

Model Description

1. Purpose

The purpose of the model is to simulate how changing climate conditions influence polar bear predation and northern common eider populations. It is also intended to test how changing patterns of polar bear predation will influence the distribution of common eider nests, and how polar bear foraging on eider nests might influence the body condition of individual polar bears.

This model was implemented in NetLogo 5.3.1 (Wilensky, 1999). The Netlogo code has been made available at github.com/cjdey/Agent-based-models.

Further information, including analysis and inference from this model, can be found in Dey et al. 2018. *Cons Biol* 0:0

2. Entities, state variables and scales

This ABM includes 2 types of digital agents representing polar bears and common eider nests/hens. The polar bear agents are characterized by having a sex, age, structural body size (body length), body mass, individual identification number and location.

The eider agents have a clutch size (for each season), nest initiation date (for each season), nest energy (representative of the available energy for consumption by a predator), age, individual identification number and location.

Bear and eider agents interact on a two-dimensional rectangular landscape representing a coastline and island archipelago. The landscape is composed of square cells each representing an area of 50 m by 50 m, with a total landscape area of 100 km by 17.5 km (Figure S1). The cells belong to one of three types; mainland cells, island cells and water cells.

The model proceeds in discrete time-steps representing 30 minutes (i.e. 48 steps per day). Each model run includes 50 sequential eider breeding seasons – the model begins each year on the date that the first eider nest is to be initiated and runs until all eider agent nesting has been completed for that year. Then, the model skips forward to the start of the next breeding season.

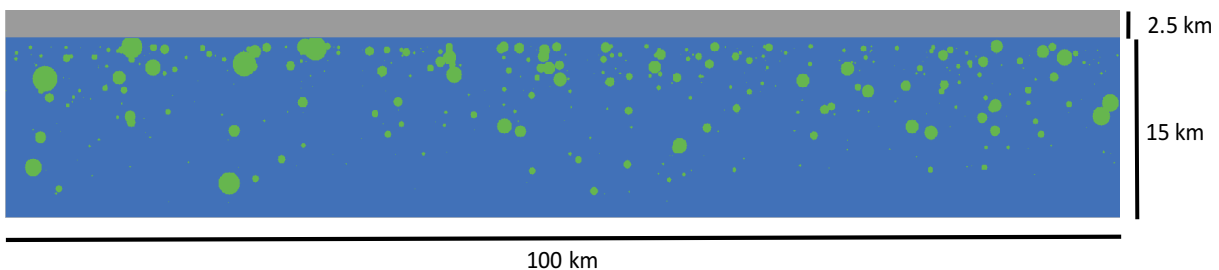


Figure 1. Depiction of a landscape used in the agent-based model. The landscape is composed of square cells each representing 50 m x 50 m in area. Blue cells indicate

water cells, green cells indicate island cells and grey cells indicate mainland cells. For each model run a new landscape was created under the rules outlined in Section 2.5.

3. Process Overview and Scheduling

The model simulates interactions between polar bears and common eiders over 50 eider breeding seasons. Certain model processes are run only on the first day of each season. First, the climate information (ice-breakup and ice-freeze-up date) for the upcoming season are determined (see *Sea ice phenology and the timing of agent appearance* submodel). During this time-step polar bear agents also experience mortality (simulating mortality on bears during the intermission since the last eider breeding season), update their structural body size and mass (simulating changes in size that would occur during on-ice foraging) and update their age and parental status (see *Polar bear growth and death* submodel). Then, the eider agents experience mortality, age, choose a new nest location and determine the date they will initiate their nest during the upcoming seasons (see *Eider nesting* submodel).

During the first time-step of each season, all of the eider agents and polar bear agents are inactive (i.e. they are not visible, they do not act and they do not update any personal information). The eider agents are activated on their nest initiation date (which varies among individuals), and at the site they have chosen for their nest. All of the polar bear agents are activated on the ice-breakup date, at a random offshore location (with 50 cells of the offshore edge of the landscape) to simulate their arrival from the offshore sea ice.

During other time steps, then, polar bear agents assess their state, sense the environment, choose and perform a behavior and update their personal information. Then, the eider agents countdown their remaining incubation time and update the amount of energy in their nest.

4. Design Concepts

4.1 Basic Principles

This model is based on the premise that climate has a different influence the phenology of different species, and climate change can therefore lead to changes in interspecific interactions. Historic and simulated sea ice data are used to determine the relative appearance of polar bears and common eider agents in near-shore Arctic environments. Polar bear arrival in near-shore environments is tightly linked to the break-up of sea ice (Cherry et al., 2013; Stirling et al., 1999), and is therefore advancing rapidly as Arctic environments warm. Common eider nesting dates are advancing at a much slower rate than polar bear onshore migration timing (Jean-Gagnon, 2015; Love et al., 2010), and climate warming is therefore expected to create a greater temporal overlap between nesting eiders and polar bears in near-shore environments (see also Rockwell and Gormezano 2009).

We simulated the behavior of polar bears during the ice-free period using bioenergetics, foraging ecology and expert knowledge of polar bear behavior. In general, polar bear agents attempt to minimize net energy loss during the ice-free period (Derocher and

Stirling, 1990; Ferguson et al., 1997; Knudsen, 1978). If polar bear agents are not energetically stressed (i.e. they will be able to fast for the duration of the ice-free period without severe negative consequences), they will only forage for eider nests in an opportunistic manner. However, if the polar bear agents are energetically stressed, they will actively search for eider nests.

We modeled eider behavior using knowledge of this species' demography and reproductive ecology. These agents change their nest site selection dependent on whether they were successful, or failed the previous year (e.g. if they were depredated). Additionally, they age, reproduce and die according to known vital rates. Finally, climate change has direct influences on some vital rates (breeding propensity and clutch size) in our model.

4.2 Emergence

Nest predation emerges from complex interactions between polar bear behavior, eider nesting behavior and sea ice metrics. The main aspects contributing to these emergent patterns, that are considered by this model, are:

- (i) **Changes in temporal overlap between bears and eiders in near-shore environments.** The timing of nest initiation relative to the timing of ice-breakup (and bear arrival) influences the relative amount of temporal overlap between bears and eiders in near shore environments. This influences the amount of time that eider nests are available as prey.
- (ii) **Changes in available energy in eider nests across the incubation phase.** Avian nests contain more energy earlier in the incubation phase since embryos use energy for metabolic processes (Romanoff, 1967). As a result, the benefit of foraging for nests increases when fresher nests can be found (e.g. when bears arrive earlier in the breeding season).
- (iii) **Changes in the length of the ice-free period.** Polar bears lose body mass during the ice-free period because they generally cannot hunt for their primary prey, seals (Order: *Pinnipedia*). As climate warming increases the length of the ice-free period, bears must spend longer periods of time in a negative energetic state, and will become increasingly reliant on ancilliary prey (e.g. eider nests) to prevent starvation. Therefore, bears should be more motivated to search and forage on eider nests as the length of the ice-free season increases
- (iv) **Learning and memory of eider nest locations.** Eiders often nest in high density aggregations which may persist at specific sites for many years. Since polar bears are known to return to reliable food sources (Lunn and Stirling, 1985), they will be able to learn the location of eider colonies, and return in subsequent seasons.
- (v) **Changes in the distribution of eider nests.** Nest site choice by eiders is influenced by previous nesting success, including nest depredation (Öst et al., 2011; Waltho and Coulson, 2015). Therefore, predation by polar bears will causes changes in the location of nests, and also in the distribution

- (clumpiness) of eider nests, which will influence the costs and benefits of foraging.
- (vi) **Changes in eider population size.** Changes in reproductive output have the potential to influence eider population size and therefore influence the benefit and cost of polar bear foraging on eider eggs.

4.3 Adaptation

The polar bear agents adapt their behavior to meet their predicted energetic needs for a given season, based on rules outlined in the *Polar bear decision making and movement* and *Polar bear bioenergetics* submodels. In brief, they predict their body condition at the end of the ice-free period, and if it will be below a critical threshold they actively search for eider nests to eat. The polar bear agents also have the capacity to remember the location of eider nests, and to learn about the energetic value of eider nests, in order to optimize their foraging behavior.

The eider agents adapt to polar bear predation by moving their nest between years. Eider agents that were depredated the previous year will move further than those that had successful nests (Öst et al., 2011). As a result, repeated bear predation in a single location will cause a decrease in nest density in that area over time.

4.4 Objectives

The polar bear agent's main goal is to survive the ice-free period with sufficient energetic reserves that they can commence hunting for seals once the ice returns. This objective can be met by (a) minimizing energetic expenditure, or (b) foraging for ancillary prey (i.e. common eider nests).

The common eider agent's goal is to reproduce. The eider agents themselves are never depredated by polar bear agents, but their reproductive effort may be terminated by polar bear agents.

4.5 Learning

Polar bear agents have 3 types of memory which allows them to learn the location and value of resources (eider nests) in their environment.

Polar bear agents remember all islands they have visited in the current year (i.e. working memory), and use this information to avoid revisiting the same island during a single year (see *Polar bear decision making and movement* submodel).

Polar bear agents learn about the location of eider nests in their environment (i.e. island reference memory). They remember the location of islands on which they ate nests during previous years, as well as the number of nests that they ate on each island. At the end of each year, they update the expected number of nests available for each island in their reference memory, $\delta_{i,y}$, based on a Bayesian linear operator model (Bernstein et al.,

1988), which increases the weight of more recent information, and devalues (i.e. ‘forgets’) older information based on the equation:

$$\delta_{i_y} = \theta_i \cdot g_i + (1 - \theta_i) \cdot \delta_{i_{y-1}}$$

where g_i is the actual number of nests eaten on a particular island during the current year, θ_i is the memory factor and $\delta_{i_{y-1}}$ is the expected number of nests from the start of the previous year. If $\theta_i = 0$, new information is irrelevant and the expected number of nests for each island remains constant. If $\theta_i = 1$, old information is irrelevant and the expected number of nests for each island is equal to the actual consumption, $g_{i_{y-1}}$, from the previous year.

Finally, polar bear agents keep track of the expected amount of energy they will gain from eating each nest, δ_n (i.e. nest energy reference memory). They update this information during each time step that they eat new nests, again through a Bayesian linear operator model:

$$\delta_{n_x} = \theta_n \cdot g_n + (1 - \theta_n) \cdot \delta_{n_{x-1}}$$

where g_n is the actual rate of energetic gain per nest from the current time step x , and θ_n is the memory factor.

Polar bear agents were initialized with δ_i values of 0 for all islands. This value simulates a population with no experience foraging on eider nests.

The initial expected gain rate δ_n for each individual polar bear agent was drawn from a uniform distribution between 2.32 MJ per nest and 3.93 MJ per nest, which are the available energy values for nests that are just prior to hatching, or freshly laid, respectively.

4.6 Prediction

Bear agents predict what their body condition will be at the end of the ice-free period, and use this information to determine if they are in a condition of high or low energetic stress. In order to make this prediction, the bear agents assume they will lose mass at the rate for resting, fasting bears (see *Polar bear bioenergetics* submodel) until the Julian date equivalent to the ice freeze-up date from the previous year (see *Sea ice phenology and timing of agent appearance* submodel). If their projected body condition at freeze-up is lower than a threshold level (Q_{crit}), the bear agent is considered to be in a state of high energetic stress. Otherwise, the bear will be in a low energetic stress state. The bear agents update their energetic stress level at the end of each day, after incorporating daily net energy gains and losses into their body mass.

4.7 Sensing

Bear agents are able to use olfactory cues to detect nearby eider agents. We assumed that bears could detect that there were nests in a given cell if:

$$n_{nests}^{0.5} > distance$$

where $n_{\text{ nests }}$ is the number of active nests in a given cell, and *distance* is the distance (in cells) from the bear agent.

Bear agents also use visual cues to orient themselves when swimming. We assumed that bear agents can see island cells up to 60 cells (3 km) in a 180-degree cone in the direction they are facing. Polar bear agents cannot detect eider nests using vision, but only use it to guide their movement among islands.

4.8 Interaction

Polar bear agents prey on eider agents as defined in the *Polar bear foraging* submodel. We assumed the bears only eat eider nests, as predation on adult eiders is rare. Polar bear agents do not directly interact with one another in this model. Nor do eider agents directly interact with one another.

4.9 Stochasticity

A large number of model processes were influenced by stochasticity. In each case, we selected statistical distributions that were most appropriate to the particular process, and random values were drawn from those distributions. In particular, landscape generation was based on random assignments for island seed location, island size and the initial distribution of nests. While the first 25 model years were based on historical sea ice data, the sea ice metrics in model years 26-50 were stochastically determined based on extrapolations of previous climatic trends. Furthermore, the spring body mass of polar bear agents, as well as their behavior and movement, had stochastic elements. Similarly, the nesting dates, clutch size, breeding propensity and nest site selection rules for eider agents included stochasticity.

4.10 Collectives

There are no collectives considered in this model.

4.11 Observation

A variety of measures were taken from this model depending on the analysis in question. For more detail see (Dey et al., 2018, 2017)

5. Initialization

Island generation

$n_{\text{island-seeds}}$ cells were selected to be the center of circular islands. The x-coordinates of the cells were selected from a uniform distribution of all possible x-values, while the y-coordinates were selected from:

$$y = \text{Beta}(\alpha = 0.63, \beta = 1.927) * y_{\text{range}}$$

where y_{range} is the range of non-mainland y-values. This distribution and values reproduce the realistic pattern that islands are more likely to occur near the mainland than further from the mainland.

Island seeds were then assigned an island radius (in cells) drawn from:

$$island\ radius = \sqrt{\frac{\gamma(\alpha=0.22243, \lambda=0.00385)}{\pi}}$$

All cells within the island radius of each island seed were changed to 'island cells' and each island was assigned a unique ID number. When the island radius of two (or more) island centers overlapped, the islands were combined into a single island (with a single ID). As a result, the number of islands, $n_{islands}$ is less than or equal to $n_{island-seeds}$, and is not directly controlled. However, the describe procedures create a realistic landscape, in that the islands can have complex shapes rather than being constrained to be circular.

Initial nest distribution

Eider agents were assigned to islands based on a negative binomial distribution:

$$island\ ID = NB(r = 1, p = \frac{100 * C}{n_{islands}})$$

where C is the clumpiness coefficient, and $n_{islands}$ is the number of islands in the landscape. The eider agent would randomly select a cell on this island to nest unless all cells on that island had more than 250 nest agents already established there. This simulates a maximum nesting density of 1000 nests / ha, which is similar to the highest nest density observed in nature (1024 nest/ha; Chaulk et al. 2004). If all cells in the selected island had 250 nests, eider agents would randomly choose another island cell with less than 250 nests.

We calculated a rate of nest failure for each island, F_i , that was indicative of the habitat quality on that island. Our value for F_i was based on the landscape wide average nest failure rate F , and the number of nests present on each island during model setup, assuming that more nests would be present on islands with higher habitat quality (i.e. lower values of F_i).

$$F_i = F - \frac{\beta \cdot (\mu_{IslandID} - islandID)}{100}$$

where $\mu_{IslandID}$ is the mean Island ID of the nest agents during the initialization. The value β determines the degree to which island habitat quality differs from the landscape wide mean habitat quality (F), when β is low, all islands have similar habitat quality, when β is high, islands differ greatly in habitat quality.

Initial age of eider agents

To specify the common eider agent's initial age at the start of each model run we simulated a stable distribution of common eider ages using the age-specific mortality rules described in the *Common eider demography* submodel (below). To produce this

distribution, we created a simulated population of 10000 agents, with a random age drawn from a uniform distribution between 0 and 20. We then allowed this simulated population to age and die for 1000 years, and ensured the mean age was no longer changing. Each agent that died was reinitialized as a hatchling to ensure the population size remained constant in this simulation. The common eider agents in the model were then randomly sampled from this distribution to obtain their initial age.

Initial age and sex of polar bear agents

We simulated a stable distribution of bear ages and sexes under the age and sex-specific mortality rules described in the *Polar bear growth and death* submodel. This was required so that the mean age of polar bear agents did not vary from the start to the end of the model run. In order to produce this distribution, we created a simulated population of 10000 agents, with a random sex and an age drawn from a uniform distribution between 3 and 25. We then allowed this simulated population to age and die for 1000 years, and ensured the mean age, and sex ratio, were no longer changing. The polar bear agents in the model were then randomly sampled from this distribution to obtain their initial age and their sex. We initialized 1/3 of the female polar bear agents in each reproductive category (i.e. no attendant offspring, attendant cub, attendant yearling).

Number of agents

In all model runs we used 40 polar bear agents and 5000 eider agents.

6. Input data

Table 1. Values and associated references for parameters used in this model. Parameters determined through complex calculations, or those defined by probability distributions (rather than single values) are outlined in the text rather than in this table.

Symbol	Definition	Value	Units	References	Notes
<i>Eider nest agents</i>					
λ_e	Annual adult survival rate	92.25	%		Determined via model calibration
B_h	Historic mean nesting date	165	Julian date	Waltho & Coulson 2015	For a North American population at 64° N. Estimated from Figure 6.3 and Figure 6.4, p. 157
S_{95}	Spread of 95% of laying period	28	days	Waltho & Coulson 2015	For a population at 64° N. Figure 6.3, p. 157
V	Nesting phenology adjustment	0.2	days / day advance	Jean-Gagnon 2015	Table 3, p. 39. See also Section 7

			in ice- breakup		
U	Length of incubation period	26	days	Goudie <i>et al.</i> 2000	species no. 546
F	Landscape wide likelihood of nest failure	15	%	Swennen 1983	Table 3, p. 248
μ_s	Mean log (nest dispersal distance) for successful breeders	2.80	m	Öst <i>et al.</i> 2011	Calculated from values on p. 331, see Section 3.6
σ_s	Standard deviation log (nest dispersal distance) for successful breeders	1.40	m	Öst <i>et al.</i> 2011	Calculated from values on p. 331, see Section 3.6
μ_f	Mean log (nest dispersal distance) for failed breeders	3.72	m	Öst <i>et al.</i> 2011	Calculated from values on p. 331, see Section 3.6
σ_f	Standard deviation log (nest dispersal distance) for failed breeders	1.81	m	Öst <i>et al.</i> 2011	Calculated from values on p. 331, see Section 3.6
C	Clumpiness coefficient	0.4		Dey <i>et al.</i> 2017	Determined via model calibration
β	Nesting habitat quality variation	0.2		Dey <i>et al.</i> 2017	Determined via model calibration

Polar bear agents

d	Average time between ice break-up and polar bear onshore date	24.6	days	Stirling <i>et al.</i> 1999	p. 300
σ_d	Standard deviation in time ice break-up and polar bear onshore date	5.5	days	Stirling <i>et al.</i> 1999	p. 300
L_m	Asymptotic length (males)	237	cm	Derocher 1991	Table 6-1, p. 135
L_f	Asymptotic length (females)	198	cm	Derocher 1991	Table 6-1, p. 135
W_m	Asymptotic mass (males)	579	kg	Derocher 1991	Table 6-2, p. 136

W_f	Asymptotic mass (females)	255	kg	Derocher 1991	Table 6-2, p. 136
k_{mL}	von Bertalanffy growth rate (males – body length)	0.381	years ⁻¹	Derocher 1991	Table 6-1, p. 135
k_{fL}	von Bertalanffy growth rate (females – body length)	0.530	years ⁻¹	Derocher 1991	Table 6-1, p. 135
k_{mW}	von Bertalanffy growth rate (males – mass)	0.206	years ⁻¹	Derocher 1991	Table 6-2, p. 136
k_{fW}	von Bertalanffy growth rate (females – mass)	0.605	years ⁻¹	Derocher 1991	Table 6-2, p. 136
A_{0mL}	Age at 0 size (males – body length)	-1.219	years	Derocher 1991	Table 6-1, p. 135
A_{0fL}	Age at 0 size (females – body length)	-1.166	years	Derocher 1991	Table 6-1, p. 135
A_{0mW}	Age at 0 size (males – mass)	-3.383	years	Derocher 1991	Table 6-2, p. 136
A_{0fW}	Age at 0 size (females – mass)	-0.944	years	Derocher 1991	Table 6-2, p. 136
E_m	Mass specific metabolic rate of movement	10.0	kJ/kg/hour	Whiteman <i>et al.</i> 2015	Calculated from supplementary information
E_r	Mass specific resting metabolic rate	2.438	kJ/kg/hour	Watts <i>et al.</i> 1987	Mean calculated from values in Table 1, p. 689
θ_n, θ_i	Memory factor for nests and islands, respectively	0.5		Hamblin and Giraldeau, 2009	Optimal memory factor from this study
Q_{crit-m}	Threshold body condition for energetic stress (males)	51.1	kg/m ²	Stirling <i>et al.</i> 2008	Mean for individuals with fatness index 2. Fig 3 p. 572.
Q_{crit-f}	Threshold body condition for energetic stress (females)	38.6	kg/m ²	Stirling <i>et al.</i> 2008	Mean for individuals with fatness index 2. Fig 3 p. 572.

R_l	Activity rate for bear agents with low energetic stress	12.4	%	Whiteman <i>et al.</i> 2015	Minimum value from Figure 2, p. 296
R_h	Activity rate for bear agents with high energetic stress	26.6	%	Whiteman <i>et al.</i> 2015	Maximum value from Figure 2, p. 296
λ_{am}	Annual survival for prime age (5-19) adult males	90	%	Regehr <i>et al.</i> 2007	Table 1, pg 2678
λ_{af}	Annual survival for prime age (5-19) adult females	93	%	Regehr <i>et al.</i> 2007	Table 1, pg 2678
λ_{sub-m}	Annual survival for subadult males	81	%	Regehr <i>et al.</i> 2007	Table 1, pg 2678
λ_{sub-f}	Annual survival for subadult females	86	%	Regehr <i>et al.</i> 2007	Table 1, pg 2678
λ_{sen-m}	Annual survival for senescent males (>20 years)	75	%	Regehr <i>et al.</i> 2007	Table 1, pg 2678
λ_{sen-f}	Annual survival for senescent females (>20 years)	81	%	Regehr <i>et al.</i> 2007	Table 1, pg 2678
λ_{coy}	Annual mortality for cubs of the year	59.5	%	Aars <i>et al.</i> 2005	mean value for male and female cub-of-the-year survival for Foxe Basin. Table 2, p. 37
T_h	Handling time per nest	1/60	time-steps	Dey <i>et al.</i> 2017	
a'	Search efficiency	1	cells/time-step	Dey <i>et al.</i> 2017	

*Values taken from figures were estimated using WebPlotDigitizer version 3.9 (Rohatgi, 2015).

Data on the estimated date of ice-breakup and freeze-up for Foxe Basin was used to define the climate variables for the first 25 model years of each model run (see *Sea ice phenology and timing of agent appearance* submodel below).

7. Submodels

7.1 Sea ice phenology and timing of agent appearance

At the start of each model year, we defined an ice break-up date and an ice freeze-up date for that year. For the first 25 model years, we used historical ice data from the National Snow and Ice Data Center for Foxe Basin for 1990-2014 as our estimated ice break-up and freeze-up dates. For the next 25 model years, we simulated the sea ice metrics using a linear extrapolation of the ice-breakup date and ice-freeze up dates from 1990-2014, including appropriate inter-annual variance:

$$I_b = 181.86 - 0.64 * (year - 1989) + N(\mu = 0, \sigma = 6.99)$$

$$I_f = 300.33 + 0.73 * (year - 1989) + N(\mu = 0, \sigma = 8.31)$$

Where I_b and I_f are the break-up and freeze-up dates respectively. See Section 3.4 for more details on sea ice parameterization.

The distribution of common eider nest initiation dates is approximately normal (Waltho and Coulson, 2015). We defined a distribution of nest initiation dates for the eider agents based on the mean nesting date for a given year, B , and the spread of 95% of nesting, S , in Waltho and Coulson (2015):

$$N(\mu = B, \sigma = \frac{S}{2 \cdot 1.96})$$

Because common eider nesting phenology is influenced by climate (with earlier nesting in warmer springs; Jean-Gagnon 2015), we adjusted the mean nesting date for each season based on the sea ice conditions for that particular year of the simulation. First, we first defined a temporary variable, S_a , representing the number of days the ice-breakup date was advanced from the average level between 1990 and 2015:

$$S_a = \frac{\sum_{1990 \leq i \leq 2014} (I_{b(i)})}{25} - I_b$$

Then, we advanced the mean nesting date by V days, from the historic mean nesting date, B_h , for every day that the spring was advanced from historical levels:

$$B = B_h - (V \cdot S_a)$$

We also used the ice break-up date for each particular year to determine the date of arrival (appearance) of the polar bear agents. The mean onshore date of polar bears is strongly correlated with the date of ice break-up ($r = 0.975$, Stirling et al. 1999). We calculated the arrival date (in the landscape) of each polar bear agent based on the ice break-up date, and the average time between ice break-up and polar bear arrival in terrestrial environments, d :

$$arrival\ date = N(\mu = (I_b + d), \sigma = \sigma_d)$$

7.2 Polar bear submodel

Polar bear growth and death

Prior to the beginning of each season, polar bear agents experienced mortality according to their annual survival rate for their age and sex class (see Table 1). If a bear died, it was

replaced by a 3 year old bear with a random sex, since young bears typically stay with their mother for their first 2 years (Ramsay and Stirling, 1986, 1988).

Adult females were assumed to have attendant cubs if they had no attendant offspring during the previous year, and females that had attendant yearlings the previous year were assumed to have no attendant offspring. If an adult female had an attendant cub during the previous year, we assumed the cub survived to be a yearling with a survival rate of λ_{coy} .

Polar bear agents tracked their age (in years) and were classified as subadults or adults dependent on whether they were ≥ 5 years of age (similar to Taylor et al. 2006). They updated this information prior to the start of each breeding season. Additionally, they updated their body length and mass prior to the start of each breeding season. We estimated the polar bear body length from the von Bertalanffy growth curves for the Foxe Basin subpopulation, presented in Derocher (1991). Body length was dependent on age, such that:

$$L(A) = L_{\infty} \cdot (1 - e^{-k(A-A_0)})$$

where A is the agent's age in years, L_{∞} is the asymptotic body length, k is the von Bertalanffy growth rate and A_0 is the age at 0 size. The values used for L_{∞} , k and A_0 were sex-specific and are defined in Table S1.

Similarly, we estimated body mass, m , using the von Bertalanffy growth curves for body mass in Derocher 1991 (again, for the Foxe Basin subpopulation). However, we also incorporated intra-age variation in body mass by allowing the body mass to be drawn from a normal distribution with a mean equal to the expected value from the von Bertalanffy curve, and a standard deviation of 67.6 kg (for males) and 55.3 kg (for females).

Polar bear decision making and movement

A polar bear agent's behavioral decisions are dependent on their individual state, as well as their knowledge of the environment. Additionally, we incorporated physiological constraints (i.e. the need to sleep and rest) into the model, in order to ensure realistic time budgets for our polar bear agents.

Polar bears spend the majority of their time during the summer months inactive (Stirling 1974). Polar bear activity rates, determined using accelerometers, are thought to vary between 12.4% (R_l) and 26.6% (R_h) depending on the time of year (Whiteman et al. 2015). We used these values as the activity rates for polar bear agents that had low and high energetic stress respectively, since we assumed that bears that were energetically stressed (and therefore need to search and forage for prey) would exhibit behavior similar to bears in winter, which are actively foraging for prey. Polar bear agents rested for $(1 - R) \cdot t_s$ time-steps, if they had been awake for more than $t_s - ((1 - R) \cdot t_s)$ time-steps, and were on an island or mainland cell (i.e. they would not rest if in water).

If the polar bear agents were not resting, they would first evaluate whether it was profitable to forage in the local cell. We assumed that polar bears could not estimate expected or marginal rates of energetic gain (e.g., Charnov 1976), but instead made the simpler

assumption that polar bear agents could estimate whether foraging would lead to a net energetic gain (see *Foraging* below).

If local foraging was not expected to lead to an energetic gain (e.g. if there were no nests in the cell), the polar bear agents sensed the nearby cells to determine if they could detect any nests (i.e. by ‘smell’, see 4.7 Sensing). If nests were detected in one or more cells, the agent moved to one of the closest cells in which nests were detected.

If no nests were detected in nearby cells, the agents exhibited one of three types of behavior depending on their energetic state and memory. These behavior states were based on the principle of risk-sensitive foraging (Bateson, 2002; Caraco et al., 1980), such that bears that in good condition (i.e. low energetic stress) picked behavioral options that lead to low risk of wasting energy (i.e. risk-averse), while bears in poor condition (i.e. high energetic stress) picked behavioral options with high variance (i.e. risk prone) in an attempt to meet their energetic demands.

The ‘migration’ behavior state was intended to simulate the completion of the onshore migration by polar bears in a low energetic stress state. Although common eiders rarely nest on the mainland, the mainland provides other resources (e.g. food such as berries and other vegetation, shelter) that can be beneficial to bears that are not energetically stressed. Polar bear agents in the ‘migration’ behavior state headed towards the mainland using biased random movement, with different parameters depending on their local environment (see Table 2). When possible, they move from island to island to enable resting and to increase the chance of finding eider nests. Once on the mainland, they rest for the remainder of the model year. The ‘random search’ behavior mode simulates a bear actively searching for nests, but without any knowledge of nest location on the landscape. These agents make relatively direct movements between island, and more tortuous movement while on islands, in order to search for nests. Agents in ‘memory-informed search’ state act similarly to the agents in the ‘migration’ state, except they orient towards the island from their reference memory that has the greatest number of expected nests (see Section 4.5). They search for nests on route to this destination by moving between islands when possible.

In all cases, the agent’s working memory prevents them from revisiting any island they had already visited during the current year, and prevents them from swimming away from the mainland (i.e. out to sea) unless they are moving towards an island they can see. Additionally, bear agents continually used their olfactory abilities to detect nests while on route, and if they were able to detect any nests while moving, they abandoned their current course and moved towards the sensed nests. Bear agents moved a maximum distance, d_{max} , in each time step that was determined by their sex and status, such that $d_{max} = 12, 20, 17, 18$ cells for males, solitary females, females with cubs-of-the-year and females with yearlings, respectively (see Section 3.5 for more details).

Table 2. Movement rules for polar bear agents.

Behavioral Mode		
Migration	Random search	Memory-informed search

Water cell	1. Face mainland 2. If there are islands in sight range, face one and move ¹ towards it 3. If not, correlated random movement ² towards mainland	1. Maintain current heading 2. If there are islands in sight range, face one and move ¹ towards it 3. If not, correlated random movement ² towards current heading	1. Face the island from memory with the greatest number of expected nests 2. If there are islands in sight range, face one and move ¹ towards it 3. If not, correlated random movement ² towards best island from reference memory
Island cell	1. Face mainland 2. Correlated random movement ² towards mainland	1. Maintain current heading 2. Correlated random movement ²	1. Face the island from memory with the greatest number of expected nests 2. Correlated random movement ² towards best island from reference memory
Mainland cell	1. Rest for remainder of model year	1. Maintain current heading 2. Correlated random movement ²	1. Face the island from memory with the greatest number of expected nests 2. Correlated random movement ² towards best island from reference memory

¹Agents move up to d_{max} cells per time step, if the destination is $> d_{max}$ cells away they move d_{max} cells and maintain the same destination for the next time-step.

²Agents first update their heading by selecting a normally distributed value with parameters $N(\mu = \text{current heading}, \sigma = 45^\circ)$, then move up to d_{max} cells

Polar bear bioenergetics

Polar bear agents lost energy at every time step, and the amount of energy depended on the activity during the time step. If the polar bear agent was resting or sleeping, the amount of energy lost, E_c , was determined by their resting mass specific basal metabolic rate, E_r and their current body mass:

$$E_c = E_r m$$

where m is the body mass of the polar bear agent.

If the polar bear agent was active (swimming, walking or foraging) they lost energy at the mass specific metabolic rate of movement E_m , such that:

$$E_c = E_m m$$

To these baseline energetic costs, we also added the energetic cost of milk production for adult female bears, equivalent to 10.9 MJ / day for females with attendant cubs, and 2.6 MJ / day for females with attendant yearlings (Arnould and Ramsay, 1994).

The only way in which polar bear agents could gain energy was through foraging on eider nests (detailed below).

At the end of each day, polar bear agents convert net energetic changes into changes in body mass. We assumed all changes in mass were due to changes in body fat (Atkinson et al., 1996) which has an estimated energy density of 39.3 MJ / kg (Blaxter, 1989).

Polar bear foraging

Polar bear agents can gain energy only by consuming nests. They have perfect knowledge of the number of nests in the cell that they occupy, and can calculate the number of nests they would consume in a single time-step. We used the Holling's disc equation (type II functional response; Holling 1959) to determine the number of nests a bear would consume in the next time step:

$$P_{nests} = \frac{a' n_{nests}}{1 + a' T_h n_{nests}}$$

where n_{nests} is the number of active nests in the cell that the polar bear agent is in. This equation describes the number of prey a predator will consume after incorporating searching (a') and handling time (T_h), and is widely thought of as the null model for prey consumption rates (Brown, 1991). Polar bear agents will forage if foraging will lead to an expected net energetic gain, defined as:

$$P_{nests} \cdot \delta_x > E_m \cdot m$$

If the above inequality is true, the polar bear agent will forage in the current cell by transferring the nest energy from P_{nests} random nests to themselves. The depredated eider agents will then become inactive for the remainder of the season.

7.3 Common eider demography submodel

To investigate how the direct and indirect effects of climate change will impact common eider populations, we created a common eider demography submodel that 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 Figure 2, with individuals moving through life stages according to the following rules:

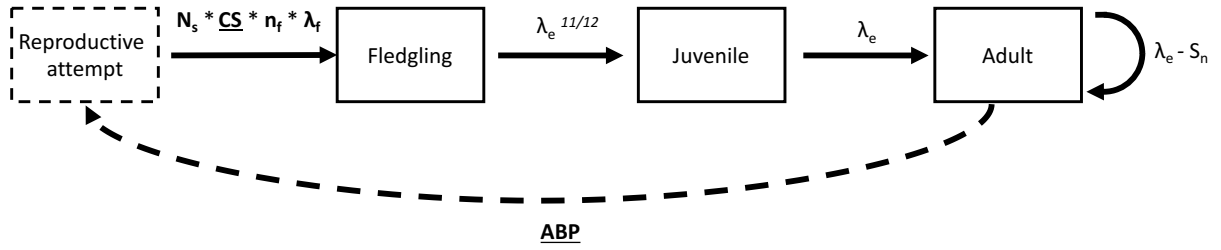


Figure 2. Outline of life stage model for common eider agents. A complete description of the common eider demography model is presented in the methods. Vital rates included in the model are shown in this figure including adult survival rate (λ_e), fledgling survival rate (λ_f), adult survival senescence (S_n), annual breeding propensity (ABP), nesting success (N_s), clutch size (CS), and proportion of hatchlings that are female (n_f). Vital rates shown in bold vary among years according to rules outlined in the common eider demography submodel. Underlined vital rates (clutch size, and annual breeding propensity) are also linked to annual climatic conditions in some model runs.

Adult, 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, λ_e and a Weibull model of survival senescence (Ricklefs and Scheuerlein, 2002) with coefficients determined from empirical curves of adult survival in Waltho & Coulson (2015). An adult had a possibility of death of:

$$(1 - \lambda_e) + 4.74 \times 10^{-11} \cdot (age - 2)^{7.431}$$

where *age*, is the age of the common eider agent in years. 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 hatchling survival rules, below), and therefore their possibility of death was $1 - \lambda_e^{11/12}$.

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. Several studies have noted a link between climate conditions and breeding propensity (Hanssen et al., 2013; Jónsson 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 2002-2013 at Mitivik 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 break-up date for Foxe Basin as the sole fixed effect. Then, we used this statistical model to interpolate and extrapolate the annual breeding propensity (ABP) using the equation:

$$ABP = \text{logit}^{-1} (-0.456 + (-1 * 0.011 * (I_b - 190)) + N(\mu = 0, \sigma = 0.448))$$

where logit^{-1} represents the inverse logit, -0.45611 is the intercept from the logistic regression, 0.011 is the slope of the linear predictor from the logistic regression, 0.448 is the standard deviation from the logistic regression, and N represents the normal (Gaussian) distribution. In model runs WITH CLIM-BP, we used the annual ice breakup date as , and therefore the expected value for ABP increases as the ice breakup date advanced (i.e., more common eider agents breed in years with earlier ice breakup). In model runs WITHOUT CLIM-BP, we substituted 190 for I_b , which is the ice breakup date from the first year of the model runs. In this condition, annual breeding propensity still varied among years (due to the sampling of the Gaussian distribution), but the expected value did not depend on the annual ice breakup date. In our model, the expected breeding propensity of common eider hens did not change with age.

Nest site selection

Common eider females are highly philopatric to nesting sites. The distance between nests from successive years was determined by:

$$D_{disp} = \ln N(\mu, \sigma)$$

Where μ and σ represent the mean log (dispersal distance), and standard deviation of log (dispersal distance), respectively. For hens that were successful during the previous year, we used values of μ_s and σ_s while for hens that were unsuccessful during the previous year we used μ_f and σ_f . First time breeders were assumed to disperse from their natal site with similar rules to those of failed breeders. Eider agents dispersed the maximum distance possible, as determined by the availability of island cells and their D_{disp} value (i.e. they moved to one-of the furthest island cells that was $\leq D_{disp}$ cells away).

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 & Coulson (2015). We then 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 Figure 8.1 in Waltho and Coulson, 2015). Therefore, the mean common eider clutch size (\overline{CS}) for a given year was determined by:

$$\overline{CS} = 8.658 - (0.027 * B) + N(\mu = 0, \sigma = 0.304)$$

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:

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

Nest energy

The energy available in avian eggs decreases across the incubation phase as energy is inefficiently converted to tissue by developing embryos (Romanoff 1967). This decrease is not constant over time and we modeled the energy change in each nest such that the energetic content of eggs remains constant for the first 2/3 of incubation and then decreases linearly over the remaining 1/3 of incubation, according to the equation:

$$\text{If } U_r > \frac{U}{3}, \text{ available nest energy} = 984 \text{ kJ/egg} * 4 \text{ eggs}$$

$$\text{If } U_r < \frac{t_s \cdot U}{3}, \text{ available nest energy} = U_r \cdot 50.4 + (580 \text{ kJ/egg} * 4 \text{ eggs})$$

where U_r is the remaining incubation time in number of days.

Nesting success and hatchling survival

For females that bred, 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 fledgling stage (see Figure 2). First, we determined whether each female successfully completed the incubation stage (nesting success, N_s) 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_i , such that each day, each nest had a chance of failure of:

$$\text{daily rate of failure} = F_i^{(\frac{1}{26})}$$

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 hen's nest:

$$n_f = \text{Binom} (n = \text{CS}, p = 0.5)$$

Then, we calculated whether each female hatchling survived to 30 days old. The survival rate for hatchlings (λ_f) varied among years and was sampled from the distribution of hatchling survival presented in (Wilson *et al.*, 2012):

$$\lambda_f = \text{Beta} (\alpha = 1.272, \beta = 5.423)$$