Forecasting the outcome of multiple effects of climate change on northern common eiders

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Abstract

Contemporary climate change has complex effects on animal populations caused by the (non-linear) combination of multiple direct and indirect effects on individuals. These interactions make predictions of the ecological response to climate change challenging; however, predictive models are required to effectively manage wildlife populations and conserve biodiversity. Here, we demonstrate how agent-based models (ABMs) can be used to predict population responses under multiple effects of climate change. We consider the case of northern common eiders (Somateria mollissima borealis), a culturally and ecologically important seabird which is experiencing dramatic environmental change due to losses in Arctic sea ice. Our model shows that losses in Arctic sea ice will lead to increases in nest predation by polar bears in areas where these species are sympatric. However, climate-mediated increases in breeding propensity and clutch size could have a large positive effect on eider population size. When considered together, these effects are predicted to result in a relatively stable eider population size over a 50-year period. Additionally, assuming eider populations are influenced by climate change in the manner proposed in this study, our model suggests that future eider populations will not be more susceptible to extrinsic perturbations (e.g. severe weather events, disease outbreaks) than were historical populations. As a result, our study demonstrates increasing climatic suitability and increasing nest predation will not lead to major changes in population size in northern common eiders, and emphasizes the importance of considering multiple, interacting effects on wildlife populations experiencing climate change.

1. Introduction

Climate change is predicted to have global impacts on the abundance and distribution of earth's biota (Hof et al., 2012; Jenouvrier, 2013; Zarnetske et al., 2012). If a species' survival or reproductive success is related to local temperature, precipitation, snow/ice cover, humidity, or extreme weather conditions, then changes in these climatic variables can have direct impacts on the fitness of individuals and populations. This 'climate envelope' approach has been widely used to understand the ecological consequences of climate change (Duncan et al., 2009; Pearson and Dawson, 2003), however, climatic change can also indirectly impact species by influencing the biotic interactions that regulate their abundance and distribution (Blois et al., 2013; Harley, 2011; Hof et al., 2012; Milazzo et al., 2013; Zarnetske et al., 2012).

Even if a species is physiologically insensitive to shifts in local climate, they may be indirectly influenced by changes in the abundance or behaviour of predators, prey, competitors, hosts and parasites. Importantly, many species will be influenced by multiple direct and indirect effects of climate change, which can lead to unexpected biological responses (Cannone et al., 2007; Harley et al., 2006). There is increasing recognition that ecologists should be able to make predictions regarding the effects of climate change, even if it that means our predictions will sometimes be inaccurate (Evans et al., 2012; Sutherland, 2006). Predictions related to climate change are routinely made in other fields (e.g. economics, climatology) and are desired by wildlife managers, decision-makers and other stakeholder groups who can use them for pre-emptive conservation action. While some studies have produced large (i.e. global or continental) scale predictions of the
ecological response to climate change (e.g., Cramer et al., 2001; Cheung et al., 2009), these studies may be at too coarse of a scale to effectively inform certain conservation actions. Instead, reliable landscape- or population-level predictions of both environmental and biological changes would be highly beneficial for many conservation practitioners. However, predicting the impacts of climate change on animal populations is challenging, in part because a population’s response is typically a non-additive combination of multiple different biotic and abiotic effects that are experienced (Bjornstad, 2001; Hassell et al., 1976). Indeed, most animal populations can be considered complex systems, which have a heterogeneous composition, many interacting elements, feedback mechanisms, tipping points and lagged responses (Mitchell, 2009; Taylor, 2005). In general, using empirical methods to make predictions of complex animal populations is infeasible because of issues related to scale, boundedness, and temporal or spatial separation between cause and effect (Game et al., 2014). As such, there is an urgent need to develop reliable mathematical or simulation-based models for ecological systems experiencing a changing climate (Evans et al., 2012).

In comparison to many other ecological systems, making predictive models of the effects of climate change on Arctic systems may be relatively tractable. Arctic areas are experiencing rapid climate change, yet are low in biodiversity (Gaston, 2000; Stroeve et al., 2007). As a result, the abiotic effects of climate change effects on Arctic species should be strong. Additionally, because Arctic areas are relatively low in biodiversity, the changes in biotic interactions should be less complex than for species in temperate or tropical areas (owing to fewer biotic interactions overall). Furthermore, Arctic areas are still relatively free from industrial, agricultural and transportation infrastructure (Sanderson et al., 2002; Venter et al., 2016), and therefore the most extensive environmental change in Arctic areas in the short-term future is likely to be a changing climate. For these reasons, Arctic systems represent an important test-bed for the field of predictive ecology, especially in regards to ecological responses to climate change.

The northern common eider (Somateria mollissima borealis; hereafter we use the term ‘northern common eider’ when referring to the focal subspecies, and the term ‘common eider’ when referring to the species generally) is a sea duck found in the Eastern Canadian Arctic, Greenland and Iceland, an area that is experiencing rapid warming and dramatic losses in sea ice (Ding et al., 2014). This culturally and ecologically important species is being influenced by climate change through several mechanisms. Many studies have suggested that there is generally a positive relationship between warmer conditions and increased reproduction for common eiders. Specifically, earlier sea ice breakup leads to earlier nesting (Chaulk and Mahoney, 2012; Love et al., 2010), more total nests being initiated (i.e. higher breeding propensity; Mehlum, 2012; Hansen et al., 2013; Jónsson et al., 2016) and increases in clutch size (Chaulk and Mahoney, 2012; Jónsson et al., 2009; Lehikoinen et al., 2006; Mehlum, 2012), which results in increased recruitment (D’Alba et al., 2016; Lehikoinen et al., 2006; Mendenhall and Milne, 1985; Swennen, 1991).

However, northern common eiders are also sympatric with polar bears (Ursus maritimus) across much of their range, and several studies have noted that polar bear predation of common eider nests is increasing (Iverson et al., 2014; Prop et al., 2015; Smith et al., 2010). Polar bears primarily hunt marine mammals from the sea ice, but declines in Arctic sea ice have forced polar bears into terrestrial environments where (and when) northern common eiders nest. Because sea ice loss is expected to continue (e.g., Overland and Wang, 2007), predictive models also suggest that polar bear predation of eider nests will increase in the future (Dey et al., 2017). While the energetic value of bird eggs to polar bear populations is probably low (Dey et al., 2017; Rode et al., 2015), polar bear predation could have dramatic effects on local bird populations and could influence traditional activities such as egg and down collection.

Here, we use agent-based models (ABMs) to predict the effects of climate change on northern common eider populations, and then use several data sources to validate our predictions based on recently observed changes in common eider populations. Agent-based modelling is simulation-based approach which allows for the incorporation of interindividual variation, can account for complex interactions within and among species, as well as between individuals and their environments, and is also flexible in the types of social and biological systems that can be modelled (McLane et al., 2011; Wilensky and Rand, 2015). In our model, individual animals are represented as digital agents, and can interact with one another and with their environment based on programmed behavioural rules, which are developed with ecological theory and species-specific knowledge. Population-level responses are then allowed to emerge from the interactions among agents. We used agent-based modelling to address three primary research questions related to climate-change effects on northern common eiders: (1) How will direct climate-mediated changes in northern common eider vital rates (breeding propensity and clutch size), and indirect effects (i.e. increased nest predation by polar bears) independently affect northern common eider populations? (2) How will the indirect and direct effects of climate change interact to influence northern common eider population dynamics and, (3) Will future northern common eider populations be more susceptible to perturbations (e.g. disease outbreaks, severe weather) than are current populations? In addressing these questions, we aim to demonstrate the utility of agent-based modelling in creating predictive models for animal populations experiencing climate change, as well as providing useful predictions to support wildlife conservation efforts in Arctic areas.

2. Methods

2.1. Modelling challenges

Predicting changes in northern common eider populations is important because they have an important role in Arctic socio-ecological systems (Walther and Coulson, 2015). However, northern common eiders exhibit many of the general characteristics which make ecological prediction challenging. They are a long-lived species, and therefore would be expected to have slow population responses to changes in reproductive success. They have a “boom and bust” (i.e. high variance) reproductive strategy, such that measuring reproductive success over short-periods is unlikely to predict population dynamics. Northern common eiders exhibit behavioural plasticity with respect to breeding decisions (e.g. timing and location of nesting; Sonsthagen et al., 2009; Öst et al., 2011; Jönsson and Løvkvistsson, 2013), which could impact their exposure to nest predation and their reproductive success. Finally, northern common eider nest predators (like polar bears) have the capacity to learn and remember eider colony locations (Fagan et al., 2013; Lunn and Stirling, 1985), which can modify predator behaviour and feedback on the fitness of nesting birds (Fig. 1). As a result, forecasting changes in northern common eider populations due to climate change requires a framework that can incorporate interactions between changes in common eider demography, spatial ecology, nesting phenology, polar bear learning and memory, and the direct effects of climate on common eider reproductive success.

2.2. Model overview

We used agent-based modelling to predict how direct and indirect aspects of climate change will affect northern common eider population dynamics. To perform this analysis, we extended the spatially explicit ABM presented in Dey et al. (2017), which was developed to predict the degree to which polar bear predation of common eider eggs would increase given predicted declines in sea ice, and the bioenergetics consequences of egg consumption for polar bears. Briefly, this model includes two types of digital agents that represent individual polar bears and female common eiders. The behaviour of these agents is
governed by species-specific submodels (details below). These agents interact on a simulated Arctic island archipelago landscape and behave according to behavioural rules generated from ecological theory, as well as known behavioural patterns of common eiders and polar bears. When possible, our model was developed with data from common eider and polar bear populations in Fosse Basin and Hudson Strait, Canada, an area experiencing rapid changes in sea ice dynamics, and where polar bears are increasingly foraging for seabird eggs (Iverson et al., 2014). Climatic change was incorporated using historical and predicted sea ice break-up and freeze-up dates for the period of 1990–2039 for Fosse Basin (Dey et al., 2017), and these climatic variables influence the phenology of both polar bear and common eider agents (Chaulk and Mahoney, 2012; Love et al., 2010; Stirling et al., 1999). The model runs for 50 consecutive common eider breeding seasons (i.e., it begins on the day of the first nesting attempt by a common eider and continues until the last common eider is finished nesting, then it skips ahead to the next breeding season); therefore, changes in common eider population dynamics due to winter conditions (e.g., Guerry et al., 2016) are outside of the scope of this model. Each model run begins with 5000 common eider agents and 40 polar bear agents, which were based on estimates of the population density of polar bears and common eiders in Hudson Strait. Full details of the model are presented in (Dey et al., 2017). This previous model underwent thorough model verification and corroboration using the TRACE procedure (Augusiak et al., 2014; Grimm et al., 2014).

Because our previous model focused on the behaviour and bioenergetics of polar bears, the common eider agents were simplistically represented (their population size was consistent across model years, and climate conditions only influenced nesting phenology, but not other reproductive variables). In the current study, we modify the previous model through the addition of a common eider demography submodel, which allows for changes in common eider population size, and for climate change to drive variation in common eider vital rates. Furthermore, we conduct new calibration, verification, and validation procedures for our new model components using datasets not previously used in the earlier model development. We used our extended model to test how certain climate-dependent common eider vital rates (breeding propensity and clutch size), as well as polar bear nest predation, would impact common eider population size over a 50-year period. Additionally, we tested whether common eider populations experiencing climate change were more susceptible to future perturbations in several different vital rates (in addition to breeding propensity and clutch size). Finally, we tested how uncertainty in key model variables influenced the common eider population projections.

The changes to our model are detailed below. The complete code required to run the current version of the model, as well as a model description (using the ODD protocol; Grimm et al., 2010) is available at github.com/cjdey/Agent-based-models.

2.3. Common eider demography submodel

In our previous model, the common eider agent population size was stable throughout each model run (i.e., the model was restricted to have no change in common eider population size). Common eider agents did not track their age, and although they experienced mortality, they were replaced by a single new agent if they died. Additionally, while common eider nesting phenology was influenced by the sea ice breakup date in our previous model, no demographic vital rates were influenced by climatic conditions. To investigate how the direct and indirect effects of climate change will impact common eider populations, we created a common eider demography submodel that more accurately represented demographic processes, and allowed for changes in population size. This submodel included stochastic components for certain vital rates similar to stochastic matrix population models (Boyce et al., 2006). Additionally, two vital rates (breeding propensity and clutch size) were linked with annual climate conditions, based on evidence from previous common eider studies. The submodel followed the general outline shown in Fig. 2, with individuals moving through life stages according to the following rules:

2.4. Adults, juvenile and fledgling survival

Adult common eider agents (> 2 years old) experienced death between model years (i.e. during the non-breeding season). The rate of mortality was determined by the baseline adult survival rate, \( \lambda_n \), and a Weibull model of survival senescence (Ricklefs and Scheuerlein, 2002) with coefficients determined from empirical curves of adult survival in Waltho and Coulson (2015). An adult had a possibility of death of:

\[
(1 - \lambda_n) + (4.74 \times 10^{-31}) \times (\text{age} - 2)^{7.411}
\]

Fig. 1. Major effects on sea ice loss on northern common eiders. The loss of Arctic sea ice has direct impacts on common eider nesting behaviour, polar bear (a nest predator) behaviour and common eider clutch size. Polar bear foraging behaviour is also influenced by their learning and memory for common eider colony locations and the energetic benefit of eating eggs (which is influenced by clutch size). Similarly, common eiders adjust their nesting behaviour in response to nest predation, creating complex feedback loops which ultimately impacts reproductive success and population size.
where age, is the age of the common eider agent in years. The adult survival rate ($\lambda_a$) was inversely determined through calibration (see Electronic Supplementary Materials). Juvenile common eider agents (1–2 years old) were assumed to survive at similar rates to adult common eider agents (Wilson et al., 2012) and did not experience survival senescence. Juvenile common eider agents also did not reproduce. As a result, they had a possibility of death of $1 - \lambda_e$. Fledgling common eider agents (1 month–1 year old) were also assumed to survive at similar rates to adult common eider agents. However, these agents had already survived for 1 month (see hatching survival rules, below), and therefore their possibility of death was $1 - \lambda_{ff}^{11/12}$.

### 2.5. Breeding propensity

Only adult common eider agents had the potential to breed and the probability that a common eider hen bred in a specific year varied among model years (Fig. 2). Several studies have noted a link between climate conditions and breeding propensity (Hanssen et al., 2013; Jönsson et al., 2016; Mehlum, 2012) and therefore we conducted model runs with two different conditions. In the WITHOUT CLIM-BP model, the breeding propensity of the common eider agents was independent of the annual climatic conditions, but stochastically varied among years (see below). In model runs WITH CLIM-BP, the breeding propensity of the common eider agents was linked with the annual climate conditions. We used an empirical dataset of common eider hen breeding propensity (2668 hens sampled from 2002 to 2013 at Mittivik Island, Nunavut, Canada) to parameterize our breeding propensity rules for both conditions. We fit a logistic regression (with a logit link) to the breeding propensity data (1 = bred, 0 = did not breed) using the annual ice breakup date as the response variable, mean nesting date as the fixed effect, and site as a random intercept. We derived the slope and variance of the relationship between mean clutch size and the mean nesting date, using clutch size data from three locations presented in Waltho and Coulson (2015). Then we fit a linear mixed model to the datasets using mean annual clutch size as the response variable, mean nesting date as the fixed effect, and site as a random intercept. We derived the slope and variance of the relationship between mean clutch size and mean nesting date from this statistical model, and set the intercept of the relationship such that the expected clutch size in the first model year was equal to $4.12$ (which is the estimated mean clutch size for common eiders at 60°N from Fig. 8.1 in Waltho and Coulson, 2015). Therefore, the mean common eider clutch size ($CS$) for a given year was determined by:

$$CS = 8.658 - (0.027 \times B) + N (\mu = 0, \sigma = 0.304)$$

where $B$ is the mean nesting date for the model year. Since the mean nesting date $B$, is linked to the ice breakup date (see Dey et al., 2017), the mean clutch size will increase as the ice breakup date advances (in model runs WITH CLIM-CS). In model runs WITHOUT CLIM-CS, we substituted 168 for $B$, which is the mean nesting date for the first model year. Therefore, the mean clutch size would still vary among model years (due to the stochasticity in the equation), but the expected mean clutch size would be constant among model years. In our model, the expected clutch size of common eider hens did not change with age.

Regardless of model condition, each common eider agent then sampled the following distribution to determine their individual clutch size ($CS$) for the year:  

$$CS \sim \text{Poisson} (\lambda = CS - 1) + 1$$

### 2.6. Clutch size

For females that bred, we determined the clutch size ($CS$) of each individual’s nest for the year, under two different conditions. In model runs WITHOUT CLIM-CS, mean clutch size varied among model years, but was not linked with annual climate conditions. In model runs WITH CLIM-CS, clutch size was linked to the annual climate conditions, since several previous studies have noted that mean clutch size of common eiders is increased in years with earlier sea ice breakup (Chaulk and Mahoney, 2012; Lehikoinen et al., 2006; Mehlum, 2012). We first determined the slope (and variance) of the relationship between mean clutch size and the mean nesting date, using clutch size data from three locations presented in Waltho and Coulson (2015). Then we fit a linear mixed model to the datasets using mean annual clutch size as the response variable, mean nesting date as the fixed effect, and site as a random intercept. We derived the slope and variance of the relationship between mean clutch size and mean nesting date from this statistical model, and set the intercept of the relationship such that the expected clutch size in the first model year was equal to $4.12$ (which is the estimated mean clutch size for common eiders at 60°N from Fig. 8.1 in Waltho and Coulson, 2015)). Therefore, the mean common eider clutch size ($CS$) for a given year was determined by:

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### 2.7. Nesting success and hatching survival

For females that breed, we determined the number of female hatchlings that survived to 30 days (since only female common eiders are included in the model), at which point they transitioned to the fledging stage (see Fig. 2). First, we determined whether each female successfully completed the incubation stage (nesting success, $N_n$) of reproduction. Independent of polar bear predation, nests could fail due to a background rate of nest failure (e.g. due to nest abandonment, or predation by traditional nest predators), similar to our previous model. Background nest failure was based on the local rate of nest failure $F_l$ (which simulates variance in local habitat quality, see Section 2.5 of the TRACE document in Dey et al., 2017 for details), such that each day, each nest had a chance of failure of:

$$\text{daily rate of failure} = F_l (\frac{1}{2})$$

If a nest had not failed during incubation, we calculated the number of female hatchlings ($n_f$) produced, based on the clutch size ($CS$) of that
Then, we calculated whether each female hatching survived to 30 days old. The survival rate for hatchlings \( \lambda_f \) varied among years and was sampled from the distribution of hatching survival presented in (Wilson et al., 2012):

\[
\lambda_f = \text{Beta} \left( \alpha = 1.272, \beta = 5.423 \right)
\]

### 2.8. Changes to polar bear submodel

To explore the impact of polar bear depredation on common eider population dynamics, we ran model runs without bears (no polar bear agents included) and with bears. In model runs with bears, we included a stable population of 40 polar bear agents, similar to our previous model (based on an estimation of the population density of polar bears in Foxe Basin, Dey et al., 2017). The polar bear agent behavior rules are fully outlined in Dey et al. (2017), and were not modified for this study. Briefly, polar bear agent behavior was dependent on their energetic state, their sensory abilities (visual and olfactory), and their memory of the environment (gained through experience). Polar bear agents that are in poor condition actively search for nests, while those in good condition only forage on nests that they encounter opportunistically.

Some studies have predicted declines in polar bear population size due to declines in sea ice (Atwood et al., 2016; Hunter et al., 2010; Lunn et al., 2016; Molnar et al., 2010; O’Neill et al., 2008; Regehr et al., 2016). To evaluate the potential impact of declines in polar bear population size on our model outcomes (common eider population dynamics), we also ran some model runs with a declining polar bear population (with bear decline). In these model runs, we initially included 40 polar bear agents, but removed 1 randomly selected polar bear agent every 2 years during the future period of the model (i.e. model years 2015–2039). This process resulted in a decrease in the model’s polar bear population of 30% (over a 25-year period), which is of similar magnitude to the predicted decline in global polar bear populations in a recent simulation model (Regehr et al., 2016). We chose this simple method of removing polar bear agents, rather than a mechanistic model of polar bear population declines, because changes in polar bear population are dependent on changes in many processes which are outside of the scope of this model (e.g. mating success, winter foraging success, reproductive physiology, juvenile survival, harvest, etc.).

### 2.9. Further model details

For details related to model initialization, model calibration, model resolution and scope, and model verification, please see the Electronic Supplemental Materials.

### 2.10. A note on nomenclature

The model variant without bears, without clim-bp and without clim-cs was termed the baseline model and was used as a null model against which to test the effect of changes in common eider population dynamics. This model also represents a situation in which climatic change does not occur, since no model processes are linked to climate conditions. The model variant with bears, with clim-bp and with clim-cs was termed the climate change model, and was used as a most likely scenario for northern common eider populations experiencing climate change.

### 2.11. Model validation

We validated our model using pattern-oriented modelling procedures (Grimm et al., 2005; Grimm and Railsback, 2012). When models simultaneously recreate multiple patterns observed in empirical systems that were not included in the design of the model, users can be confident that the model represents the essence of a system, and is therefore useful for prediction and inference. Our original model recreated empirical patterns of polar bear bioenergetics, polar bear behavior, and common eider colony dynamics (Dey et al., 2017). To further validate our current model, we tested whether our model reproduced patterns of common eider age distribution, and patterns of variation in common eider reproduction, observed in real populations. Additionally, we qualitatively compare whether our model produces similar adult survival rates, patterns of vital rate sensitivity and changes in population size, as real populations. These tests are detailed below.

There is limited data available on age distributions of common eiders, and to our knowledge, no such data on the borealis subspecies. However, by intensively banding and sighting female eiders at the Coquit Island colony, Coulson (1984) presents data on the age since first reproduction of > 1100 Somateria mollissima mollissima individuals. We tested whether our model showed similar patterns of age since first reproduction as Coulson’s data. First, we ran 100 model runs of our baseline model. This model variant was chosen because Coulson’s data is from a historical population where climate change effects were unlikely to have a strong impact on the age distribution, and no polar bears impact reproductive success in that area. For each model run, we calculated the distribution of years since first reproduction for the eider agents that were alive at the end of the run (i.e. at the end of model year 2039). Then, we converted these values, as well as Coulson’s values, to proportions of the total adult population, and compared the distributions visually (Fig. S2). This comparison demonstrates that the age since first reproduction from our model strongly matches those from the Coquit Island population.

The spatial distribution of nesting common eiders is known to have a positive relationship with the abundance of nests, across multiple spatial scales (Chaulk et al., 2006). We tested whether this pattern was also present in our model, by comparing the incidence of nesting common eiders (i.e. the proportion of islands that had nesting common eiders) with the common eider abundance (i.e. mean nests per island), across all islands within 10 non-overlapping 10 km × 10 km (100 km²) grid cells from our model environment. We measured the incidence and abundance during the last model year (2039), for 100 model runs of the climate change model. Our modelled common eider population demonstrated a positive incidence – abundance relationship, similar to real common eider populations (slope between incidence and log(abundance) from linear mixed model with model run as a random intercept = 0.023, SE = 0.00086, t = 26.81, P < 0.001, Fig. S3). Qualitatively similar results were produced in the baseline model.

In addition to the above validation testing, our model recreated three other patterns observed in empirical populations, providing further evidence that the modelled common eider population is representative of real common eider populations. First, the inversely determined adult survival rate \( \lambda_a = 0.9225, \) Table S1) is within the range of adult survival values found in previous field studies (0.81–0.96) (Waltho and Coulson, 2015). Second, our perturbation analysis (see Model analysis section, below), shows that our modelled common eider population is most sensitive to changes in adult survival rate, with much lower sensitivity to other vital rates. This result is similar to findings from other common eider population studies (Wilson et al., 2012), and consistent with theoretical expectations for long-lived birds (Sæther and Bakke, 2000). Finally, while there is limited data available on changes in common eider population size over most of their range (Waltho and Coulson, 2015), colony sizes have been generally stable across multiple sites in Hudson Strait from 1990 to present. This is an area that is experiencing rapid sea ice loss and where polar bears are increasingly foraging on seaduck nests (Iverson et al., 2014). As a result, stable modelled eider population sizes over this time period (in the climate change variant; see e.g. Fig. 3D) is also qualitatively supportive of consistency between the models and the empirical system.
2.12. Model analysis

Because our model contained many stochastic components, the results of model runs varied. To derive inferences from our model outputs, we ran batches of model runs using BehaviorSpace (Wilensky and Shargel, 2002), and imported the results into R (R Core Team, 2015) for statistical analysis using the lme4 (Bates et al., 2015), ggplot2 (Wickham, 2009) and heplots (Fox and Friendly, 2016) packages.

To analyze the effects of polar bear predation, and climate-linked changes in common eider vital rates on common eider population size, we ran 100 model runs for each of 5 sets of model conditions (the four variants shown in Fig. 3, plus the baseline variant). We then compared the final population size among variants using a linear model. Log-transformed final common eider population size was used as the response variable, and model variant was included as the sole fixed effect.

To test whether a decline in polar bear population would influence common eider population size, we ran two additional model variants, each for 100 model runs. These variants were (a) a model with polar bear agents that experienced a declining population (i.e. with bear decline) but without climate-linked vital rates for common eiders (i.e. a model variant equivalent to Fig. 3C, but with a declining polar bear population), and (b) a model with polar bear agents that experienced a declining population and an common eider population with climate-linked breeding propensity and clutch size (i.e. a model variant equivalent to Fig. 3D, but also with a declining polar bear population). We then compared the log-transformed final common eider population size of model runs with bear decline to the similar variant without bear decline, using two linear models.

To test how additional extrinsic perturbations (e.g. extreme weather events) to the common eider population will impact common eider population size, we conducted one-at-a-time sensitivity analysis (Thiele et al., 2014). In this analysis, we conducted a batch of model runs in which common eider vital rates (nest success, juvenile survival, hatchling survival, fledgling survival, clutch size, breeding incidence, adult survival) were changed, one at a time for a short period. We allowed each model run to progress under standard conditions until model year 2030. Then, we ‘perturbed’ the population by decreasing one common eider vital rate by 10%, for a period of 5 model years. We repeated this procedure 100 times for each vital rate (see Fig. 4) and, repeated the whole simulation for two model variants (the baseline model and the climate change model). We also conducted 100 model runs of each model variant, in which no vital rates were perturbed, for comparative purposes.

To statistically compare the effects of perturbations in different vital rates, and whether the effects of perturbation differed between the baseline model, and the climate change model, we first calculated the rate of change in population size across the 5-year perturbation period using the equation:

\[ \text{Growth rate} = \frac{P(t_2) - P(t_1)}{P(t_1) \times (t_2 - t_1)} \]

where \( P(t_1) \) indicates the population size at the end of model year 2029, and \( P(t_2) \) indicates the population size at the end of model year 2034. We used this value as the response variable in a linear model with the model variant, the vital rate that was perturbed, and the interaction of these variables, as fixed effects.

2.13. Global sensitivity testing

To test the impact of parameter uncertainty on model outcomes, we performed a global sensitivity analysis (Thiele et al., 2014). To perform this analysis we allowed 3 key model parameters to vary (simultaneously) within intervals of uncertainty, and used multivariate regression techniques to partition variance in model outcomes (Broeke et al., 2014; Burgers et al., 2010). We first created 500 sets of parameter values by drawing each parameter from uniform distributions with lower limits equal to 50% of the original parameter value, and upper limits equal to 150% of the original parameter value. Then, we ran one model run for each parameter set, and recorded the final common eider population size as the model output of interest. The parameters we allowed to vary were the number of polar bear agents (uncertainty interval: 20–60), the slope of the relationship between ice breakup date and common eider breeding propensity (uncertainty interval: 0.0056–0.0166) and the slope of the relationship between ice breakup date and mean common eider clutch size (uncertainty interval: 0.0135–0.0405). Note that our previously conducted models with bear decline (see above) are different than the runs with different bear population sizes in this analysis because runs with bear decline include a decreasing bear population size over time, whereas the global sensitivity models have set bear populations within each model run.

To determine the sensitivity of the model output to uncertainty in the parameter values, we then ran a linear model using log-transformed final common eider population size as the response variable, and the three parameters as the fixed effects. To facilitate comparison among fixed effects, we scaled and centered the fixed effects prior to analysis (Schielzeth, 2010). We also calculated eta² for each parameter, which describes the percentage of variance in the response variable that is explained by each parameter (Cohen, 1973). If eta² values are high, then the model output is sensitive to uncertainty in the parameter value.

3. Results

The final common eider population size was responsive to the conditions of the model. Relative to the baseline model variant, including a link between annual climatic conditions and common eider clutch size (i.e. with clim-CS) did not significantly increase the final common eider population size (LM: \( \exp(\beta) = 1.147, \ t = 1.627, P = 0.104 \), Fig. 3A), although the mean final population size was 17% higher than in baseline conditions. However, a link between climate and common eider breeding propensity (i.e. with clim-bp) resulted in a significant increase in common eider population size to approximately double the initial population size (\( \exp(\beta) = 2.03, t = 8.457, P < 0.001 \), Fig. 3B). In contrast, the presence of polar bear agents (i.e. with bears) significantly decreased the final common eider population size relative to the baseline model, (\( \exp(\beta) = 0.519, \ t = -7.782, P < 0.001 \), Fig. 3C), and the mean population size decreased by approximately 50% of the starting value over the 50-year modelling period. These changes in population size are equivalent to long-term common eider population growth rates of 0.55% (interquartile range (IQR) = −0.66, 1.36) per year (with clim-CS), 2.40% (IQR = 0.51, 3.88) per year (with clim-bp), and −0.87% (IQR = −1.35, −0.63) per year (with bears).

Importantly, the positive effects of changes in common eider vital rates, and the negative effects of polar bear nest predation, nearly completed cancelled out (Fig. 3D). Model runs with climate linked common eider vital rates, and polar bear presence (i.e. the climate change model), did not have significantly different common eider population sizes than the baseline model (\( \exp(\beta) = 1.037, \ t = 0.430, P = 0.667, \) Fig. 3D). The mean change in population size in the climate change model was equivalent to a long-term population growth rate of 0.23% per year (IQR = −0.64, 0.86), which was similar to the 0.18% per year (IQR = −0.74, 0.91) mean growth rate in the baseline model.

Including a declining polar bear population had marginal effects on common eider population size. For model runs without climate linked common eider vital rates (i.e. without clim-CS and without clim-bp), common eider population size was not significantly different for runs with a declining polar bear population relative to those with a stable polar bear population (LM: \( \exp(\beta) = 1.015, \ t = 0.193, P = 0.847 \)). Similar results were found for model runs with clim-CS and with clim-bp (LM: \( \exp(\beta) = 1.035, \ t = 0.442, P = 0.659 \)).

Perturbation of common eider vital rates led to changes in common eider population size (Fig. 4). The modelled common eider population
was most affected by decreases in adult survival, and perturbation of other vital rates showed small changes in common eider population size (Fig. 4). However, relative to the BASELINE model, the CLIMATE CHANGE model did not demonstrate any significant overall difference in sensitivity to vital rate perturbation (Table 2), nor did the effect of perturbing any individual vital rates differ among model variants (i.e. no interaction with P-values < 0.05, Table 2).

Uncertainty in key model parameters influenced the final common eider population size, but the effects were small. The model was most sensitive to the relationship between ice breakup date and common eider breeding propensity, and this variable explained 7.6% of the variance among model runs in our global sensitivity testing (LM: exp(β) = 1.18). The number of polar bear agents explained only 2.8% of the variance (LM: exp(β) = 0.91), while the relationship between ice breakup date and common eider clutch size explained 0.3% of the variance (LM: exp(β) = 1.03). Indeed, the highest fitted common eider population size from the linear model (i.e. the fitted value for runs with a low number of bears, and high climate-breeding propensity and climate-clutch size slopes) was 8189 (a long-term growth rate of 1.27% per year), while the lowest fitted value (i.e. with high number of bears, and low climate-breeding propensity and climate-clutch size slopes) was 3021 (a long-term growth rate of −0.79% per year), demonstrating only moderate change in modelled common eider population size even with extreme differences in parameter values.
4. Discussion

Climate change can have complex effects on wildlife populations by directly influencing multiple vital rates, and by influencing interactions among species. While most species are expected to follow the general prediction of poleward range expansions (Pearson and Dawson, 2003), and increases in population sizes at higher latitudes due to poleward shifts in climatic niches (Jiguet et al., 2010; Maclean et al., 2008), biotic interactions can prevent these changes. Here, we show that despite climate-mediated changes in northern common eider nesting phenology, breeding propensity, clutch size, spatial distribution, predator behaviour, and predator population size, our models predict stable northern common eider population sizes over a 50-year period (Dey et al., 2017; this study). While polar bear predation of eider nests would drive decreases in common eider population, these effects are offset by increases in eider breeding propensity and (to a lesser extent) increases in eider clutch size. Additionally, our model predicts that these multiple effects will not cause future northern common eider populations to be more susceptible to extrinsic perturbations than are current populations. Incorporating these various effects into analytical models would be extremely challenging, however our ABM allows population responses to emerge from these lower-level processes, while also accounting for heterogeneity among individuals and complex spatial dynamics.

While we found that climate change will have limited effects on northern common eider population growth, it is important to point out that the link between climate and specific vital rates is idiosyncratic to specific species, and may even differ among subspecies or subpopulations. Indeed, there are 5–7 subspecies of common eiders which encompass a large variance in life-history (e.g. migratory vs resident populations, phenotypic variance, dietary variance) and are geographically widespread (Waltho and Coulson, 2015) which should promote climate resilience at the species level. In our model, northern common eider breeding propensity and clutch size were linked to the date of sea ice breakup. However, the breeding phenology of many common eider populations is not limited by sea ice phenology and some common eider populations are not sympatric with polar bears (e.g. populations in New England, the Baltic Sea and the North Atlantic). Other species may be influenced by climate change in a completely different manner than are common eiders and therefore our study should not be interpreted as supporting a general trend of species resilience to climatic change. While variation in species responses to climate change implies that there may be a need to develop de novo models for each population, species or community of interest, agent-based modelling could provide a general methodology for predictive modelling of climate change effects.

In long-lived species such as common eiders, population growth rate is highly sensitive to changes in adult survival (Wilson et al., 2012). However, empirical studies show that adult survival rates in common eiders are relatively invariant (Hario et al., 2009; Jónsson and Lúðviksson, 2013; Wilson et al., 2007) and most retrospective variation in population growth rate is due to variability in components of fecundity (Wilson et al., 2012). While a recent study has found heterogeneity in common eider survival related to variation in the North Atlantic Oscillation (Guery et al., 2016), there is not a consistent trend with global warming and sea ice loss. Therefore, incorporating such variation is unlikely to change the general outcomes of our model, although it could increase the accuracy of year to year predictions. Nonetheless, if persistent changes in adult survival were to occur in future common eider populations, it is likely that changes in population size would follow.

Our study does add to a growing list of counter-intuitive ecological responses to climatic change. For example, studies of the effect of warming on spider-grasshopper-plant communities indicate that warming increased the indirect effect of spiders on plants, which was opposite of the initial expectations based on the thermal response of individual species (Barton et al., 2009). Similarly, Suttle et al. (2007) found that increasing spring precipitation in a grassland ecosystem initially favoured native plants over invasive plants, however, invasive plants were ultimately able to dominate because of increases in soil nitrogen. Such unexpected responses to climate change illustrate the complexity of ecological systems and the challenge of predicting ecological responses to environmental change, especially without mechanistic models.

Despite the challenges, predicting the effects of environmental change on ecological communities is an important goal for many ecologists. Our study demonstrates how agent-based modelling can incorporate ecological complexity and be used to make reliable predictive models. Our results show that even predictions for single species should incorporate both biotic and abiotic changes, and that such changes must be considered simultaneously, rather than sequentially, because changing biotic interactions can have complex effects on population size. Furthermore, our study demonstrates that a stable population size does not imply a lack of climate change effects on an animal population, nor does it imply adaptation to changing climatic conditions. Instead, stable population size could be maintained by antagonistic effects of climate change on different vital rates - a finding that deserves further consideration in species that are apparently climate resilient.

Acknowledgments

The authors thank community members from Cape Dorset, Coral Harbour, Iqaluit, Kangiqsujuaq, Aupaluk, Kangirsuk, Iqaluit and Kimmirut, for logistical assistance with common eider research. This research was funded by a Mitacs Accelerate Cluster grant (IT04216) (in collaboration with Baffinland) to HGG and CADS, and a Liber Ero Fellowship to CJD. Additional funding was provided by Environment and Climate Change Canada, Carleton University, the University of Windsor, the Weston Foundation, the Nunavut Inuit Wildlife Secretariat, ArcticNet Centers of Excellence, Oceans North, the Polar Continental Shelf Project, and the PEW Charitable Trust.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.02.007.