted in a positive contribution of reproductive rates, and a negative contribution of the numbers of individuals in the adult age class, to the realised population growth rate.

5. The patterns of density dependence in this population of barnacle geese were different from those recorded in income breeding birds, where density regulation mainly occurs through an effect on early-life survival. This indicates that the population dynamics of capital breeders, such as the barnacle goose, are likely to be more reproduction-driven than is the case for income breeders.

KEYWORDS
barnacle geese, capital breeder, density dependence, integrated population model, perturbation analysis, population dynamics

1 | INTRODUCTION

Population dynamics are determined by a combination of density dependence and environmental stochasticity, acting through an influence on species' vital rates (Lande, Engen, & Saether, 2003; Turchin, 1995), thereby controlling the underlying mechanisms regulating and limiting population growth (Grant & Benton, 2000; Ricklefs, 1983). Consequently, density dependence has received much attention as a fundamental mechanism driving population dynamics (Lande et al., 2002; Ricklefs, 2000). Gaining a mechanistic understanding of how density dependence drives population fluctuations requires a consideration of demographic structure (Coulson et al., 2001; Lande et al., 2002). For long-lived species, the mechanisms through which density dependence acts are often largely determined by age-specific variation in life history (Fowler, 1981; Lande et al., 2002). For example, younger age classes may be more vulnerable to density-dependent effects (Gaillard & Yoccoz, 2003). Alternatively, older breeding individuals may be more resource demanding and hence can suffer more from resource competition (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Lok, Overdijk, Tinbergen, & Piersma, 2013). Ignoring this variation among age classes in their response to density can ultimately bias inferences about underlying processes affecting fluctuations in population size (Gamelon et al., 2016).

Accurately estimating the strength of density dependence therefore requires long time series of high-quality demographic data (Both, Visser, & Verboven, 1999; Coulson et al., 2001) as well as a robust modelling approach to analyse them, accounting for all potential sources of error (Freckleton, Watkinson, Green, & Sutherland, 2006; Shenk, White, & Burnham, 1998). A challenge in studies of population dynamics is access to data covering a sufficiently wide range of population sizes for obtaining unbiased estimates of density-dependent effects (Brook & Bradshaw, 2006). Populations establishing themselves in new areas represent a unique opportunity for analysing density-dependent processes (Nicoll, Jones, & Norris, 2003; Redfield, 1973). However, examples are few, since long-term studies tend to focus on well-established populations. Here, we take the rare advantage of analysing the dynamics of a high Arctic barnacle goose, *Branta leucopsis*, population that colonised Kongsfjorden, Svalbard, in the 1980s (Loonen, Tombre, & Mehlum, 1998; Owen, 1984). Barnacle geese are predominantly capital breeders, partly due to the unpredictability of environmental conditions at the high Arctic breeding grounds. Although the "degree of capital breeding" can vary, depending on environmental conditions (Hobson, Sharp, Jefferies, Rockwell, & Abraham, 2011), they utilise resources accumulated during the spring migration to initiate breeding (Hahn, Loonen, & Klaassen, 2011). The inter-annual environmental stochasticity in the high Arctic can lead to resource competition and potentially strong density-dependent effects (Bruggeman, Swem, Andersen, Kennedy, & Nigro, 2015).

In a comparative study of age-structured density-dependent effects in other bird species, Sæther et al. (2016) revealed a remarkably simple pattern. They found that density dependence mainly acted through an influence on survival, especially during the first year. Furthermore, the relative influence of survival rates of older individuals on the population growth rate, expressed by the elasticity (Caswell, 2001), increased when population size approached carrying capacity. However, the generality of these findings still remains uncertain because all species included in the analyses can be characterised as income breeders to varying degrees (Durant, Massemin, Thouzeau, & Handrich, 2000; Meijer & Drent, 1999), where energy required for reproduction is acquired at the breeding grounds (Drent & Daan, 1980).

We examine how variation in population size affects different vital rates of the capital breeding barnacle geese. This high Arctic migrant must bring sufficient amounts of endogenous reserves to the breeding grounds to meet the energetic requirements for egg laying and incubation (Hahn et al., 2011). Using 28 years (1990–2017) of population counts and individual-based mark–recapture data from a local population in Svalbard, we develop an integrated population model (IPM (Abadi, Gimenez, Arlettaz, & Schaub, 2010; Schaub & Abadi, 2011)) to investigate patterns of density regulation and changes in demographic rates and age structure. By parameterising a post-breeding, age-structured population projection matrix, we quantify the elasticities of the population growth rate to density-dependent demographic rates across a range of population sizes, using a prospective perturbation analysis (Caswell, 2001). We also quantify the contributions of vital rates and population structure to the realised population growth rate, using a transient retrospective perturbation analysis (Caswell, 2007; Koons, Iles, Schaub, & Caswell, 2016).

2 | MATERIALS AND METHODS

2.1 | Study species and site

The study population of barnacle geese breed and rear their young in Kongsfjorden, Svalbard, close to the settlement of Ny-Ålesund (78°55'N, 11°56'S). They are long-lived birds (up to 28 years) and form monogamous breeding pairs. During the summer breeding season (May to September), they breed on islands in the fjord and rear their young along the coastline later in the season. Successful breeding pairs lay a single clutch of three to five eggs on average during June and offspring fledge in August (Owen & Black, 1989). The total flyway Svalbard population winters at Solway Firth, UK, and migrates to breeding sites across Svalbard in summer, via spring staging areas along the coast of mainland Norway.

2.2 | Data collection

Following their colonisation in the 1980s, a local mark–recapture programme was initiated in 1990 where individuals are caught and marked with unique colour bands and metal identification rings. Sex is determined by cloacal inspection and behavioural observations (Loonen, Oosterbeek, & Drent, 1997). Although fledglings are clearly distinguishable from older birds, thereafter the difference is

difficult to determine and therefore only individuals of known age (i.e. marked as fledglings) were included in the survival analysis, which was age class-dependent. Re-sightings of marked birds take place twice per day in the area around Ny-Ålesund, and catches take place at least twice during a season. Data on reproduction are recorded on the two main nesting islands during the hatching phase; nests are visited on the islands at one- to two-day intervals to record the number of goslings, and families are followed throughout the season to determine the number of fledglings per breeding pair at the end of the season in August.

Count data of the number of yearlings and adults in Kongsfjorden came from two sources; from 1990 to 1996, total population size was estimated from the number of marked individuals observed, divided by the average proportion of marked geese in catches, known as a Petersen estimate (Begon, 1979). After 1996, counts of the number of yearlings and adults occurred during the moulting phase (end of July). Only counts of yearlings and adults (combined) were included since the timing of counts was often before first-year birds fledged and pre-fledging mortality is high (Loonen et al.,1998).

2.3 | Integrated population model

The mark–recapture dataset used for this analysis consisted of 3,487 individuals, marked between 1990 and 2017. Using an integrated population model framework (Abadi, Gimenez, Arlettaz, et al., 2010), we simultaneously analysed mark–recapture, reproduction and population count data. Based on the life cycle of the barnacle goose (Figure 1), we developed age-structured, post-breeding state equations with three age classes (fledglings, yearlings and adults) to estimate the annual probability of reproduction, R, fecundity, fec and age class-specific (apparent) survival $\phi_{a \supset f, y, ad}$, (Figure 2b,c). Reproductive rates, R and fec, determine the number of fledglings produced in August, the first survival rate for the fledgling age class describes survival in the first year of life, from August at year t to August at year $t + 1$, the yearling age class to the second year and adults from the third year onwards.

Mark–recapture data were analysed as individual capture histories and modelled with a Cormack–Jolly–Seber model (Lebreton, Burnham, Clobert, & Anderson, 1992). Survival parameters were estimated as
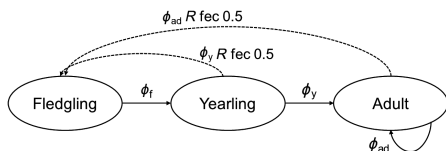
FIGURE 1 Age class-structured life cycle of the barnacle goose based on fledgling (f), yearling (y) and adult (ad) age classes. ϕ_a is the probability of an individual in age class a surviving to the next year, R is the probability of a female producing a fledgling and fec is the number of fledglings per successful female breeder. Age class-specific contributions to reproduction are based on breeder survival (ϕ_y or ϕ_{ad}), R and fec, multiplied by 0.5 to account for sex ratio, in accordance with a post-breeding census

functions of time and age, from year t to $t + 1$ and for fledglings (ϕ_f), yearlings (ϕ_y) and adults (ϕ_{ad}). Apparent survival was modelled on the logit scale, with a Bernoulli distribution, and varied with age (a) and year (t); logit $(\phi_{a,t+1}) = \mu_{\phi_a} + \varepsilon_{\phi_{a,t+1}}$. We found no difference in survival between sexes, but the recapture rate of females (0.62; 0.56, 0.67) was higher than that of males (0.41; 0.36, 0.47), as a consequence of higher philopatry in females (Black, Prop, & Larsson, 2014).

Reproductive data of the annual number of fledglings produced, for the female portion of the population, were defined by two parameters describing reproduction at year $t + 1$ (R and fec). R was the annual probability of a female producing at least one fledgling, and fec was the average number of fledglings per successfully breeding female. Reproduction was considered from the second year of life and was independent of age. The probability that a female produces at least one fledgling (R) was modelled with a Bernoulli distribution, where logit $(R_{t+1}) = \mu_R + \varepsilon_{R,t+1}$. The number of fledglings per successfully breeding female (fec) was modelled with a Poisson distribution, where log $(fec_{t+1}) = \mu_{fec} + \varepsilon_{fec, t+1}$. Annual reproduction at year $t + 1$ was therefore the product of breeder survival $\phi_{a,t}$, the probability of reproduction R_{t+1}, the number of fledglings per successfully breeding female fec_{t+1} and 0.5, assuming an equal offspring sex ratio, since reproductive rates were only based on females.

To account for a potential correlation in environmental effects on vital rates, we modelled the temporal variance in ϕ_a, R and fec assuming that the variance originated from a random process with a mean of zero, but with vital rate- and age class-specific deviations (Schaub, Jakober, & Stauber, 2013). Ɛ is a matrix of the temporal residuals for each rate, as described by Link and Barker (2005). Temporal residuals were treated as a realisation from a multivariate normal distribution (MVN) with zero mean, $\varepsilon \sim MVN(0, \Sigma)$, where Σ is the variance–covariance matrix (Schaub et al., 2013), with the scaled inverse Wishart distribution as the prior for Σ (Gelman & Hill, 2006, p.286). With this approach, we estimated the temporal variance of each parameter and the covariances between parameters as the sub-diagonals of the matrix. Since the recapture probability was not expected to be correlated with vital rates, the temporal variance was modelled independently with a fixed effect of sex (s) and a random effect of year (t); logit $(p_{s,t+1}) \sim Normal(\mu_{p,s}, \sigma^2_{p,t+1})$.

The state process equations model the annual expected numbers of individuals in each age class, based on the underlying demographic rates. We modelled reproduction into the first age class as a Poisson process and survival to subsequent age classes as Binomial processes to incorporate demographic stochasticity (Lande et al., 2003). The model describing the number of individuals in each class at year $t + 1$ can be written as.

$$N_{f_{t+1}} \sim Poisson\left(R_{t+1} \, fec_{t+1}(N_{y_t}\phi_{y_t} + N_{ad_t}\phi_{ad_t})/2\right), \quad (1)$$

$$N_{y_{t+1}} \sim Binomial(\phi_{f_t}, N_{f_t}) \text{ and} \quad (2)$$

$$N_{ad_{t+1}} \sim Binomial(\phi_{y_t}, N_{y_t}) + Binomial(\phi_{ad_t}, N_{ad_t}). \quad (3)$$

Estimating the number of unmarked individuals entering the marked population is important for correctly estimating vital rates,
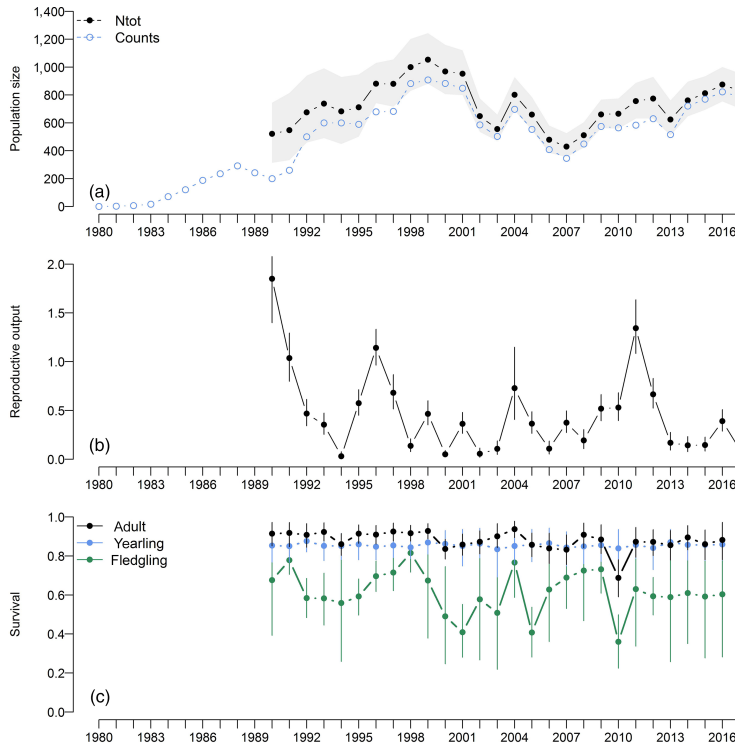
FIGURE 2 (a) Model estimates of total population size from 1990 to 2017 (black) with 95% CRIs (grey shading). Population count data are shown based on counts of nests in Kongsfjorden from 1980 to 1990 (Fuglei, Øritsland, & Prestrud, 2003), on a Petersen index from 1990 to 1996 (see Methods) and total fjord counts of the number of yearlings and adults in Kongsfjorden from 1996 to 2017. The consistent discrepancy between model estimates and total counts is due to the exclusion of fledglings from total counts. (b) Posterior means and 95% CRIs of the reproductive output (product of R and fec). (c) Annual estimates of age class-specific survival rates (ϕ_f, ϕ_y and ϕ_{ad})

but can be challenging in demographic studies (Schaub, Aebischer et al. 2010, Lieury, Gallardo et al. 2015). Changes in the numbers of unmarked birds in the study area were accounted for by estimating the annual proportion of unmarked fledglings and older birds (Abadi, Gimenez, Ullrich, Arlettaz, & Schaub, 2010). We estimated the rate of addition of unmarked fledglings (U_f) and older birds ($U_{y,ad}$). This allows unmarked individuals to enter the population at each time step, assuming the same vital rates as marked individuals. The numbers of unmarked fledglings (N_{U_f}) and older birds ($N_{U_{y,ad}}$) were modelled as a Poisson process;

$$N_{U_{f_{t+1}}} \sim \text{Poisson}\,(N_{f_t} U_{f_t}) \text{ and} \tag{4}$$

$$N_{U_{y,ad_{t+1}}} \sim \text{Poisson}\,\left((N_{y_t} + N_{ad_t})\, U_{y,ad_t}\right), \tag{5}$$

where N_f, N_y and N_{ad} correspond to the numbers of marked fledglings, yearlings and adults, and N_{U_f} and $N_{U_{y,ad}}$ to the number of unmarked fledglings and older birds (yearlings and adults). We calculated the annual total number of marked and unmarked birds, N_{tot}, by summing N_f, N_y, N_{ad}, N_{U_f} and $N_{U_{y,ad}}$.

We modelled annual population counts using a state-space model, which combines the state process model, describing the true state of the system, with an observation process model (de Valpine & Hastings, 2002). Total counts were available for yearlings and adults; however, counts of fledglings (C_{f,c_t}) were not available, since

total fjord counts often took place before fledging in August (see Section 2.2). Therefore, C_{f,c_t} was included as a matrix of NAs and estimated as a latent variable. We assumed a log-normal distribution for the population count data and the variance in the observation probability was assumed to differ for the period where counts were based on a Petersen index (1990–1996) and the period where total fjord counts were conducted (1997–2017). The observation model links the counts ($C_{a,c,t}$) to the latent population numbers by;

$$\log\,(C_{f,c_t}) \sim \text{Normal}\,\left(\log\left(N_{f_t} + N_{U_{f_t}}\right), \sigma_{C_c}^2\right) \tag{6}$$

for fledglings and

$$\log\,(C_{y,ad,c_t}) \sim \text{Normal}\,(\log\,(N_{y_t} + N_{ad_t} + N_{U_{y,ad_t}}), \sigma_{C_c}^2) \tag{7}$$

for yearlings and adults, where the variance in $\sigma_{C_c}^2$ represents the observation error for counts estimated using the Petersen index or the total fjord counts (c). The combined likelihood of the state and observation process models is therefore given by; $L_{sp}(N \mid \phi, R, \text{fec}) \times L_{ob}(C \mid N, \sigma_{C_c}^2)$.

The IPM was implemented in a Bayesian framework with non-informative priors (see Appendix S1). Posterior distributions of parameters were obtained using Markov Chain Monte Carlo simulations, implemented in JAGS (Plummer, 2003) via the program JAGSUI, version 1.4.4 (Kellner, 2015), in R version 3.4.0 (Team, 2017). Four separate

chains were run for 1,000,000 iterations, with a burn-in of 100,000 iterations and thinning every 90th sample, resulting in 40,000 posterior samples from which posterior means and 95% Bayesian credible intervals (CRIs) were estimated. Convergence was assessed by ensuring R̂ values for each parameter were less than 1.1 (Brooks & Gelman, 1998).

2.4 | Density dependence

We conducted post hoc linear regressions to estimate the effect of population size on vital rates and the population growth rate, using the 40,000 posterior samples of vital rates and population sizes from the IPM analysis, similar to Schaub et al. (2013). We regressed the logit of age class-specific survival (ϕ_a) at year t to $t + 1$ against total numbers of individuals (N_{tot}) at year t, to approximate the strength of density dependence on survival. The logit of the probability of reproduction (R) and the log of fecundity (fec) at year t were regressed against the annual numbers of yearlings and adults ($N_{y,ad}$). We formulated linear equations describing the strength of density regulation on ϕ_a, R and fec, where the intercept of each regression corresponds to the mean of each demographic rate, the regression coefficient to the strength of density dependence and the residuals to the remaining variance not explained by density. We regressed the population growth rate (λ) on total numbers of individuals (N_{tot}), to assess whether there was a net effect of density on population growth. We also tested for a temporal trend in vital rates and age class-specific numbers by fitting a linear regression with a continuous year effect. We also conducted density-dependent regressions with a continuous year effect, to ensure that any negative effects of density dependence on vital rates were not caused by temporal trends. Regression coefficients were estimated for all 40,000 posterior samples, from which mean and 95% CRIs were calculated, as well as the probability of the coefficients to be less than zero ($P(\beta < 0)$).

2.5 | Population dynamics

We parameterised an age-structured, post-breeding population projection matrix based on the state process equations. The asymptotic population growth rate (λ) was approximated as the maximum eigenvalue, and reproductive values and the stable age distribution were approximated as the left and right eigenvalues, respectively, of the projection matrix, using each sample of vital rates from the posterior distribution to calculate means and 95% CRIs (Caswell, 2001). We adopted an asymptotic prospective perturbation analysis, to quantify the sensitivity of λ to a proportional change (elasticity) in each demographic rate (Caswell, 2000).

Short-term, transient dynamics can differ from asymptotic dynamics, particularly in highly stochastic environments, influencing population dynamics through feedbacks between vital rates and population structure (Koons et al., 2016; Stott, 2016). We performed a transient prospective perturbation analysis to calculate the transient elasticities of the population vector (N_t) to lower-level vital rates (Caswell, 2007). We also performed a transient retrospective analysis (LTRE) (Koons, Arnold, & Schaub, 2017; Koons et al., 2016),

to determine the contributions of vital rates and population structure to the realised population growth rate, $\lambda_{realised,t}$ (Appendix S6).

Demographic rates were predicted over the observed range of total population sizes using the regression coefficients described in the previous section, to determine how density dependence influenced the sensitivity and elasticity of λ to each demographic rate. Since some matrix elements were the product of multiple demographic rates, we calculated the elasticity of λ to each demographic rate (lower-level elasticities) analytically, by differentiation of each matrix element with respect to the parameter and application of the chain rule (Caswell, 2000). Sensitivities and elasticities were calculated using the 40,000 posterior samples of the regression coefficients and demographic rates, at a hundred population sizes, ranging from the minimum to maximum estimated N_{tot}. This resulted in 40,000 sensitivity and elasticity estimates for each demographic rate, which were used to calculate means and 95% CRIs.

3 | RESULTS

3.1 | Temporal trends in population size and structure

Following their colonisation of the breeding grounds in Kongsfjorden, western Svalbard, the estimated population size grew from 521 individuals (95% CRIs: 314, 745) in 1990 to a maximum of 1,054 (881, 1,244) individuals in 1999, before fluctuating around 700 individuals (Figure 2a). The number of fledglings, N_f, (slope = −1.33; CRI = −2.02, −0.55) and yearlings, N_y, (−1.28; −2.09, −0.41) declined, and the probabilities of the regression slopes being negative were both 1.00 ($P(\beta < 0)$. This decline was largely driven by the first and last years of the study. The number of adults, $N_{ad,}$ increased (9.38; 6.25, 12.10), and the probability of this slope being positive was 1.00, indicating an ageing population (Appendix S3: Figure S3.1). The numbers of unmarked fledglings in the population (N_{U_f}) also showed a tendency for a negative trend (−2.45; −6.37, 1.22) where the probability of a negative slope was 0.89. The number of unmarked yearlings and adults ($N_{U_{y,ad}}$) increased over the study period (8.80; 5.49, 12.68), and the probability of this slope being positive was 1.00 (Appendix S3: Figure S3.2).

3.2 | Age class-specific demographic rates

The mean probability of an adult female (i.e. older than one year) breeding successfully (R) was 0.13 (0.09, 0.17), and the mean number of fledglings per successfully breeding female (fec) was 2.12 (1.85, 2.44). R (logit scale) showed a tendency for a decline over time (−0.0029; −0.0119, 0.0063); however, credible intervals overlapped 0 and the probability of the slope being negative was 0.70. fec (log scale) declined over time (−0.0111; −0.0160, −0.0046), where the probability of a negative slope ($P(\beta < 0)$) was 1.00. The temporal variance of R was larger than fec, and fledgling survival (ϕ_f) had a larger variance than survival of older age classes (Figure 3). Covariances between survival rates were generally positive, and R was positively correlated with ϕ_{ad}, although credible intervals overlapped 0 (Figure 3). We calculated the
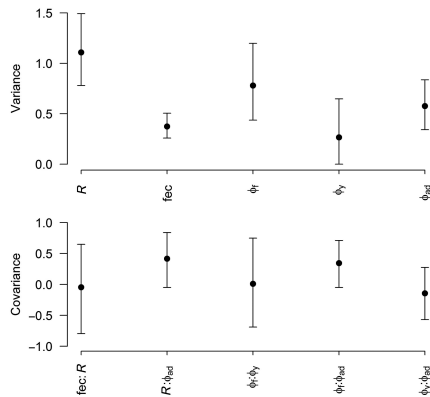
FIGURE 3 Mean parameter estimates of temporal variance and covariance in R, fec, ϕ_f, ϕ_y and ϕ_{ad}, with associated 95% CRIs

product of R and fec as a measure of annual reproductive output (per mature female), which declined rapidly in the first years of the study and was close to 0 in 1994, 2000 and 2002 (Figure 2b). As is typical in long-lived species, mean adult and yearling survival were high while fledgling survival was lowest (Table 1). The covariance between fledgling and adult survival was larger than yearling and adult survival, with a probability of 0.79 $\left(P\left(\text{cov}(\sigma_f^2, \sigma_{ad}^2) > \text{cov}(\sigma_y^2, \sigma_{ad}^2) \right) \right)$. Fledgling and yearling survival co-varied to a lesser extent $\left(P\left(\text{cov}(\sigma_f^2, \sigma_y^2) < \text{cov}(\sigma_y^2, \sigma_{ad}^2) \right) = 0.58; P\left(\text{cov}(\sigma_f^2, \sigma_y^2) < \text{cov}(\sigma_f^2, \sigma_{ad}^2) \right) = 0.83 \right)$. Survival of adults (−0.024; −0.034, −0.013) and yearlings (−0.004; −0.015, −0.002) declined from 1990 to 2017, and fledgling survival (−0.008; −0.028, 0.022) showed a tendency for decline; however, credible intervals overlapped 0 and the probability of a negative slope was 0.75, compared to 0.91 and 1.00 for yearling and adult survival, respectively (Figure 2c).

3.3 | Density regulation at the breeding grounds

The number of yearlings and adults in Kongsfjorden had a negative effect on the probability of reproduction (R) and the number of fledglings per successfully breeding female (fec) (Table 1). This translated into a direct, negative effect of total population size on the population growth rate. No statistically significant negative effect of local density on survival was observed, although there was a tendency for a negative effect on fledgling survival (Table 1). The estimated density dependence coefficients were similar when temporal trends in vital rates and population size were accounted for (Appendix S5).

3.4 | Age-structured population dynamics

The mean population growth rate over the study period was 1.05 (0.65, 1.53). However, annual population growth rates showed large variation from 0.68 (0.54, 0.85) in 2001, the year prior to a major crash in reproductive success, to 1.27 (0.79, 1.73) in 1991, during the growth phase after colonisation. The stable age distribution of

fledglings, yearlings and adults, based on mean vital rate estimates, was 0.04 (0.02, 0.05), 0.03 (0.02, 0.04) and 0.94 (0.92, 0.96), respectively, indicating that individuals were mostly distributed in the adult age class. Adult and yearling classes had the highest reproductive values, 0.94 (0.92, 0.97) and 0.92 (0.87, 0.97), respectively, vs. 0.67 (0.55, 0.75) for the fledgling age class.

Mean sensitivities and elasticities of the asymptotic population growth rate (λ) to vital rates were calculated from a population projection matrix based on posterior samples of age-specific demographic rates. The mean sensitivity of λ to the probability of reproduction (R) was higher than to the number of fledglings (fec), while the elasticities of λ to R, fec and ϕ_f were the same (Table 1). The sensitivity and elasticity of λ to variation in survival were substantially higher for the rate of the adult age class than for the survival rates of yearlings and fledglings, which were not statistically significantly different (Table 1).

We parameterised population projection matrices where vital rates were functions of population size (Caswell, 2001), based on density dependence coefficients for each vital rate. Elasticities of the population growth rate to R, fec, ϕ_f and ϕ_y were consistently lower than ϕ_{ad} and declined with population size at the same rate (Figure 4a). Conversely, the elasticity to ϕ_{ad} increased as the population approached the carrying capacity.

Transient elasticities of the population vector at $t = 5$, N_5, rapidly converged to the same pattern as in the asymptotic elasticities, with increasing elasticity to adult survival and decreasing elasticities to other vital rates as population size increased (Appendix S6: Figure S6.1). Based on the transient LTRE, contributions of vital rates to the realised population growth rate, $\lambda_{realised,t}$, reflected the strength of density dependence acting on each rate (since reproductive rates were negatively affected by N_{tot}, reproductive rates made a positive contribution to $\lambda_{realised,t}$) (Figure 4b). Additionally, the population vector reduced population growth through a negative effect on the number of adults, which made up the largest proportion of total population size.

4 | DISCUSSION

Colonising populations should eventually stop increasing as a consequence of density dependence in certain vital rates (Redfield, 1973). However, few studies of colonising populations – particularly in migratory species – have identified which age-specific reproductive and survival rates undergo density regulation and how this in turn affects the population dynamics (Fowler, 1981, 1987). Sæther et al. (2016) found no evidence for density regulation of reproduction, when analysing density dependence in different vital rates of income breeding birds. In contrast, density regulation in several duck species, which are closer to being capital breeders, was found to occur primarily through negative feedbacks on reproduction (Elmberg, Gunnarsson, Nummi, Pöysä, & Sjöberg, 2003; Elmberg, Gunnarsson, Pöysä, Sjöberg, & Nummi, 2005). Similarly, in our study population of barnacle geese and in other goose species (Cooch, Lank, Rockwell, & Cooke, 1989; Sedinger et al., 1998), density dependence largely regulated population growth via a negative feedback on reproductive success prior to fledging.

TABLE 1 Estimates of population growth rate λ and demographic rates at mean population size, with corresponding sensitivities and elasticities of the population growth rate and coefficients (β) describing the effect of N (local population, i.e. the total population size N_{tot} or the numbers of yearlings and adults $N_{y,ad}$) on demographic rates, with associated 95% credible intervals. Coefficients describing the strength of density dependence, fec and λ were distributed on the log scale, while R, ϕ_f, ϕ_y and ϕ_{ad} were distributed on logit scale

Par	Mean	Sensitivity of λ	Elasticity of λ	N	β on link scale ($\times 10^3$) (95% CRIs)	$P(\beta < 0)$
R	0.13 (0.09 0.17)	0.21 (0.17, 0.24)	0.03 (0.02, 0.04)	$N_{y,ad}$	−1.73 (−2.61, −0.75)	1.00
fec	2.12 (1.85, 2.44)	0.04 (0.02, 0.06)	0.03 (0.02, 0.04)	$N_{y,ad}$	−0.48 (−0.84, −0.13)	1.00
ϕ_f	0.63 (0.53 0.72)	0.04 (0.03, 0.06)	0.03 (0.02, 0.04)	N_{tot}	−0.04 (−1.36, 1.25)	0.52
ϕ_y	0.86 (0.82 0.90)	0.03 (0.02, 0.04)	0.03 (0.02, 0.04)	N_{tot}	0.03 (−0.60, 0.73)	0.46
ϕ_{ad}	0.89 (0.87 0.91)	0.97 (0.96, 0.98)	0.94 (0.92, 0.96)	N_{tot}	0.41 (−0.34, 1.20)	0.14
λ	1.05 (0.65, 1.53)			N_{tot}	−0.54 (−0.81, −0.36)	1.00
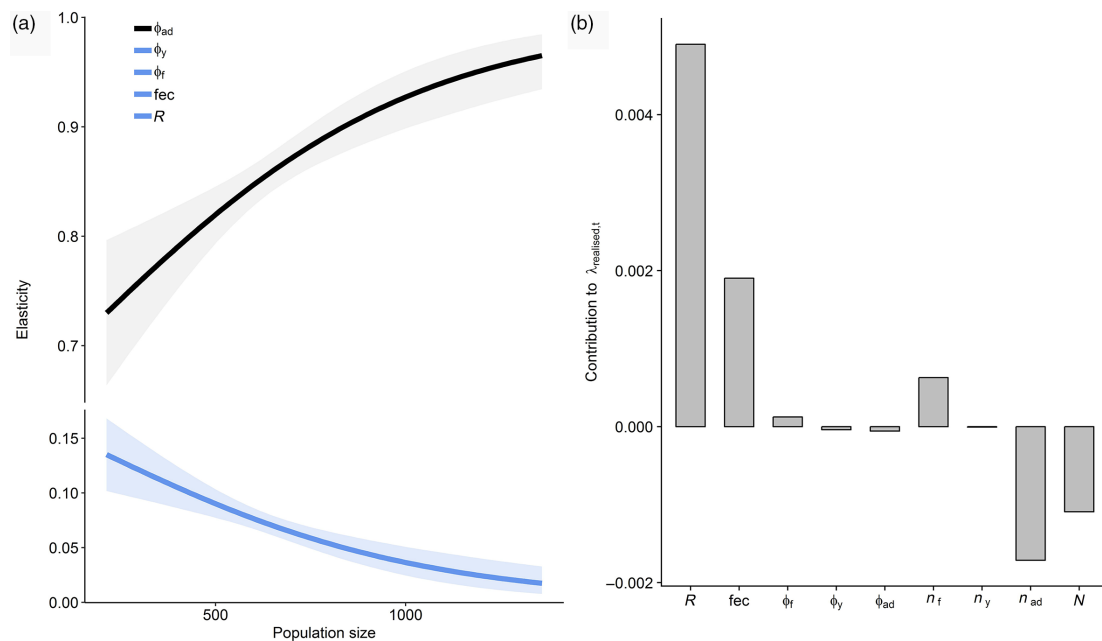
FIGURE 4 (a) Elasticities of the asymptotic population growth rate to vital rates, in relation to total population size, with 95% CRIs. Elasticities to R, fec, ϕ_f and ϕ_y were the same, and consequently, lines are overlapping. (b) Contributions of demographic rates and normalised components of the population structure to the realised population growth rate, $\lambda_{realised,t}$

A central concept in classifying reproductive tactics is the capital–income dichotomy, which separates species where reproductive success relies on body stores (capital) from species that invest in offspring using resources directly at the breeding grounds (Drent & Daan, 1980; Jönsson, 1997; Stearns, 1992). Analyses of ungulates have revealed that the pattern of temporal covariation in demographic traits differs between those two life-history types. In capital breeders such as bighorn sheep (*Ovis canadensis*), ewes successfully weaning a lamb were heavier than those losing their lamb (Festa-Bianchet, Gaillard, & Jorgenson, 1998), whereas in the income breeding roe deer (*Capreolus capreolus*), there was no detectable difference in female body mass between years with successful and unsuccessful fawn production (Andersen, Gaillard, Linnell, & Duncan, 2000).

Waterfowl, such as geese and ducks, are closer to the capital breeding end of the spectrum, in which the endogenous nutrients brought to the breeding grounds may affect their reproductive success (Hahn et al., 2011; Klaassen, Abraham, Jefferies, & Vrtiska, 2006). This indicates that population dynamics of capital breeders, such as barnacle geese, can be characterised by a "tap-type", rather than a "tub-type", of dynamics (Sæther et al., 2006; Sæther, Sutherland, & Engen, 2004), that is processes influencing the mean body condition prior to the breeding season affect reproductive success and hence strongly affect population dynamical characteristics.

In this study, we found strong support for density dependence acting through a negative feedback on reproduction. Stronger density regulation of reproduction than survival in barnacle geese may

therefore be explained by their status as capital breeders, with processes during the breeding season making a larger contribution to population dynamics. In contrast, Sæther et al. (2016) found that annual variation in population growth rates of income breeding bird species was mainly explained by temporal variation in survival. In addition, barnacle geese are also nidifugous (i.e. offspring leave the nest shortly after hatching and receive minimal parental care thereafter) in contrast to altricial species, where offspring hatch in an undeveloped state (Lack, 1968). Sæther, Ringsby, and Røskaft (1996) proposed that factors affecting the population dynamics of nidifugous species would occur during the breeding season, but would occur during the non-breeding season in altricial species. Consequently, the vulnerability of barnacle goose young to fluctuations in the availability of food resources may be greater than in altricial species. In support of this, the majority of species included in the analysis of Sæther et al. (2016) were altricial birds. Furthermore, studies have shown that herbivores in particular are strongly affected by environmental stochasticity and density dependence, which often acts through density regulation of reproduction since the temporal variance in adult survival is limited (Gaillard et al., 1998; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000; Sæther, 1997). This pattern may therefore be especially clear in herbivores since their body condition is strongly dependent on the amount of food available prior to or during a season. In our study, population density influenced both the probability of reproduction and the number of fledglings, conditional on successful reproduction. Such density effects may be attributed to competition for food resources prior to the breeding season, with consequent carry-over effects on reproduction (Sedinger, Schamber, Ward, Nicolai, & Conant, 2011). Additionally, density-dependent reproduction is likely also explained by competition for nest sites and/or food resources during the brood rearing phase, where increased food competition at the breeding grounds has been linked to higher pre-fledging mortality in barnacle geese (Larsson & Forslund, 1994; Loonen et al., 1997). Finally, the number of Arctic foxes in Kongsfjorden has increased in parallel with goose numbers, affecting reproduction directly through predation but also indirectly by limiting available foraging area and exacerbating resource competition (Loonen et al.,1998).

In this population, survival appeared to be density-independent after the first year of life. Food conditions can influence both reproduction and survival in high Arctic geese through effects on body condition (Newton, 1977), which is a known determinant of survival in geese, since fat build-up is paramount to successful migration (Loonen et al., 1997; Newton, 1977). Both reproduction and survival showed a tendency for decline over the study period. Vital rates are typically high during the growing phase of a colonising population (Redfield, 1973), and this decline could be attributed to gradual habitat deterioration at the breeding grounds (Kuijper, Ubels, & Loonen, 2009) or by processes at other migratory stages. The continued increase in the total Svalbard flyway population, which convenes at the wintering grounds, may potentially also explain the decline in survival rates. No evidence of this was found when regressing age-specific survival rates against annual total population size, accounting for a linear temporal trend. However, we cannot rule out that this substantial linear increase in the Svalbard

flyway population is, at least in part, responsible for the concomitant decline observed in local survival rates. When the year 1990 was removed from the analysis of density dependence (Appendix S5.2), we did find some support for density-regulated fledgling survival ($P(\beta < 0)$) = 0.93), potentially caused by post-fledging mortality during the first migration attempt, for example driven by food availability at the breeding grounds (Owen & Black, 1989). Similarly, in lesser snow geese, deteriorating food conditions was the main driver of increased first-year mortality (Francis, Richards, Cooke, & Rockwell, 1992). Therefore, density dependence may also act on fledgling survival by determining their first migration success, through limited resources at the breeding grounds. Deteriorating conditions and increased competition could also increase the amount of permanent emigration to other breeding grounds (causing a decline in apparent survival), rather than direct mortality, but we could not differentiate between these processes in the survival analysis.

Similar to Sæther et al. (2016), the elasticity of the population growth rate to adult survival increased as the population approached its carrying capacity. At small population sizes, the relative influence of reproductive rates and early-life survival on λ was high, but it declined with increasing population size. This is in agreement with Lack's hypothesis (1954; 1966) that, when a population is far from its carrying capacity, the system is driven by reproduction to a greater extent. However, Lack (1966) also argued that variation in reproduction should be largely independent of density, whereas in our study, population reproduction was strongly density-dependent. This discordance could stem from the aforementioned differences between income and capital breeders, which may alter the critical annual phase driving population dynamics (Sæther et al., 2004; Vander Werf, 1992). Thus, our analysis follows what would be predicted by Lack's hypothesis (1954) that, although reproductive rates vary as a density-dependent consequence of fluctuations in resources during the breeding season, the dynamics are still strongly influenced by adult survival as the population approaches its carrying capacity.

The elasticities of the population growth rate to demographic rates were typical for a long-lived species, where elasticities to reproductive rates and early-life survival are lower than to adult survival (Gaillard et al., 1998; Gaillard & Yoccoz, 2003). Survival often increases with age during the first few years of life in long-lived species, and such a pattern has also been observed for reproduction in geese (Rockwell, Cooch, Thompson, & Cooke, 1993). However, reproductive rates could not be modelled as age dependent in our study. Reproductive output also varied greatly among years in this barnacle goose population. This is a common pattern observed in several species of waterfowl, where elasticities to survival are high and reproduction tends to be more labile to environmental variation, allowing reproductive rates to contribute more to population dynamics (Koons, Gunnarsson, Schmutz, & Rotella, 2014). We have shown that in addition to the effects of environmental variation, the variability in reproductive rates can also be caused by density-dependent feedbacks. The large contribution of reproductive rates to population dynamics is also expected for long-lived birds with high survival rates and long life spans where, despite the low elasticity of λ to reproductive rates, their variance allows them to contribute substantially to realised population growth (Cooch, Rockwell, & Brault,

2001; Koons et al., 2014). The inter-annual variation was greater in the probability of producing a fledgling than in the number of fledglings per successful breeder, possibly since weather conditions influence initial nest success to a greater extent than the actual number of young (Prop & de Vries, 1993). Transient analysis can potentially reveal much about population dynamics in such variable environments (Ezard et al., 2010; Koons et al., 2017, 2016). In this case, the similarities between transient vs. asymptotic elasticities and contributions may be attributable to (a) the fact that vital rates were predicted deterministically as functions of vital rate-specific density dependence and (b) that this population reached the carrying capacity so quickly. Consequently, transient dynamics rapidly resembled asymptotic dynamics.

Understanding how density dependence influences the population dynamics and population trajectories of local populations colonising high Arctic breeding grounds is essential for their management and conservation, locally and internationally. This study gives insight into the dynamics behind the rapid expansion of migratory birds across the Arctic, currently a topic of management interest (AEWA, 2018; Trinder, 2014). These findings appear to oppose a recent study of the total flyway population of Svalbard barnacle geese at the wintering grounds, where no evidence of density regulation was observed (Trinder, 2014). Such a disparity can occur because density dependence in the total flyway population is concealed by range expansion on Svalbard, that is is only observable at a local scale. However, the limits of future range expansion are difficult to predict as climate change alters the area of suitable habitat for geese in the Arctic (Jensen et al., 2008; Post et al., 2009). The discrepancy between local and total Svalbard population dynamics indicates that, by ignoring local patterns, managers may miss changes occurring in Arctic migrant goose populations. Local density regulation can be seen as an early warning signal for future limitation of total flyway populations, when range expansion is no longer possible. We emphasise the need for a greater focus on local population dynamics and the suitability of remaining habitat at the high Arctic breeding grounds, especially when the re-introduction of hunting of migratory geese wintering in Europe is being called into question (AEWA, 2018).

AUTHORS' CONTRIBUTIONS

K.L.M., B.B.H. and V.G. conceived the ideas and designed the methodology; M.L. collected the data; K.L.M., V.G. and C.C. analysed the data; and K.L.M., B.B.H. and B.E.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

1   Supporting information:

2   **'Density-dependent population dynamics of a high Arctic capital breeder, the barnacle**

3   **goose'**

4   Kate Layton-Matthews, Maarten J. J. E. Loonen, Brage Bremset Hansen, Christophe F. D. Coste, Bernt-Erik

5   Sæther and Vidar Grøtan

6

7   **Appendix S1.** Prior distributions for integrated population model parameters of barnacle geese. The

8   distributions are given the following abbreviations; Normal distribution (N), Uniform distribution (U)

9   and Wishart distribution (W).

10

Parameter	Prior distribution
Mean demographic rates	
μ^R	U(-5,5)
μ^{fec}	U(-5,3)
μ^ϕ	U(-5,5)
U_f	U(0,1)
$U_{y,ad}$	U(0,1)
Mean recapture probability	
μ^p	U(-5,5)
Temporal variability	
Σ	$W(\mathbf{I}, 7)^{-1}$ ($\mathbf{I}$=6x6 identity matrix)
σ_p	U(0, 10)
σ_C	U(0, 100)
Initial population sizes (numbers are rounded and truncated to positive values)	
N_f	N(100,1000)
N_y	N(100,1000)
N_{ad}	N(100,1000)
N_{unm_f}	N(100,1000)
$N_{unm_{y\&ad}}$	N(100,1000)

11 **Appendix S2.** Counts of the total population of Svalbard barnacle geese

12 The total wintering population has been increasing close to exponentially since the implementation of

13 hunting bans in the 1950s. In a recent study of the total population at Solway Firth, UK, Trinder (2014)

14 found no evidence of density-dependent effects on vital rates or the population growth rate.

15

16
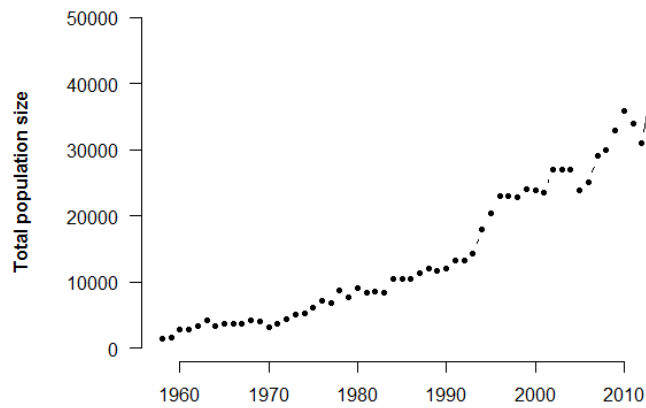
24 **Figure S2.** Annual population size for the total Svalbard barnacle goose population at the wintering

25 grounds, obtained from Trinder (2014).

26   **Appendix S3.** Estimated annual age class proportions of barnacle geese.
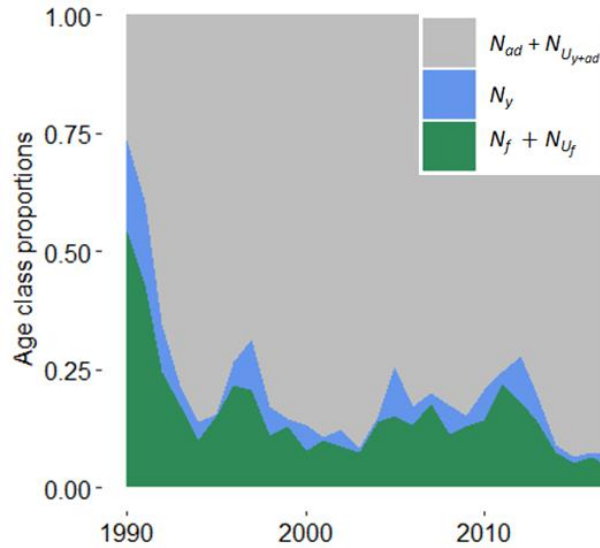
27

28   **Figure S3.1.** Annual proportions of the estimated numbers of fledglings ($N_f + N_{U_f}$), yearlings (N_y) and

29   adults ($N_{ad} + N_{U_{y,ad}}$).
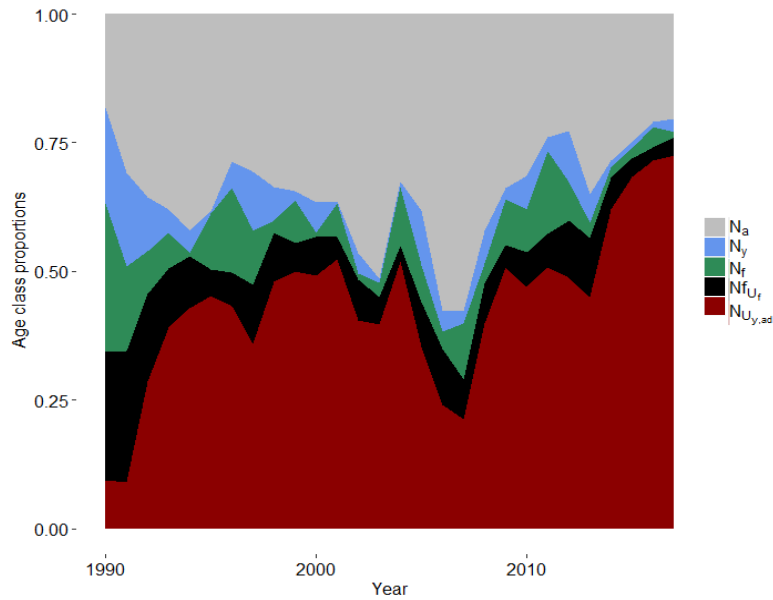
30   **Figure S3.2.** Annual proportions of the estimated numbers of fledglings (N_f), yearlings (N_y) and adults

31   (N_{ad}) during 1990-2017 with unmarked fledglings (N_{U_f}) and unmarked yearlings and adults ($N_{U_{y,ad}}$)

32   shown separately.

33   **Appendix S4.** Annual estimates of the probability of *R*, the probability of a female reproducing at

34   least one fledgling and *fec*, the number of fledglings per successfully breeding female.
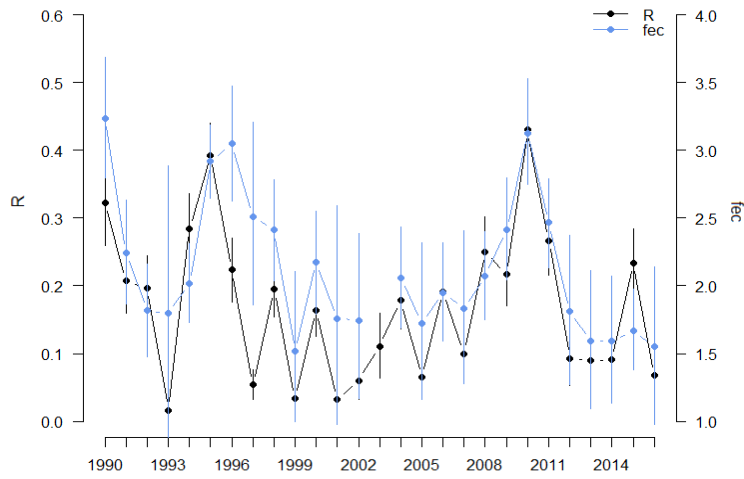
35

36   **Figure S4.** Annual posterior means and 95% CRIs of reproductive parameters *R* and *fec*.

Appendix S5: Estimating the strength of density dependence, accounting for a temporal trend

To ensure that a negative density-dependent feedback was not attributed to what was in fact a spurious effect of temporal trends, we regressed vital rates against estimates of population size (as described in *Methods: Density dependence*) and included a continuous year effect, to remove any monotonic change (Table S5.1). Additionally, to ensure that density dependence was also not only driven by the steep decline from 1990 to 1991, density dependence regressions were performed only including the years 1991–2017 (Table S5.2). Estimates are shown with associated 95% credible intervals and coefficients describing the strength of density dependence, fec and λ were distributed on the log scale, while R, ϕ_f, ϕ_y and ϕ_{ad} were distributed on logit scale.

Table S5.1 Estimates of coefficients (β) describing the effect of N, i.e. the total population size or the numbers of yearlings and adults, on demographic rates, accounting for a temporal trend (i.e. linear year effect).

Parameter	N	β on link scale (x10^3) (95% CRIs)	$P(\beta < 0))$
R	$N_{y,ad}$	-1.77 (-2.68, -0.76)	1.00
fec	$N_{y,ad}$	-0.41 (-0.79, -0.05)	1.00
ϕ_f	N_{tot}	-0.06 (-1.43, 1.26)	0.53
ϕ_y	N_{tot}	0.03 (-0.60, 0.76)	0.46
ϕ_{ad}	N_{tot}	0.40 (-0.30, 1.13)	0.12
λ	N_{tot}	-0.47 (-0.66, 0.22)	1.00

Table S5.2 Estimates of coefficients (β) describing the effect of N, i.e. the total population size or the numbers of yearlings and adults from 1991-2017 (i.e. 1990 was not included).

Parameter	N	β on link scale (x10^3) (95% CRIs)	$P(\beta < 0))$
R	$N_{y,ad}$	-2.05 (-3.05, -1.02)	1.00
fec	$N_{y,ad}$	-0.24 (-0.68, 0.16)	0.88
ϕ_f	N_{tot}	-0.95 (-2.42, 0.36)	0.93
ϕ_y	N_{tot}	0.10 (-0.63, 1.06)	0.40
ϕ_{ad}	N_{tot}	-0.32 (-1.13, 0.37)	0.81
λ	N_{tot}	-0.47 (-0.66, 0.22)	1.00

Appendix S6: A comparison of transient and asymptotic prospective and retrospective

60 **perturbation analyses**

61 *Appendix 6.1: Prospective perturbation analysis*

62 We performed a prospective perturbation analysis of transient population dynamics using matrix

63 calculus, based on the methods developed by Caswell (2007) and also described in Ezard *et al.* (2010).

64 The sensitivity of total population size (N_t) at time *t*, to lower-level vital rates contained in θ, was

65 calculated as;

66 $$\frac{\partial N(t)}{\partial \theta^T} = c^T \frac{\partial n(t)}{\partial \theta^T} \ , \qquad\qquad\qquad eqn\ S1$$

67 where c is a vector of 1s for each age class and n is the number of individuals in each component of the

68 population vector at time *t*. The elasticities of N_t to changes in θ, were then calculated as;

69 $$\frac{\theta}{N_t} \ \frac{\partial N_t}{\partial \theta^T} \ . \qquad\qquad\qquad eqn\ S2$$

70 We show the sensitivities and elasticities of the asymptotic population growth rate, λ, and the population

71 vector at t = 5, N_5 to lower-level vital rates, as functions of increasing population size (figure S1). We

72 chose *t* = 5 as the transient time period, since it reflected a time window of sufficient population growth

73 in the study population. Sensitivities and elasticities of λ and N_5 were very similar; where elasticities to

74 adult survival increased but elasticities to all other rates decreased with population size (figure S1).

75 *Appendix 6.2 Retrospective perturbation analysis (LTRE)*

76 We performed a retrospective perturbation analysis, namely a life-table response experiment (LTRE),

77 to calculate the contributions of density-dependent vital rates and components of the population

78 structure, to transient and asymptotic dynamics, based on methods developed by Caswell (2007) and

79 Koons *et al.* (2016) (see also Koons, Arnold and Schaub (2017)). Vital rates and the numbers of

80 individuals in each age class were predicted using linear regressions, with total population size as an

81 explanatory variable (see *Methods: Density dependence*). The numbers of yearlings declined, while the

82 numbers of fledglings and adults increased with population size.

83 For the transient analysis, we decomposed the realised population growth rate ($\lambda_{realised,t}$) into

84 contributions of vital rates and population structure. We implemented a transient LTRE to decompose

85 the variance in $\lambda_{realised,t}$, into contributions from the variance in lower-level vital rates and components

86 of the population structure ($n_{f,t}$, $n_{y,t}$ and $n_{ad,t}$,);

87 $$\text{contribution}_\theta{}^{\text{var}(\lambda_{realised,t})} \approx \sum_j \text{cov}(\theta_{i,t}, \theta_{j,t}) \ \frac{\partial \lambda_t}{\partial \theta_{i,t}} \frac{\partial \lambda_t}{\partial \theta_{j,t}}, \qquad\qquad eqn\ S3$$

88 where θ also includes n_t. Contrary to Koons *et al.* (2016), we used non-normalised values for the

89 components of the population vector, rather than forcing them to sum to one. This was more applicable

90   to study the consequences of density dependence for population dynamics, by allowing actual rather

91   than relative numbers in the population vector to influence vital rates and the population growth rate.

92   Lower-level vital rates contained in the time-varying matrix, $\mathbf{A_t}$, and components of the total population

93   vector, $\mathbf{N_t}$, were included in a vector, Θ, and we calculated the sensitivity of $\lambda_{realised,t}$ to changes in each

94   parameter. Using these sensitivities and covariances among all elements of Θ, we obtained a first-order

95   approximation of the variance in $\lambda_{realised,t}$, where sensitivities were calculated at the means of predicted

96   vital rates and components of $\mathbf{N_t}$. The contribution of the variance in each element of Θ was calculated

97   by summing over the covariances (Horvitz, Schemske & Caswell 1997). We also decomposed the

98   variance in the asymptotic population growth rate, λ_t, into contributions of the variance in vital rates by

99   the same approach as the transient analysis (asymptotic LTRE).

100   Contributions of vital rates to the asymptotic growth rate (λ) and realised growth rate ($\lambda_{realised,t}$) showed

101   a similar pattern although the scale of these contributions differed (figure S2),. The contribution of vital

102   rates to λ (and $\lambda_{realised,t}$) reflected the strength of density dependence on each rate, where negative density

103   dependence resulted in a positive contribution of the reproductive components and fledgling survival

104   (R and fec, and ϕ_f) since population growth rates also declined as population size increased. Yearling

105   and adult survival (ϕ_y and ϕ_{ad}) negatively contributed to λ and $\lambda_{realised,t}$, due to the lack of density

106   dependence on these rates. The total population vector ($\mathbf{N_t}$) had a negative contribution to $\lambda_{realised,t}$

107   through the adult component $\mathbf{n_{ad}}$, since adults largely made up the population and therefore contribute

108   most to density dependence. $\mathbf{n_f}$ contributed positively, likely through its dependency on reproductive

109   parameters at each time step. $\mathbf{n_y}$ had little effect on the $\lambda_{realised,t}$ due to its low sensitivity and low numbers

110   in the population.

111   Transience is a burgeoning field in population dynamics (Caswell 2007; Koons *et al.* 2016; Koons,

112   Arnold & Schaub 2017), and its potential importance in addition to conventional, asymptotic

113   approaches has received a lot of attention in recent years (Ezard *et al.* 2010; Stott 2016; Maldonado-

114   Chaparro *et al.* 2018). Transient analysis can be applied in several ways, through perturbation of matrix

115   elements and/or the population structure and time variance can be incorporated in multiple ways (Stott

116   2016). Many approaches, such as that of Koons *et al.* (2016), which we applied for this study, are

117   focused on including stochasticity in vital rates and the population structure, within a fixed matrix

118   design. Therefore, incorporating density dependence, rather than only environmental stochasticity, may

119   require some alterations to this approach since interpretation of the contributions of the population

120   structure is not very intuitive in this framework. For instance, Caswell and Takada (2004) showed that

121   elasticity analysis is more relevant when investigating the effects of environmental changes, given

122   density-dependent vital rates, and so elasticity analysis of density-dependent matrices could be

123   incorporated into this existing transient framework.
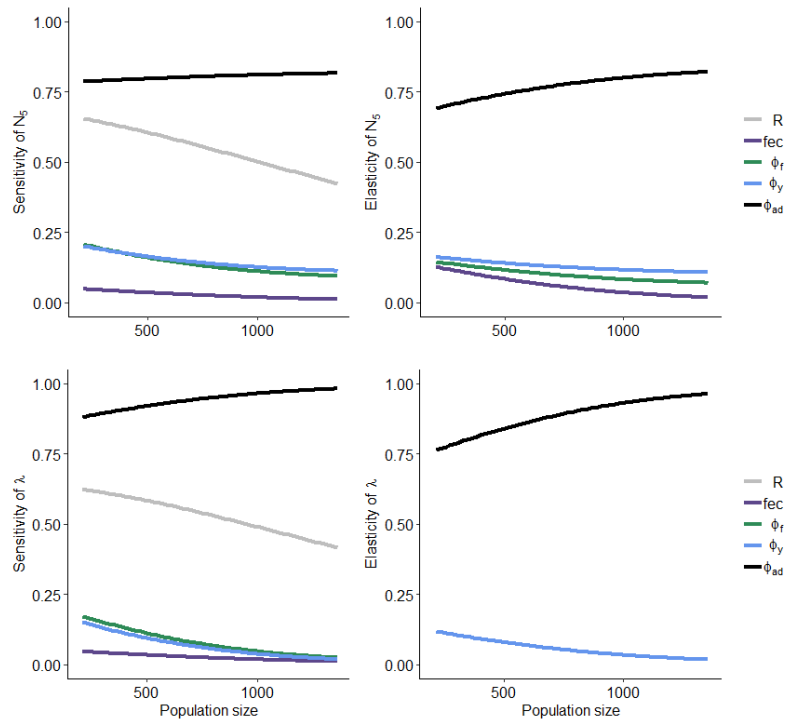
Figure S6.1. Sensitivities (left column) and elasticities (right column) of the population vector at $t = 5$, N_5, (top row), and the asymptotic growth rate, λ, (bottom row), to lower-level vital rates at different population sizes. Since elasticities to R and fec were equal in the transient analysis (to N_5), and elasticities to R, fec, ϕ_f and ϕ_y were equal in the asymptotic analysis (to λ), some parameters therefore cannot be seen.
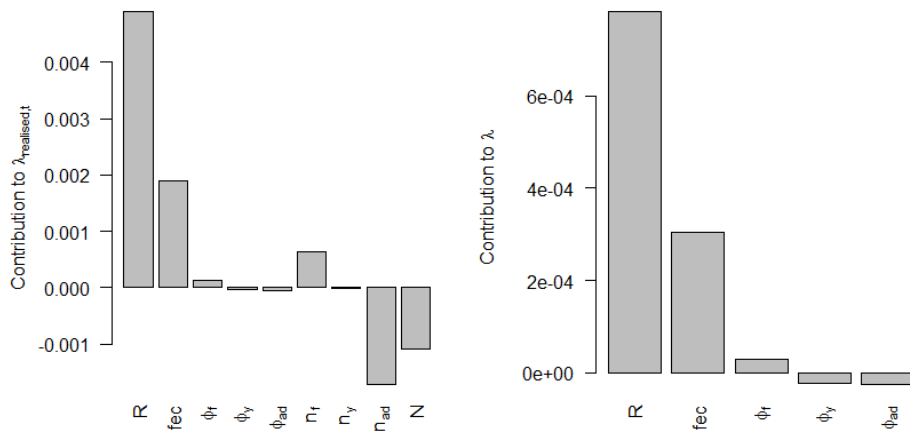
Figure S6.2. Contributions of demographic rates (and normalised components of the population structure for the transient analysis) to the transient realised population growth rate, $\lambda_{\text{realised},t}$ (left) and the asymptotic population growth rate, λ, (right).

8

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166

Appendix 7: Integrated population model for the barnacle goose

Kate Layton-Matthews

29 April 2019

Model structure

3 age classes (fledgling, yearling & adult).

Reproduction possible from second year of life.

Post-breeding census.

All rates are time-dependent, survival is age dependent and recapture is sex dependent.

Data

1) Population counts: countsT = annual counts of (1) fledglings (NAs) and (2) yearling **and** adults
2) Reproduction:
    nbf = annual number of females
    nfem = annual number of females
    J = annual number of fledglings per breeding female
3) CH = mark-recapture data (individual capture histories)
4) age_mat = matrix of ages (1-3) with the same dimensions as mark-recapture data
5) f = indicator variable of an individual's first capture
6) sex = indicator variable for sex of indivual

Functions used to run the IPM

Functions to create a matrix with information about the latent state z, and a matrix of initial values for latent state z (Kery & Schaub, 2012).

```
# Latent state (between two "1" the individual has survived -> 1)
known.state.cjs <- function(ch){
  state <- ch
  for (i in 1:dim(ch)[1]){
    n1 <- min(which(ch[i,]==1))
    n2 <- max(which(ch[i,]==1))
    state[i,n1:n2] <- 1
    state[i,n1] <- NA
  }
  state[state==0] <- NA
  return(state)
}

# Function to create a matrix of initial values for latent state z
cjs.init.z <- function(ch,f){
  for (i in 1:dim(CH)[1]){
    if (sum(ch[i,])==1) next
    n2 <- max(which(ch[i,]==1))
    ch[i,f[i]:n2] <- NA
  }
  for (i in 1:dim(CH)[1]){
```

```
    ch[i,1:f[i]] <- NA
  }
  return(ch)
}
```

Model definition

```
sink("IPM_branta.txt")
cat("

    model
    {
#*******************************
# 1: Priors and constraints
#*******************************
  # Recapture
    for (g in 1:2){
      for (t in 1:(n.occasions-1)){
        p[g,t] <- 1 / (1 + exp(-(mean.p[g] + epsilon.p[t])))
      } #t
      mean.p[g] ~ dunif(-5,5) # prior for mean, sex-specific recapture rate
    } #g
    for (t in 1:(n.occasions-1)){epsilon.p[t] ~ dnorm(0,tau.p)} #t
    sigma.p ~ dunif(0,10)
    tau.p <- pow(sigma.p,-2)
    sigma2.p <- pow(sigma.p, 2)

  # Survival
    for (u in 1:3){
      for (t in 1:(n.occasions-1)){
        s[u,t] <- 1 / (1 + exp(-(mu.s[u] + epsilon[t,u])))
      } #t
    } #u

    for (u in 1:3){mu.s[u] ~ dunif(-5,5)} #u  # prior for mean age-specific survival rates

## Vital rate priors
    xi.1 ~ dunif(0,10)
    xi.2 ~ dunif(0,10)
    xi.3 ~ dunif(0,10)
    xi.4 ~ dunif(0,10)
    xi.5 ~ dunif(0,10)
    for (t in 1:(n.occasions-1)){
      eps.raw[t,1:5] ~ dmnorm(zeros[], tau.raw[,])
      epsilon[t,1] <- xi.1 * eps.raw[t,1]
      epsilon[t,2] <- xi.2 * eps.raw[t,2]
      epsilon[t,3] <- xi.3 * eps.raw[t,3]
      epsilon[t,4] <- xi.4 * eps.raw[t,4]
      epsilon[t,5] <- xi.5 * eps.raw[t,5]
    } #t

    tau.raw[1:5,1:5] ~ dwish(W[,], 6)
    sigma.raw[1:5,1:5] <- inverse(tau.raw[,])
```

```r
# Temporal variances
  sigma.s1 <- xi.1*sqrt(sigma.raw[1,1])
  sigma.s2 <- xi.2*sqrt(sigma.raw[2,2])
  sigma.s3 <- xi.3*sqrt(sigma.raw[3,3])
  sigma.s4 <- xi.4*sqrt(sigma.raw[4,4])
  sigma.s5 <- xi.5*sqrt(sigma.raw[5,5])

# Temporal covariances
  rho.s.12 <- sigma.raw[1,2]/sqrt(sigma.raw[1,1] * sigma.raw[2,2])
  rho.s.13 <- sigma.raw[1,3]/sqrt(sigma.raw[1,1] * sigma.raw[3,3])
  rho.s.23 <- sigma.raw[2,3]/sqrt(sigma.raw[2,2] * sigma.raw[3,3])
  rho.s.35 <- sigma.raw[3,5]/sqrt(sigma.raw[3,3] * sigma.raw[5,5])
  rho.s.45 <- sigma.raw[4,5]/sqrt(sigma.raw[4,4] * sigma.raw[5,5])

# Unmarked rates
  for (t in 1:(n.occasions-1)){
    unm.A[t] ~ dunif(0,1) # prior for mean yearling and adults unmarked rate
    unm.F[t] ~ dunif(0,1) # prior for mean fledgling unmarked rate
  } #t

# Observation error
  # Peterson
  tauy.p ~ dgamma(0.001, 0.001)
  sigma2.y.p <- 1 / tauy.p

  # Fjord
  tauy.f ~ dgamma(0.001, 0.001)
  sigma2.y.f <- 1 / tauy.f

# Initial population sizes
  nf ~ dnorm(100,0.0001)I(0,)  # fledglings
  Nf[1] <- round(nf)
  ny ~ dnorm(100,0.0001)I(0,)  # yearlings
  Ny[1] <- round(ny)
  na ~ dnorm(100,0.0001)I(0,)  # adults
  Na[1] <- round(na)
  UNMARKED.A[1] ~ dnorm(100,0.0001)I(0,)  # Unmarked yearlings+unmarked adults
  UNMARKED.F[1] ~ dnorm(100,0.0001)I(0,)  # Unmarked fledglings

#*************************************************
# 2: Likelihoods
#*************************************************
# Reproduction data
  for (t in 1:(n.occasions-1)){
  # R
    nbf[t] ~ dbin(d[t],nfem[t])
    d[t] <-  1 / (1 + exp(-(mu.R + epsilon[t,5])))
  # Fecundity
    J[t] ~ dpois(R[t])
  R[t] <- exp(mu.f + epsilon[t,4] + log(nbf[t]))
  fec[t] <-  exp(mu.f + epsilon[t,4])
  } #t
  mu.R ~ dunif(-5,5) # prior for mean R
```

3

```
   mu.f ~ dunif(-5,3) # prior for mean fec

 # Capture-recapture data
   for (i in 1:nind){
     z[i,f[i]] <- 1
     for (t in (f[i]+1):n.occasions){
   # State process
       z[i,t] ~ dbern(mu1[i,t])
       mu1[i,t] <- s[x1[i,t-1],t-1] * z[i,t-1]
   # Observation process
       y[i,t] ~ dbern(mu2[i,t])
       mu2[i,t] <- p[sex[i],t-1] * z[i,t]
     }#t
   }#i

 # Population count data
   # System process
   for (t in 2:n.occasions){
     Nf.temp[t] <- (s[2,t-1]*fec[t-1]*0.5*d[t-1]*Ny[t-1]) +
                   (s[3,t-1]*fec[t-1]*0.5*d[t-1]*Na[t-1])
     Nf[t] ~ dpois(Nf.temp[t])
     Ny[t] ~ dbin(s[1,t-1],Nf[t-1])
     mean2[t] ~ dbin(s[2,t-1],Ny[t-1])
     mean3[t] ~ dbin(s[3,t-1],Na[t-1])
     Na[t] <- mean2[t] + mean3[t]
     UNMARKED.A[t] <- Ntot.A[t-1]*unm.A[t-1]
     UNMARKED.F[t] <- Ntot.F[t-1]*unm.F[t-1]
   } #t

   for (t in 1:n.occasions){
     Ntot.A[t]<- Ny[t]+ Na[t] + UNMARKED.A[t]
     Ntot.F[t] <- Nf[t] + UNMARKED.F[t]
     Ntot[t] <- Ntot.A[t] + Ntot.F[t]
     log.Ntot.A[t] <- log(Ntot.A[t])
   }

   # Observation process
   # Petersons index
   for (t in 1:6){
   counts[t,1] ~ dlnorm(log.Ntot.A[t],tauy.p)
   counts[t,2] ~ dnorm(Ntot.F[t],tauy.p)
   }

   # Fjord counts
   for (t in 7:n.occasions){
   counts[t,1] ~ dlnorm(log.Ntot.A[t],tauy.f)
   counts[t,2] ~ dnorm(Ntot.F[t],tauy.f)
   }
 }
   ",fill = TRUE)
sink()
```

Model inputs and settings (for jagsUI)

Bundle data

```
data <- list(y = CH, nbf=nbf, nfem=nfem, J=nfled, W=diag(5),zeros=rep(0.0,5),
             counts = as.matrix(countsT), f = f, nind = dim(CH)[1],
             n.occasions = dim(CH)[2], z = known.state.cjs(CH), x1 = age_mat, sex=fs)
```

Initial values

```
inits <- function(){list(z=cjs.init.z(CH, f), mu.s=runif(3,0,1), mu.d=runif(1,0,1),
                    mu.f=runif(1,0,1),   mean.p=runif(2,0,1),   sigma.p=runif(1,0,5),
                    sigma.y=runif(1,0,10), tauy.f=runif(1,0,5), tauy.p=runif(1,0,5))}
```

Parameters monitored

```
parameters <- c("sigma2.y.p","sigma2.y.f","s","mu.s","mu.d","mu.f","d","fec","p","mean.p",
               "sigma.s1","sigma.s2","sigma.s3","sigma.s4","sigma.s5","sigma2.p",
               "rho.s.12","rho.s.13","rho.s.23","rho.s.45","rho.s.35",
               "Nf", "Ny", "Na","Ntot","unm.F","unm.A","UNMARKED.A","UNMARKED.F")
```

Model

```
ipm.mod <- jags(model.file ='IPM_branta.txt',data = data, parameters.to.save = parameters,
               inits = inits,n.chains = 4, n.iter = 1000000, n.burnin = 100000,
               n.thin = 90, parallel=TRUE)
```

Model output

```
print(ipm.mod, digits=3)
```

Paper II

PRIMARY RESEARCH ARTICLE

Global Change Biology **WILEY**

Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming

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Abstract

Climate change is most rapid in the Arctic, posing both benefits and challenges for migratory herbivores. However, population-dynamic responses to climate change are generally difficult to predict, due to concurrent changes in other trophic levels. Migratory species are also exposed to contrasting climate trends and density regimes over the annual cycle. Thus, determining how climate change impacts their population dynamics requires an understanding of how weather directly or indirectly (through trophic interactions and carryover effects) affects reproduction and survival across migratory stages, while accounting for density dependence. Here, we analyse the overall implications of climate change for a local non-hunted population of high-arctic Svalbard barnacle geese, *Branta leucopsis*, using 28 years of individual-based data. By identifying the main drivers of reproductive stages (egg production, hatching and fledging) and age-specific survival rates, we quantify their impact on population growth. Recent climate change in Svalbard enhanced egg production and hatching success through positive effects of advanced spring onset (snow melt) and warmer summers (i.e. earlier vegetation green-up) respectively. Contrastingly, there was a strong temporal decline in fledging probability due to increased local abundance of the Arctic fox, the main predator. While weather during the non-breeding season influenced geese through a positive effect of temperature (UK wintering grounds) on adult survival and a positive carryover effect of rainfall (spring stopover site in Norway) on egg production, these covariates showed no temporal trends. However, density-dependent effects occurred throughout the annual cycle, and the steadily increasing total flyway population size caused negative trends in overwinter survival and carryover effects on egg production. The combination of density-dependent processes and direct and indirect climate change effects across life history stages appeared to stabilize local population size. Our study emphasizes the need for holistic approaches when studying population-dynamic responses to global change in migratory species.

1 | INTRODUCTION

The climate is changing most rapidly in the Arctic, as a consequence of Arctic amplification (Arft et al., 1999; Serreze & Barry, 2011). Climate change has disrupted abiotic and biotic processes (Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Post et al., 2009) and thereby the population dynamics of many species, through altered snowpack characteristics (Hansen et al., 2019), phenological mismatch (Clausen & Clausen, 2013; Doiron, Gauthier, & Lévesque, 2015; Post & Forchhammer, 2008) and changes in vegetation productivity ('Arctic greening') and structure (e.g. Fauchald, Park, Tømmervik, Myneni, & Hausner, 2017).

Earlier snow melt has long been recognized as one of the prevailing indicators of Arctic climate change (Foster, 1989). The snowfree season, and thus the growing season, is extremely short at high latitudes. Earlier snow melt may therefore benefit Arctic wildlife populations (Gareth, 2004) and especially herbivores. Warmer temperatures and advancing springs have increased plant productivity (Bjorkman, Elmendorf, Beamish, Vellend, & Henry, 2015; Jensen et al., 2008), providing more food for both resident and migratory herbivores (Hill & Henry, 2011; Van der Wal & Stien, 2014) and potentially increasing reproduction, survival and, in turn, population sizes. Positive trends associated with climate change have been observed in some Arctic herbivore populations (Albon et al., 2017; Forchhammer et al., 2008; Morrissette, Bêty, Gauthier, Reed, & Lefebvre, 2010). However, there has been little evidence for a general pattern of increase (Post et al., 2009). This may be partly explained by negative effects of 'trophic mismatch' (i.e. poor timing of reproduction in relation to resource peaks), limiting the potential benefits of earlier and warmer springs (Clausen & Clausen, 2013; Doiron et al., 2015; Saino et al., 2011), as well as changing winter conditions (Forchhammer, Post, Stenseth, & Boertmann, 2002; Hansen et al., 2019, 2013; Kohler & Aanes, 2004). In addition, climate change effects may be indirect through other species in the Arctic community, across trophic levels (Forchhammer et al., 2008; Hansen et al., 2013; Post et al., 2009), causing changes in 'bottom-up' and 'top-down' processes (Forchhammer et al., 2002; Gauthier, Bêty, Giroux, & Rochefort, 2004). Arctic herbivore populations are often strongly influenced by bottom-up processes (i.e. food resource availability; Barrio et al., 2016). Fluctuations in Arctic fox, *Vulpes lagopus*, abundance also has distinct top-down effects on population dynamics, affecting reproductive success in geese (Gauthier et al., 2004; Loonen, Tombre, & Mehlum, 1998) and survival in voles (Ehrich et al., 2017) and lemmings (Angerbjorn, Tannerfeldt, & Erlinge, 1999).

The Arctic is the breeding grounds for many migratory species (Dickey, Gauthier, & Cadieuz, 2008). Long-distance migrants (such as those breeding in the high Arctic) occupy widely separated habitats across the annual cycle and are therefore exposed to different climate regimes and trends, and also potentially contrasting density-dependent effects (Both, Bouwhuis, Lessells, & Visser, 2006; Hüppop & Winkel, 2006; van Oudenhove, Gauthier, & Lebreton, 2014). The time spent on migration often accounts for a large proportion of the annual cycle and individuals are dependent on food resources at each migratory stage. Therefore, climate-induced changes in plant productivity and the timing of the plant growing season can be a major source of mortality (Newton, 2006, 2007). Consequently, migrants may be particularly vulnerable to climate change (Robinson et al., 2009), as possibly reflected in the declining trends reported for several long-distance migrant populations (Both et al., 2006). However, predicting their population responses to climate change clearly depends on understanding how climate—and other drivers—affects vital rates at each stage of the annual cycle. Reproductive success in Arctic nesting geese is largely determined by weather conditions during the breeding season (Bêty, Gauthier, & Giroux, 2003; Madsen et al., 2007; Prop & de Vries, 1993), but conditions earlier in the annual cycle may also affect individuals at later stages via carryover effects. Especially in capital breeders, nutrients accumulated prior to the breeding season determine body condition and thereby affect reproduction (Inger et al., 2010; Sedinger, Schamber, Ward, Nicolai, & Conant, 2011). Carryover effects can contribute substantially to reproductive success and thus population dynamics in Arctic goose populations (Marra, Hobson, & Holmes, 1998; Norris, 2005).

The extent to which climate change affects population dynamics also depends on a species' life history (Sæther et al., 2013). In long-lived species such as geese, population growth is often more sensitive to variation in survival than reproduction. Consequently, reproduction may be more susceptible to environmental variability (Gaillard & Yoccoz, 2003; Morris & Doak, 2004) and therefore climate change (Koons, Gunnarsson, Schmutz, & Rotella, 2014). It is also crucial to account for intrinsic regulation of population dynamics through density dependence when studying the effects of environmental variation (Sæther et al., 2006). Total flyway population sizes have been steadily increasing in most European Arctic-nesting goose populations, largely due to hunting bans since the 1950s (Fox & Madsen, 2017) and shifts in agriculture (Fox & Abraham, 2017). This increase has resulted in range expansion across the Arctic (Kondratyev, Zaynagutdinova, & Kruckenberg, 2013; Owen & Norderhaug, 1977). While local density-dependent effects on reproduction have been found in some populations (Bruggeman, Swem, Andersen, Kennedy, & Nigro, 2015; Ebbinge, Heesterbeek, Ens, & Goedhart, 2002; Layton-Matthews et al., 2019), density dependence may also be expected to affect survival at other stages in the annual cycle (Frederiksen & Bregnballe, 2000).

Arctic nesting geese play a key trophic role both as herbivores (Bazely & Jefferies, 1989; Fujita & Kameda, 2016) and prey (Bêty, Gauthier, Korpimäki, & Giroux, 2002), providing nutrient transfer within and between temperate and Arctic ecosystems (Hahn, Loonen, & Klaassen, 2011; Hessen, Tombre, van Geest, & Alfsnes, 2017). Substantial differences in local population trends of geese at their Arctic breeding grounds have been reported (Jensen et al., 2008; Lameris et al., 2018; Morrissette et al., 2010). Disentangling the drivers of these trends is key to a predictive understanding of future climate change implications. Besides the potential issue of mismatch in migratory timing with peak food abundance (Dickey et al., 2008; Kölzsch et al., 2015; Lameris et al., 2017), future climate change will likely disrupt other processes affecting reproduction and survival, for instance through trophic interactions (Ims, Jepsen, Stien, & Yoccoz, 2013). Here, we assess the contributions of climate, trophic interactions and density dependence to population dynamics of a local, non-hunted population of Svalbard barnacle geese, *Branta leucopsis*. Using individual-based mark–recapture data, we determine the main drivers of each reproductive stage (egg laying, hatching and fledging) and age class-specific survival, across their annual cycle. We quantify the contributions of direct and indirect drivers to population growth using a retrospective perturbation analysis and investigate how temporal trends in environmental variables influence population growth.

2 | MATERIALS AND METHODS

2.1 | Study population

The Svalbard barnacle goose population overwinters at Solway Firth, Scotland (UK; 55°N, 3.30°W), before flying to Svalbard for breeding in summer, with a spring stopover at Helgeland on the coast of mainland northern Norway (65°45′N, 12°E; Figure 1). Barnacle geese are close to the capital end of the capital–income breeding spectrum, investing between 23% and 88% of body stores acquired further south in egg production (Hahn et al., 2011). We studied a population breeding close to the settlement of Ny-Ålesund, northwestern Svalbard (78°55′N, 11°56′E) that arrives in late May and nests on islands in the fjord (Kongsfjorden). Hatching occurs around the 1 July (range: 19 June–19 July) and after hatching, families leave the nesting islands to forage along the coast. Offspring fledge at the end of August and individuals leave the breeding grounds in September (Figure 1). Barnacle geese typically begin breeding as 2 year olds (Forslund & Larsson, 1992; Owen, 1980).

2.2 | Data collection

Individual mark–recapture data from both sexes were collected from the nesting islands and coastal area around Ny-Ålesund (see Section 2.2). Using these data, we assessed the effects of climate, population size and predation (see Section 2.3) on three stages of reproduction (egg laying, hatching and fledging), as well as on apparent survival of fledglings (0 year old) and adults (1–28 years old). We identified the
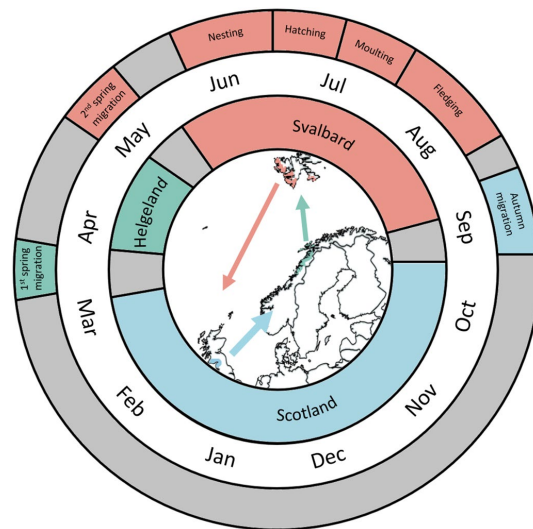
FIGURE 1 Migration route and timing of key events for Svalbard barnacle geese. Barnacle geese overwinter at Solway Firth, Scotland (blue), before travelling to western Svalbard for breeding (pink) via a stopover on the coast of mainland Norway (green). The timing of migrations and reproductive events (nesting, hatching, moulting and fledging) are shown in the outer circle (NB: failed breeders can moult earlier than shown here)

best models with covariates of reproduction using a path analysis framework and model selection (see Section 2.4) and determined the best-fitting survival model using model selection (see Section 2.5). We developed a population matrix projection model using the best-fitting models of vital rates, to quantify the contribution of covariates to population growth using a retrospective perturbation analysis (see Section 2.6).

The study area consists of two nesting islands, Storholmen and Prins Heinrichsøya, and the area close to the settlement of Ny-Ålesund, where goose families forage on tundra vegetation. The analysis was conducted on individual-based data from 1990 to 2017 (ringing of individuals began in 1989). Three thousand two hundred and ninety nests were monitored over this 28 year period. The islands were visited at 1 or 2 day intervals during the nesting period. Females with a clutch (*n* = 5,828) were identified and the clutch size (maximum number of eggs per nest) was recorded (*n* = 2,111). Data on clutch size were not recorded in the years 1994, 1997, 2000, 2002 and 2004 as the islands were not visited.

Over the study period, 3,487 individuals (goslings and older birds) have been caught around Ny-Ålesund and ringed with unique, engraved colour and metal rings, during the moulting phase in July and early August. During a catch, sex was determined by cloacal inspection. During the brood-rearing phase in July–August, twice-daily ring readings took place and whether a female had any offspring

(n = 5,872) and the number of goslings associated with the parent was recorded (n = 2,799). The maximum number of fledged goslings per female was recorded in mid-August (n = 1,976). Observational data for modelling hatching and fledging were not recorded for the year 2004. Annual sample sizes for each parameter are shown in Appendix S1.

2.3 | Covariates

We included covariates describing population size, weather and predation that could affect reproductive and survival rates over the annual cycle, for the years 1990–2017.

2.3.1 | Scotland: Wintering grounds

For the wintering period in Scotland, mean daily minimum and maximum temperature and precipitation data were taken from the Eskdalemuir weather station (55°39′N, 3°21′W), 40 km from Solway Firth, provided by the UK Meteorological Office (metoffice.gov.uk, 2018). Annual averages were calculated for the period October–March ($T_{scot,min}$, $T_{scot,max}$, P_{scot}; minimum and maximum temperatures were used since mean temperature values were not available). Svalbard flyway population size (N_{scot}), recorded at the wintering grounds in Scotland (Trinder, 2014; WWT, 2017), was included to determine whether density-dependent effects at the wintering grounds, via flyway population size, affected survival.

2.3.2 | Helgeland: Spring stopover site

For the spring stopover site at Helgeland, daily mean temperature and precipitation values for the period April–May were based on data from the Vega weather station (65°38′N, 11°52′E), within the spring range of barnacle geese. Annual means for the period April–May were calculated from the daily data ($T_{helg,am}$, $P_{helg,am}$). We also tested for an effect of the sum of positive temperatures above 6°C ($T_{helgsum6}$), since net grass growth is positive above this threshold (Prop, Black, Shimmings, & Owen, 1998). Data were obtained from the Norwegian Meteorological Institute (eklima.met.no, 2018).

2.3.3 | Svalbard: Breeding grounds

Covariates describing initial conditions at the breeding grounds (Ny-Ålesund, Svalbard) included cumulated snowfall from November to April ($snow_{sval}$, see Peeters et al., 2019) and date of spring onset (range: 13 May–21 June). Spring onset (SO_{sval}) describes the date (Julian day) at which the 10 day smoothed daily temperature crossed 0°C and remained above this threshold for at least 10 days (Le Moullec, Buchwal, van der Wal, Sandal, & Hansen, 2019). Daily mean temperature and precipitation data were used to calculate averages for mid-June to mid-July ($T_{sval,jj}$, $P_{sval,jj}$) and mid-July to mid-August ($T_{sval,ja}$, $P_{sval,ja}$). These covariates may influence conditions during hatching and fledging since mean temperature is a good predictor of plant phenology, while variation in rainfall relates to plant growing conditions (Jia, Epstein, & Walker, 2009; Prop & Black, 1998), potentially explaining variation in reproduction via indirect effects on food resource availability. Data were taken from the manned Ny-Ålesund weather station, operated by the Norwegian Meteorological Institute. Annual estimates of adult numbers in the study population around Ny-Ålesund (i.e. a subset of the total Svalbard breeding population) were included ($N_{sval,ad}$), to test for density-dependent effects (see Layton-Matthews et al., 2019 for details). The Arctic fox is the main predator of eggs and goslings, but also adults (Eide, Stien, Prestrud, Yoccoz, & Fuglei, 2012; Fuglei, Øritsland, & Prestrud, 2003; Pedersen et al., 2018). Consequently, gosling survival can be strongly influenced by fox predation (Loonen et al., 1998; Morrissette et al., 2010). We used a measure of Arctic fox predation (fox_{sval}) around Ny-Ålesund, based on annual records of the proportion of known den sites with pup production during the summer period from 1993 to 2017 (the annual Arctic fox monitoring program of the Norwegian Polar Institute). We assumed a linear increase from zero dens with pups in 1990 to 1993, since data were not available for 1991 and 1992 (Fuglei et al., 2003).

In a post hoc analysis, we investigated the correlations between climate variables included in the best-fitting reproductive models and variables describing the timing of snow melt, the timing of plant growth onset and plant productivity. To assess whether the estimated spring onset date (SO_{sval}) was a good proxy for timing of snow melt (i.e. when nest sites become available), we regressed SO_{sval} against a measure of the timing of snow melt at Ny-Ålesund for the years 1993–2016 (Maturilli, Herber, & König-Langlo, 2015). We regressed $T_{sval,jj}$ against a measure of the onset of the plant growing season, defined as the mean (Julian) date when the pixel-specific Normalized Difference Vegetation Index (NDVI) values exceeded 70% of mid-summer NDVI (Karlsen, Anderson, Van der Wal, & Hansen, 2018; Karlsen, Elvebakk, Høgda, & Grydeland, 2014), which was available for the years 2000–2014. $P_{sval,ja}$ was regressed against average standing crop of *Poa arctica*, an important food source for barnacle geese (i.e. a proxy for food availability). Repeated measurements were taken between July and August from exclosures (to prevent grazing), as part of a long-term plant experiment at Ny-Ålesund for the years 2004–2016 (Appendix S2).

2.4 | Reproduction

Reproduction was modelled in three stages to investigate the step-wise mechanisms determining recruitment of fledglings. Egg laying (C and E) was based on data from the nesting islands and (post-) hatching (H and G) and fledging (F) were based on data from ringed individuals around Ny-Ålesund.

Two variables were used to describe the egg laying phase, C and E, where C is the proportion of nesting females observed with a clutch, and E is the number of eggs per clutch. To estimate C, data on whether a female was observed with at least one egg in the nest (0/1) were fitted as a binomially distributed response variable. To estimate E, data on the number of eggs per clutch (range:

1–9) were fitted as a normally distributed response variable. The variables H and G quantified the average gosling production per female breeder. H, hatching success, is the estimated proportion of females with at least one gosling around Ny-Ålesund. Observation data were fitted using a binomial distribution for the response. G is the expected number of goslings per successful female and data were modelled with a Poisson distribution (note that 'hatching' refers to the first observation of a female with goslings when they return from the nesting islands). F describes the proportion of goslings fledging and data were modelled with a binomial distribution. All models were fitted as (generalized) linear mixed-effects models, with female ID and year as random effects in addition to other covariates. All models were fitted using canonical link functions. Since reproductive success in barnacle geese has been shown to increase until age 5 (Black, Prop, & Larsson, 2014; Forslund & Larsson, 1992), we tested for age (class) effects in an initial analysis. We began with a model with five age classes (where the fifth class includes individuals ≥5 years old) and progressively reduced the number of classes. Akaike's information criterion adjusted for small sample sizes (AIC_c) was used to identify the best-fitting age model (Burnham & Anderson, 2002).

Covariates included in the candidate model set of egg laying (C and E) included $T_{scot,min}$, $T_{scot,max}$, P_{scot} and N_{scot} in Scotland, $T_{helg,am}$, $P_{helg,am}$ and $T_{helgsum6}$ at Helgeland (i.e. carryover effects) and SO_{sval}, $snow_{sval}$ and $N_{sval,ad}$ on Svalbard. The candidate model set of hatching (H and G) included $T_{sval,jj}$, $P_{sval,jj}$, fox_{sval} and $N_{sval,ad}$ and the candidate model set of fledgling probability (F) included $T_{sval,ja}$, $P_{sval,ja}$, fox_{sval} and $N_{sval,ad}$.

Confirmatory path analysis (Shipley, 2000, 2009) was used to identify the important intrinsic and extrinsic drivers of reproduction. We constructed a path diagram with all proposed links between covariates and response variables and tested the proposed independence relationships among variables using d-separation tests (Appendix S3; Shipley, 2009, 2016). To account for dependencies among reproductive stages, the response variable E was entered as a predictor in the models of the later reproductive stages H and G, and G was included in the model of F (Appendix S4.1). Best-fitting models for each of the five reproductive parameters were identified separately (C, E, H, G and F). To evaluate the best-fitting model of reproduction with covariates, we ranked models according to their AIC_c and also examined whether they explained a significant amount of deviance by performing an analysis of deviance using the package 'afex' (Singmann, Bolker, & Westfall, 2015).

Means and 95% confidence intervals were calculated for all covariate effects in the best-fitting models of each response variable. (Generalized) linear mixed-effects models were modelled in R, version 3.5.0 (R Core Team, 2018) using the package 'lme4' (Bates, Mächler, Bolker, & Walker, 2014), and d-separation tests were performed using 'piecewiseSEM' (Lefcheck, 2016). All covariates were standardized, including reproductive parameters when entered as explanatory variables.

2.5 | Survival

We estimated age-specific, apparent (we could not distinguish between mortality and permanent emigration) survival rates based on mark–recapture data from Ny-Ålesund. Survival rates were estimated with a Cormack–Jolly–Seber framework, in the RMark interface (Laake, 2013) for program MARK (White & Burnham, 1999). Survival rates were modelled for two age classes, fledglings (ϕ_f) and adults (ϕ_{ad}), where ad is a pooled age class from 1 to 28 years (i.e. maximum observed age) old. Survival rates were not found to be sex specific. Detection probability was modelled as sex, but not age, specific since female philopatry is often higher than male philopatry (Black et al., 2014) and no effect of age was found in a previous analysis of this study population (Layton-Matthews et al., 2019). Accordingly, this analysis also showed that detection probabilities were higher for females (mean: 0.62; 95% confidence interval: 0.60, 0.65) than males (0.55; 0.54, 0.56). Survival was modelled from August (i.e. at the time of fledgling) until August the following year. Based on a survival model with two age classes, ϕ_f and ϕ_{ad}, we developed a candidate model set with all combinations of standardized covariates from the winter and spring locations (see Section 2.3) that were not highly correlated.

Covariates from the wintering grounds and the spring stopover site were included in the candidate model set of survival (Appendix S4.2), since substantial natural mortality occurs during migration and particularly the autumn migration when individuals fly directly from Svalbard to Scotland (Owen & Black, 1989, 1991b). Summer conditions likely influence body condition and mortality during the autumn migration, however, since we were not able to distinguish seasonal survival rates, only covariates from later stages in the annual cycle (i.e. the wintering grounds and spring stopover site) were included. Arctic fox abundance (fox_{sval}) was included as a potential cause of mortality during the summer prior to the census. To determine the best-fitting additive model of survival with covariates, we first ranked models according to AIC_c and then performed an analysis of deviance in program MARK. After identifying the best additive model, we determined the best model with interaction effects between age class and covariates using the same approach.

To investigate the potential influence of climate change on reproduction and survival, we tested for temporal trends in the estimated vital rate parameters and covariates from the best-approximating models, by fitting linear regressions with a continuous year effect as an explanatory variable.

2.6 | Population dynamics

We constructed a 2 × 2 population projection matrix, based on a post-breeding census, corresponding to the fledgling and adult age classes. In accordance with a post-breeding census, recruitment of fledglings included adult (i.e. breeder) survival, ϕ_{ad}, since they must survive almost a full year before reproducing. The top left matrix element is zero since 1 year old birds generally do not reproduce. The reproductive rates H (which was no longer conditional on C and E), G and F were divided by 2 to calculate the number of fledglings per

female. C and E were not included, since this would inflate reproductive rates (both E and H are the expected number of offspring per female at different stages of the reproductive cycle). Consequently, covariates influencing C and E were included as effects on H instead. The resulting population projection matrix was

$$\begin{bmatrix} 0 & \dfrac{(\phi_{ad} \times H \times G \times F)}{2} \\ \phi_f & \phi_{ad} \end{bmatrix}.$$

We calculated the asymptotic population growth rate (λ) as the dominant eigenvalue of the population projection matrix, calculated at the mean value of covariates included in the best-fitting models. We accounted for uncertainty in model regression coefficients by assuming that regression coefficients arise from a multivariate normal distribution, where the coefficients and variance–covariance matrix from each model provided the means and variance–covariance matrix (Gelman & Hill, 2006). Vital rates were predicted using the regression coefficients sampled 10,000 times from the multivariate normal distribution. Population matrices were constructed with each sample of vital rates to calculate the mean population growth rate with 95% confidence intervals. Using this approach, we determined the change in λ when vital rates in the population matrix were predicted at a low value of a covariate (5th quantile) and a high value (95th quantile). This difference in λ was decomposed into vital rate contributions using a life table response experiment (LTRE), a common retrospective perturbation analysis (Caswell, 1989; Horvitz, Schemske, & Caswell, 1997). The contribution of a covariate was calculated as the product of (a) the difference in the affected vital rate between the two matrices (5th vs. 95th); and (b) the sensitivity of λ to that vital rate. Sensitivities were calculated analytically using the chain rule (Caswell, 2001). Analysis of the projection matrix was conducted in R using our own code and the 'popbio' package (Stubben & Milligan, 2007).

3 | RESULTS

3.1 | Reproduction

The best-fitting path model for reproduction included dependencies among reproductive phases (i.e. egg laying, hatching and fledging),

as well as effects of population size, climate, predation and carryover effects from the spring stopover site and wintering grounds (Figure 2). None of the response variables were found to be age dependent.

The model of clutch success (C) with the lowest AIC_c included date of spring onset (SO_{sval}), where a later onset had a negative effect (Figure 2). This model also included positive carryover effects of the average maximum daily temperature from October to March ($T_{scot,max}$) at the wintering grounds in Scotland and mean April–May precipitation at the spring stopover site at Helgeland ($P_{helg,am}$; Appendix S5.1.1). However, the difference between the lowest AIC_c model and one with only SO_{sval} was negligible ($\Delta AIC_c = 0.35$). $T_{scot,max}$ and $P_{helg,am}$ were only present in five and four of the top nine models, respectively, and did not explain a significant amount of variance, based on the analysis of deviance (Appendix S5.2). However, the difference in AIC_c with SO_{sval} and the null model was greater than 2 ($\Delta AIC_c = 2.40$). Therefore, the best-approximating model of C only included an effect of SO_{sval}.

The model of clutch size (E) with the lowest AIC_c also included a negative effect of SO_{sval}, a negative carryover effect of population size at the wintering grounds (N_{scot}) and a positive effect of $P_{helg,am}$ (Appendix S5.1.2; Figure 3a–c). SO_{sval} and $P_{helg,am}$ were present in all nine of the top models and explained a significant amount of variation (Appendix S5.2). N_{scot} was present in eight of nine of the top models and explained a significant amount of deviance ($p = .03$). The difference in the lowest AIC_c model and a model without N_{scot} was 1.64, and so the best-approximating model of E included SO_{sval}, $P_{helg,am}$ and N_{scot}.

The lowest AIC_c model of hatching success (H) included positive effects of clutch size (E), which was present in all top 10 models, and mid-June to mid-July temperature ($T_{sval,jj}$; Figure 3d). Although the next best model ($\Delta AIC_c = 1.04$) only included an effect of E, $T_{sval,jj}$ was present in four of five top models and the amount of variance it explained was close to being significant at the .05 level ($p = .08$). A negative effect of $N_{sval,ad}$ was only included in 40% of the top nine models (Appendix S5.1.3) and so the best-approximating model of H included E and $T_{sval,jj}$.

The lowest AIC_c model of the number of goslings (G) included a positive effect of E and weak negative effects of $N_{sval,ad}$ and fox_{sval}.
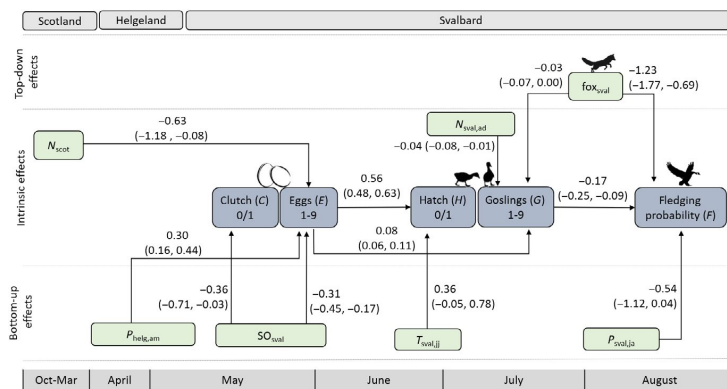
FIGURE 2 Best-fitting path model diagram for the reproductive stages, with standardized slope coefficients and associated 95% confidence intervals in brackets
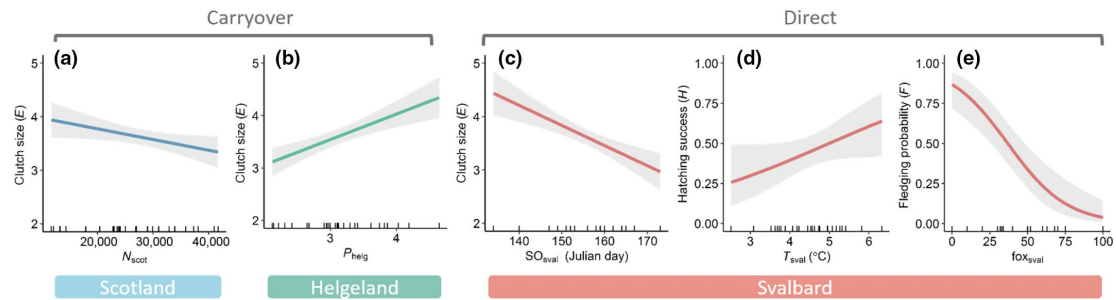
FIGURE 3 Model predictions with 95% confidence intervals, describing (a, b) the carryover effects of (a) flyway population size in Scotland (N_{scot}) and (b) spring precipitation at Helgeland ($P_{helg,am}$), and (c–e) the direct effects of (c) the onset of spring (SO_{sval}) at the Svalbard breeding grounds on clutch size (E), (d) summer temperature on Svalbard ($T_{sval,jj}$) on hatching success (H) and (e) fox abundance (fox_{sval}) on fledging probability (F). Data distributions are shown on the x-axis as rugs

FIGURE 4 Model predictions with 95% confidence intervals describing the effect of (a) Scotland winter temperature ($T_{scot,min}$) and (b) total flyway population size (N_{scot}) on the survival rate of fledglings (ϕ_f) and adults (ϕ_{ad}). Data distributions are shown on the x-axis as rugs
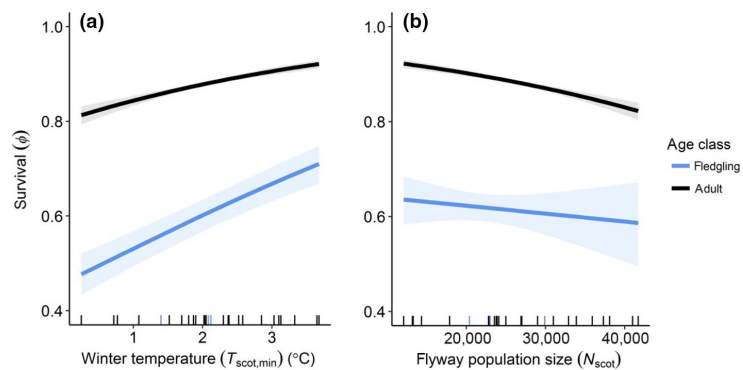
E was consistently present in all 10 of the top-ranking models, while $N_{sval,ad}$ was present in 60% and fox_{sval} in 70% (Appendix S5.1.4). Both $N_{sval,ad}$ and fox_{sval} were close to, but not, significant at the .05 level ($P_{Nsval,ad}$ = 0.07; $P_{foxsval}$ = 0.08). A weak positive effect of $T_{sval,jj}$ and a weak negative effect of $P_{sval,jj}$ were both present in 40% of the top 10 models. Since $N_{sval,ad}$ and fox_{sval} were both consistently present in the top models and close to being significant, we considered the best-approximating model of G to include E, $N_{sval,ad}$ and fox_{sval}.

The lowest AIC_c model of fledging probability (F) included negative effects of G, fox_{sval} (Figure 3e) and mid-July to mid-August precipitation on Svalbard ($P_{sval,ja}$; Appendix S5.1.5). G was included in all eight top-ranking models, fox_{sval} was included in seven of eight and the amount of variance both covariates explained was significant ($p < .01$). Although the second-best model did not include $P_{sval,ja}$ (ΔAIC_c = 1.29) and $P_{sval,ja}$ did not explain a significant amount of variation at the .05 significance level ($p = .07$), this variable was included in three of four top-ranked models with a consistently strong negative effect. Consequently, we considered the best-approximating model of F to include G, fox_{sval} and $P_{sval,ja}$.

There was a strong positive correlation between SO_{sval} and the timing of snow melt, where the standardized correlation coefficient was 0.65 (0.24, 1.07) (R^2 = 0.31), and a negative correlation between mid-June to mid-July temperature ($T_{sval,jj}$) and the date of plant growth onset (−0.78;

−1.15, −0.41; R^2 = 0.61). $T_{sval,jj}$ was also strongly negatively correlated (−0.89; −1.06, −0.72) with the date at which temperature sum on Svalbard reached 180°C (plant growing degree-days, GDD) (Van Wijk et al., 2012). There was also a negative correlation (−0.64; −1.06, −0.21; R^2 = 0.49) between mid-July to mid-August precipitation and the standing crop of the grass *P. arctica*, an important food species for barnacle geese (Appendix S2).

3.2 | Survival

Apparent survival was lower for fledglings (0.62; confidence interval: 0.59, 0.65) than for adults (0.83; 0.80, 0.84). The best-fitting model of survival included a positive effect of minimum winter temperature in Scotland ($T_{scot,min}$) and a negative effect of flyway population size in Scotland (N_{scot}; Figure 4a), as well as weak negative effects of fox abundance at Ny-Ålesund (fox_{sval}) and precipitation at Helgeland ($P_{helg,aprmay}$) and a positive effect of the sum of positive temperatures above 6°C at Helgeland ($T_{helg,sum6}$; Appendix S5.3). However, only $T_{scot,min}$ and N_{scot} explained a significant amount of variance based on the analysis of deviance (Appendix S5.4). A model with an interaction effect between age class and N_{scot} was a better fit than the best additive model (ΔAIC_c = 4.18) since N_{scot} had a more negative effect on adults than fledglings (Figure 4b; Appendix S5.5).

3.3 | Temporal trends

Date of spring onset (SO$_{sval}$) became earlier over the study period (−0.05; −0.10, −0.01) and was a predictor of clutch success and clutch size, which also exhibited positive temporal trends (C = 0.05; 0.01, 0.11, E = 0.06; 0.00, 0.11; Figure 5a). Mid-June to mid-July temperature ($T_{sval,jj}$) exhibited a positive temporal trend (0.06; 0.03, 0.11), as did hatching success, H, (0.07; 0.01, 0.12), while the number of goslings (G) did not show a trend (0.01; −0.06, 0.07). There was a tendency for a trend of increasing fox abundance (0.03; −0.02, 0.08), while the probability of fledging (F) declined dramatically over the study period (−0.06; −0.12, −0.01). Total flyway population size (N_{scot}) showed a consistent increase over the study period (0.12; 0.11, 0.14), while both fledgling, ϕ_f, and adult, ϕ_{ad}, survival exhibited significant

declines (Figure 5b). Other covariates did not exhibit a clear trend; summer precipitation in Svalbard, $P_{sval,ja}$, (0.00; −0.05; 0.05), mean minimum temperature in Scotland, $T_{scot,min}$ (0.00; −0.04, 0.05; Appendix S6), and adult population size in Svalbard, $N_{sval,ad}$ (0.03; −0.02, 0.08; Figure 5c).

3.4 | Population dynamics

The mean asymptotic population growth rate (λ) was 1.05 (0.92, 1.17) based on vital rate estimates with covariates at their observed mean values. Best-fitting models of vital rates with covariates used in this analysis are shown in Appendix S4.3. λ was more sensitive to adult survival than to reproductive rates (H, G, F) and fledgling survival (Appendix S7).
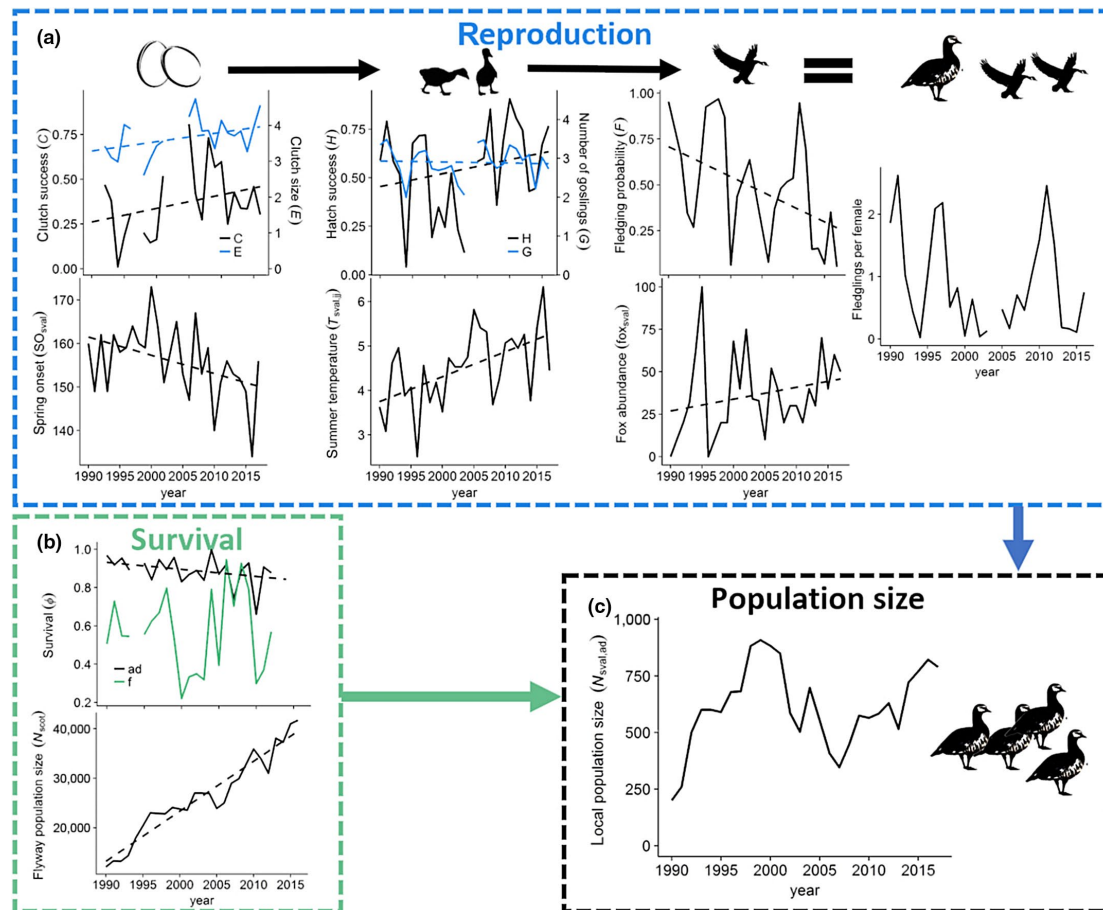
FIGURE 5 Trends in barnacle geese parameters and associated explanatory variables. For reproduction, from left to right: (a) clutch success (C) and clutch size (E) the predictor spring onset (SO$_{sval}$); hatch success (H) and the predictor mid-June to mid-July temperature ($T_{sval,jj}$); fledging probability (F) and the predictor Arctic fox abundance (fox$_{sval}$); and number of fledglings per female ($H \times G \times F$). For survival (b), apparent survival rates of fledglings (ϕ_f) and adults (ϕ_{ad}; based on a model with additive age class and time effects) and the predictor counts of total flyway population size in Scotland (N_{scot}). For local population size (c), annual estimates of adult numbers in the local Svalbard breeding population ($N_{sval,ad}$)

TABLE 1 Mean population growth rates estimated at the 5th (λ_{5th}) and at the 95th (λ_{95th}) quantile of important covariates affecting one or more vital rates. 95% credible intervals are shown in brackets

Covariate	Covariate description	Vital rate	λ_{5th}	λ_{95th}
SO_{sval}	Julian day of spring onset, Svalbard	H	1.09 (1.01, 1.18)	1.01 (0.96, 1.08)
$T_{sval,jj}$	(Mid) June–July temperature, Svalbard	H	1.02 (0.96, 1.09)	1.07 (1.00, 1.15)
$P_{helg,am}$	April–May precipitation, Helgeland	H	0.98 (0.93, 1.04)	1.12 (1.03, 1.20)
fox_{sval}	Fox abundance proxy, Svalbard	G, F	1.15 (1.08, 1.21)	0.93 (0.90, 0.97)
$N_{sval,ad}$	Local adult population size, Svalbard	G	1.06 (0.99, 1.13)	1.04 (0.98, 1.10)
$P_{sval,ja}$	(Mid) July–August precipitation, Svalbard	F	1.09 (1.02, 1.16)	0.98 (0.93, 1.04)
N_{scot}	Flyway population size, Scotland	ϕ_f, ϕ_{ad}	1.10 (1.03, 1.17)	1.01 (0.94, 1.07)
$T_{scot,min}$	Min. winter temperature, Scotland	ϕ_f, ϕ_{ad}	0.97 (0.92, 1.03)	1.10 (1.03, 1.18)
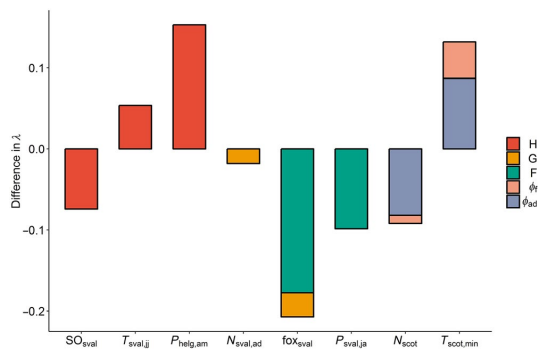
FIGURE 6 The difference in population growth rate λ when covariates on the x-axis were calculated at the 95th versus 5th quantile of their observed range. Colours represent the relative contribution of associated vital rates (H, G, F, ϕ_f and ϕ_{ad}) to these differences in the population growth rate

The population growth rate was reduced when vital rates were estimated at an early (95th quantile) and late (5th quantile) date of spring onset in Svalbard (SO_{sval}), which was attributed to reduced hatching success (H) rather than egg laying which could not be included in the analysis of the population projection matrix (Table 1; Figure 6). $T_{sval,jj}$ had a similarly large effect on λ, while carryover effects of $P_{helg,am}$ had a larger positive effect via hatching success (Table 1). Increased Arctic fox abundance (fox_{sval}) reduced λ from positive to negative growth, mostly through effects on fledging probability (F), but also on G (Figure 6). Minimum winter temperature in Scotland ($T_{scot,min}$) had a strong positive effect on survival rates and, thereby, a large contribution to variation in λ, predominantly through adult survival (Figure 6).

4 | DISCUSSION

Here, we have demonstrated how rapid climate change in high-arctic Svalbard increased barnacle goose egg production and hatching success, through positive effects of advanced spring onset and warmer summers, respectively (Figures 2, 3, and 5). However, these positive effects of climate change on early reproduction were offset by a temporal decline in fledging probability due to increased predator abundance, strongly affecting population growth (Figures 5 and 6). Although there was a positive effect of winter temperatures at Solway Firth on adult survival (Figure 4) and a positive carryover effect of rainfall at the spring stopover site on egg production (Figure 3), these drivers outside the breeding season exhibited no trend during the study. In contrast, a steady increase in total flyway population size caused negative trends in overwinter survival and carryover effects on egg production. As a likely net result of these opposing trends in population-dynamic drivers, across the annual cycle, there was no trend in local population size (Figure 5).

4.1 | Breeding season

Due to the short Arctic summer and constrained plant growing period, the time window for reproduction is highly constrained in Arctic herbivores. Timing of breeding is therefore one of the main determinants of reproductive success in Arctic nesting geese (Cooke, Rockwell, & Lank, 1995; Skinner, Jefferies, Carleton, Abraham, & Dagger, 1998). Capital breeding is a common strategy in high latitude environments (Gustine, Barboza, & Lawler, 2010; Kerby & Post, 2013), allowing feeding and reproduction to be partially decoupled in space and time (Jönsson, 1997; Newton, 1977; Sainmont, Andersen, Varpe, & Visser, 2014). For Arctic geese, this allows them to allocate nutrients from the wintering grounds and spring stopover sites to reproduction (Drent & Daan, 1980; Hahn et al., 2011).

In this study, clutch success and clutch size were negatively affected by the date of spring snow melt. The timing of snow melt largely dictates when individuals can start breeding and is an important determinant of breeding success in Arctic geese (i.e. greater snow geese, *Chen caerulescens*, Reed, Gauthier, & Giroux, 2004; pink-footed geese, *Anser brachyrhynchus*, Madsen et al., 2007; pale-bellied brent geese, *Branta bernicla hrota*, Barry, 1962). Later spring onset also reduced clutch sizes, likely since individuals that delay nesting use retained reserves for their own maintenance instead of for egg production (Davies & Cooke, 1983; Ryder, 1970).

Long-distance migrants occupy several spatially distinct locations with contrasting habitats, and individuals can therefore be affected by multiple climate and density regimes across their annual cycle (Norris & Taylor, 2005). Consequently, the combination of reproductive and migratory strategies can result in a large contribution of carryover effects to population dynamics (Inger et al., 2010; Morrissette et al., 2010). In our study population, spring precipitation had a positive effect, and overwintering population size had a negative effect, on clutch size. Although food resources at the spring stopover site on mainland Norway are generally abundant due to a predominance of agricultural land, a rainier spring is possibly associated with improved food quality since it slows down the plant growing season, resulting in higher leaf protein content (Bø & Hjeljord, 1991; Doiron, Gauthier, & Lévesque, 2014; Jonasson, Bryant, Chapin III, & Andersson, 1986). This, in turn, improves body condition and energy stores in herbivores (Mysterud, Langvatn, Yoccoz, & Chr, 2001; Ydenberg & Prins, 1981).

In many northern herbivores, spring plant phenology controls the timing of reproduction and therefore reproductive success (Langvatn, Albon, Burkey, & Clutton-Brock, 1996; Post, Bøving, Pedersen, & MacArthur, 2003; Sedinger & Raveling, 1986). Warmer summer temperatures were negatively correlated with the date of plant growth onset and increased hatching success in this barnacle goose population. Similar effects of the timing of plant growth onset have been found in other goose populations (Cooke et al., 1995; Prop & de Vries, 1993). Warmer temperatures advance the timing of plant availability and can enhance plant productivity (Jia et al., 2009) which, at such high latitudes, does not necessarily mean a strong reduction in forage quality. For nesting geese, this can reduce their foraging time away from the nest, increasing hatching success (Black et al., 2014; Greve, Elvebakk, & Gabrielsen, 1998; Prop & de Vries, 1993). In support of our findings, several breeding populations of waterfowl (including barnacle geese) in Zackenberg, eastern Greenland, suffered almost complete breeding failure because of extremely late snow melt and onset of plant growth in 2018 (Jannik Hansen, personal communication).

In highly seasonal environments such as the high Arctic, the dynamics of herbivore populations are strongly linked to seasonality in resource availability since their body condition, and thus reproductive success, is dependent on when vegetation is available (Albon et al., 2017; Douhard et al., 2013; Langvatn et al., 1996; Sæther, 1997). Many species of herbivores, and especially waterfowl such as geese, are precocial, that is, offspring leave the nest early and in a relatively developed state. Goslings are largely dependent on their own resource acquisition and are vulnerable to fluctuations in food (vegetation) resources (Lindholm, Gauthier, & Desrochers, 1994; Loonen, Bruinzeel, Black, & Drent, 1999). Plant productivity has been identified as a key driver of gosling growth rates in several species and limited food supply increases pre-fledging mortality (Lindholm et al., 1994; Loonen, Oosterbeek, & Drent, 1997; Williams, Cooch, Jefferies, & Cooke, 1993). Increased precipitation during the peak plant growing season had a negative effect on fledging success in this study population. The mechanisms behind this remain uncertain but could be related to cloud clover and generally poorer plant growing conditions, reducing the standing crop of an important food source, the grass *P. arctica*.

However, these effects of weather in early reproductive phases were largely offset by predation of goslings. Predation by Arctic foxes is the main top-down regulator of reproduction in many Arctic nesting goose populations, causing annual fluctuations in egg productivity and gosling survival (Bêty et al., 2002; Gauthier et al., 2004; Loonen et al., 1998; Samelius & Alisauskas, 2000). In our study population, the brood-rearing phase is when offspring are most vulnerable to predation (Loonen et al., 1998) and increased local abundance of Arctic foxes over time had a dramatic negative effect on gosling survival (i.e. fledging success).

Previous studies of Arctic geese have indicated density-dependent effects during the breeding season (Cooch, Lank, Rockwell, & Cooke, 1989; Larsson & Forslund, 1994; Layton-Matthews et al., 2019), through competition for food (e.g. Larsson & Forslund, 1994; Loonen et al., 1997) and nesting sites (Ebbinge et al., 2002). This study lends some support for food competition as the main driver, since the number of goslings per parent (i.e. family size) had a negative effect on the proportion fledging. Barnacle geese provide parental care through vigilance and warming, and this parental care decreases with increasing family size (Forslund, 1993), which would then appear as 'negative density dependence'.

4.2 | Non-breeding season

Both weather and density-dependent effects at the wintering grounds caused annual variation in survival. Winter conditions influence body condition in Arctic herbivores via effects on resource availability (Albon et al., 2017; Guillemain, Elmberg, Arzel, Johnson, & Simon, 2008; Miller & Barry, 2009). Effects of varying overwinter resources are less well documented for migratory herbivores but could be important in terms of direct mortality as well as carryover effects later in the annual cycle. In Arctic geese, body reserves are fundamental for surviving migration (Klaassen et al., 2014; Owen & Black, 1989, 1991b; Prop & Black, 1998). Higher average daily minimum temperature in Scotland during winter increased survival rates of both fledglings and adults, increasing population growth. Poor weather conditions at the wintering grounds have been shown to reduce overwintering survival in other goose species (Kery, Madsen, & Lebreton, 2006; Owen & Black, 1991b; Schaub, Kania, & Köppen, 2005). Severe winters, with extended periods below freezing, reduce plant availability and productivity through

frost damage and increased snow cover (Fox, Elmberg, Tombre, & Hessel, 2017). Barnacle geese are probably most food limited in mid-winter, resulting in reduced body condition until initiation of plant productivity in February–March, prior to the spring migration from Scotland (Owen, Wells, & Black, 1992). A large proportion of natural mortality also likely occurs during autumn migration (Owen, 1982; Owen & Black, 1991a). However, in an East-Atlantic population of pale-bellied brent geese, survival was also extremely low in severe winters with food depletion (Clausen, Frederiksen, Percival, Anderson, & Denny, 2001) and in the Pacific black brant, *Branta bernicla*, mortality largely occurred during late spring due to disease, predation and starvation (Ward, Rexstad, Sedinger, Lindberg, & Dawe, 1997). Thus, although the mechanisms and timing vary, environmental conditions during the non-breeding season seem an important source of natural mortality and carryover effects on reproduction.

Despite the dramatic increases in Arctic goose populations globally, there has been little evidence of density regulation through flyway populations at the wintering grounds (Kery et al., 2006; Larsson & Forslund, 1994; Trinder, 2014). This is likely explained by continued range expansion in the Arctic, as well as temperate wintering grounds (Fox et al., 2010), and improved food quality due to the transition to agricultural land (Fox & Abraham, 2017), which has facilitated this continued growth. However, we observed a negative effect of the total flyway population on annual survival rates and a carryover effect on clutch size. Consequently, density dependence may have begun to play an increasing role in regulating goose population growth, although its effects are only apparent in local, well-established populations but not at the flyway population level (Layton-Matthews et al., 2019; Trinder, 2014). Survival estimates from populations at the wintering grounds are inflated by individuals from newly colonized areas in the Arctic, where resources are temporarily in excess. Thus, despite the increase in carrying capacity (Van Eerden, 1996), density-dependent processes at the wintering grounds may have important implications for future management of Arctic goose populations. Flyway population size affected survival more in adults than fledglings, whose autumn migration is a more likely cause of mortality (Owen & Black, 1989). However, the strength of the density dependence found here should be interpreted with caution, as removal of the trend from N_{scot} (i.e. accounting for increases in carrying capacity) reduced its effect on survival rates (to −0.04; −0.11, −0.01).

4.3 | Net implications of climate change

The dramatic warming of the Arctic (Stocker et al., 2014) has resulted in an earlier snow-free tundra, advanced plant phenology and increased productivity. We show that this has benefitted barnacle geese in the early reproductive stages by increasing clutch success, clutch size and hatching success over time. However, the potential benefits of advanced phenology likely depend on the capacity of Arctic geese to align their migratory cues (Lameris et al., 2017), thereby avoiding trophic mismatch. In some Arctic species, migratory

strategies are relatively dynamic (Clausen, Madsen, Cottaar, Kuijken, & Verscheure, 2018; Eichhorn, Drent, Stahl, Leito, & Alerstam, 2009; Lameris et al., 2017); however, migration timing is at least partially fixed (Kölzsch et al., 2015; Lameris et al., 2018; Van der Jeugd et al., 2009). The reliability of resources at spring stopover sites will also determine their ability to respond to future change (Fox et al., 2014; Prop, Black, & Shimmings, 2003). Furthermore, although the timing of spring onset and vegetation green-up contributed substantially to variation in population growth (i.e. the retrospective analysis), so did a change in predation pressure from Arctic foxes. Consequently, the potential benefits of an advancing and warming Arctic for early reproductive stages are offset by indirect climate change effects limiting later reproductive stages. The tendency for increasing fox numbers, which is likely the main explanation for the observed strong decline in fledging probability, seems mainly a result of the irruptive population of reindeer (*Rangifer tarandus platyrhynchus*) in this area, following their reintroduction (Aanes, Sæther, & Øritsland, 2000; Fuglei et al., 2003). Reindeer carcasses represent an important food source for Arctic foxes in winter and spring. High carcass availability in spring (e.g. following harsh winters) also boosts fox pup production (Hansen et al., 2013). Since the abundance of Svalbard reindeer is generally increasing because of climate warming (e.g. Albon et al., 2017), an overall higher fox density may be likely in the future. This would restrict growth in goose populations directly though the predation of eggs and juveniles (McDonald, Roth, & Baldwin, 2017) and potentially indirectly by increasing density-dependent effects through a reduction in the available foraging area for geese (Loonen et al., 1998). A steady increase in breeding populations of geese in general is likely having a further positive effect on fox pup overwinter survival (Ims et al., 2013). Additionally, recently increasing numbers of polar bears, *Ursus maritimus*, 'stranded' by the loss of sea ice, have resulted in severe declines in hatching success in some breeding populations of geese on Svalbard (Prop et al., 2015). Thus, increased predation pressure by Arctic foxes and polar bears—that is, indirect climate change effects—may counteract the benefits of climate warming for early stages of reproduction, contributing to the lack of a positive trend in local population size.

No temporal trend was observed in winter climate in Scotland. Nevertheless, moderately warmer and wetter winters are predicted for Scotland under future global warming, with fewer frost days and an earlier growing season (Jacob et al., 2014; Jenkins, Perry, & Prior, 2009). According to our results, this would reduce goose mortality with a large effect on local population growth. However, the consequences of warmer winters for plant productivity, and therefore barnacle geese, are still uncertain (Crawford, 1997; Kreyling, 2010).

In conclusion, current and near-future climate change involves contrasting trends in important environmental drivers across migratory stages and therefore does not necessarily pose a negative outlook for Arctic geese. Earlier springs and warmer summers appear beneficial for reproduction in populations where individuals can sufficiently adjust their phenology (but see Lameris et al., 2018), and even a slight future warming trend at the wintering grounds may increase survival. However, extrapolation

to future levels of warming is problematic (Bilt et al., 2019) and changes occurring further up the food web may counteract bottom-up benefits of Arctic warming. Additionally, and importantly, our results indicate that density regulation both at the breeding grounds in Svalbard and, especially, at the wintering grounds in the United Kingdom, will act to curb population growth caused by climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supporting information:

'Contrasting consequences of climate change for migratory geese: predation, density dependence and carryover effects offset benefits of high-arctic warming'

Kate Layton-Matthews, Brage Bremset Hansen, Vidar Grøtan, Eva Fuglei and Maarten J. J. E. Loonen

Appendix 1. Sample sizes for estimated reproduction and survival parameters.

Table S1. Annual sample size (N) for parameter *C, E, H, G, F*, ϕ_f and ϕ_{ad}. N_C is the total number of marked females observed on the nesting islands and N_E the number of females with a clutch. N_H is the number of females observed at Ny-Ålesund and N_G is the number of females with at least one gosling. N_F is the number of females observed with at least one fledgling. $N_{fledgling}$ describes the number of marked fledglings observed at Ny-Ålesund to estimate ϕ_f and N_{adult} is the number of marked adults to estimate ϕ_{ad}.

Year	Sample size						
	N_C	N_E	N_H	N_G	N_F	$N_{fledgling}$	N_{adult}
1990	54	16	54	33	33		101
1991			107	65	65	177	218
1992	210	55	186	70	70	107	389
1993	232	87	222	103	93	55	445
1994	267	9	257	12	7	1	516
1995	234	56	231	157	117	128	464
1996	279	82	273	168	155	228	561
1997			196	110	67	130	408
1998	331	67	257	43	18	89	655
1999	346	84	344	115	71	2	656
2000	426	97	381	86	74	5	891
2001	322	163	293	155	99	54	654
2002			209	58	47		482
2003	212	57	179	22	17	10	448
2004						15	309
2005	248	172	243	131	101	68	555
2006	227	109	219	114	63	6	491
2007	273	78	223	164	101	33	594
2008	193	120	174	59	25	6	395
2009	228	123	214	127	96	66	457
2010	252	110	218	164	87	54	492
2011	177	83	174	132	80	133	330
2012	222	112	184	128	95		413
2013	200	81	197	76	55	4	354
2014	214	93	188	87	55	1	392
2015	233	101	217	134	100	10	430
2016	262	96	248	164	106	177	458
2017	186	60	184	122	79		327

Appendix 2. Predictions of post-hoc linear regressions between environmental variables

The estimated correlation between (a) spring onset date and timing of snowmelt, (b) mid-June to mid-July temperature and onset of plant growth and (c) mid-July to mid-August precipitation and biomass of *P. arctica*. Timing of snow-melt at Ny-Ålesund was measured using satellite data (Maturilli, Herber & König-Langlo 2015). The measure of the onset of the plant growing season was defined as the mean (Julian) date when the pixel-specific Normalized Difference Vegetation Index (NDVI) values exceeded 70% of mid-summer NDVI. NDVI values were calculated from MODIS Terra data for a polygon of size 2.3 km close to Ny-Ålesund, which were available from Karlsen *et al.* (2014; 2018). The measure of average standing crop of *P. arctica* was taken from a long-term experiment at Ny-Ålesund. Measurements were taken during July to August from exclosures (to prevent grazing), the leaf length of four individual shoots was measured at five-day intervals, at ten exclosures, and standing crop was calculated as the average sum of leaf lengths per shoot (mm/shoot) over the growing season (Krikke 2014).
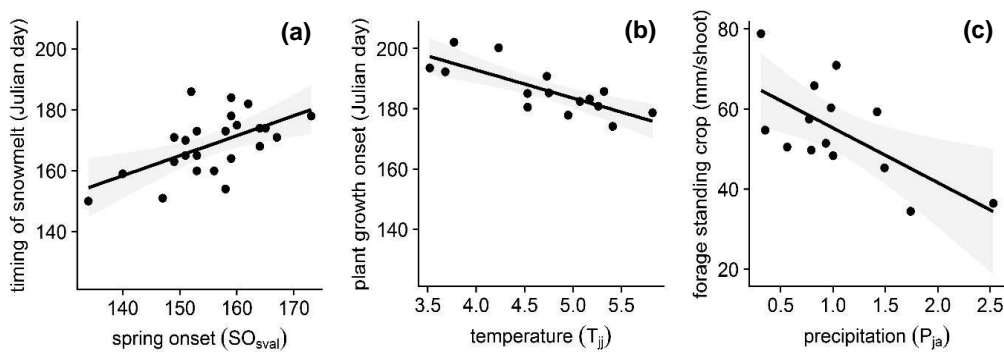
Figure S2. Predicted correlations between (a) timing of snow-melt and spring onset (b) onset of plant growth and temperature mid-June to mid-July, $T_{sval,jj}$, and (c) mid-July to mid-August precipitation, $P_{sval,ja}$, and biomass of *P. arctica* (i.e. average standing crop), shown as slopes with 95% confidence intervals estimated used the delta method (Powell 2007) with the data distribution.

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Appendix 3. D-separation tests and Fisher's C test for confirmatory path analysis

Confirmatory path analysis was used to identify the best model of reproduction, all proposed independence relationships among variables were tested using d-separation tests (Shipley 2009; Shipley 2016). Each d-separation gives the necessary conditions for two variables to be independent, conditional on a set of other variables. We determined a basis set of independence statements, containing all pairs of variables without a direct link (Shipley 2000; Shipley 2016). We tested the null probability of each conditional independence statement in the basis set and evaluated the fit of the path diagram with a Fisher's C test (Shipley 2000); $C = \sum \ln(p_i)$, where p_i is the null probability of each independence statement and C follows a Chi-squared distribution of $2k$ degrees of freedom. The Fisher's C test statistic for hypothesised path model of reproduction was 36.39 (df =34, p-value = 0.36), supporting the null hypothesis that all conditional independence claims were respected. Therefore, we could conclude that no links were missing from the model and that the path diagram fitted well.

Table S3. Tests of conditional independence for the basis set as specified by the a-priori hypothesised path model. X_||_Y {Z_i, Z_j.. indicates that X and Y are probabilistically independent conditional on Z covariates.

Basis set	Partial slopes (SE)	F value	Null probability
G_||_snow {SO, N_{ad}, E, T_{jj}, P_{jj}, fox}	0.01 (0.02)	0.63	0.53
C_||_ T_{jj} {SO, snow, N_{ad}}	0.15 (0.25)	0.61	0.54
E _||_ T_{jj} {SO, snow, N_{ad}}	0.16 (0.16)	0.96	0.35
F_||_T_{jj} {SO, snow, N_{ad}, E, fox, G, T_{ja}, P_{ja}}	-0.54 (0.32)	-1.69	0.09
C_||_P_{jj} {SO, snow, N_{ad}}	-0.03 (0.20)	-0.15	0.88
E _||_P_{jj} {SO, snow, N_{ad}}	0.08 (0.14)	0.61	0.55
F_||_P_{jj} {SO, snow, N_{ad}, E, fox, G, T_{ja}, P_{ja}}	-0.33 (0.25)	-1.33	0.18
C_||_fox {SO, snow, N_{ad}}	-0.33 (0.19)	-1.72	0.09
E_||_fox {SO, snow, N_{ad}}	-0.12 (0.13)	-0.93	0.37
C_||_ T_{ja} {SO, snow, N_{ad}}	0.16 (0.18)	0.88	0.38
E_||_T_{ja} {SO, snow, N_{ad}}	0.00 (0.12)	0.03	0.98
H_||_ T_{ja} {SO, snow, N_{ad}, E, T_{jj}, P_{jj}, fox}	0.32 (0.21)	1.51	0.13
G _||_ T_{ja} {SO, N_{ad}, E, T_{jj}, P_{jj}, fox}	0.00 (0.02)	0.04	0.97
C_||_P_{ja} {SO, snow, N_{ad}}	0.07 (0.22)	0.30	0.77
E_||_P_{ja} {SO, snow, N_{ad}}	-0.04 (0.15)	-0.28	0.78
H_||_P_{ja} {SO, snow, N_{ad}, E, T_{jj}, P_{jj}, fox}	-0.35 (0.24)	-1.46	0.14
G_||_P_{ja} {SO, N_{ad}, E, T_{jj}, P_{jj}, fox}	-0.03 (0.02)	-1.55	0.12

References

Shipley, B. (2000) A new inferential test for path models based on directed acyclic graphs. Structural Equation Modeling, 7, 206-218.

Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. Ecology, 90, 363-368.

Shipley, B. (2016) Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference with R. Cambridge University Press.

Appendix 4. Hypothesised diagrams of the reproductive path model (included the 5 response variables; *C, E, H, G* and *F*) and survival (ϕ_f and ϕ_{ad}) models, including all potential covariates. Candidate model sets were constructed for each response variable, with all possible combinations of covariates, and an AIC-model selection approach was used to select the best-approximating model.

Figure S4.1. Hypothesised path model for reproduction with proposed links between covariates, from
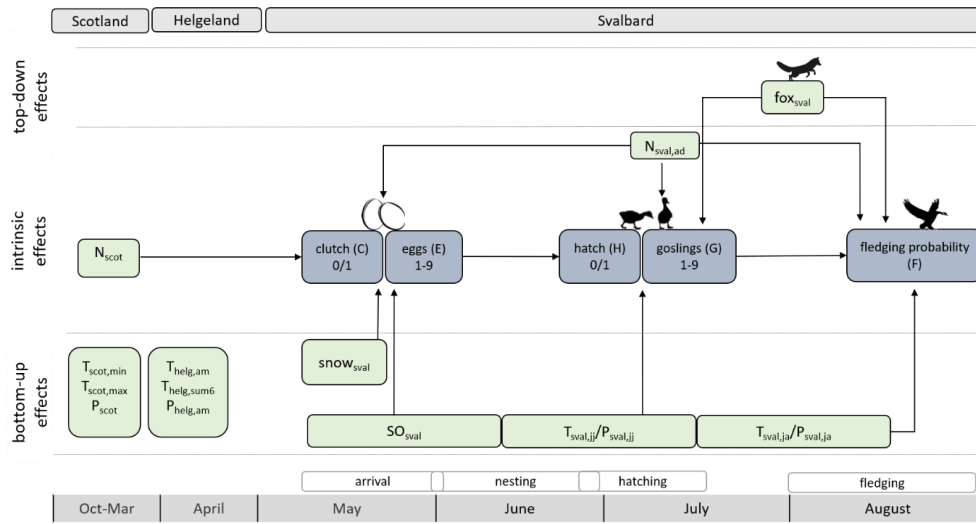
which a candidate model set was constructed (N.B. only one arrow is shown here for dependent parameters (i.e. *C* and *E*; *H* and *G*)).
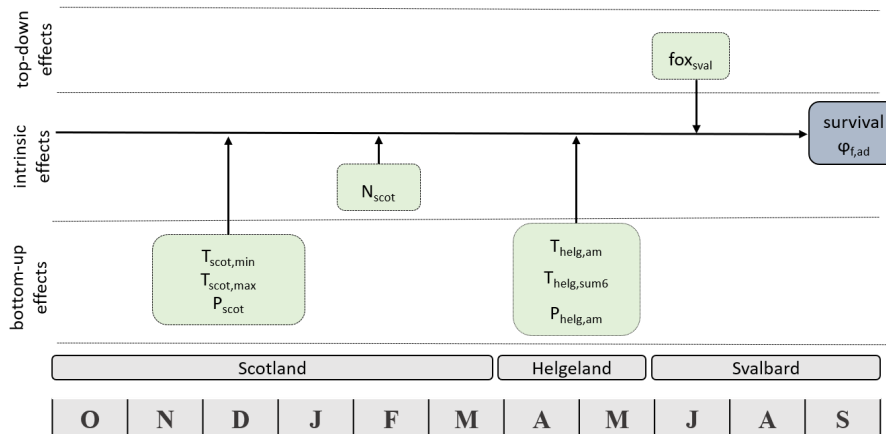
Figure S4.2. Illustration of hypothesised covariate effects on survival over the annual cycle (i.e. Scotland, Helgeland and Svalbard). All possible combinations of these covariates were included in the candidate model set and compared using AIC_c and analysis of deviance.

Table S4.3. Models of vital rates including covariates used in population projection matrix analysis. Parameters describing the egg-laying phase (C and E) are not included, since this would inflate reproductive rates as both E and H are the expected number of offspring per female at different stages of the reproductive cycle.

Par	Model with slope coefficients and 95% confidence intervals
H	$-0.15(-0.48,0.18) + -0.39(-0.79,-0.01)\mathbf{SO_{sval}} + 0.63(0.30,0.95)\mathbf{P_{helg,am}} + 0.22(-0.18,0.61)\mathbf{T_{sval,jj}}$
G	$1.03(1.00,1.07) + -0.03(-0.07,-0.01)\mathbf{fox_{sval}} + -0.03(-0.07,-0.01)\mathbf{N_{sval,ad}}$
F	$0.03(-0.52, 0.58) + -0.17(-0.25,-0.09)\mathbf{G} + -1.23(-1.77,-0.69)\mathbf{fox_{sval}} + -0.54(-1.12, 0.04)\mathbf{P_{sval,ja}}$
$\phi_{f,ad}$	$0.46(0.32,0.60) + 1.56(1.41,1.71)\mathbf{age_{ad}} + 0.25(0.19,0.31)\mathbf{T_{scot,min}} + -0.058(-0.21, 0.09)\mathbf{N_{scot}}$

Appendix 5. Model selection tables

S5.1. Reproduction: AIC-based approach

Candidate model sets for each reproductive parameter, where all models included year and id as random effects. The tables below show the mean slope coefficient for each covariate effect in the model, degrees of freedom (df), AIC adjusted for small sample size (AIC_c), difference in AIC_c from a model and the lowest AIC_c model (ΔAIC_c) and the proportion of variance explained by the fixed effects (R^2).

Table S5.1.1. *C* (clutch success). Candidate model set (8 top-ranking models) and null model for the generalised linear model of clutch success, fitted with a binomial distribution.

SO_{sval}	$P_{helg,am}$	$T_{scot,max}$	$T_{helg,am}$	$T_{helg,sum6}$	$N_{sval,ad}$	N_{scot}	P_{scot}	$T_{scot,min}$	$snow_{sval}$	df	AIC_c	ΔAIC_c	R^2
-0.41	0.27	0.25								6	6230.41	0.00	0.04
-0.39	0.23									5	6230.76	0.35	0.03
-0.36										4	6230.76	0.35	0.02
-0.39	0.26	0.27		0.22						7	6231.27	0.87	0.04
-0.38		0.20								5	6231.36	0.95	0.03
-0.37									-0.17	5	6231.52	1.12	0.03
-0.37	0.26	0.27	0.20							7	6231.58	1.17	0.04
-0.43	0.25							0.17		6	6231.58	1.18	0.03
				Null model						3	6233.15	2.75	0

Table S5.1.2. *E* (clutch size). Candidate model set (8 top-ranking models) and null model for the linear model of clutch size.

SO_{sval}	$P_{helg,am}$	N_{scot}	$T_{helg,am}$	$T_{helg,sum6}$	$N_{sval,ad}$	P_{scot}	$T_{scot,max}$	$T_{scot,min}$	$snow_{sval}$	df	AIC_c	ΔAIC_c	R^2
-0.31	0.31	-0.63								7	5742.86	0.00	0.15
-0.31	0.31									6	5744.50	1.64	0.13
-0.33	0.32	-0.71						0.11		8	5746.19	3.34	0.16
-0.32	0.31	-0.75		-0.12						8	5746.25	3.39	0.16
-0.31	0.31	-0.67			0.10					8	5746.33	3.48	0.15
-0.34	0.32	-0.73	-0.11							8	5746.41	3.55	0.15
-0.32	0.33	-0.69					0.10			8	5746.42	3.57	0.16
-0.31	0.31	-0.68			0.02					8	5747.46	4.60	0.15
				Null model						4	5752.30	9.45	0

Table S5.1.3. *H* (hatching success). Candidate model set (10 top-ranking models) and null model for generalised linear model of hatching success, fitted with a binomial distribution.

	Parameter				df	AIC_c	ΔAIC_c	R^2
E	$\mathbf{T_{sval,jj}}$	$\mathbf{N_{sval,ad}}$	$\mathbf{fox_{sval}}$	$\mathbf{P_{sval,jj}}$				
0.56	0.37				5	6216.50	0.00	0.10
0.56					4	6217.53	1.04	0.06
0.56	0.36	-0.10			6	6218.29	1.80	0.11
0.56	0.37		-0.05		6	6218.44	1.95	0.10
0.56	0.37			-0.00	6	6218.50	2.00	0.10
0.56		-0.13			5	6219.19	2.70	0.07
0.56				0.11	5	6219.26	2.77	0.06
0.56			-0.02		5	6219.53	3.04	0.06
0.56	0.37	-0.11		-0.04	7	6220.27	3.77	0.06
0.56	0.37	-0.09	-0.03		7	6220.28	3.79	0.11
		Null model			3	6444.26	227.76	0

Table S5.1.4. *G* (number of goslings). Candidate model set (10 top-ranking models) and null model for generalised linear model of the number of goslings, fitted with a Poisson distribution.

	Parameter				df	AIC_c	ΔAIC_c	R^2
E	$\mathbf{N_{sval,ad}}$	$\mathbf{fox_{sval}}$	$\mathbf{P_{sval,jj}}$	$\mathbf{T_{sval,jj}}$				
0.08	-0.03	-0.03			6	8928.01	0.00	0.04
0.08	-0.03	-0.03		0.02	7	8928.19	0.18	0.04
0.08		-0.04		0.03	6	8928.82	0.81	0.04
0.09	-0.04				5	8929.15	1.14	0.03
0.08		-0.04			5	8929.23	1.23	0.03
0.08	-0.04	-0.03	-0.01		7	8929.79	1.78	0.04
0.08	-0.04			0.02	6	8930.10	2.09	0.03
0.08		-0.04	-0.00	0.03	7	8930.78	2.77	0.04
0.09	-0.04		-0.01		6	8931.04	3.03	0.03
0.08		-0.04	0.01		6	8931.14	3.13	0.04
		Null model			3	8990.28	62.27	0

Table S5.1.5. F (fledging probability)

Candidate model set (8 top-ranking models) and null model for generalised linear model of the proportion of goslings fledging, fitted with a binomial distribution.

		Parameter			df	AIC_c	ΔAIC_c	R^2
G	**fox$_{sval}$**	**P$_{ja}$**	**N$_{sval,ad}$**	**T$_{sval,ja}$**				
-0.17	-1.23	-0.54			6	4345.26	0.00	0.27
-0.17	-1.26				5	4346.55	1.29	0.25
-0.17	-1.22	-0.55		-0.15	7	4346.99	1.74	0.27
-0.17	-1.24	-0.54	0.03		7	4347.26	2.00	0.27
-0.17	-1.25			-0.10	6	4348.44	3.19	0.25
-0.17	-1.26		-0.00		6	4348.56	3.30	0.25
-0.17	-1.25		0.00	-0.10	7	4350.46	5.20	0.25
-0.17		-0.62			5	4359.06	13.81	0.06
		Null model			3	4375.22	29.97	0

5.2. Reproduction: Analysis of deviance

Since several models had similar AIC_c values, we used an analysis of deviance, conducted using the *afex* package in R (Singmann *et al.* 2015) to quantify the amount of variance explained by each covariate and whether the amount of explained variance was significant.

Table S5.2. Analysis of deviance for reproduction analyses**.** Results of the analysis of deviance are presented for each parameter, where an F statistic and P value were estimated for each covariate effect from the top-ranking model based on AIC_c.

Parameter	Covariate	F	P
C	SO_{sval}	6.25	0.01
	$P_{helg,am}$	2.95	0.09
	$T_{scot,max}$	2.35	0.13
E	SO_{sval}	14.71	<0.01
	$P_{helg,am}$	14.65	<0.01
	N_{scot}	4.90	0.03
H	E	227.79	<0.01
	$T_{sval,jj}$	3.04	0.08
G	E	60.14	<0.01
	$N_{sval,ad}$	3.23	0.07
	fox_{sval}	3.15	0.08
F	$P_{sval,ja}$	2.69	0.07
	G	15.63	<0.01
	fox_{sval}	15.82	<0.01

Table S5.3. AIC_c-based model selection for survival. Candidate model set (8 top-ranking models) and null model of apparent survival rates (all models include age class). The number of parameters for the simplest model of survival (i.e. with only age class as a predictor/null model) was 2 (par: intercept =1, age = 1).

Parameter						npar	AIC_c	ΔAIC_c	R^2
$T_{scot,min}$	N_{scot}	$P_{helg,am}$	$T_{helg,sum6}$	fox_{sval}	P_{scot}				
0.29	-0.28	-0.14	0.09	-0.16		7	34452.41	0.00	0.58
0.27	-0.25	-0.15		-0.15		6	34457.07	4.65	0.56
0.24	-0.27		0.10	-0.13	0.09	7	34463.19	10.78	0.55
0.26	-0.26		0.10	-0.08		6	34464.07	11.66	0.54
0.29	-0.25	-0.10	0.07		-0.08	7	34464.57	12.16	0.54
0.26	-0.25	-0.06	0.07			6	34465.59	13.18	0.53
0.28	-0.23	-0.11			-0.08	6	34467.01	14.60	0.53
0.26	-0.25		0.08			5	34467.35	14.94	0.52
0.25	-0.24	-0.07				5	34467.82	15.41	0.52
0.26	-0.25		0.08		-0.01	6	34469.24	16.83	0.52
0.23	-0.25			-0.11	0.08	6	34469.45	17.04	0.52
0.25	-0.24			-0.06		5	34469.92	17.51	0.51
0.24	-0.23					4	34471.15	18.74	0.50
		Null model				2	34624.81	172.4	

S5.4. Survival: Analysis of deviance

Since several models had similar AIC_c values we also performed an analysis of deviance, using the program MARK (ANODEV), to confirm that the covariates from the lowest AIC_c models explained significant variation.

Table S5.4. Analysis of deviance for survival analysis. Results are presented as an R^2 equivalent representing the variance explained by each term, calculated by ($\sigma^2_{\text{unconstrained time dependent}}$ − $\sigma^2_{\text{covariate}}$)/$\sigma^2_{\text{unconstrained time dependent}}$ (Grosbois *et al.* 2008), with the associated P-value (P).

Covariate	R^2	P
$T_{\text{scot,min}}$	0.32	<0.01
N_{scot}	0.31	<0.01
fox_{sval}	0.04	0.32
$T_{\text{helg,sum6}}$	0.04	0.38
$P_{\text{helg,am}}$	0.00	0.82

S5.5 Survival: post-hoc analysis of age-specific covariate effects on survival rates

The best additive model of survival (based on an AIC_c-model selection and analysis of deviance approach) included additive effects of $T_{\text{scot,min}}$ and N_{scot}. We tested whether the effect of $T_{\text{scot,min}}$ and N_{scot} differed between age classes (i.e. for fledglings or adults), using an AIC_c-based approach.

Table S5.5. Post-hoc AIC_c-based model selection for the best-fitting survival model with interactions between age classes and covariates. The number of parameters modelled (npar), AIC_c, ΔAIC_c from lowest-ranking model and the percentage of annual variation in apparent survival explained by the model terms (R^2) are shown.

		Parameter		npar	AIC_c	ΔAIC_c	R^2
$T_{\text{scot,min}}$	N_{scot}	age class: $T_{\text{scot,min}}$	age class:N_{scot}				
0.25	-0.06		-0.21	5	34466.96	0.00	0.52
0.22	-0.08	0.04	-0.19	6	34468.71	1.75	0.52
0.15	-0.24	0.11		5	34470.74	3.78	0.51
0.27	-0.13			4	34471.15	4.18	0.50

References

Singmann, H., Bolker, B., Westfall, J., Højsgaard, S. & Fox, J. (2015) Package 'afex' for R: Analysis of Factorial Experiments.

Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews, 83, 357-399.

Appendix 6. Time series of covariates from best models of reproduction and survival that do not show temporal trends (i.e. not shown in figure 5).
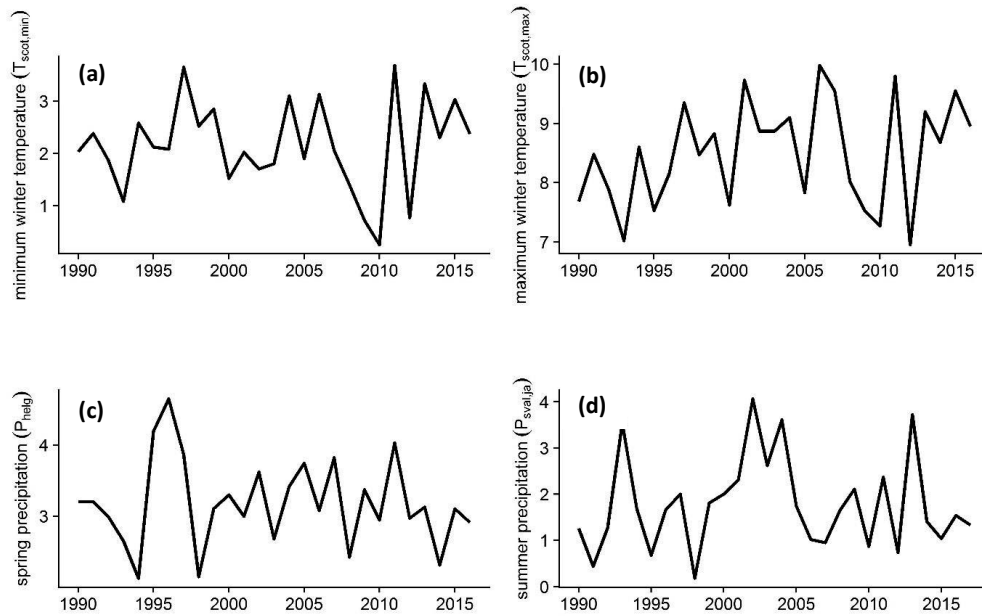
Figure S6. Annual mean (a) minimum ($T_{scot,min}$) and (b) maximum ($T_{scot,max}$) winter (October-March) temperature in Scotland, (c) April-May precipitation at Helgeland ($P_{helg,am}$) and mid-July to mid-August precipitation at Ny-Ålesund ($P_{sval,ja}$).

Appendix 7. Sensitivities of the asymptotic population growth rate
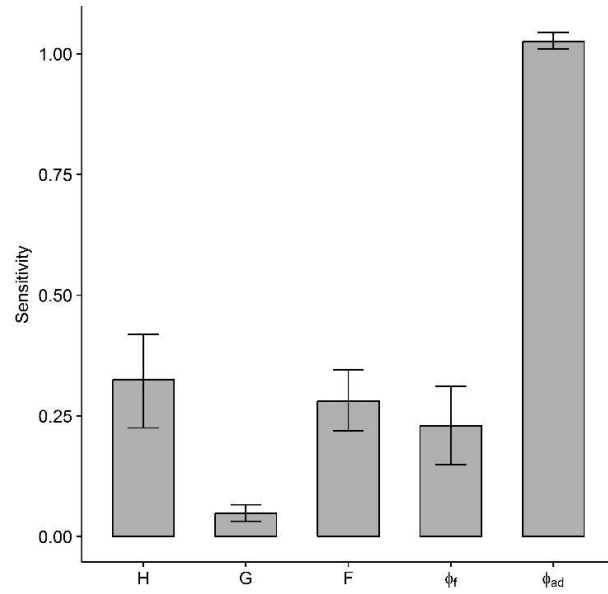
Figure S7. Sensitivities of the (asymptotic) population growth rate to lower-level parameters used in the retrospective perturbation analysis (LTRE). Here, all vital rates were estimated at mean covariate values. Error bars represent 95% confidence intervals, based on 10,000 simulations of vital rates.

Paper III

High-arctic family planning: earlier spring onset advances age at first reproduction in barnacle geese

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16   **Abstract**

17   Quantifying how key life-history traits respond to climatic change is fundamental in understanding and

18   predicting long-term population prospects. Age at first reproduction, which affects fitness and

19   population dynamics, may be influenced by environmental stochasticity but has rarely been directly

20   linked to climate change. Here, we use a case study from the highly seasonal and stochastic environment

21   in high-arctic Svalbard, with strong temporal trends in breeding conditions, to test whether rapid climate

22   warming may induce changes in age at first reproduction in barnacle geese, *Branta leucopsis*. Using

23   long-term mark-recapture and reproductive data (1991-2017), we developed a multi-event model to

24   estimate individual age at first reproduction (i.e., goslings produced). The annual probability of

25   reproducing for the first time was negatively affected by population density but only for two-year olds,

26   the earliest age of maturity. Furthermore, advanced spring onset positively influenced the probability of

27   reproducing and even more strongly the probability of reproducing for the first time. Thus, because

28   climate warming has advanced spring onset by two weeks, this likely led to an earlier age at first

29   reproduction by more than doubling the probability of reproducing at two-years old. This may, in turn,

30   impact important life-history trade-offs and long-term population trajectories.

Introduction

Global warming may have dramatic eco-evolutionary consequences [1, 2] by changing long-term population dynamics [3] and the evolution of life-history traits [4, 5]. The fastest warming occurs in the Arctic [6], where, as a consequence, the timing of snow melt and vegetation growth onset in spring is advancing rapidly [7, 8]. Since the snow-free season is extremely short at high latitudes, prolonged snow cover often has detrimental effects on reproduction in ground-nesting birds [9]. Accordingly, advancing springs due to recent climate warming have proven beneficial [3, 10]. Changes in age-specific breeding success can trigger changes in key life-history traits like the age at which individuals mature [11] or reproduce [12] for the first time. Age at first reproduction (AFR) is linked to the fast-slow life-history continuum, where longer-lived species generally exhibit delayed, and larger individual variation in, AFR [13, 14]. An individual's AFR will affect their fitness, due to costs and benefits associated with different life-history strategies [14, 15]. Earlier AFR can be beneficial, by increasing the total number of reproductive events, but can come at a cost if resources are used that would otherwise be allocated to growth, survival or future reproduction. Environmental stochasticity and density dependence can also induce variability in AFR [16, 17], as high resource competition or poor breeding conditions can lead to individuals delaying maturation [18] or reproduction [11]. While weather conditions are known to influence annual AFR in some species [e.g., common tern, *Sterna hirundo*, 19, red deer, *Cervus elaphus*, 20], the link between long-term climate change and trends in AFR remains largely unexplored [but see 21, 22].

Geese migrating to Arctic breeding grounds experience highly variable spring conditions. Consequently, their reproductive success exhibits large inter-annual fluctuations, while adult survival is generally high and buffered against variability [23, 24], a common pattern in long-lived species. In Arctic geese, there is substantial age-related variation in reproduction [25], as well as temporal variation associated with timing of nesting, density dependence and food availability [26-28]. Although temporal variation in their age at first reproduction has been documented [29, 30], potential environmental causes of this variation have received little attention. Accurately estimating age at first reproduction can be challenging due to detection issues and because an individual's breeding state is not always ascertainable. Multi-event models are widely used to quantify state uncertainty, such as mortality [31] or breeding status [32], by evaluating them as a hidden Markov process [33]. Here, using a multi-event framework, we studied causes of variation in AFR, defined as the first production of goslings, in the female portion of a population of Svalbard barnacle geese, *Branta leucopsis*. We hypothesise that an early spring, which has proven beneficial for reproduction overall in this population [34], reduces individual AFR. Since spring onset is advancing rapidly, this predicts, in turn, a temporal decline in AFR.

Materials and Methods

Study species and data collection

68 Our study population of breeding barnacle geese is located around Ny-Ålesund (Kongsfjorden),
69 Svalbard (78.9°N, 11.9°E). The Svalbard flyway population overwinters at Solway Firth, UK (55°N,
70 3.30°W), then travels north in spring with a stop-over along mainland Norway before arriving at the
71 Svalbard breeding grounds. Barnacle geese are long-lived (up to 28 years old) and become sexually
72 mature at two years of age [25, 35]. They are partial capital breeders, utilising reserves acquired at
73 wintering and stopover sites earlier in the annual cycle to initiate reproduction [36, 37]. Over a 26-year
74 period (1991 - 2017), 480 female goslings were caught at Ny-Ålesund and ringed with unique colour
75 and metal bands during moulting (July/August). Geese nest on islands during May-June. After hatching,
76 families return to Ny-Ålesund to forage, where ringed adults and associated goslings are recorded,
77 resulting in 3006 individual observations used to model AFR (appendix 1a). Males were excluded from
78 the dataset due to lower recapture rates [35]. Date of spring onset (SO) and adult population density
79 (POP) were included as time-varying covariates. Accumulated winter snowfall [38] was included
80 initially, but showed no evidence of an effect. SO is the (ordinal) day when the 10-day smoothed daily
81 temperature crosses 0°C and remains above for at least 10 days [39] and has been shown to affect egg
82 production [34]. POP is an annual estimate of adult numbers in the study population, which negatively
83 affects gosling production and fledgling recruitment [34, 40].
84
85 *Statistical analysis*
86 Mark-recapture data were used to estimate age at first reproduction (AFR), where reproduction is
87 defined as a female producing goslings (recorded at the foraging grounds, see appendix 1a). Data
88 consisted of individual capture histories of female barnacle geese, recorded as observed with at least
89 one gosling, observed without goslings, or not observed, in a given year. A multi-event model, run in
90 program E-SURGE [Multi-Event SURvival Generalized Estimation; version 2.1.4, 41], was used to
91 separate *states*, representing the 'true' reproductive status of an individual in a given year, and *events*,
92 i.e., the observed state of an individual. We modelled four *states*, pre-breeder (PB), non-breeder (NB),
93 breeder (B) and dead (†). PB was any individual not breeding at year *t* that had never bred previously.
94 NB included individuals not breeding at year *t* but that had bred in a previous year. B was any female
95 that produced at least one gosling at year *t* and † includes dead and permanently emigrated individuals.
96 Three *events* were considered: 'not seen', 'seen as breeder' and 'seen as non-breeder'. Only individuals
97 in the B state could give rise to a 'seen as breeder' event, whereas both PB and NB states contributed to
98 'seen but not breeding' events, and individuals in all three states could be recorded in a 'not seen' event
99 (figure 1). See table 1 for definitions.
100   Goodness-of-fit (GOF) tests on a simplified, multi-state dataset (n = 687, four states: PB, B,
101 NB, not observed) in program U-CARE [version 2.3.4, 41] indicated transience, which was accounted
102 for by modelling age-dependent apparent survival, and trap-history-dependent recapture, which was not
103 considered problematic for this analysis (see appendix 1b for details). Details on model implementation
104 are found in appendix 1c.

105   Following [40] and the GOF tests, annual survival probabilities were modelled for goslings,
106   yearlings and adults, including year effects, and recapture probabilities were modelled as year-specific.
107   Transition probabilities (ψ) to the breeding state were assumed to be the same from NB and B states ($\psi^{NB/B \rightarrow B}$).
108   We compared models with covariates (SO, POP) on transition probabilities from PB to B ($\psi^{PB \rightarrow B}$)
109   and from NB and B to B ($\psi^{NB/B \rightarrow B}$). An age effect was included on $\psi^{PB \rightarrow B}$, where females of
110   four years or older were pooled due to reduced sample sizes thereafter. Model selection was based on
111   Akaike's Information Criterion corrected for small sample sizes (AICc). A model was considered a
112   better fit when ΔAICc was reduced by at least 2 [42]. Confidence intervals for parameter estimates were
113   calculated using the Delta method [43].
114   Using the Viterbi algorithm in E-SURGE, we reconstituted the 30 most-probable life histories
115   for each individual, and their probabilities, based on the highest-ranked model. From the output we
116   estimated the AFR distribution in the population and the annual proportion of breeding 2-year-olds
117   (appendix 2).
118
119   **Results**
120   The best-fitting model (table 2) explaining the pre-breeder to breeder transition ($\psi^{PB \rightarrow B}$) included an
121   effect of spring onset (SO) and an interaction effect between age class and population density (POP).
122   The non-breeder/breeder to breeder transition ($\psi^{NB/B \rightarrow B}$) also included a SO effect ($\psi^{NB/B \rightarrow B}$ (logit
123   scale) β = -0.29; 95% CI = -0.40, -0.17), which was weaker than on $\psi^{PB \rightarrow B}$ (-0.44; -0.63, -0.25), as the
124   mean estimate of $\psi^{PB \rightarrow B}$ was outside the confidence interval of $\psi^{NB/B \rightarrow B}$. In other words, the probability
125   of producing goslings decreased with delayed spring onset and more so for first-time breeders (figure
126   2a). POP had a negative effect on the probability to reproduce for the first time for females of age two
127   (-0.60; -0.93, -0.28) but no effect on ages three and older (0.12; -0.09, 0.34) (figure 2b).
128   Based on estimated individual age at first reproduction (AFR), 35% of individuals reproduced
129   for the first time as 2-year-olds, while 88% and 97% had reproduced by 5 and 10 years of age,
130   respectively (appendix 2). The top-ranked model suggested that a substantial number of individuals that
131   were not observed as 2-year-olds were breeding (appendix 2). Furthermore, the estimated proportion of
132   two-year olds reproducing each year more than doubled over the study (figure 2c) and the date of spring
133   onset, SO, advanced by approximately two weeks (β = -0.55, SE $\pm$ 0.19, p-value < 0.01, figure 2d). This
134   provides support to our prediction of declining AFR over time with advancing spring phenology.
135   Population densities, POP, showed no significant temporal trend (β = -0.01, SE $\pm$ 4.1, p-value = 0.99,
136   figure 2e).
137
138   **Discussion**
139   This long-term study of Svalbard barnacle geese documents empirically the link between global
140   warming and age at first reproduction, a key life-history trait. Although some ('poor') individuals
141   produce goslings for the first time later in life, AFR appears strongly linked to annual fluctuations in

142 nest-site and resource availability. Earlier spring onset increased the probability of producing goslings,

143 especially for females reproducing for the first time, suggesting that inexperienced breeders are more

144 affected by environmental variation. Advancing spring onset, associated with ongoing climate warming,

145 led to an increasing proportion of reproducing two-year olds (i.e., age of sexual maturity) over the study.

146 Density dependence, also operating through resource availability, only affected the probability of

147 producing goslings for two-year olds. This suggests that barnacle geese generally start breeding as two-

148 year-olds and only poor conditions – i.e., cold springs or high densities – force them to delay. In such

149 cases, AFR is likely to change over time with long-term trends in breeding conditions.

150 Spring phenology can affect AFR since it impacts both clutch success/size and hatching success,

151 through effects on the timing of nesting and food availability during incubation [26, 27, 34]. Colder

152 springs delay snowmelt, and therefore nest-site availability, but also the timing of food availability by

153 delaying plant growth onset [34]. Similarly, under delayed snowmelt, female geese initially utilise

154 retained reserves for self-maintenance rather than egg production [44] and take more frequent, and

155 longer, breaks from incubation to forage, increasing egg predation risk [28, 45].

156 Density dependence affects reproduction and thereby potentially the age at which females

157 produce goslings. Here, two-year-olds were less likely to produce goslings in years with higher densities

158 (i.e., higher intraspecific competition), supported by similar findings from a Baltic population of

159 barnacle geese [30]. Reproductive success was also found to be age-dependent in the Baltic population

160 [25], explained by increasing experience/social status with age. This may explain the impact of increased

161 competition on young geese that are forced to settle at sub-optimal nesting sites as densities increase

162 [46]. Better nest sites have more forage available, limiting time spent off the nest for incubating females,

163 limiting egg-predation risk. The same mechanism may also have contributed to stronger effects of spring

164 onset on pre-breeders (typically younger individuals), since late springs increase snow cover and thereby

165 nest-site availability.

166 Global warming is having profound effects on reproduction in Arctic geese and other Arctic

167 herbivores [34, 47]. Our results, from one of the most rapidly warming places on Earth [6], indicate that

168 climate change is affecting key life-history traits like age at first reproduction. Climate change is

169 advancing spring, providing an explanation for the increasing proportion of two-year olds reproducing

170 and thereby earlier AFR. Reproduction is the main driver of population dynamics in geese and any

171 changes have substantial population-level effects [40]. However, increased production of goslings will,

172 to some extent, shift the age structure towards a larger proportion of young individuals that are more

173 sensitive to density-dependent processes, potentially countering benefits of earlier AFR somewhat.

174 Additionally, here, age at first reproduction refers to production of goslings, but survival to fledging is

175 highly variable and susceptible to predation [34, 48]. Earlier AFR may also incur a cost through reduced

176 future reproduction or survival, which was not possible to test here, but care should be taken when

177 inferring population-dynamic implications. For long-distance migrants like Arctic geese, following the

178 food-peak across migratory sites is an important evolutionary strategy [49, 50]. However, they may,

179   eventually, be unable to keep up with fast-changing spring conditions [51], leading to phenological

180   mismatch in food-web interactions [52, 53], with potentially negative reproductive consequences [54].

181   Nevertheless, this population shows no current indication of mismatch effects [34]. On the contrary,

182   Arctic climate change appears to allow for higher gosling production and earlier age at first

183   reproduction, which may have positive consequences for population persistence.

184

185   **Acknowledgements**
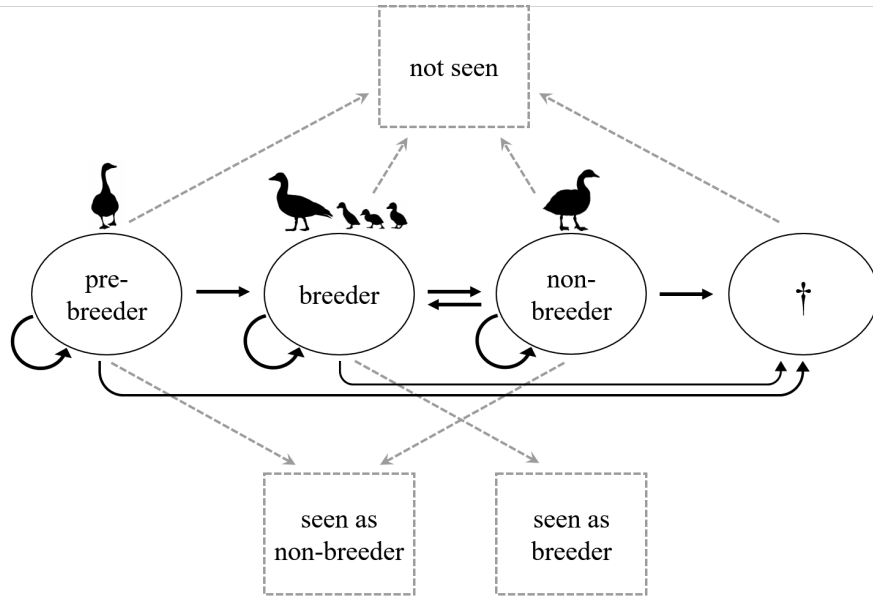
Figure 1. Multi-state model of barnacle geese. Circles represent 'true', unobservable states, with black
arrows indicating transitions between states from time t-1 to t. Squares are observable events and grey-
dotted arrows show which event(s) would be observed given an individual's state.
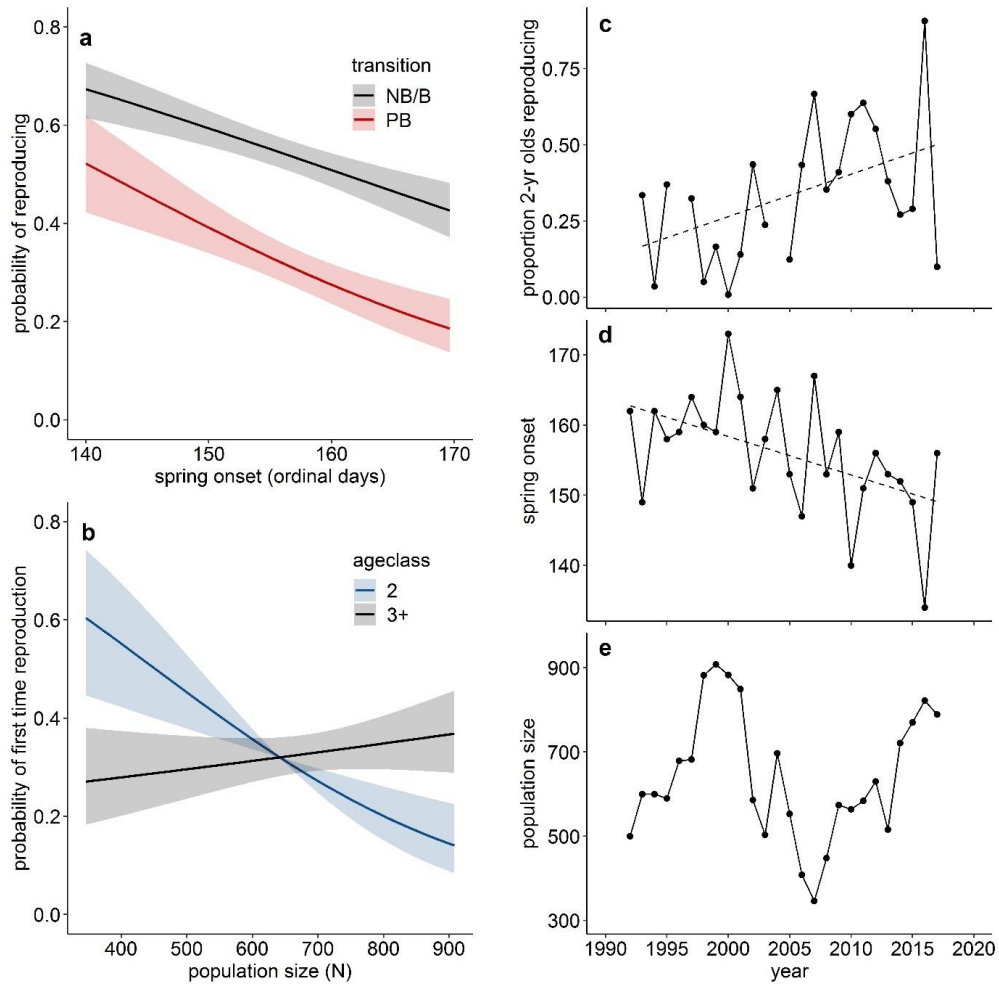
Figure 2. (a) Effect of spring onset date, SO, on reproduction probability of first-time (pre-breeders, PB) and experienced (non-breeders or breeders, NB/B) mothers. (b) Population density, POP, effects on age classes 2 and 3+ in PB. Annual (c) estimated proportion of 2-year-olds reproducing, (d) SO and (e) POP. Dashed lines indicate (c) trend towards an increasing proportion of 2-year-old individuals reproducing for the first time, estimated with E-SURGE (*see Methods*), and (d) advancing spring phenology.

204　**Table 1.** Explanations of terminology.

205

Terminology	Meaning	Definition
AFR	Age at first reproduction	The age at which a female first produces goslings that survive to the foraging area (around Ny-Ålesund).
State	True annual state	PB, B, NB and †. Not always observable. An individual without goslings may be PB or NB, depending on its reproduction history.
Transition	Shift between states from year t-1 to year t	Transition probability from any (living) state at t-1 (i.e., B, PB, NB) to state B at year t represents the breeding probability at year t.
Event	Annual observed reproductive situation	Events include seen as a breeder (i.e., with goslings), non-breeder and not observed.
PB	Pre-breeder	State of females that have yet to produce goslings for the first time. *Note: reproduction probability of PB refers to individuals in PB at t-1 that transitioned into B at t.*
B	Breeder	State of birds producing one or more goslings in a given year.
NB	Non-breeder	State of birds not producing goslings during breeding season but having bred previously.
†	Dead	State dead includes dead and permanently emigrated individuals.
SO	Spring onset date	(Ordinal) day when 10-day smoothed daily temperature crosses 0°C and remains above for at least 10 days
POP	Population density	Annual estimated number of adults in the study population at Ny-Ålesund

206

207

Table 2. Ten highest-ranked models of transition probabilities for PB and NB/B to B. k = number of parameters for transition estimations, excluding survival and recapture ($k = 54$).

Rank	Model $\psi^{PB \to B}$	Model $\psi^{B/NB \to B}$	k	AICc	ΔAICc
1	age$_{2\text{-}3+}$ × POP + SO	SO	6	9760.9	0
2	age$_{2\text{-}3+}$ × POP + SO	SO + POP	7	9762.1	1.2
3	age$_{2\text{-}4+}$ × POP + SO	SO	7	9762.4	1.5
4	age$_{2\text{-}3+}$ × POP age$_{2\text{-}4+}$ × SO	SO	9	9763.4	2.5
5	age$_{2\text{-}4+}$ × POP + SO	SO + POP	8	9763.5	2.6
6	age$_{2\text{-}3+}$ × POP age$_{2\text{-}3+}$ × SO	SO	8	9764.9	4.0
7	SO	SO	4	9773.3	12.4
8	SO + POP	SO	5	9773.5	12.6
9	age$_{2\text{-}4+}$ × SO + POP	SO	7	9774.3	13.4
10	SO	SO + POP	5	9774.6	13.7

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211

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343

1 Supporting information:

2 **'High-arctic family planning: earlier spring onset advances age at first reproduction in**

3 **barnacle geese'**

4 Mari Aas Fjelldal, Kate Layton-Matthews, Aline Magdalena Lee, Vidar Grøtan, Maarten J.J.E. Loonen and Brage
5 Bremset Hansen

6

7 **Appendix 1.** Additional fieldwork details, GOF tests and E-SURGE implementation

8 **Appendix 1a.** Further details of data collected and study system.

9 Each year, geese arrived at the breeding grounds during May to nest on islands in Kongsfjorden.

10 Goslings hatched around 1st July (range = 19th June to 19th July). Straight after, individuals with newly

11 hatched goslings returned to the coastline to forage around the settlement of Ny-Ålesund. From the

12 beginning of June to the end of August, twice-daily observations were made of individuals and their

13 offspring (goslings) in the study area (around Ny-Ålesund), registering the parental ID (i.e., ringed

14 individuals) and their associated number of goslings. Since parents immediately leave the nesting islands

15 after hatching with their offspring and moved to the foraging grounds, we used these observations of

16 families in the foraging area to determine whether a female had produced goslings (i.e., they would be

17 allocated the 'seen as breeder' event). On average, goslings were 3.65 (standard deviation = 2.23) days

18 old when first observed. If a female was never observed with goslings during the breeding season then

19 they would be allocated the 'seen as non-breeder' event. If a female was never observed during the

20 breeding season a given year then she would be allocated the 'not seen event'. Recorded breeder events

21 therefore do not capture females that produce eggs but lose their clutch before arriving at the foraging

22 grounds. These females would be allocated the 'seen as non-breeder' event, given that none of their

23 produced offspring that survived until the first recordings at the foraging grounds.

24

25 **Appendix 1b.** Results from Goodness-of-fit tests

26 The Goodness-of-fit test showed significance for transience in the data (p < 0.001), meaning that newly

27 recruited individuals were less likely to be recaptured than individuals with an already established

28 capture history. Because all individuals were marked as goslings in this study, this indicated a difference

29 in apparent survival rates between goslings and adults, as new individuals (goslings) were less likely to

30 be recaptured than individuals with an established recapture history (adults). This was accounted for in

31 the models by adding age-dependent apparent survival. The Goodness-of-fit tests also gave a significant

32 result for trap-history-dependent recapture (p < 0.001). This could be explained by the study system, as

33 barnacle geese showed high fidelity to their breeding and foraging sites. Females using the Ny-Ålesund

34 area for foraging, after leaving the nesting islands, were likely to come back to this site year after year

35 increasing the probability of being recaptured and thus leading to the detection of "trap-happy"

36 individuals. This study consequently analysed data on a non-random sampled population. However, this

37 should not affect the measures of external forces on AFR.

38 **Appendix 1c.** E-SURGE implementation

39 Models were implemented in E-SURGE through three main steps: firstly, by constructing matrices for

40 states and events and defining which among-year transitions were possible; an individual with the

41 underlying state PB was restricted from transitioning directly into the NB state, as it needed to previously

42 have bred before it could become a non-breeder. NB and B individuals were restricted from transitioning

43 back to the PB state. The event-matrices defined which underlying states generated observed events;

44 individuals with the states PB or NB were assigned the recorded event "seen but not breeding", while B

45 individuals was be assigned to the event "seen as successful breeder". All states could have been

46 assigned the event "not observed". The matrices were built for estimating survival, transition, and

47 recapture probabilities, and read from rows to columns with each symbol representing the probability

48 for the specific transition. The "-" indicates parameters constrained to a probability of 0. States included

49 in the matrices were; pre-breeder (PB), non-breeder (NB), breeder (B), and "dead" (†). The model

50 construction included five matrices in this setup: one for the initial state; one for survival, defined as the

51 first matrix after the initial state and therefore gave the condition to the following matrices that only

52 surviving individuals could transition between states. The third matrix described transitions between

53 breeding states, where the PB state is prevented from becoming a NB and NB, and B states were

54 prevented from transitioning into the PB state. Fourth, the recapture matrix, defined that individuals

55 from all states could be recorded as "not observed". Finally, one matrix connected states and events,

56 where it defined that individuals in the PB and NB states will be recorded as non-breeding events if

57 recaptured, while the B state was recorded as a breeding event. The '*' symbol in the matrices indicates

58 redundant entries as each matrix is row-stochastic (the sum of each row sums to 1).

59 **Initial state matrix**: All the individuals were captured and ringed as goslings, meaning they were all

60 registered as PB at the first occasion.

61 $\qquad$ PB $\quad$ NB $\quad$ B

62 $$\begin{bmatrix} * & - & - \end{bmatrix}$$

63

64 **Survival matrix**: Diagonal matrix for survival probabilities.

65 $\qquad$ PB $\quad$ NB $\quad$ B $\quad$ †

66 $\quad$ PB $\begin{bmatrix} y & - & - & * \\$

67 $\quad$ NB $\quad - & y & - & * \\$

68 $\quad$ B $\quad - & - & y & * \\$

69 $\quad$ † $\quad - & - & - & * \end{bmatrix}$

70

71 **Reproduction matrix**: Estimation of reproductive probability, and transition between adult states.

72

	PB	NB	B	†
PB	*	–	p	–
NB	–	*	p	–
B	–	*	p	–
†	–	–	–	*

77 **Recapture matrix:** Recapture probability at the population. NO = not observed, RPB = recaptured pre-
78 breeder, RNB = recaptured non-breeder, RB = recaptured breeder.

79

	NO	RPB	RNB	RB
PB	*	b	–	–
NB	*	–	b	–
B	*	–	–	b
†	*	–	–	–

84 **Event matrix**: The actual observed reproductive status of an individual was limited to if it is detected
85 with or without goslings (seen as breeder or seen as non-breeder). It was assumed that no observed
86 individual was registered with the wrong event.

87

	Not seen (0)	Seen B (1)	Seen NB (2)
NO	*	–	–
RPB	–	–	*
RNB	–	–	*
RB	–	*	–

92

93   The second main step in the E-SURGE implementation was the model construction, where the
94 models that were to be evaluated through model selection were defined. As an example we present the
95 model construction of the highest ranked model from table 2.

96

97 Initial state: i
98 Transition 1 (survival):   a(1,2,3:4)+t
99 Transition 2 (reproduction): a(1,2:4).f(1).[i+t*x(1)]+a(1,2,3:4).f(1).[t*x(2)]+f(2:3).to(3).[i+t*x(1)]
100 Recapture: firste+nexte.t
101 Event: from

102

103   In the third step, known probabilities were specified, including the capture probability for the

104   first occasion (i.e. the gosling stage), which was fixed to one, and the breeding probability for yearlings,

105   which was fixed at zero.

106   **Appendix 2.** Results from Viterbi algorithm in E-SURGE

107   We used the Viterbi algorithm in E-SURGE to reconstitute the 30 most probable life histories for each

108   individual, and their probabilities, based on the highest-ranked model. For most records the cumulative

109   probability of these 30 life histories was close to one (figure S1.1), indicating that this number of life

110   histories was sufficient to capture most of the uncertainty in the estimates. For each record, we calculated

111   the relative probability of each of the 30 suggested life histories and weighted the number of individuals

112   by this probability. For example, if there was a 0.1 probability that an individual with a given record of

113   observations was a breeder at age two, this individual would contribute 0.1 individuals to the count of

114   two-year-old breeders in that year. From the output we estimated the AFR distribution in the population

115   and the annual proportion of breeding two-year-old individuals. Comparing this estimated AFR

116   distribution with the distribution of observed breeding events in the data, we found that E-SURGE

117   estimated a higher rate of breeding in two-year-olds than would be predicted from the observed data

118   alone (figure S1.2). This demonstrates the usefulness of multi-event models in accounting for

119   unobserved events.

120
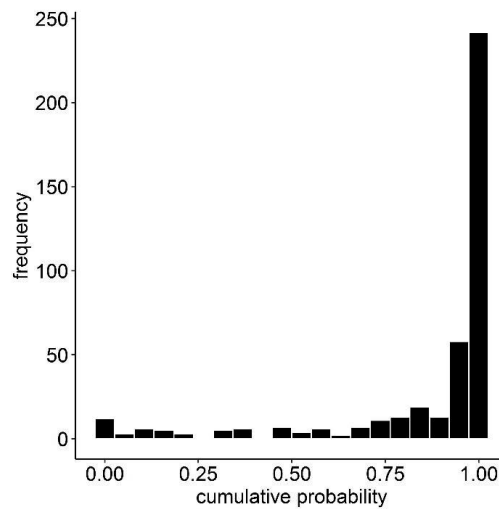
121   **Figure S1.1.** Histogram of the cumulative probabilities of the 30 most probable life histories for each

122   recorded capture history.
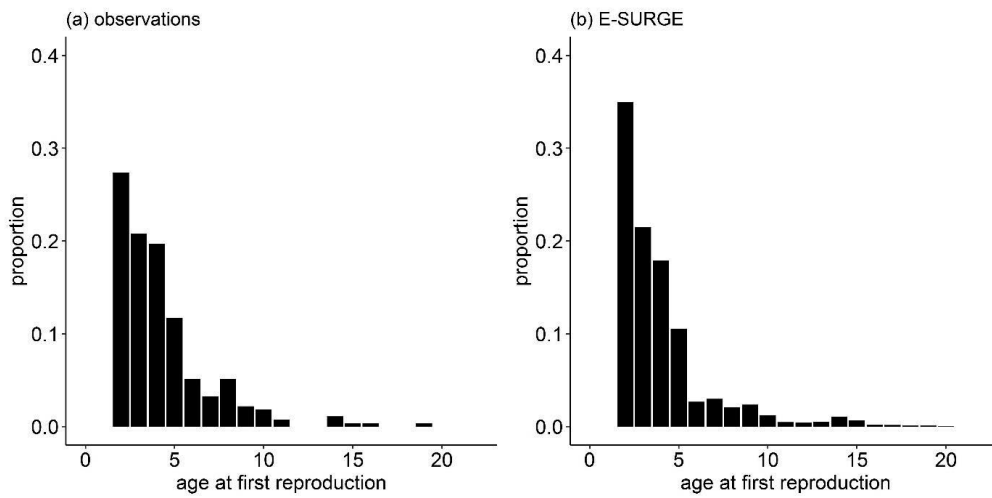
Figure S1.2. Observed and estimated proportions of ages at first reproduction. Histogram shows the proportions of each age class at which female barnacle geese produced a gosling for the first time (a) based on the observational data ($n_{individuals,obs} = 274$) and (b) estimated from the highest-ranked model using the Viterbi algorithm in E-SURGE, which estimated a larger proportion of 2-year-old individuals reproducing than were recorded in the data ($n_{individuals,est} = 362$). NB: estimated proportions for the highest age classes (i.e., from 15 and above) are so low that they involve fewer than one individual in the data set starting to breed, and fewer than five individuals from ages 10 to 15.

Paper IV

1 **Environmental change reduces body mass, but not population growth, in an Arctic**

2 **herbivore**

3

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25 **Abstract**

26 Environmental change influences fitness-related traits and demographic rates, which are often linked to

27 resource-driven variation in body mass in herbivores. Coupled body mass-demographic responses may

28 therefore be important for herbivore population dynamics in fluctuating environments, such as the Arctic.

29 We apply a transient Life-Table Response Experiment ('transient-LTRE') to demographic data from

30 Svalbard barnacle geese (*Branta leucopsis*), to quantify their population-dynamic responses to changes in

31 body mass. We partitioned contributions from direct demographic and body mass-mediated processes to

32 variation in population growth. Despite a 10% decline in body mass (1980-2017) and positive effects of

33 mass on reproduction and fledgling survival, this had negligible population-dynamic consequences.

34 Population growth rates were mainly reproduction-driven, in part through positive responses to rapid

35 advances in spring phenology. The virtual lack of body mass-mediated effects indicates that herbivore

36 population dynamics may be more resilient to changing body condition than expected, with implications

37 for their persistence under environmental change.

Introduction

Fluctuations in fitness-related traits and population size are jointly affected by environmental stochasticity and density dependence (Lande *et al.* 2003; Sæther *et al.* 2016). Body condition, measured as proxies such as body mass or mass/tarsus ratio (Schamber *et al.* 2009), is a key fitness-related trait, reflecting energy reserves available to survive, grow and reproduce (Labocha & Hayes 2012). Individual body condition is constantly responding to weather and density-dependent processes, as they influence food availability and energy expenditure (Sæther 1997; Parker *et al.* 2009). Particularly in herbivores, this can have direct effects on reproduction and survival (Festa-Bianchet *et al.* 1997; Sæther 1997; Post & Stenseth 1999). Short-term effects of weather and density can also lead to cohort effects on body mass, with lasting impacts on reproduction (Albon *et al.* 1987; Choudhury *et al.* 1996) and population size (Beckerman *et al.* 2002). Simultaneous changes in body mass and vital rates occur when both respond to variation in weather or density (Parmesan 2006). This coupling can have complex population-dynamic consequences (Post *et al.* 1997; Ozgul *et al.* 2010). Associating changes in fitness-related traits with variation in population growth is challenging when environment-trait-demography associations vary temporally (e.g., seasonally, Paniw *et al.* 2019b) or among life-history components (e.g., Douhard *et al.* 2013).

Arctic environments are highly seasonal and stochastic. Consequently, Arctic herbivores are exposed to variable weather conditions, causing fluctuations in their body mass and population size (Forchhammer *et al.* 2002; Couturier *et al.* 2008; Albon *et al.* 2017). Weather patterns are now being affected by climate change (Scheffer *et al.* 2001), which is occurring most rapidly in the Arctic (Serreze & Barry 2011). Climate change effects on body condition (Albon *et al.* 2017), reproduction (Post & Forchhammer 2008; Layton-Matthews *et al.* 2019a), survival (Hansen *et al.* 2014), and population size (Forchhammer *et al.* 2002; Hansen *et al.* 2019) have been documented in resident and migratory Arctic herbivores. The mechanism by which body mass influences environment-demography relationships can take two forms: through trait-mediating (Ozgul *et al.* 2010; Plard *et al.* 2015; Albon *et al.* 2017) or trait-modifying effects (Herfindal *et al.* 2006; Harrison *et al.* 2013). A trait acts as a mediator when it *explains* a relationship between environmental conditions and vital rates, e.g., temperature affects body mass, which in turn affects survival,

64 whereas a modifying effect requires a body mass-temperature interaction effect on survival. Since body

65 mass is so influential on the life-history processes of Arctic herbivores, we may expect responses in the

66 population growth rate to changes in this trait (Albon *et al.* 2017). However, for trait (i.e., body mass)-

67 mediated effects on population growth to arise, three conditions must be met. Firstly, body mass must

68 fluctuate at the relevant life-history stage for a given, potentially age-specific, demographic rate. Secondly,

69 the demographic rate must be sensitive to changes in mass. Thirdly, the population growth rate must, in

70 turn, be sensitive to variation in the demographic rate (Gaillard & Yoccoz 2003). If a condition is not met,

71 then no pathway exists for trait variation to lead to variation in population growth.

72   Populations are constantly being perturbed by short-term, temporal variation in the environment

73 (Bierzychudek 1999; Clutton–Brock & Coulson 2002). This can lead to 'transient population dynamics'

74 (Hastings 2004; Koons *et al.* 2005; Ezard *et al.* 2010), as fluctuating environments cause changes in the

75 underlying population structure (e.g., age structure, Koons *et al.* 2016) or trait distributions (e.g., body

76 mass, Ozgul *et al.* 2010). Changes in population structure can have delayed, transient effects on future

77 population growth, especially when there is substantial variation in the vital rates of different classes of

78 individuals (Beckerman *et al.* 2002; De Roos *et al.* 2003). For instance, if poor conditions reduce cohort

79 body mass, vital rates can be affected for several subsequent years through delayed effects, mediated by

80 early-life body mass (e.g., Albon *et al.* 1987). Recent extensions of matrix (MPM) and integral (IPM)

81 projection models have attempted to quantify population-dynamic consequences of such delayed or

82 'lagged' effects (Koons *et al.* 2005; Lande *et al.* 2006; Kuss *et al.* 2008). Transient life-table response

83 experiments (transient-LTREs) partition variance in the realised population growth rate into contributions

84 from underlying demographic rates. Transient-LTREs can be used to decompose contributions from

85 temporal variation in vital rates and population structure/trait distributions (e.g., cohort effects), thereby

86 explicitly incorporating past environments through lagged parameter effects (Maldonado-Chaparro *et al.*

87 2018). Here, we investigated the consequences of changes in body mass - through trait-mediated processes

88 - for the population dynamics of Svalbard barnacle geese, *Branta leucopsis*. We analysed individual female

89 mark-recapture and body mass data spanning 28 years. We quantified environmental and density effects on

4

90 survival, reproduction, growth, and fledging body mass and used these regression models to construct an

91 environmentally-driven, stochastic integral projection model (Rees & Ellner 2009; Metcalf *et al.* 2015).

92 Using a recently developed transient-LTRE, we decomposed variation in the realised population growth

93 rate (λ_t) into vital rate contributions through demographic and trait-mediated pathways, separated into direct

94 and delayed effects. Variation in λ_t was largely reproduction-driven, through direct and delayed effects (i.e.,

95 changes in age structure), while body mass-mediated pathways contributed negligibly to population growth.

96 We further decomposed vital rate contributions into variation from modelled covariates and unexplained

97 variation (i.e., random effects). Variation in λ_t through the reproduction probability could be, in part,

98 explained by the timing of spring onset at the breeding grounds, while variation through adult survival was

99 partially explained by overwinter temperature and population density.

100

101 **Methods**

102 *Study species*

103   Arctic geese are migratory capital breeders, relying, to some extent, on accumulated body reserves for

104 reproduction (Jönsson 1997; Hahn *et al.* 2011). Therefore, an individual's condition prior to the breeding

105 season affects their reproductive success (Ankney & MacInnes 1978; Ebbinge & Spaans 1995; Prop &

106 Black 1998). Svalbard barnacle geese overwinter in Scotland, UK (55° N, 3.30° W). They fly to Svalbard

107 for breeding in summer, stopping over in spring along the coast of mainland Norway. The study population

108 breeds close to Ny-Ålesund, western Spitsbergen (78°55' N, 11°56' E). Geese arrive at the end of May and

109 nest on islands in the fjord, Kongsfjorden. Hatching occurs from late June. Families leave the nesting islands

110 to forage thereafter, until offspring fledge at the end of August and geese migrate back to Scotland by

111 October.

112

113 *Demographic data*

114 All analyses were female based. Over the main study period (i.e. the mark-recapture period; 1990-2017), a

115 total of 1669 females were caught in July-August and ringed with unique colour and metal identification

116   bands. Recapture data were based on daily observations of ringed individuals around Ny-Ålesund during

117   the entire foraging period from late June to August (n_{obs} = 7280). Some years were missing recapture or

118   body mass data (see Appendix 1 for annual sample sizes). Reproduction was assessed based on observations

119   of sexually mature adults with offspring at the beginning of August, i.e., when goslings fledge. Individuals

120   ringed in their first year of life were recorded as 'fledglings' (*fl*) and older individuals as 'adults' (*ad*) - a

121   pooled class of up to 28-year-old individuals. Body mass was also measured during a catch ($n_{measurements}$: *fl*

122   = 696, *ad* = 2108). We analysed body mass rather than other indices of body condition, since body mass is

123   a reliable measure of condition in geese (Schmutz 1993; Lindholm *et al.* 1994). We also tested for a

124   temporal trend in cohort body mass (1980-2017), by fitting a linear regression with year as an explanatory

125   variable.

126

127   *Analytical approach*

128   First, we fitted (generalised) linear mixed-effects models ((G)LMMs) to describe fledgling mass (C_0),

129   growth (i.e., change in mass from *t* to *t*+1, *G*), overwinter survival (ϕ) and reproduction: the probability of

130   reproducing (*R*) and fledged brood size (*fec*). For each regression model, we quantified effects of age class,

131   body mass and covariates, using model selection. Based on the best-approximating models, we constructed

132   an IPM to model temporal dynamics of population size and body mass distribution. We decomposed

133   variation in the population growth rate (λ_t), using a transient-LTRE, into direct effects of demographic rates

134   versus indirect effects through fluctuations in age class-structure and body mass distribution. Contributions

135   to variation in λ_t were further decomposed into variation from modelled covariates versus random effects.

136

137   *Regression models*

138   We fitted a model to fledgling body mass data with an LMM, to model the mean and distribution of

139   fledgling masses, C_0, including catch date as a predictor since gosling growth increased linearly over the

140   season (Appendix 2). We also fitted an LMM to body mass data of both age classes, describing mass-

141   dependent growth between years (e.g., due to ontogeny and phenotypic plasticity, *G*), with fledgling body

142   masses adjusted for catch date. Reproduction and mark-recapture data were modelled with GLMMs. To

143   estimate apparent survival (ϕ), mark-recapture data were modelled with a Cormack-Jolly-Seber framework

144   using the *RMark* interface (Laake 2013) for program MARK (White & Burnham 1999). Reproduction was

145   modelled as two response parameters. *R* describes the annual reproduction probability i.e., whether or not

146   a female had at least one fledgling (0/1), which was fitted as a binomial response. Fledged brood size, *fec*,

147   describes the number of fledglings per mother and was fitted as a Poisson response. Only observations from

148   2-year-olds onwards (i.e., the age of sexual maturity, Owen 1980; Forslund & Larsson 1992; Fjelldal *et al.*

149   in press) were included in the reproductive models, and the model of *fec* only included successfully

150   reproducing individuals ($R = 1$). All (G)LMM's using the *lme4* package (Bates *et al.* 2015) and were fitted

151   with year as a random effect.

152   We identified effects of age class, body mass, density and external covariates (see below,

153   *Covariates*) on C_0, G, R, fec and ϕ, using Akaike's Information Criterion corrected for small sample sizes

154   (AICc, Burnham & Anderson 2002) to identify the most parsimonious model. Note that body mass was de-

155   trended for model selection of G and C_0, to avoid spurious correlations caused by declining trends. A set of

156   candidate models were fitted for each rate including all possible subsets of covariates and interactions

157   between age class, body mass and covariates (global models are shown in Appendix 3, Table S1). If two or

158   more models had ΔAICc < 2, the one with least parameters was selected as the most parsimonious. For

159   survival, AICc-based model selection was performed in *RMark*, but the final model was fitted in a Bayesian

160   framework to model age class-, and year-, specific random effects. Markov Chain Monte Carlo (MCMC)

161   simulations were implemented in JAGS via the *rjags* package (Plummer 2013), assuming that annual

162   variation in survival originated from a random process with zero mean and age class-specific deviations

163   (see Schaub *et al.* 2013; Layton-Matthews *et al.* 2019b for details). All priors were non-informative.

164   Missing body mass observations were imputed by drawing from a normal distribution, where priors were

165   set for the age-specific mean body mass and variance (Gimenez *et al.* 2006).

166

167   *Covariates*

7

168   Covariates reflecting weather, population density over the annual cycle, and predator abundance effects on

169   barnacle goose demography (Layton-Matthews *et al.* 2019a) were included in the regression models of

170   reproduction (R, *fec*), survival (ϕ), growth (G) and fledgling mass (C_0). From the overwintering grounds at

171   Solway Firth, Scotland (*win,* i.e., winter: October$_t$ –March$_{t+1}$), we included annual mean winter temperature

172   (T_{win}) and total flyway population counts (N_{win}). From the spring staging grounds at Helgeland, (*spr*, i.e.,

173   spring: April-May), we included spring precipitation (P_{spr}) using data from the Vega weather station (65°38′

174   N, 11°52′ E). Climate covariates from the breeding grounds in Svalbard (*sum,* i.e., summer) included the

175   date of spring onset, SO_{sum}, which is the ordinal day when the 10-day smoothed daily temperature crossed

176   0°C and remained above for at least 10 days (Le Moullec *et al.* 2019), temperature (mid-June to mid-July,

177   T_{sum}) and precipitation (mid-July to mid-August, P_{sum}). Estimates adult population size in Kongsfjorden

178   (N_{sum}, Layton-Matthews *et al.* 2019b), were also included, as well as an index of Arctic fox (*Vulpes lagopus*)

179   abundance (*fox$_{sum}$*), i.e. the proportion of occupied known dens, since predation by Arctic foxes has been

180   shown to influence gosling survival (Fuglei *et al.* 2003; Layton-Matthews *et al.* 2019a). More details on

181   covariates can be found in Layton-Matthews *et al.* (2019a).

182

183   *Stochastic integral projection model*

184   We constructed a stochastic integral projection model, describing the temporal dynamics of population size

185   (n) and body mass distribution (z) of the fledgling (*fl*) and adult (*ad*) age classes, following the life cycle in

186   Figure 1. The growth kernel, $G^{(t)}(z',z)$, describes the probability density function of body masses z' in

187   August in year $t+1$ of an individual of body mass z in year t. Annual age-class specific survival, $\phi^{(t)}(z,a)$,

188   describes the probability of an individual, of age class a (*fl* or *ad*) and body mass z at year t, surviving to

189   year $t+1$. $P_{ad}^{(t)}(z',z)$ and $P_{fl}^{(t)}(z',z)$ represent survival-growth kernels for adults and fledglings, respectively,

190   describing how individuals of mass z at time t, survive and grow to reach mass z' at $t+1$, given by:

191    $P_a^{(t)}(z',z) = \phi^{(t)}(z,a)\,G^{(t)}(z',z)$ for a = *fledgling* or *adults*   (1)

192   Annual probability of reproduction, $R^{(t+1)}(z)$, describes the probability of a >1-year-old female of

193   mass z producing at least one fledgling at $t+1$, given she survives. Fledged brood size, $fec^{(t+1)}$, describes the

194   number of fledglings per mother at $t+1$, conditional on reproduction. Fledgling (body) mass kernel,

195    $C_0^{(t+1)}(z')$, describes the probability distribution of fledgling masses in August at $t+1$. This was assumed to

196   be independent of mother body mass, since a pedigree was not available. This is likely a fair assumption,

197   as offspring mass has not been linked to mother body mass but rather to structural size (e.g., head size,

198   Larsson *et al.* 1998). $F_{ad}^{(t)}(z', z)$ is the reproduction kernel, describing the number of fledglings of mass z'

199   that adults of mass z can contribute to the population at year $t+1$, given by;

200    $F_{ad}(z', z) = \phi^{(t)}(z, ad)\, R^{(t+1)}(z)\, fec^{(t+1)}\, C_0^{(t+1)}(z')\, /2$ (2)

201   Reproduction was divided by 2 since the model was female based. The structure of the IPM was:

202    $n_{fl}(z', t+1) = \int_L^U F_{ad}^{(t)}(z', z) n_{ad}(z, t) dz$ (3)

203    $n_{ad}(z', t+1) = \int_L^U P_{ad}^{(t)}(z', z) n_{ad}(z, t) dz + \int_L^U P_{fl}^{(t)}(z', z) n_{fl}(z, t) dz$ (4)

204   We numerically integrated the IPM using the 'midpoint rule' (Easterling *et al.* 2000) with lower

205   (L) and upper (U) integration limits of body mass 400 and 2500 grams (g), to avoid eviction of individuals

206   from the model. The IPM assumed density-independent population growth, since density effects were either

207   weak or exhibited strong linear trends that would restrict the model unrealistically. Stochastic population

208   dynamics were simulated over 100,000 years using a two-step MCMC resampling approach (Metcalf *et al.*

209   2015). For each year, a set of environmental/density covariate values was sampled from 28 observations in

210   this study (1990-2017). For the functions - C_0, G, R, fec, ϕ_{fl} and ϕ_{ad}, - values were sampled from their

211   respective distributions (i.e., distribution sampling, Metcalf *et al.* 2015). We used estimates of intercept and

212   yearly random effects to calculate the corresponding variance-covariance matrix and sampled parameter

213   sets assuming a multivariate normal distribution (Gelman & Hill 2006), to account for potential correlations

214   (Compagnoni *et al.* 2016). Trends in demographic rates, growth or fledgling mass were captured by the

9

215 random effects. Transition kernels for each annual projection were constructed by combining both sets of

216 sampled parameters to calculate a realised intercept for each function.

217

218 *Transient life table response experiment*

219 We used an extension of the Monte Carlo random LTRE, introduced by Rees and Ellner (2009), to

220 incorporate transient fluctuations in age class-structure and body mass distribution (Maldonado-Chaparro

221 *et al.* 2018). Rather than assuming the population was always close to its stable structure, i.e., focusing on

222 the yearly asymptotic growth rates ($\tilde{\lambda}_t$), we decomposed variance in the realised population growth rate at

223 time t (λ_t). We also included 'lagged' parameter effects in the model of λ_t, to quantify delayed effects of

224 parameters, $\theta_{i,t}$ (i.e., parameter i at time t), acting through changes in age structure or body mass distribution.

225 Variance decompositions of λ_t were modelled assuming either linear (linear model, LM) or non-linear

226 (generalised additive model, GAM) dependencies of λ_t. Following Maldonado-Chaparro *et al.* (2018), we

227 decomposed variance in $\log(\lambda_t)$. We compared the R^2 of LMs and GAMs and incorporated delayed effects

228 with increasing numbers of year lags. We also tested whether interaction effects between parameters (or, in

229 the case of the GAM models, pairwise smooths) contributed to substantial variation in $\log(\lambda_t)$. We

230 considered a model of $\log(\lambda_t)$ to be a better fit when the amount of variance explained increased by at least

231 1% (Maldonado-Chaparro *et al.* 2018).

232   Vital rate contributions were further separated out into variation from covariates included in the

233 underlying regressions versus random effects (i.e., unexplained variation). In this case, (net) contributions

234 of covariates to λ_t depended on; temporal covariances among covariates, their effect size on $\theta_{i,t}$ and the

235 sensitivity of λ_t to $\theta_{i,t}$. We assumed linear dependencies of λ_t on $\theta_{i,t}$ for the environmental decomposition

236 (see Maldonado-Chaparro *et al.* 2018). In the IPM, trait-mediated effects could contribute to intercept

237 variation in each function (e.g., G or ϕ), while trait-modified effects would cause variation in the slope

238 describing the relationship between body mass and each function. Consequently, we decomposed variation

10

239 in $\log(\lambda_t)$ at three hierarchical levels: (1) overall contributions from C_0, G, R, fec and ϕ, (2) modelled

240 environment versus random effects and (3) slope versus intercept variation.

241

242 **Results**

243 *Body mass and life history processes*

244 The best model of overwinter survival (ϕ) included the interaction effect between age class and body mass,

245 with a much stronger positive effect on fledglings (Figure 1a), and additive effects of overwintering

246 population size (N_{win}, negative effect) and winter temperature (T_{win}, positive effect) (Table 1). The best-

247 approximating growth model (G), estimating body mass at year $t+1$, only included a positive effect of mass

248 at time t (Figure 1b). The best-approximating model of the reproductive probability (R, i.e., of an adult

249 female producing fledglings) suggested a positive effect of spring precipitation (P_{spr}) and a negative effect

250 of date of spring onset (SO_{sum}), and an interaction effect between mother body mass and SO_{sum}, with a

251 strong, positive body mass effect in late springs and no effect when spring onset was early (Figure 1c-e).

252 For fledged brood size (fec), model selection suggested negative effects of Arctic fox abundance (fox_{sum})

253 and summer precipitation (P_{sum}), while the best-approximating model of fledgling mass (C_0) included an

254 interaction effect of fox_{sum} and adult population density at the breeding grounds (N_{sum}), where the latter

255 tended to have a negative effect at high fox abundance, and not at low fox abundance (Figure 1f-h). Further

256 description of the best-fitting models and model selection (Tables S2.1-2.5) can be found in Appendix 3.

257   Over the study period, average cohort body mass declined significantly (slope = -8.3 g per cohort,

258 SE = 0.8 g, p<0.001). Inter-annual changes in body mass were relatively small for adults, but larger for

259 fledgling body mass (Figure 2).

260

261 *Transient LTRE*

262 The mean stochastic population growth rate $\hat{\lambda}_t$ was 1.07 (confidence interval: 0.77, 1.59) (calculated from

263 100,000 simulations, Appendix 4, Figure S1), which was similar to the observed growth rate (1.05; 0.65,

264 1.53). The stable body mass-age class distribution reflected the bimodal distribution of the fledgling and

11

265   adult masses (Appendix 4, Figure S2). 94% of the variation in λ_t was explained by main effects of the

266   functions including a one-year time lag, with the transient linear LTRE (LM-LTRE), which increased to

267   98% with a generalised additive model (GAM-LTRE). The only pairwise smooth (i.e., interaction between

268   parameters) explaining more than 1% variance was between the intercept and slope terms of the probability

269   of reproducing (R) - since SO_{sum} was present as a predictor in both parameters. Parameter effects with more

270   than a one-year lag explained a negligible amount of variance in λ_t (<1%).

271   Sensitivity surfaces were estimated using the GAM-LTRE for $\log(\lambda_t)$, illustrating the influence of

272   each function through direct (Figure 3a) and delayed effects (Figure 3b). The direct effect of variation

273   occurring through the reproduction probability (R) was larger than survival (ϕ) or fledged brood size (*fec*).

274   λ_t was sensitive to variation through survival rates, especially adult survival (Figure 3a). Note that direct

275   effects of variation through changes in growth and fledgling mass are not included in Figure 3a since a

276   change in body mass can only affect λ the next year (i.e., through delayed effects). The population growth

277   rate was insensitive to delayed effects (Figure 3b) through G and C_0 (i.e., trait-mediated effects). The

278   sensitivity of λ_t to delayed effects (i.e., at *t*-1) through R and *fec* reflects how increased reproduction in a

279   given year has a negative impact the following year, via a shift in the age structure towards a larger

280   proportion of non-reproductive individuals.

281   Vital rate contributions from variances and covariances in $\log(\lambda_t)$, separating variance explained by

282   covariates versus the random effects, suggested large contribution from variation in the reproductive

283   probability (R) (Figure 4). R contributed 69% through direct effects and 12% through delayed effects (i.e.,

284   changes in age structure). The remaining ~20% was largely explained by direct and delayed contributions

285   from variation in adult survival (ϕ_{ad}, total contribution = 6%), fledged brood size (*fec*, 6%), and fledgling

286   survival (ϕ_{fl}, 2%). Changes in body mass acting through the fledgling mass and growth functions (i.e., trait-

287   mediated effects) made negligible contributions to variance in $\log(\lambda_t)$ (0.04% through G and 0.5% through

288   C_0). Reproduction (R, *fec*) were negatively correlated with adult survival (ϕ_{ad}), resulting in a total

289   contribution of -7% to $\log(\lambda_t)$, i.e., if ϕ_{ad} is high in a given year R will therefore be lower, reducing variation

290 in population growth overall. Both reproductive (R and fec) and survival parameters (ϕ_{fl} and ϕ_{ad}) covaried

291 positively, and both covariations contributed ca. 3% to $\log(\lambda_t)$.

292 58% of the variation in $\log(\lambda_t)$ acting through the reproductive rate (R) could be attributed to

293 modelled covariates (Figure 4). Precipitation at the spring stopover site (P_{spr}) contributed to 26% of the

294 variation, while date of spring onset at the breeding grounds (SO_{sum}) contributed 16% through intercept and

295 slope variance. 59% of the variation in $\log(\lambda_t)$ that was attributed to adult survival (ϕ_{ad}) was explained by

296 temperature (T_{win}) and population size (N_{win}) at the wintering grounds, which accounted for 1% and 2% of

297 the overall variation in $\log(\lambda_t)$. In contrast, less than 1% of the variation in fledgling survival could be

298 attributed to T_{win} or N_{win}. However, modelled T_{win} and N_{win} explained 95% of the positive covariation

299 between fledgling and adult survival, which led to a small positive contribution to variation in $\log(\lambda_t)$ of ca.

300 1% (Figure 4). Finally, 65% of the variation in fledged offspring brood size (fec) was explained by Arctic

301 fox abundance and summer precipitation, which contributed 3% each to the variation in $\log(\lambda_t)$.

302

303 **Discussion**

304 Coupled body mass-demography responses to environmental change can be key to understand and predict

305 short- and long-term population dynamics, especially in herbivores. Here, we explored population-dynamic

306 responses to declining body mass in a breeding population of Arctic geese, using recently developed

307 transient-LTRE methodology. Body mass at the fledging stage was density-dependent, supporting the

308 hypothesis that this body mass decline, which has been observed in several Arctic goose populations, is

309 caused by declining resource availability at the breeding grounds. Surprisingly, the dynamics of our study

310 population appeared buffered against such a decline in body mass, in spite of the clear influence of this

311 proxy for body condition on reproduction and survival. Instead, variation in population growth rates was

312 largely explained by direct and delayed effects through reproduction *per se*, partly caused by variation in

313 spring phenology at the breeding grounds.

314

315 *Population-growth responses to declining body mass*

13

316   The dramatic rise in goose numbers, caused by hunting bans in the 1950s and agricultural change at the

317   wintering grounds, has led to population expansion across the Arctic (Fox & Abraham 2017; Fox & Madsen

318   2017). Density-dependent processes associated with overgrazing by geese have degraded the breeding

319   grounds, resulting in declining cohort body size and mass in barnacle geese (Loonen *et al.* 1997; Larsson

320   *et al.* 1998) and other goose species (Cooch *et al.* 1991b; Reed & Plante 1997). This was supported by a

321   negative relationship between fledgling mass and adult population size found in this study, yet only evident

322   at high abundance of the Arctic fox, the main predator of the goslings and, occasionally, adults (Fuglei *et*

323   *al.* 2003). Arctic foxes seem to limit goose numbers through lethal effects on fledged brood size (*fec*) and

324   non-lethal effects on fledgling mass, probably restricting the ability to utilise all available foraging areas

325   (Loonen *et al.* 1998).

326   Despite the substantial decline in cohort body mass, between-year fluctuations in adult body mass were

327   small (<100 g/year). Fledgling body mass exhibited more inter-annual variation, a result of strong resource-

328   dependence during gosling growth (Cooch *et al.* 1991a; Lindholm *et al.* 1994). Body mass, in turn,

329   positively influenced survival and reproduction. The reserves that first-year-geese accumulate at the

330   breeding grounds are known to affect survival during migration (Owen & Black 1989; Menu *et al.* 2005),

331   which in our study population was reflected in the remarkably strong positive effect of body mass on

332   fledgling survival to the next summer. Adult survival, however, was largely unaffected by body mass and

333   varied less from year to year.

334   Several recent studies have stressed the potential importance of coupled trait-demography responses in

335   predicting herbivore population persistence under environmental change (Ozgul *et al.* 2009; 2010; Albon

336   *et al.* 2017). However, there is contrasting evidence that body condition contributes very little as a pathway

337   for environmental conditions to influence population dynamics (McLean *et al.* 2020). Here, despite a strong

338   negative temporal trend in body mass and positive effects of body mass on vital rates, there was little

339   evidence of trait-mediated effects in our study population of barnacle geese. This can be explained by the

340   fact that all three conditions required for trait-mediated pathways to arise were not met for any of the age

341   class-specific demographic rates (summarised in Table 2). More specifically, although post-fledgling

342 survival was strongly influenced by body mass, variance in this rate made a small contribution to population

343 growth since fledglings represent a small fraction of the population. Furthermore, while the population

344 growth rate was indeed sensitive to changes in adult survival, body mass had no effect on adult survival.

345 Instead, variation in ϕ_{ad} was attributed to temperature and population density at the overwintering grounds.

346 The population growth rate was sensitive to changes in reproduction probability, which was weakly

347 influenced by adult body mass (at mean environmental conditions) and - although the long-term decline in

348 adult body mass was pronounced - inter-annual variation was relatively limited. This resulted in a lack trait-

349 mediated effects through variation in reproduction. According to the demographic buffering hypothesis,

350 variability in λ reduces fitness (Tuljapurkar 1982), leading to selection for reduced variation (Gaillard &

351 Yoccoz 2003; Jongejans *et al.* 2010). Therefore, buffering of population growth against trait-mediated

352 variation may occur via such mechanisms. Individual heterogeneity in body mass, which were not captured

353 here, may also have important demographic consequences (Vindenes *et al.* 2008; Vindenes & Langangen

354 2015). This is particularly relevant for survival, where modelling age-specific random effects in a Bayesian

355 framework may have under-estimated individual heterogeneity (McCarthy & Masters 2005).

356

357 *Population-growth responses to climate change*

358 Quantifying demographic - and associated trait - responses to climate change is necessary for a mechanistic

359 and predictive understanding of population-level consequences (Jenouvrier 2013; Paniw *et al.* 2019a).

360 Arctic warming is advancing the snow melt, with widespread effects on plant phenology (Foster 1989),

361 while rising summer temperatures are influencing plant productivity (Bjorkman *et al.* 2015). For migrating

362 Arctic geese, the timing of spring at the breeding grounds dictates when nesting sites become snow-free as

363 well as the onset of plant growth, both important determinants of breeding success (Reed *et al.* 2004;

364 Madsen *et al.* 2007). Here, earlier spring onset increased fledgling production, which has been attributed to

365 females laying bigger clutches with higher hatching success (Layton-Matthews *et al.* 2019a). As a result,

366 advancing spring phenology could benefit reproduction and, thereby, population growth. However, neither

367 reproduction probability nor fledged brood size exhibited positive temporal trends (Appendix 5). This could

15

368   be explained by contrasting (direct or indirect) climate change effects, since the number of Arctic foxes –

369   and gosling predation rates – are generally increasing (Layton-Matthews *et al.* 2019a; unpublished data, E.

370   Fuglei).

371   In capital breeders, such as the barnacle goose, accumulating body stores is beneficial in

372   unpredictable environments, and this strategy is often associated with higher latitudes, e.g., the Arctic

373   (Varpe *et al.* 2009; Sainmont *et al.* 2014). Storing resources along their flyway allows geese to initiate

374   reproduction without immediate access to food (Klaassen *et al.* 2017). Consequently, several stages of their

375   reproduction are dependent on fat reserves (Bêty *et al.* 2003; Guillemain *et al.* 2008; Aubry *et al.* 2013),

376   illustrated here by the positive relationship between body mass and the probability of producing fledglings.

377   However, our results also show that benefits of heavier mass depend on spring phenology. Heavier

378   individuals were more likely to reproduce than lighter ones under poor (delayed) spring conditions, since

379   they have more 'capital' to initiate reproduction. However, in earlier springs, possibly with an excess of

380   nesting sites and food resources, benefits of accumulating fat reserves were reduced, and the influence of

381   body mass on reproduction was weaker. Further advanced springs due to continued climate change could

382   therefore tip the balance in favour of accumulating fewer resources for reproduction, potentially relaxing

383   selection on body mass if individuals gain a survival advantage by requiring fewer fat reserves for migration

384   (Larsson *et al.* 1998). Overall, population dynamics of Arctic geese appear to be largely unaffected by the

385   substantial decline in body mass, with important implications for the resilience of Arctic herbivores to

386   future environmental change. This work emphasises the importance of holistic approaches, that fully

387   capture environment-trait-demography relationships. While we are observing changes in phenotypic trait

388   distributions in response to environmental change - particularly in light of climate change (Parmesan 2006)

389   - we cannot assume that this will have consequences for population persistence. Therefore, mechanistic

390   pathways from trait variation to population-growth variation should be fully explored.

391

392

393

401 **Table 1.** Linear predictors for best-approximating regression models of each function, with mean parameter

402 estimates, used to parameterise the integral projection model (IPM). a is a dummy variable equal to 0 for

403 fledglings (*fl*) and 1 for adults (*ad*), and z refers to body mass and ***catch*** refers to catch date.

404

IPM function	Model	Best-fitting regression model
Survival	$\text{logit}(\phi_{fl,ad})$	$-2.67 + 4.32\boldsymbol{a} + 0.004z -0.003\boldsymbol{a}{:}z + 0.22\boldsymbol{T_{win}} -0.21\boldsymbol{N_{win}}$
Growth	G	$648.50 + 0.60z$
Fledgling body mass	C_0	$-3357.40 + 19.46\boldsymbol{catch} -2.37\boldsymbol{fox_{sum}} -46.30\boldsymbol{N_{sum}} -7.70\boldsymbol{fox_{sum}}{:}\boldsymbol{N_{sum}}$
Reproductive rate	$\text{logit}(R)$	$-3.76 + 0.002z + 0.86\boldsymbol{P_{spr}} -3.52\boldsymbol{SO_{sum}} + 0.002z{:}\boldsymbol{SO_{sum}}$
Fledged brood size	$\log(fec)$	$0.77 - 0.16\boldsymbol{fox_{sum}} - 0.10\boldsymbol{P_{sum}}$

405 **Table 2. S**ummary of which conditions for body mass-mediated effects on the population growth rate (for

406 each demographic rate) that were met or not (✓ = condition met).

Condition	Fledgling survival (ϕ_{fl})	Adult survival (ϕ_{ad})	Probability of reproducing (R)	Fledged brood size (*fec*)
Body mass fluctuates at the relevant stage	✓			
Demographic rate sensitive to body mass change	✓		✓	
λ sensitive to variation in demographic rate		✓	✓	✓
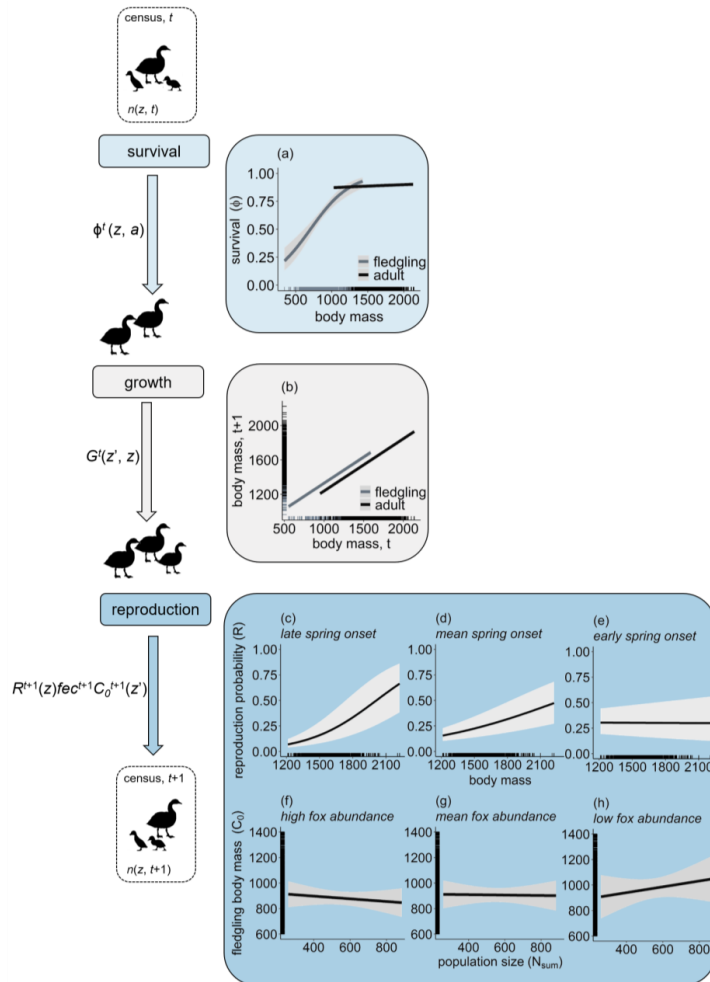
Figures

408 **Figure 1.** Life cycle of barnacle geese based on a post-breeding census (i.e., breeding occurs just before a

409 census). Individuals in age class *a* must survive with a mass-dependent probability ($\phi(z, a)$) and grow to the

410 next year ($G(z^*, z)$) in order to reproduce ($R(z)$, *fec*) and contribute fledglings of mass ($C_0(z')$) to the

411 population. Model predictions of body mass effects at *t* on; (a) fledgling (ϕ_{fl}) and adult (ϕ_{ad}) survival, (b)

412 mass at *t*+1, reproduction probability (R) of adult females at the (c) 20th quantile, (d) mean and (e) 80th

413 quantile of the date of spring onset (SO_{sum}). Effects of adult population size at Ny-Ålesund (N_{sum}) on

414 fledgling mass (C_0) at the (f) 20th, (g) mean and (h) 80th quantile of Arctic fox abundance (fox_{sum}).
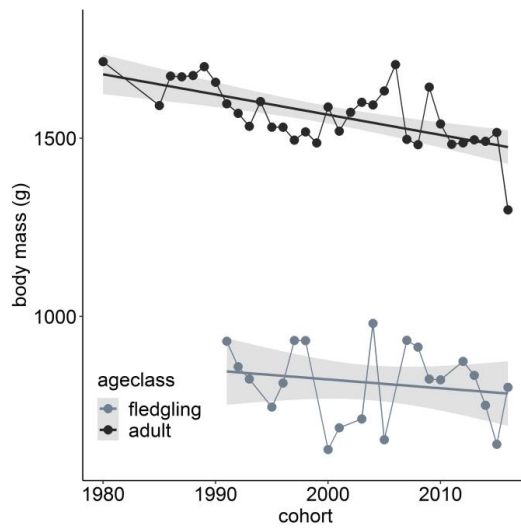
415 **Figure 2.** Temporal trends in average cohort adult (black, 1980-2016) and annual fledgling (grey, 1991-

416 2016) body mass, slope (bold line) with 95% confidence intervals (shading) were calculated based on a

417 linear regression.

418
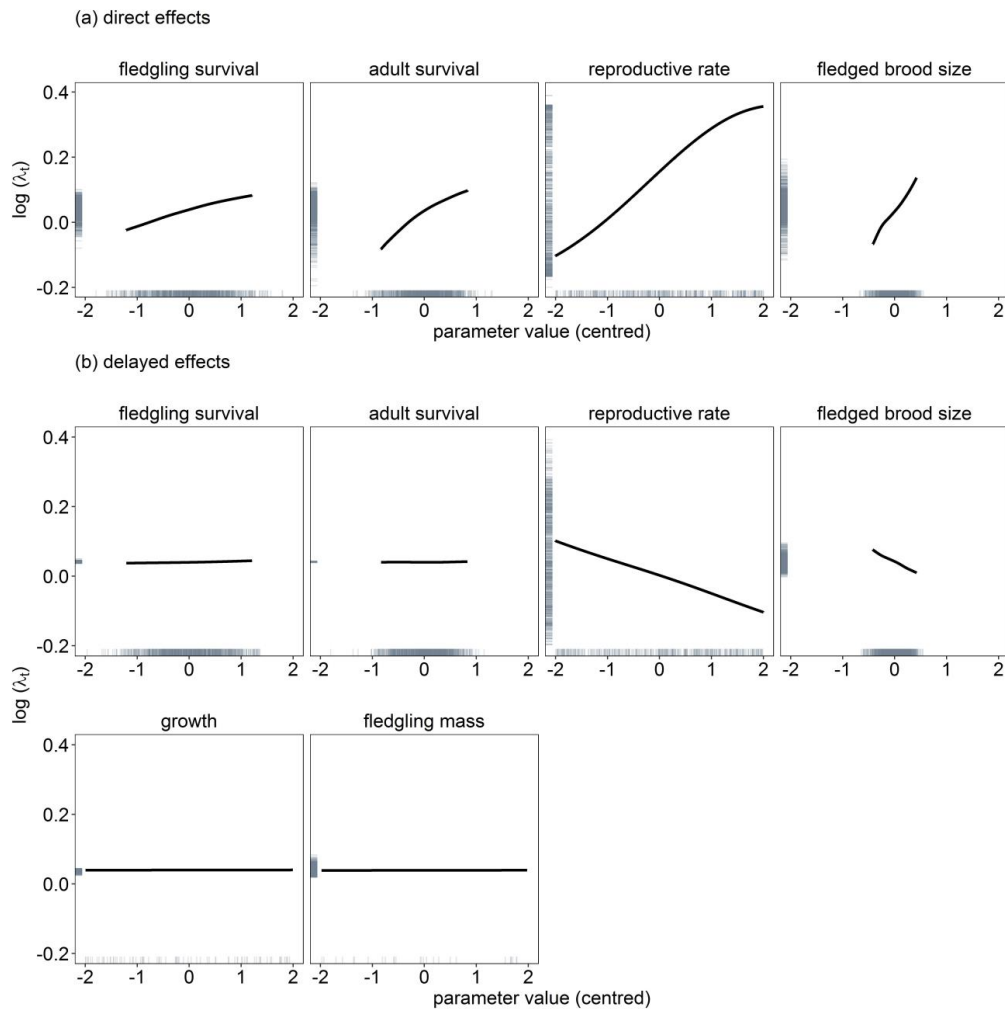
Figure 3. Sensitivity surfaces illustrating the effects of fledgling (ϕ_{fl}) and adult (ϕ_{ad}) survival, reproductive rate (R), fledged brood size (*fec*), growth (*G*) and fledgling body mass (C_0) on the population growth rate, $\log(\lambda_t)$. (a) Direct contributions from each vital rate parameter and (b) delayed contributions from delayed vital rate parameters, i.e., parameter effects at *t*-1 on $\log(\lambda_t)$. X-axis and y-axis rugs show distributions of parameters (centred values) and $\log(\lambda_t)$, respectively.

22
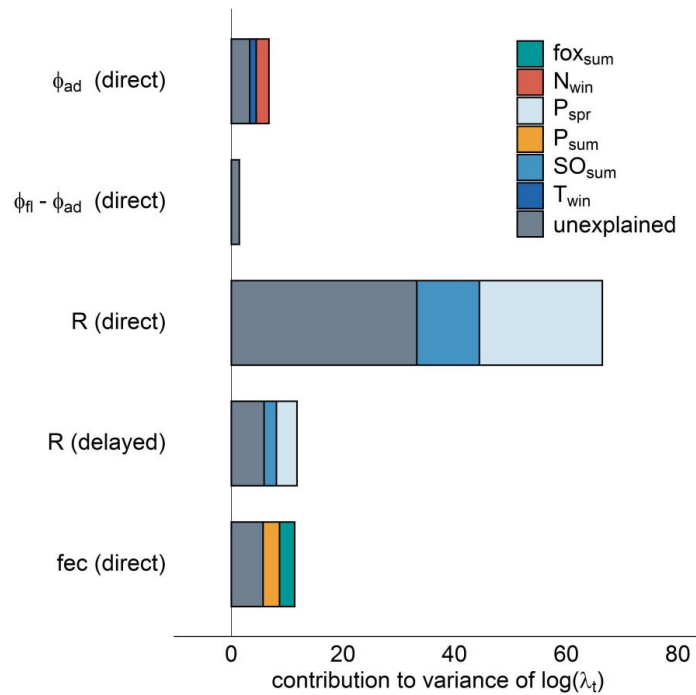
Figure 4. Percentage contributions of the five largest demographic contributions to variance in the population growth rate, $\log(\lambda_t)$. Contributions were decomposed into direct and delayed (in brackets) variances and covariances. Colours represent contributions from modelled covariates versus unexplained variation (random effects).

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648

Supporting information:

'Environmental change reduces body mass, but not population growth, in an Arctic herbivore'

Kate Layton-Matthews, Vidar Grøtan, Brage B. Hansen, Maarten J. J. E. Loonen, Eva Fuglei, Dylan Z. Childs

Appendix 1. Sample sizes of data used in regression models.

Table S1. Annual sample sizes used to estimate; G, ϕ_{fl}, ϕ_{ad}, R, fec, and C_0. Sample size for G is the number of observations of individuals (fledglings and adults) where body mass was measured at year t and $t+1$. For survival, this was the number of observations, per year, for fledglings (ϕ_{fl}) and adults (ϕ_{ad}). For R, the sample size refers to the yearly number of observations of adult females that survived from $t-1$ to t, in order to reproduce. For fec, only successful mothers were included (i.e., $R = 1$) in the sample size. The sample size for C_0 is the annual number of records of fledging body mass.

year	growth (G)	fledgling survival (ϕ_{fl})	adult survival (ϕ_{ad})	reproduction probability (R)	fledged brood size (fec)	fledgling mass (C_0)
1990	-	-	101	-	-	-
1991	115	177	218	94	41	164
1992	92	105	391	89	22	105
1993	60	55	445	175	36	55
1994	34	1	516	295	2	1
1995	84	128	464	366	61	128
1996	46	247	564	345	112	228
1997	50	130	408	321	46	129
1998	50	88	657	269	15	87
1999	56	2	656	365	46	-
2000	24	5	891	508	12	5
2001	3	54	654	538	50	51
2002	24	-	482	490	6	-
2003	80	9	449	360	6	9
2004	83	15	383	-	-	15
2005	25	65	558	209	22	65
2006	30	4	493	415	12	-
2007	15	33	595	371	41	33
2008	16	8	398	346	13	8
2009	27	66	458	284	50	64
2010	2	55	492	318	48	52
2011	8	132	330	275	52	-
2012	23	25	415	274	62	132
2013	39	17	401	301	15	25
2014	32	13	403	247	11	17
2015	19	23	438	334	14	13
2016	-	9	489	320	49	22
2017	-	-	-	256	11	-

Appendix 2. Seasonal trend in body mass measurements
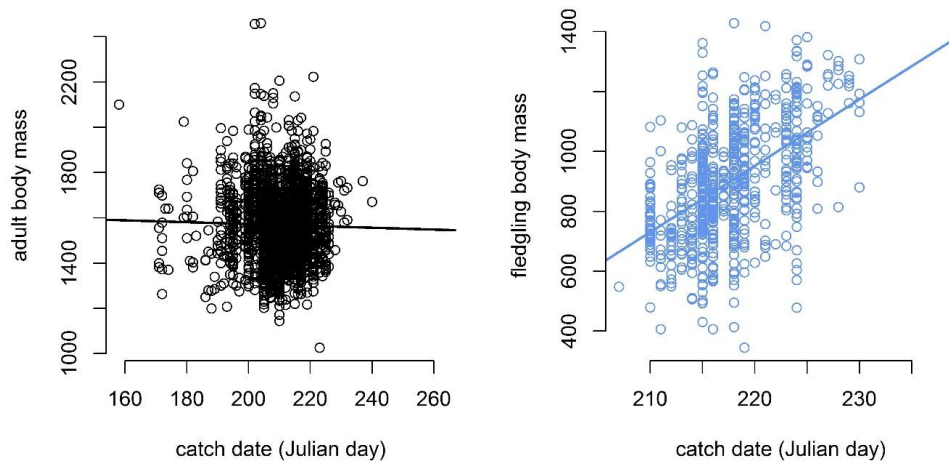
Figure S1. Distribution of body mass for adults and first year birds in relation to catch date.

Appendix 3. Model selection

Table S1. Global models for each response variable.

Parameter	Abbreviation	Global model
Growth	G	age class $\times$ body mass + $N_{sum} + fox_{sum} + SO_{sum} + P_{sum} + T_{sum} + P_{spr} + N_{win} + T_{win}$
Survival	ϕ	age class $\times$ body mass $\times$ $(fox_{sum} + P_{spr} + N_{win} + T_{win})$
Reproductive probability	R	age class $\times$ body mass $\times$ $(N_{sum} + fox_{sum} + SO_{sum} + P_{sum} + T_{sum} + P_{spr} + N_{win} + T_{win})$
Fledged brood size	fec	age class $\times$ body mass $\times$ $(N_{sum} + fox_{sum} + SO_{sum} + P_{sum} + T_{sum} + P_{spr} + N_{win} + T_{win})$
Fledgling mass	C_0	$N_{sum} + fox_{sum} + SO_{sum} + P_{sum} + T_{sum}$

Summary of candidate models of parameters

The best-fitting model of fledgling mass (C_0) included additive and interaction effects between Arctic fox abundance, fox_{sum}, and population density, N_{sum}, (Table S2.1). N_{sum} had a negative effect on fledgling mass, which was stronger with increasing fox abundance. The best-fitting growth model, estimating body mass at time $t+1$ included positive effects of mass at time t spring precipitation at Helgeland (P_{spr}) and age class. However, a model without age class and P_{spr} was within 2 ΔAICc (Table S2.2) and so a simpler model including only mass was the most parsimonious. The best-fitting model of the reproductive rate, R, (i.e., probability of an adult female producing fledglings) included positive effects of mother mass and P_{spr} (Table S2.3). This model also included a negative effect of date of spring onset, SO_{sum} and an interaction between mass and SO_{sum}, where the effect of mass increased with delayed spring onset. The second best-fitting model (1.57 ΔAICc) included negative fox and summer precipitation effects but not SO_{sum}. The most parsimonious model of fec (i.e., number of fledged offspring per mother) included negative effects of fox abundance and summer precipitation, P_{sum} (Table S2.4). The best-fitting model of survival included additive effects of age class, body mass, overwintering population size (N_{win}) and winter temperature (T_{win}), as well as age class-mass and mass-N_{win} interaction effects. However, a model without a body mass-N_{win} interaction was considered the most parsimonious since it was within 2 ΔAICc (Table S2.5).

Table S2.1. Model selection table for body mass of fledglings, C_0.

#	catch	fox_{sum}	P_{sum}	N_{sum}	SO_{sum}	T_{sum}	$fox_{sum}{:}N_{sum}$	npar	AIC_c	ΔAIC_c
1	19.41	-2.37		-46.3			-77.7	7	9037.40	0
2	19.41	-18.61		-22.98		-2.33		7	9041.62	4.22
3	19.41	-20.31	-7.41	-21.34				7	9042.09	4.68
4	19.41	-19.17		-22.77	3.27			7	9042.09	4.68
5	19.42			-27.99	0.02	-9.1		7	9042.18	4.77
9	19.45							4	9062.04	24.63
			Null model					3	9234.02	196.62

Table S2.2. AIC_c Model selection table for G, growth, i.e. effect on (body) mass at $t+1$ (mass detrended).

#	age	mass	P_{spr}	fox_{sum}	age:mass	N_{win}	T_{win}	SO_{sum}	npar	AIC_c	ΔAIC_c
1	23.93	0.52	8.37						7	29083.99	0
2		0.55	8.27						6	29084.6	0.61
3	23.61	0.52							6	29085	1.01
4	24.96	0.52	7.91	-4.17					8	29085.37	1.38
5		0.55							5	29085.54	1.55
6	-1.31	0.50	8.32		0.02				8	29085.8	1.81
7	23.79	0.52	8.13			9.86			8	29085.8	1.81
8	24.07	0.52	8.04					2.31	8	29085.9	1.91
9	23.93	0.52	8.48				1.32		8	29086.03	2.04
10	24.81	0.52		-5.14					7	29086.08	2.09

Table S2.3. Model selection table for *R*, probability of a female producing a fledgling.

#	mass	fox_{sum}	P_{spr}	P_{sum}	SO_{sum}	mass:SO_{sum}	npar	AIC_c	ΔAIC_c
1	0.002		0.86		-3.52	0.002	7	1049.25	0.00
2	0.002	-0.62	0.74	-0.58			7	1050.82	1.57
3	0.002	-0.61	0.80		-0.48		7	1051.70	2.44
4	0.002	-0.74			-3.43	0.002	7	1051.87	2.62
5		-0.64	0.85	-0.60	-0.48		7	1052.37	3.11
6	0.002		0.89	-0.58	-0.48		7	1052.79	3.53
7	0.002	-0.65	0.73				6	1052.82	3.57
9		-0.65	0.77	-0.61			6	1053.76	4.50
	0.002						4	1059.78	10.53
			Null model				3	1063.44	14.19

Table S2.4. Model selection table for *fec*, fledged brood size

#	fox_{sum}	P_{sum}	P_{spr}	N_{win}	npar	AICc	ΔAIC_c
1	-0.16	-0.10			4	2146.80	0.93
2	-0.15		0.07		4	2148.20	2.30
3	-0.15				3	2148.60	2.69
4	-0.15			-0.06	4	2149.20	3.32
		Null model			2	2154.99	9.09

Table. S2.5 Survival, ϕ, model selection table: mass = body mass, age = age class (fledgling or adult).

#	age	mass	age:mass	N_{win}	T_{win}	mass:N_{win}	mass:T_{win}	age:N_{win}	age:T_{sum}	age:mass:N_{win}	age:mass:T_{win}	npar	AICc	ΔAICc
1	4.09	0.004	-0.003	0.05	0.24	-0.0002						7	16624.65	0.00
2	4.06	0.004	-0.003	0.01	0.007	-0.0002	0.0002					8	16624.83	0.18
3	4.17	0.004	-0.003	-0.24	-0.05		0.0002					7	16625.36	0.71
4	4.04	0.004	-0.003	0.16	0.23					-0.0004, -0.0003		8	16626.07	1.42
6	4.22	0.004	-0.003	-0.24	0.23							6	16626.24	1.59
7	4.16	0.004	-0.0033	-0.24	-0.04						0.0002, 0.0002	8	16627.37	2.72
8	4.20	0.004	-0.003	-0.24	0.15				0.10			7	16627.38	2.73
11	4.21	0.004	-0.003	-0.2	0.24			-0.041				7	16628.13	3.48
12	4.20	0.004	-0.003	-0.24	0.15			-0.003	0.10			8	16629.39	4.74
	1.00	0.0005										3	16738.98	114.33
	1.32											2	16759.70	135.05

Appendix 4. Simulation of stochastic IPM
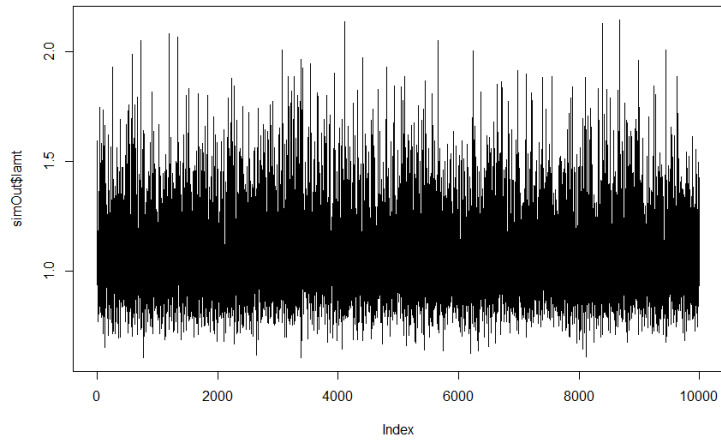
Figure S1. Stochastic growth rate, λ_t, distribution from 100,000 simulations.
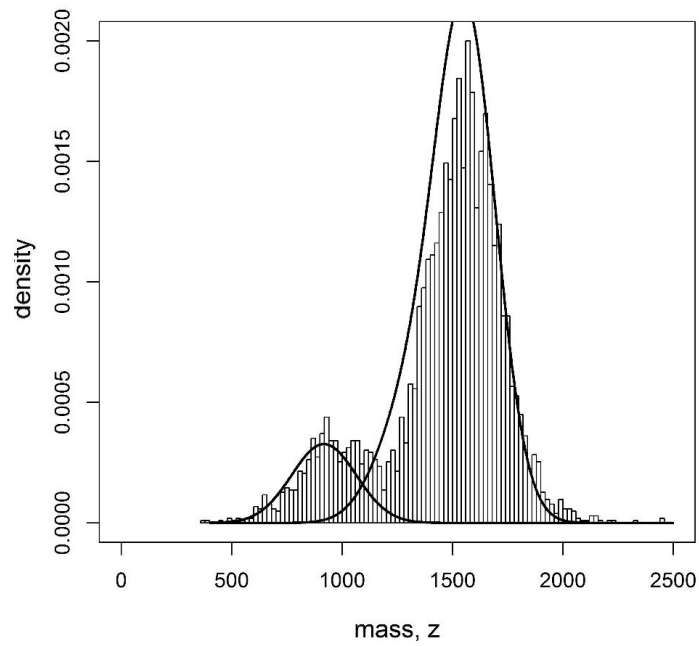
Figure S2. Estimated stable state distribution for (body) mass, z. Continuous line: estimated stable distribution of the integral projection model. Histogram: observed mass distribution.

Appendix 5. Annual parameter estimates based on regression models.
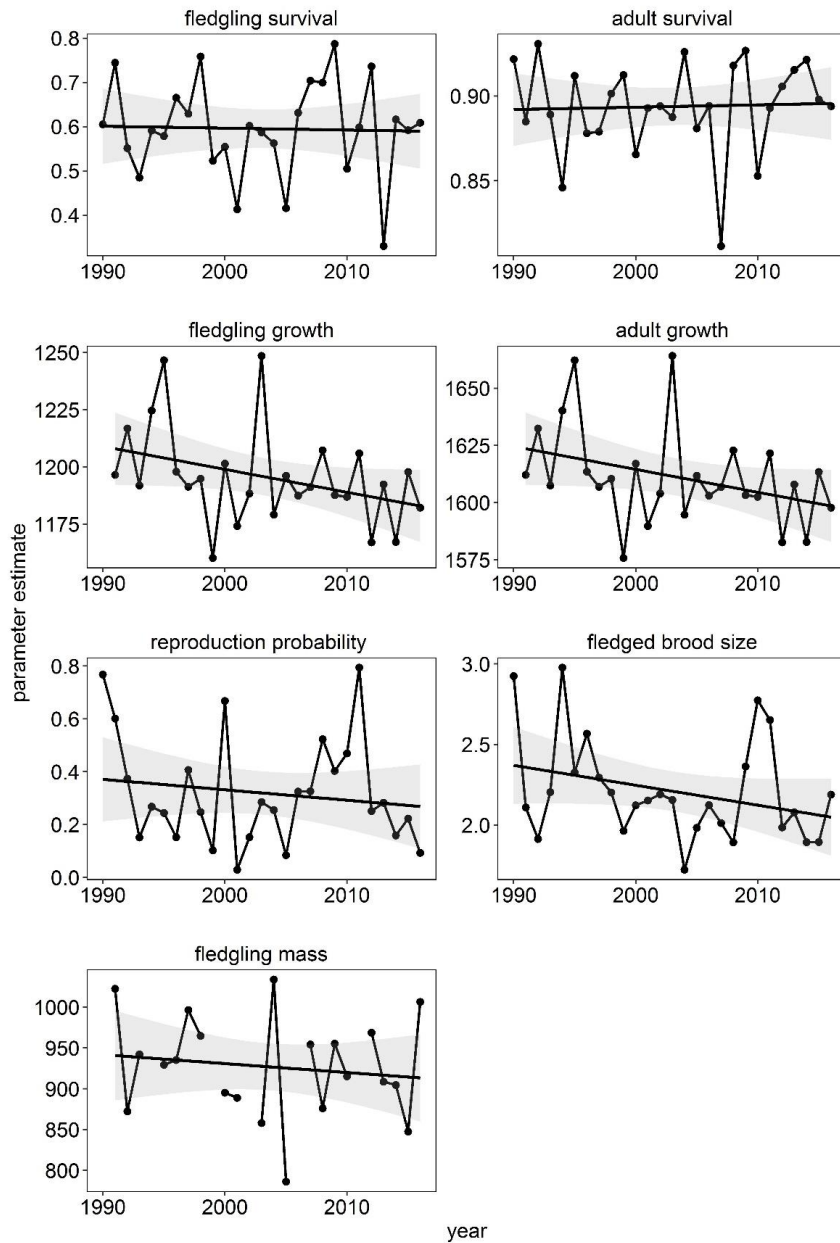
Figure S1. Annual parameter estimates based on regression models of survival of fledglings (ϕ_{fl})and adults (ϕ_{ad}), growth (G), reproduction probability (R), fledged brood size (*fec*) and fledgling mass (C_0), estimated at mean (age-specific) body mass and covariate values. Black line illustrates the temporal trend for each rate/transition, with 95% confidence intervals, estimated with a linear model.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statoliths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two symparic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis*): Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus)* habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh

2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	Phd Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	Phd Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (Salmo salar L): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	Phd Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (*Salmo Salar*) production and reproduction
2020	Rachael Morgan	Phd Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	Phd Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (Salmo salar L.): possible nutriomics approaches