Predicting Survival, Reproduction and Abundance of Polar Bears under Climate Change

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Abstract: Polar bear (*Ursus maritimus*) populations are predicted to be negatively affected by climate warming, but the timeframe and manner in which change to polar bear populations will occur remains unclear. Predictions incorporating climate change effects are necessary for proactive population management, the setting of optimal harvest quotas, and conservation status decisions. Such predictions are difficult to obtain from historic data directly because past and predicted environmental conditions differ substantially. Here, we explore how models can be used to predict polar bear population responses under climate change. We suggest the development of mechanistic models aimed at predicting reproduction and survival as a function of the environment. Such models can often be developed, parameterized, and tested under current environmental conditions. Model predictions for reproduction and survival under future conditions could then be input into demographic projection models to improve abundance predictions under climate change. We illustrate the approach using two examples. First, using an individual-based dynamic energy budget model, we estimate that 3% to 6% of adult males in western Hudson Bay would die of starvation before the end of a 120 day summer fasting period but 28% to 48% would die if climate warming increases the fasting period to 180 days. Expected changes in survival are nonlinear (sigmoid) as a function of fasting period length. Second, we use an encounter rate model to predict changes in female mating probability under sea ice area declines and declines in mate-searching efficiency due to habitat fragmentation. The model predicts that mating success will decline non-linearly if searching efficiency declines faster than habitat area, and increase non-linearly otherwise. Specifically for the Lancaster Sound population, we predict that female mating success would decline from 99% to 91% if searching efficiency declined twice as fast as sea ice area, and to 72% if searching efficiency declined four times as fast as area. Sea ice is a complex and dynamic habitat that is rapidly changing. Failure to incorporate climate change effects into population projections can result in flawed conservation assessments and management decisions.

Key words: climate change, dynamic energy budgets, *Ursus maritimus*, population viability analysis, starvation, mechanistic models

1. Introduction

Climate change effects on species and ecosystems have been identified as critical problems for conservation biology (McCarty, 2001; Mawdsley et al., 2009). Describing, understanding, and anticipating these effects are precursors to identifying mitigation strategies (Harley et al., 2006; Root and Schneider, 2006). Anticipation can be particularly challenging and requires a combination of good quantitative data along with precise hypotheses on the mechanisms by which climate change will affect a species (Ådahl et al., 2006; Krebs and Berteaux, 2006). Mathematical models can be a powerful tool in this process, and they can inform research, monitoring, and conservation planning by indicating where and how change in a population is most likely to occur. The type of projection model that can be applied depends to a large degree on how similar predicted environmental conditions are to the ones observed. Berteaux et al. (2006) discuss constraints to projecting the ecological effects of climate change, and they suggest a distinction between forecast and prediction models. Forecast models are based on correlational relationships between explanatory and dependent variables (e.g., environmental conditions and vital rates) and are useful if there is no extrapolation beyond the observed range of explanatory variables. In contrast, predictive models mechanistically describe the cause-effect relationships determining change (e.g., the link between environmental conditions and vital rates via energetic constraints), and can be used beyond the observed ranges.

The Arctic is warming faster than many other areas (IPCC, 2007), and habitat alteration is well underway. One Arctic habitat showing profound effects is the sea ice, with the perennial and annual ice cover shrinking, and sea ice thickness decreasing (Comiso, 2002; Maslanik et al., 2007; Comiso et al., 2008). The sea ice is declining at rates faster than expected (Stroeve et al., 2007), and declines are projected to accelerate (Holland et al., 2006; Serreze et al., 2007). Variability in predictive sea ice models exist but it is possible that the Arctic Ocean will be ice-free in summer by the middle to the end of the 21st century (Holland et al., 2006; Zhang and Walsh, 2006; Serreze et al., 2007; Boé et al., 2009). Among the most vulnerable to these warming trends are ice-obligate species, such as polar bear (*Ursus maritimus*), walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), and ringed seal (*Pusa hispida*) (Laidre et al., 2008; Moore and Huntington, 2008). Polar bears in particular have become the subject of intense political debate, and public interest in the future of the species is increasing (e.g., Charles, 2008). The vulnerability of polar bears to climate warming is clear (e.g., Stirling and Derocher, 1993; Derocher et al., 2004; Stirling and Parkinson, 2006; Laidre et al., 2008; Wiig et al., 2008), but few predictions exist to address how polar bear abundance might change numerically in response to a warming climate (Amstrup et al., 2007; Hunter et al., 2007).

Prediction of polar bear population dynamics under climate change is challenging, because observed and predicted environmental conditions differ substantially (Wiig et al., 2008). Consequently, few data exist to inform us how reproduction and survival (and thus population abundance) might change under future conditions. To date, only two studies have incorporated climate change trends into quantitative projections of polar bear abundance (Amstrup et al., 2007; Hunter et al., 2007), and each of these studies had to rely on some form of extrapolation or expert judgment to parameterize suggested population models due to the lack of data relating present to future conditions. These analyses are important steps, and they provide new hypotheses on how populations may respond to further warming. However, their projections may lack accuracy if unexpected non-linearities exist in vital rate response curves to future environmental conditions.

Here, we follow the framework of Berteaux et al. (2006) to suggest how predictions of population abundance under climate change could be improved. For this purpose, we first review expected and observed climate change effects on polar bears with specific focus on the biological mechanisms affecting survival and reproduction. We then summarize previous attempts to forecast polar bear abundance under climate change and discuss limitations of these studies. To improve predictions of population abundance, we suggest the development of mechanistic models aimed at predicting reproduction and survival as a function of the environment. Such predictions could inform demographic projection models to improve population viability analyses (PVA) under climate change. We illustrate the approach with two examples: a dynamic energy budget (DEB) model to predict changes in survival due to prolonged summer fasts, and an encounter rate model to predict changes in female mating success due to climate change induced habitat fragmentation and sea ice area declines. To aid further development of such mechanistic models, we discuss data collection needs to augment ongoing monitoring projects.

2. Climate Change Threats to Polar Bears

Polar bears are vulnerable to climate warming primarily because they depend on sea ice as a platform to access their main prey, ringed seals and bearded seals (Stirling and Archibald, 1977; Smith, 1980). Other marine mammals may locally complement the diet, but in general all marine prey is expected to become less accessible to polar bears as the sea ice declines.

Terrestrial food sources may be opportunistically exploited but are unlikely to substitute for the high energy diet polar bears obtain from seals (Derocher et al., 2004; Wiig et al., 2008; Hobson et al., 2009; Molnár 2009). The sea ice is also used in other aspects of polar bear life history, including traveling and mating (Ramsay and Stirling, 1986; Stirling et al., 1993). With rising temperatures, areas of open water and ice floe drift rates are expected to increase, and traveling in such a fragmented and dynamic sea ice habitat would become energetically more expensive because polar bears would have to walk or swim increasing distances to maintain contact with preferred habitats (Mauritzen et al., 2003).

The combined effects of decreasing food availability and increasing energetic demands are predicted to result in decreasing polar bear body condition and a consequent cascade of demographic effects (Stirling and Derocher, 1993; Derocher et al., 2004; Wiig et al., 2008). Pregnant females, for instance, give birth in maternity dens, when food is unavailable for 4-8 months (Atkinson and Ramsay, 1995). To meet the energetic demands of survival, gestation, and early lactation, females need to accumulate sufficient energy stores before denning. The lightest female observed to produce viable offspring weighed 189 kg at den entry (Derocher et al., 1992), and the proportion of females below such a reproduction threshold will increase with ongoing food stress (Molnár, 2009). Females above the threshold may reproduce, but their reproductive success would still decline with reduced body condition, because body condition is positively correlated with litter size and litter mass, where the latter is also positively correlated with cub survival (Derocher and Stirling, 1996, 1998). After den exit, cubs are nursed for about 2.5 years, but maternal food stress may reduce milk production, with negative consequences for cub growth and cub survival (Derocher et al., 1993; Arnould and Ramsay, 1994). Adult survival rates, in contrast, are probably only affected under more severe conditions because polar bears can survive extended periods without feeding (Atkinson and Ramsay, 1995). Subadult mortality, however, may increase before adult survival is affected, because young bears are less proficient in finding food (Stirling and Latour, 1978) and thus more vulnerable to adverse conditions. Such negative changes in reproduction and survival could lead to decreased population growth rates or population declines.

There is evidence that some of these predicted changes are underway. For example, polar bears in the Western Hudson Bay population (Fig. 1) have shown declines in body condition, reproductive success, survival, and population abundance, and these declines are thought to result from increasing food stress associated with prolonged open-water fasting periods (Derocher and Stirling, 1995; Stirling et al., 1999; Regehr et al., 2007). Appropriate time series to detect changes in body condition, reproduction, and survival do not exist for most other populations (but see Regehr et al., 2010). However, food stress has been documented for polar bears in the Beaufort Sea (Fig. 1) (Cherry et al., 2009), and recent incidents of cannibalism and an increased presence of polar bears near human settlements may provide further indicators for food stress in various populations (Amstrup et al., 2006; Stirling and Parkinson, 2006; Towns et al., 2009).

Changes in energy availability and consequent demographic effects constitute the biggest concern for polar bears under climate warming. However, energy-independent or only partially energy-related effects of climate warming are also possible, such as increased exposure and vulnerability to pollutants, the emergence of new diseases, loss of denning habitat, and conflict with humans associated with industrial development. For reviews of climate warming effects on polar bears, see Stirling and Derocher (1993), Derocher et al. (2004) and Wiig et al. (2008).

3. Towards an Understanding of the Future of Polar Bears

Qualitative predictions regarding the future of polar bears under changing environmental conditions abound (e.g., Stirling and Derocher, 1993; Derocher et al., 2004; Rosing-Asvid, 2006; Stirling and Parkinson, 2006; Moore and Huntington, 2008; Wiig et al., 2008), and some of these predictions were outlined above. Such assessments are useful to identify threats and to provide insights into complex interactions between ecological dynamics, environmental variables, and anthropogenic influences, but they cannot provide quantitative information on the manner and timeframe in which polar bear populations will be affected. However, sound quantitative projections of population abundances are necessary to correctly assess conservation status, to proactively direct conservation efforts, and to set sustainable harvest quotas (Coulson et al., 2001; Mace et al., 2008).

Currently, most projections of polar bear population abundance are accomplished using RISKMAN, a population simulation model that accounts for the three-year reproductive cycle of female polar bears (Taylor et al., 2002). In its basic components, the program is equivalent to a stage-structured matrix population model with parental care, such as the one developed by Hunter et al. (2007; illustrated in Fig. 2). RISKMAN has been used to determine harvest quotas (e.g., Taylor et al., 2002) and to assess polar bear conservation status in Canada (COSEWIC, 2008). Model parameters in these studies were based on recent mean estimates of reproduction and survival, and potential future changes in these demographic parameters due to climate change were not considered. However, our understanding of polar bear life history and ecology implies that such changes are likely.

Quantitative predictions of population dynamics under environmental change must account for potential changes in reproduction and survival to be meaningful (Beissinger and Westphal, 1998; Coulson et al., 2001), and are therefore possible if (a) predictions for future environmental conditions exist, (b) the relationship between future conditions and demographic parameters can be quantified, and (c) a population model integrating these effects can be developed (Jenouvrier et al., 2009). In some species, such as Emperor Penguins (*Aptenodytes forsteri*), a population viability approach incorporating these three steps was possible because reproduction and survival data exist for environmental conditions similar to those predicted to occur (Jenouvrier et al., 2009). For polar bears, the approach is difficult because few data exist to inform us how demographic parameters might change in the future. The only studies to attempt quantitative predictions of polar bear abundance under climate change were consequently limited by the need to extrapolate from present conditions (Amstrup et al., 2007; Hunter et al., 2007) and the reliance on expert judgment (Amstrup et al., 2007) when parameterizing proposed population models.

Hunter et al. (2007) coupled general circulation models with matrix population models (Fig. 2) to obtain population size projections for the southern Beaufort Sea (Fig. 1) under projections for future sea ice. For model parameterization, the authors estimated the functional relationship between polar bear survival, reproduction, and sea ice from six years of capture-recapture data (2001-06). By classifying these demographic data into “good” and “bad” years and assuming that future vital rates could be represented by these estimates, they analyzed the effects of an increase in the frequency of bad years on population growth and suggested a substantial extirpation risk for the Southern Beaufort Sea population within 45-100 years. Although their conclusions of extirpation risk were robust against parameter uncertainty, the authors noted wide prediction intervals in their projections, partially due to the limited range of sea ice conditions considered when estimating demographic parameters.

Amstrup et al. (2007) took an alternative approach, coupling general circulation models with a polar bear carrying capacity model and a Bayesian network model, respectively, to project population trends throughout the Arctic. They suggested likely extirpation of polar bears in two broad regions (Southern Hudson Bay, Western Hudson Bay, Foxe Basin, Baffin Bay, and Davis Strait populations, as well as Southern Beaufort Sea, Chukchi Sea, Laptev Sea, Kara Sea, and Barents Sea populations; Fig. 1), substantial declines in all other populations, and an overall loss of approximately two-thirds of the global population by mid-century given current sea ice projections. However, a lack of appropriate data linking predicted environmental conditions to polar bear population dynamics forced the authors to estimate future carrying capacities by extrapolating from present densities, and to rely on expert judgment for other stressors.

3.1 Using Mechanistic Models to Predict Changes in Survival and Reproduction

Nonlinear dynamics and process uncertainty can lead to spurious predictions of population dynamics and abundance, when vital rate estimates are extrapolated outside observed ranges or when future vital rate estimates are based on expert judgment only (Beissinger and Westphal, 1998; Berteaux et al., 2006; Sutherland, 2006). This kind of problem is illustrated, for example, by the failure of demographers to accurately predict human population growth

(Sutherland, 2006). An example illustrating the limitations of extrapolation in estimating future vital rates, specifically for polar bears, is given by Derocher et al. (2004). Based on linear advances in spring sea ice break-up, they calculated that most females in western Hudson Bay would be unable to give birth by 2100. The authors contrasted this estimate with alternative calculations based on extrapolating observed linear declines in mean female body mass, which implied unsuccessful parturition for most females by 2012.

Rather than estimating demographic parameters from limited data and attempting extrapolation, we suggest using mechanistic models that explicitly consider the cause-effect relationships by which environmental conditions affect reproduction and survival. Such models would allow independent prediction of these demographic parameters for yet unobserved environmental conditions (Berteaux et al., 2006), which could then be input into demographic projection models. In sections 3.2 and 3.3, we discuss this approach, first for changes in reproduction and survival as a consequence of changes in individual energy intake and energy expenditure towards movement, and then for changes that are mostly independent from an individual's energy budget. For both cases, we provide a simple example for illustration.

3.2 Predicting Changes in Survival, Reproduction, and Growth due to Changes in Energy Intake and Movement

Changes in energy availability through decreased feeding opportunities and an increased necessity for movement would negatively affect individual body condition, and thereby survival, reproduction and growth. Qualitatively, this causal relationship is clear, but quantitative predictions of how body condition, survival, reproduction and growth would be affected under changing environmental conditions do not exist. Empirical energetic studies on feeding, movement, somatic maintenance, thermoregulation, reproduction and growth in polar bears are available (e.g., Øritsland et al., 1976; Best, 1982; Watts et al., 1987; Arnould and Ramsay, 1994; Stirling and Øritsland, 1995), but these studies alone are insufficient for predictive purposes, because it is impractical to measure survival, reproduction and growth under all possible scenarios of energy intake and movement. For prediction, a mathematical energy budget framework is needed that synthesizes such data in a model that mechanistically describes how available energy is prioritized and allocated within the organism.

DEB models (*sensu* Kooijman, 2010) explicitly track how an individual utilizes available energy, using mechanistic rules for energy allocation and prioritization between somatic maintenance, thermoregulation, reproductive output, and structural growth. DEB models thus have the potential to predict survival, reproduction and growth, in response to expected changes in energy intake and movement associated with changing environmental conditions (Gurney et al., 1990; Nisbet et al., 2000; Kooijman, 2010), and DEB models are particularly useful to predict an individual's response to food limitation (Zonneveld and Kooijman, 1989; Noonburg et al., 1998). To date, DEB models have been applied to invertebrates, fish, amphibians, reptiles, and birds (Kooijman, 2010, and references therein), and more recently also to whales (Klanjscek et al., 2007) and ungulates (De Roos et al., 2009).

Assuming strong homeostasis (Molnár et al., 2009), a 2-compartment DEB model that tracks changes in storage energy (E; units: MJ) and structural volume (V; units: m^3) through time (t) can be written as follows:

$$(1) \qquad \begin{aligned} \frac{dE}{dt} &= F_{\mathrm{IE}} - F_{\mathrm{EA}} - F_{\mathrm{EM}} - F_{\mathrm{ET}} - F_{\mathrm{EG}} - F_{\mathrm{ER}} \\ \frac{dV}{dt} &= g^{-1} F_{\mathrm{EG}} \end{aligned}$$

where F_{IE} represents the influx of energy from the environment through food acquisition and assimilation, and F_{EA}, F_{EM}, F_{ET}, F_{EG}, and F_{ER} represent the respective rates of storage energy utilization for activity, somatic maintenance, thermoregulation, structural growth, and reproduction. The parameter g represents the energetic cost of growing a unit volume of structure (Klanjscek et al., 2007). For simplicity, we assume additivity of fluxes (Wunder, 1975), and that all energy is channeled through storage (Kooijman, 2010), although other formulations are possible (e.g., Lika and Nisbet, 2000; Klanjscek et al., 2007). Note also that the fluxes in equation (1) are not independent from each other: energy intake (F_{IE}), for example, likely depends on how much energy is allocated to movement (F_{EA}), and energy allocation to growth (F_{EG}) is usually assumed possible only after maintenance requirements (F_{EM} and F_{ET}) are met (Kooijman, 2010).

The challenge in formulating a DEB model for a given species is threefold. First, a method is needed that allows estimation of energy stores (E) and structural volume (V), second, the functional forms of the fluxes F_{XY} need to be determined, and third, these functions need to be parameterized. A full DEB model for polar bears is currently lacking, but the first step was taken by Molnár et al. (2009) who described a polar bear body composition model that distinguishes between storage and structure. Their model allows estimation of E from total body mass and straight-line body length, and estimation of V from straight-line body length. Molnár et al. also suggest that somatic maintenance rate (F_{EM}) in polar bears should be proportional to lean body mass (i.e., the mass of all tissue that is not body fat), and they parameterize this DEB model component from body mass changes in fasting adult males. Below, we extend their model to include costs of movement (F_{EA}) and illustrate the usefulness of the DEB approach for prediction by estimating future changes in adult male survival due to expected extensions of the summer open-water fasting period in western Hudson Bay. A full DEB model would also allow prediction of polar bear reproduction and growth under food limitation, but insufficient data exist to fully determine the necessary model components F_{ER}, and F_{EG}. Directed studies, however, may fill these data gaps, and we outline key data requirements below to aid further model development.

3.2.1.Example: Predicting Changes in Survival due to Prolonged Fasting – Time to Death by Starvation

Polar bears in the Western Hudson Bay population (Fig. 1) are forced ashore when the sea ice melts in summer (Derocher and Stirling, 1990). On land, energetically meaningful food is unavailable, and bears rely on their energy stores for survival (Ramsay and Stirling, 1988; Hobson et al., 2009). In recent years, spring sea ice break-up in western Hudson Bay has been occurring progressively earlier, resulting in shortened on-ice feeding and prolonged on-shore fasting for polar bears in this population (Stirling and Parkinson, 2006). Further extensions to the open-water period are expected under continued climatic warming, and polar bear survival rates for this period may eventually drop if bears cannot accumulate sufficient storage energy for the fast. To illustrate how future changes in survival due to prolonged fasting can be predicted, we use a DEB model to estimate how long a bear can survive on its energy stores before death by starvation. For simplicity, we consider adult males only.

We apply the DEB model for fasting, non-growing and non-reproducing polar bears in a thermoneutral state from Molnár et al. (2009), with an additional component to account for energy allocated to movement:

$$\frac{dE}{dt} = \underbrace{-\ m\,\mathrm{LBM}}_{\text{Somatic maintenance}} \quad \underbrace{-\left(aM^{b} + cM^{d}v\right)}_{\text{Movement}} \tag{2}$$

The model assumes a somatic maintenance rate proportional to lean body mass, *LBM*, with m representing the energy required per unit time to maintain a unit mass of lean tissue (Molnár et al., 2009). Energy costs of movement, by contrast, are dependent on total body mass, M, because both lean tissue and body fat need to be moved. Movement costs are represented by an allometric equation, where the first part of the sum, aM^b, represents the metabolic cost of maintaining posture during locomotion (in addition to somatic maintenance). The second part, cM^dv, reflects the positive linear relationship between energy consumption and velocity, v (Schmidt-Nielsen, 1972; Taylor et al., 1982).

Using the body composition model of Molnár et al. (2009), equation (2) can be rewritten as:

$$(3)\quad \frac{dE}{dt} = -\underbrace{m\left(\alpha^{-1}(1-\varphi)E + \rho_{\mathrm{STR}} kL^3\right)}_{\text{Somatic maintenance}} - \underbrace{\left(a\left(\alpha^{-1}E + \rho_{\mathrm{STR}} kL^3\right)^b + c\left(\alpha^{-1}E + \rho_{\mathrm{STR}} kL^3\right)^d v\right)}_{\text{Movement}}$$

where α represents the energy density of storage, φ is the proportion of storage mass that is fat, and $\rho_{\mathrm{STR}}k$ is a composite proportionality constant to estimate structural mass from straight-line body length, L. Body composition and maintenance parameters were estimated as m = 0.089 MJ kg^{-1} d^{-1}, α = 19.50 MJ kg^{-1}, φ = 0.439, $\rho_{\mathrm{STR}}k$ = 14.94 kg m^{-3} (Molnár et al., 2009), movement parameters as a = 0, c = 0.0214 MJ km^{-1}, d = 0.684 (Molnár 2009). For model development and parameterization details, see Molnár (2009) and Molnár et al. (2009).

Time to death by starvation can be estimated for a bear of straight-line body length L and initial energy stores $E(0) = E_0$ by numerically integrating equation (3) and solving for time T when $E(T) = 0$. Here, we considered two scenarios, one for resting bears (v = 0) and one for bears moving at average speed v = 2 km d^{-1}, which corresponds to observed on-land movement rates (Derocher and Stirling, 1990). For resting bears, energy density (E/LBM) was the sole determinant of time to death by starvation, whereas for moving bears starvation time also depended on L. However, variation due to changes in L was small, so we used the mean observed length of 2.34 m in all subsequent calculations. For both scenarios, time to death by starvation increased nonlinearly with energy density (Fig. 3).

Predictions for changes in adult male survival in western Hudson Bay as a function of fasting period length were then obtained by linking the time to death by starvation response curves to observed energy densities. For this purpose, we used mass and length data from 97 adult male polar bears (≥7 years of age) caught on-land in 1989-96 in western Hudson Bay (see Molnár et al., 2009, for handling procedures). All animal handling protocols were consistent with the Canadian Council on Animal Care guidelines. Body masses were scaled to August 1 (mean on-shore arrival date during 1990s; Stirling et al., 1999) using the mass loss curve in Molnár et al. (2009). Energy densities on August 1 were calculated from these body masses using the body composition model of Molnár et al. (2009).

Adult male survival rate as a function of observed energy densities can be estimated for any fasting period length by considering the proportion of bears that would starve to death before the end of the fasting period. For illustration we discuss survival predictions for a fasting period length of 120 days, typical of the 1980s, and 180 days which reflects potential future conditions (the fasting period has been increasing by about 7 days per decade since the early 1980s; Stirling and Parkinson, 2006). Observed energy densities were normally distributed, and with a fasting period of 120 days about 3% of these bears are expected to die of starvation before the end of the fasting period when resting (line A in Fig. 3) and about 6% when moving (line B in Fig. 3). If the fasting period is extended to 180 days (i.e., due to earlier spring ice break-up and delayed fall freeze-up), about 28% of these males would die with no on-land movement (line C in Fig. 3) and about 48% if moving (line D in Fig. 3). Expected changes in adult male survival are nonlinear due to the normal distribution of energy densities, and to a smaller degree due to the nonlinearity of the time to death by starvation curves. Estimates for changes in survival are conservative because death may happen sooner if the strong homeostasis assumption is violated near death. Furthermore, with progressively earlier spring sea ice break-up, energy densities at on-shore arrival are expected to be reduced relative to those observed during the 1990s due to shortened on-ice feeding (Stirling and Derocher, 1993), thereby further reducing expected time to death by starvation.

Such declines in body condition have already been documented in western Hudson Bay (Derocher and Stirling, 1995; Stirling et al., 1999).

Predictions of starvation time and resultant changes in survival are also possible for other groups, such as subadults or adult females with offspring, if the additional energy expended on lactation and growth, respectively (F_{ER} and F_{EG} in equation (1)), can be quantified. Generally, adult males may be the least affected group because they do not spend energy on growth or lactation. However, due to their proportionally higher lean tissue content in storage, they cannot fast as long as non-reproducing adult females (Molnár et al., 2009).

3.3 Predicting Non-Energy Related Changes in Demographic Parameters

Some effects of climate change will not be directly energy-related. Mechanistic models, specific to the proposed cause-effect relationships, may nevertheless be used for prediction in many cases, but a comprehensive discussion of all possible effects and models is impossible. However, to illustrate the potential of mechanistic models in predicting changes in vital rates, even when the primary mechanism for change is not energy-related, we explore how habitat fragmentation and declines in sea ice area would affect female mating success.

3.3.1 Example: Potential Climate Change Impacts on Female Mating Success

Derocher et al. (2004) put forth two contrasting hypotheses regarding changes in female mating success under climate warming. First, increased areas of open water and increased ice floe drift rates may impede mate-finding and result in reduced pregnancy rates because adult males rely on contiguous female tracks for mate location. By contrast, declines in sea ice area may facilitate mate-finding to increase pregnancy rates by increasing bear density during the mating season. Here, we assess the respective importance of these contrasting effects. Specifically, we use the mating model of Molnár et al. (2008) to show how quantitative predictions for changes in female mating success due to changes in habitat fragmentation (mate-searching efficiency) and sea ice area can be obtained.

Polar bear pairing dynamics during the mating season are driven by mate location, pair formation, and pair separation, and can be described by the following system of differential equations (Molnár et al., 2008):

$$\underbrace{\frac{dm}{dt}}_{\text{Solitary available males}} = \underbrace{-\frac{sq}{A}m\,f}_{\text{Pair formation}} + \underbrace{\mu\,p}_{\text{Pair separation}} \tag{4a}$$

$$\underbrace{\frac{df}{dt}}_{\text{Unfertilized females}} = \underbrace{-\frac{sq}{A}m\,f}_{\text{Pair formation}} \tag{4b}$$

$$\underbrace{\frac{dp}{dt}}_{\text{Breeding pairs}} = \underbrace{\frac{sq}{A}m\,f}_{\text{Pair formation}} - \underbrace{\mu\,p}_{\text{Pair separation}} \tag{4c}$$

$$\underbrace{\frac{df^{*}}{dt}}_{\text{Fertilized females}} = \underbrace{\mu\,p}_{\text{Pair separation}} \tag{4d}$$

where $m(t)$, $f(t)$, $p(t)$, and $f^{*}(t)$ represent the respective numbers (at time t) of solitary males searching for mates, solitary unfertilized females, breeding pairs, and solitary fertilized females. The left-hand sides of equations (4a-d) represent the respective rates of change in these quantities, and these rates depend on pair formation and pair separation. Pair formation is modelled using the law of mass action, and pairs are formed at rate sq/A, where s represents searching efficiency (units: km^2 d^{-1}), q is the probability of pair formation upon encounter (i.e., mate choice), and A is habitat area (units: km^2). Pairs remain together for μ^{-1} time units (units: d), thus separating at rate μ. The mating season begins at $t = 0$, when $m(0) = m_0$, $f(0) = f_0$, $p(0) = 0$, $f^*(0) = 0$, and lasts T time units. Female mating success is defined as the proportion of females fertilized at the end of the mating season and is estimated as $1-f(T)/f_0$. To explore how changes in sea ice area and habitat fragmentation would affect female mating success, we rewrote the model of Molnár et al. (2008) considering bear numbers rather than densities, thereby explicitly representing sea ice area, mate-searching efficiency and mate choice. We also assumed maximal male mating ability (i.e., all solitary males search for mates at all times), considering a simplified version of the model in Molnár et al. (2008). However, it is noteworthy that male mating ability may also decline under climate warming induced food stress, and such declines could reduce female mating success (Molnár et al., 2008).

The model explicitly considers the mechanisms determining female mating success, describes observed pairing dynamics well, and can thus be used to predict female mating success from initial male and female numbers, m_0 and f_0, and model parameters s, q, A, and μ (Molnár et al., 2008). We consider changes in sea ice area (A) and mate-searching efficiency (s), and illustrate predictions using the example of Lancaster Sound (Fig. 1), where $m_0 = 489$, $f_0 = 451$, sq/A = 0.00021 d^{-1}, $\mu^{-1} = 17.5$ d and $T = 60$ d were estimated for 1993-1997, implying a female mating success of 99% (Molnár et al., 2008). Female mating success depends on the ratio sq/A and is predicted to decline non-linearly if searching efficiency s

declines faster than habitat area A, and to increase non-linearly otherwise. For example, assuming that m_0, f_0, μ^{-1}, T, and q remain constant in Lancaster Sound, female mating success is predicted to decline from 99% to 91% if s declined twice as fast as A, and to 72% if s declined four times as fast as A. By contrast, if A declined faster than s, mating success would remain essentially unchanged at around 100% in this population (Fig. 4).

The parameters s and A may change independent of each other because mate-searching efficiency depends on movement speeds, movement patterns, detection distance, and male tracking ability, parameters that are affected more by the degree of habitat fragmentation (areas of open water between ice floes) than by total habitat area. The degree to which s and A will be affected by climate change cannot be predicted from the mating model itself. However, such predictions could be obtained independently for s from mechanistic encounter rate models that account for changes in movement patterns, tracking ability and detection distance due to habitat fragmentation (Kiørboe and Bagøien, 2005). The degree of future habitat fragmentation and changes to sea ice area (A) could in turn be predicted from sea ice models. Resultant predictions for s and A could then be input into the mating model to obtain more specific predictions of female mating success under climate change than presented here. Potential future changes in mate choice (q) should hereby also be considered, because mate choice may vary adaptively as a function of male densities, sex ratios, and expected mating success (Kokko and Mappes, 2005). Potential declines in s may be compensated by increases in q, because pair formation rate is determined by the composite term sq/A (but note that q cannot be increased to values larger than 1). The predictions outlined here are insensitive to the parameters μ^{-1} and T, but may be affected significantly by harvest-induced changes in m_0 and f_0 (Molnár et al., 2008).

4. Integrating Predicted Changes in Demographic Parameters into Population Models

The stage-structured population dynamics of polar bears can be formalized in matrix models (Fig. 2), which are useful for population projections and PVAs (Hunter et al., 2007). However, such analyses are only accurate if future vital rates (reproduction and survival) are accurately represented by existing estimates, or if future changes in vital rates can be accurately predicted from present conditions. The lack of data on vital rates under not yet experienced conditions has thus been a major limitation to PVA accuracy (Beissinger and Westphal, 1998; Ludwig, 1999; Coulson et al., 2001; Sutherland, 2006). To avoid this problem, we have advocated mechanistic models to predict changes in survival and reproduction because such models can often be developed and parameterized independent of environmental conditions. A second advantage of such mechanistic models is their ability to identify expected nonlinearities and threshold events in vital rate response curves to environmental conditions (Figs. 3, 4), which will affect PVAs (Ludwig, 1999; Harley et al., 2006)

The mathematical integration of vital rate predictions into matrix population models is often straightforward, and we outline this process for the two examples considered above. Adult male survival rate from one spring to the next (parameter σ_{10} in the matrix model of Hunter et al. (2007); Fig. 2) can be written as the product of adult male survival during the fasting and feeding periods, respectively. Expected changes in survival during the fasting period (Fig. 3) can thus be incorporated to predict changes in σ_{10} due to this survival component. The probability of a female without offspring breeding (β_4 in Fig. 2) can similarly be decomposed into the probabilities of successful mating, successful implantation, successful parturition, and early cub survival. Expected changes in mating success caused by habitat fragmentation and sea ice area declines (Fig. 4) could thus also be incorporated into a matrix population model.

The biggest limitation to this component-wise approach of predicting changes in reproduction and survival relates to uncertainty in initial conditions. For example, the distribution of energy densities at the beginning of the fasting period in any given year, and thus the period-specific survival rate, may depend on the date of sea ice break-up in that year (and thus the length of the preceding on-ice feeding period), but also on the lengths of the feeding and fasting periods in previous years (i.e., time lags). This problem of uncertainty could be avoided if a full DEB model was available that tracks the energy intake and expenditure of polar bears through the entire year. Population projections would in that case be a matter of tracking individuals over time. However, until a fully predictive model becomes available, a component-wise analysis of expected changes in vital rates and resultant effects on population growth is possible because the direction of the expected changes in initial conditions is often clear. For example, polar bear energy densities at on-shore arrival in western Hudson Bay are already declining and are expected to decline further. Models that assume all else equal (in particular, on-shore arrival energy densities as observed during the 1990s) to predict future fasting period survival rates as a function of predicted fasting period lengths would thus be conservative and could set boundaries to expected changes in survival. Until different effects of climate change on vital rates, addressed by different mechanistic models, can be connected into a single predictive framework, component-wise prediction of changes in vital rates (treating different aspects of climate change on polar bears separately) could provide a series of conservation indicators that should be considered in conservation assessments and population management.

5. A Call for Data

The type of data required to further mechanistic models for reproduction and survival is in many cases different from data collected for monitoring these demographic parameters (such as mark-recapture data). The development of such models will require the integration of field research to specifically address the mechanisms determining change in reproduction and survival. The areas of investigation will be specific to the mechanisms considered, and as it is impossible to provide a comprehensive summary of all potential modelling approaches, it is similarly impossible to outline all data that might prove useful for model development, parameterization, and validation. However, because most expected climate change effects on polar bears are energy-related, we believe that DEB models may provide one of the most useful venues for understanding and predicting climate change effects on polar bears. Changes in growth, reproduction, and survival, in response to expected changes in feeding and movement can be predicted from DEB models, provided that sufficient physiological data can be gathered to specify energy allocation rules and parameterize model terms (Gurney et al., 1990; Noonburg et al., 1998; Kooijman et al., 2008; Kooijman, 2010). Long-term research on polar bears has already provided much of the required physiological data for DEB development, and missing pieces could be addressed with directed studies. To aid the development of a full polar bear DEB model, we next outline key data requirements.

DEB models consider two distinct components of energy flow: net energy intake from the environment (the difference between terms F_{IE} and F_{EA} in equation (1)) and the allocation of assimilated energy within the organism towards somatic maintenance, thermoregulation, reproduction, and growth (F_{EM}, F_{ET}, F_{ER}, and F_{EG}). The physiological terms F_{EM}, F_{ET}, F_{ER}, and F_{EG} can be understood independently from the environment, and they could be determined under current conditions. In fact, the term for somatic maintenance (F_{EM}) has already been specified (Molnár et al., 2009; cf. also equations (2) and (3)), and the thermoregulation term F_{ET} can probably be determined from published data (e.g., Best, 1982). By contrast, insufficient data exist to fully determine the model terms F_{ER}, and F_{EG}, which specify the magnitude of energy allocation towards reproduction and growth and the conditions under which energy allocation to these processes ceases.

Reproduction in female polar bears consists of a short gestation period (*ca.* 60 days; Derocher et al., 1992), and a lactation period that normally lasts up to 2.5 years (Derocher et al., 1993). The energetic costs of gestation are small compared to those of lactation (Oftedal, 1993), so that data collection should prioritize quantifying milk energy transfer. Milk energy transfer rates may depend on maternal body condition (e.g., storage energy or energy density), cub demand, and cub age. Cub demand, in turn, may be determined by cub body condition, cub growth, and the amount of solid food consumed (Lee et al., 1991; Oftedal, 1993; Arnould and Ramsay, 1994). Although it may be straightforward to formulate lactation within a DEB model (e.g., Klanjscek et al., 2007), relatively large amounts of data may be required for model parameterization due to the number of factors involved. Milk energy transfer data covering a range of feeding conditions (e.g., on-shore fasting and on-ice feeding) as well as a range of maternal and cub body conditions are required for model development. Data on the presence or absence of lactation in relation to maternal energy stores, particularly during the on-shore fasting period in southern populations, may provide further insight into the mechanisms determining cessation of lactation. Cessation of lactation has been reported for food-stressed females (Derocher et al., 1993), implying a storage energy (or energy density) threshold below which lactation stops. The existence of such a threshold is supported by DEB theory (Lika and Nisbet, 2000), and would have implications for lactation (and consequent cub survival) for females food-stressed by climate warming.

The allocation of energy to structural growth is probably the least understood component in the energy budget of polar bears. It may also be the most difficult term to specify in a DEB model, because energy allocation to growth may depend on energy intake (Lika and Nisbet, 2000; Kooijman, 2010), and may also be size-dependent (Nisbet et al., 2004). Structural growth data, estimated through changes in straight-line body length, is needed for bears of different ages, sizes and body conditions with known energy intake. Captive bears may aid in determining this model component because energy intake is known and changes in storage energy and body length could be determined. Growth in bears under food limitation should also be considered to specify the conditions under which energy allocation to growth ceases. While growth data from food-stressed bears may not be available from captive studies, such data could also be obtained from cubs and subadults caught during the on-shore fasting period in southern populations. Energy intake for nursing cubs could in this case be measured through isotope dilution methods (Arnould and Ramsay, 1994), or approximated through changes in maternal energy stores. For both growth and reproduction (and, in fact, for all DEB components), longitudinal data (i.e., repeated measurements of individuals over weeks or months) is preferable over population cross-sections because individual-based processes are assessed.

Changes to the second component of an individual's energy budget, net energy intake (F_{IE}-F_{EA}), under changing environmental conditions cannot be predicted from single-species DEB models. Multi-species DEB models, modelling the flow of energy between trophic levels (Nisbet et al., 2000), may be able to provide such predictions, but insufficient data on the polar bear-seal predator-prey system currently prevents the construction of such models. Little is known about Arctic seal abundance, distribution, and population dynamics, and even less is known about the mechanisms regulating the polar bear-seal predator-prey system. To date, only a handful of studies have documented kill frequency and meal size in polar bears, and these studies are restricted in space and time (Stirling, 1974; Stirling and Latour, 1978; Stirling and Øritsland, 1995). Kill frequencies are unknown for most populations and almost all seasons. A mechanistic link between habitat characteristics, prey population dynamics, and polar bear energy intake is also missing. Comprehensive feeding data are needed to illuminate these links and should become a research priority if we are to move towards a predictive framework for changes in polar bear energy intake (and consequent changes in reproduction and survival) under climate warming. The collection of detailed dietary information can be difficult because polar bears forage in remote sea ice habitats, but new statistical methods, such as state-space models (Franke et al., 2006) or behavioural change point analyses (Gurarie et al., 2009), could be used to extract feeding events from GPS movement data. Moreover, given longitudinal mass and length data, energy intake could also be inferred from DEB models, provided that the energy expenditure terms F_{EA}, F_{EM}, F_{ET}, F_{ER}, and F_{EG} can be specified a priori.

In addition to the new set of research priorities outlined here, we advocate continued mark-recapture studies to estimate survival and reproduction. Although such studies may be of limited use for predicting polar bear population dynamics under climate change (given the lack of long-term studies for most populations and the discussed problems associated with extrapolating vital rates into yet unobserved environmental conditions), they are useful for monitoring past and current change, crucial to population management, conservation status assessment, and the setting of harvest quotas. Additionally, in the context outlined here, mark-recapture studies may provide valuable reproduction and survival data that could be used to validate proposed DEB and other mechanistic models aimed at predicting these demographic parameters.

6. Conclusions

There is no doubt that climate warming is occurring, and climatologists and other scientists have provided a number of predictive models for temperature, precipitation, sea ice, permafrost, and other issues (IPCC, 2007). Ecologists, by contrast, are still facing considerable challenges to obtain quantitative predictions for the resultant effects on species and ecosystems. It is clear that many species are already affected (Walther et al., 2002; Parmesan, 2006), but quantitative predictions are lacking for most species, and existing predictions are often associated with large uncertainty, largely due to limited data and insufficiently understood causal chains (Berteaux et al., 2006; Krebs and Berteaux, 2006; Sutherland, 2006). The mechanistic framework advocated here may help to incorporate cause-effect relationships into ecological predictions, could link expected effects of climate change over various levels of biological organization, and could alert us to the presence of yet unobserved nonlinearities in reproduction and survival in response to changing environmental conditions.

Whether or not climate change effects on survival and reproduction are incorporated into PVAs may have significant effects on conservation status assessments and other aspects of population management. Polar bears were listed globally as “Threatened” in 2008 under the U.S. *Endangered Species Act* due to the threats posed by climate change (Federal Register, 2009). In contrast, the assessment of polar bears in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) did not account for possible climate change effects, and their finding of “Special Concern” (COSEWIC, 2008) identified a lower level of threat than the U.S. assessment. The U.S. and Canadian assessments used similar population projection models in their PVAs, but they differed in their approaches towards model parameterization. The COSEWIC report used mean reproduction and survival rates from earlier studies and projected these forward, specifically stating that they “…do not account for the possible effects of climate change.” (COSEWIC, 2008: page iii). The U.S. approach included environmental trends in their PVA, but they assumed that future vital rates would correspond to estimates from three “good” and two “bad” habitat years observed between 2001 and 2005 (Hunter et al., 2007). Mechanistic models for reproduction and survival were not used in either approach, but may affect status assessments in both countries. If there are nonlinear relationships between environmental conditions and polar bear vital rates, as suggested by the two models considered above, then population projections may be direr than suggested by existing assessments.

Moreover, polar bear vital rates may also be affected by other stressors, not always directly caused but possibly amplified by climate change, such as harvest, pollution, or the emergence of new diseases. Harvest-induced changes in population composition, for instance, may lead to a mate-finding Allee effect (Molnár et al., 2008). Increased exposure of polar bears to persistent organic pollutants (Derocher et al., 2004) may affect their endocrine system (Skaare et al., 2002), their immune system (Bernhoft et al., 2000), and by extension survival and reproduction (Derocher et al., 2003). Climate change may lead to the emergence of new diseases in Arctic wildlife (Bradley et al., 2005). These stressors should also be considered in status assessments and population management (Amstrup et al., 2007) and the suggested approach for predicting changes in reproduction and survival remains applicable. However, the degree to which these effects will be amenable to prediction depends on the level at which causal chains are understood and the availability of data to develop appropriate mechanistic models (Jonzén et al., 2005; Berteaux et al., 2006; Krebs and Berteaux, 2006). Molnár et al. (2008), for instance, developed a mechanistic model for the polar bear mating system (cf. equation (4)) to predict female mating success from male and female densities for yet unobserved population compositions, and they showed that a sudden reproductive collapse could occur if males are severely depleted. Their results could be incorporated into a 2-sex population matrix model and would allow predicting the effects of a continued sex-selective harvest on female mating success, and thus population growth. The effects of increasing pollution levels on reproduction and survival could also be predicted with mechanistic models, specifically pharmacokinetic models coupled with DEB models (Klanjscek et al., 2007), but no such efforts are underway for polar bears. By contrast, potential future effects of emerging diseases on vital rates remain currently unquantifiable in polar bears due to unclear causal chains and a lack of empirical data.

The methods we have outlined in this paper for polar bears are broadly applicable to other species. Linking energy availability to demographic parameters will be a key means of understanding species responses to climate change. The increase in fasting period modelled here can be considered a form of shifting phenology and can be applied to any species. For example, breeding schedules in birds are closely tied to the phenology of their food supplies, and the disruption of this pairing can affect reproductive success (Visser et al., 1998; Thomas et al., 2001). DEB modeling may be a means to explore these relationships to aid conservation planning.

It seems clear that not all species will be currently amenable to the mechanistic framework outlined above. For mechanistic models to be successful in prediction, initial conditions must be well described, all important variables must be included in the model, and model variables must be related to each other in an appropriate way (Berteaux et al., 2006). Whether or not these conditions are fulfilled cannot be known a priori (Berteaux et al., 2006). However, modelling is an iterative approach, where proposed models should be tested against independent data to decide whether the models were successful in predicting. Models can then be improved and tested again, until they converge to satisfactory performance. Arctic species, in particular, may be among the most amenable to prediction because low species diversity, relatively simple food webs, and a limited range of species interactions result in comparatively simple relationships between environmental variables and their effects on individuals and populations.

Mechanistic models are not the only means of predicting the climate change effects on species, but given their potential to predict into yet unobserved conditions, we believe they have been underutilized and present a fruitful line of research to address conservation challenges in a changing world.

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Figure Legends:

Figure 1: Circumpolar polar bear populations. BB: Baffin Bay; DS: Davis Strait; FB: Foxe Basin; GB: Gulf of Boothia; KB: Kane Basin; LS: Lancaster Sound; MC: M'Clintock Channel; NB: Northern Beaufort Sea; NW: Norwegian Bay; QE: Queen Elizabeth Islands; SB: Southern Beaufort Sea; SH: Southern Hudson Bay; VM: Viscount Melville Sound; WH: Western Hudson Bay. The figure is from Aars et al. (2006).

Figure 2: Schematic representation of the polar bear life cycle, as modeled by Hunter et al. (2007), using a stage-structured two-sex matrix population model with parental care. Stages 1-6 are females, stages 7-10 are males. σ_i is the probability of survival for an individual in stage *i* from one spring to the next, σ_{L0} and σ_{L1} are the probabilities of at least one member of a cub-of-the-year (COY) or yearling (yrlg) litter surviving from one spring to the next, *f* is the expected size of yearling litters that survive to 2 years, and β_i is the conditional probability, given survival, of an individual in stage *i* breeding, thereby producing a COY litter with at least one member surviving to the following spring. The figure is redrawn from Hunter et al. (2007).

Figure 3: Estimated time to death by starvation for fasting adult male polar bears, when resting (solid line) and when moving at average speed v = 2 km d^{-1} (dotted line). The horizontal dotted line indicates a fasting period of 120 days, the horizontal dashed line a fasting period of 180 days. Crosses show the cumulative distribution of energy densities at the beginning of the fasting period (right axis) for 97 adult males caught in 1989-1996 in the

Western Hudson Bay population. Lines A-D illustrate the proportion of these males that would die from starvation following a fast of 120 days and 180 days, with and without movement, respectively (see text for details).

Figure 4: Potential climate change impacts on female mating success (the proportion of females fertilized at the end of the mating season), arising from declines in mate-searching efficiency, s, and sea ice habitat area, A, assuming constant mate choice. Predictions are shown for the population of Lancaster Sound, with male and female numbers assumed unchanged relative to 1993-1997, and the estimate of s/A for this period marked by a circle. Also indicated are scenarios where s declines twice (square) and four times (diamond) as fast as A, respectively. A scenario where A declines faster than s by a factor of 1.5 is indicated by a triangle (see text for details).

Figure 1:

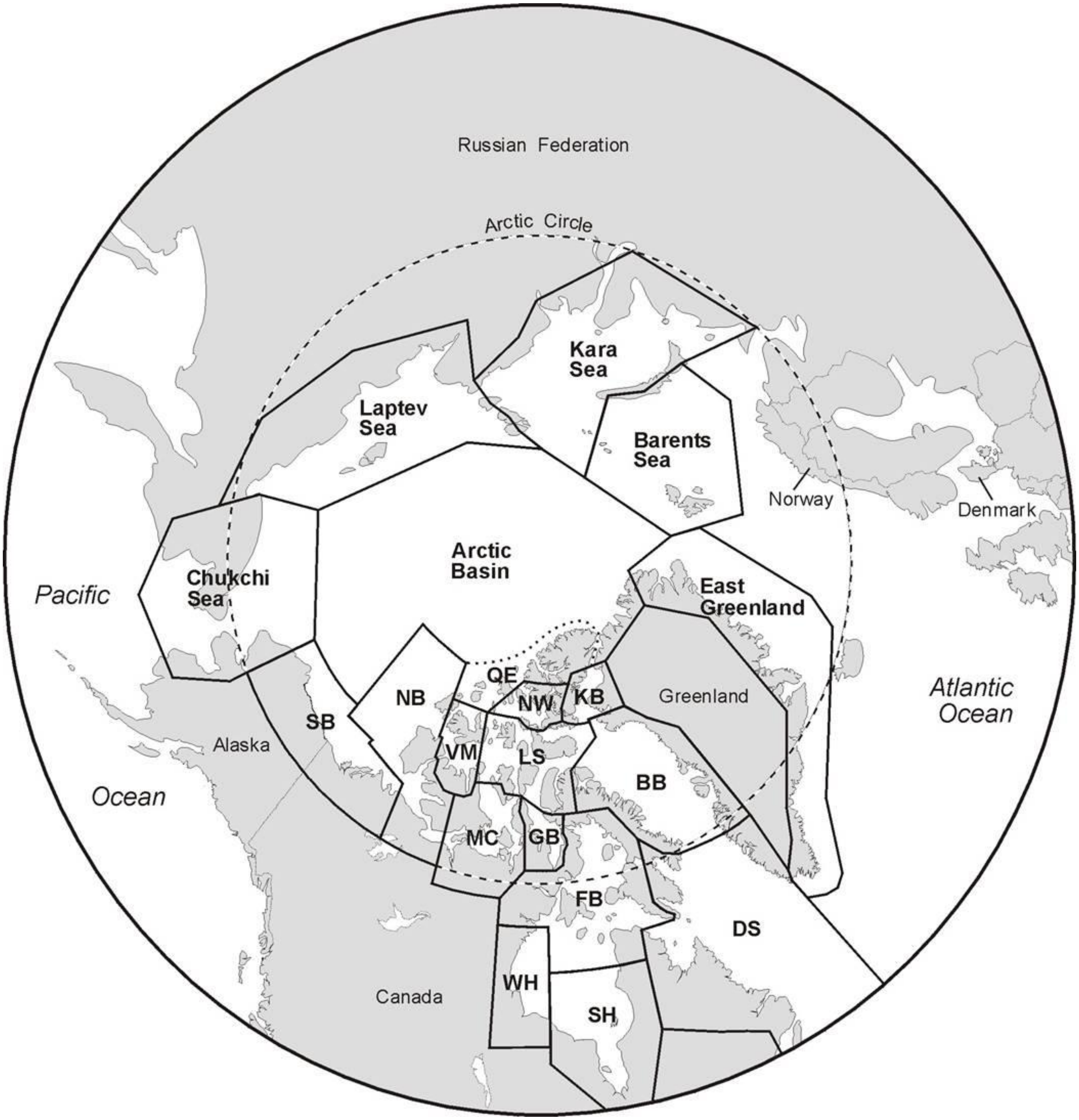

Russian Federation
Arctic Circle
Kara Sea
Laptev Sea
Barents Sea
Norway
Denmark
Arctic Basin
Chukchi Sea
Pacific
East Greenland
Atlantic Ocean
Greenland
QE
NW
KB
NB
SB
Alaska
VM
LS
BB
Ocean
MC
GB
FB
DS
WH
SH
Canada

Figure 2:

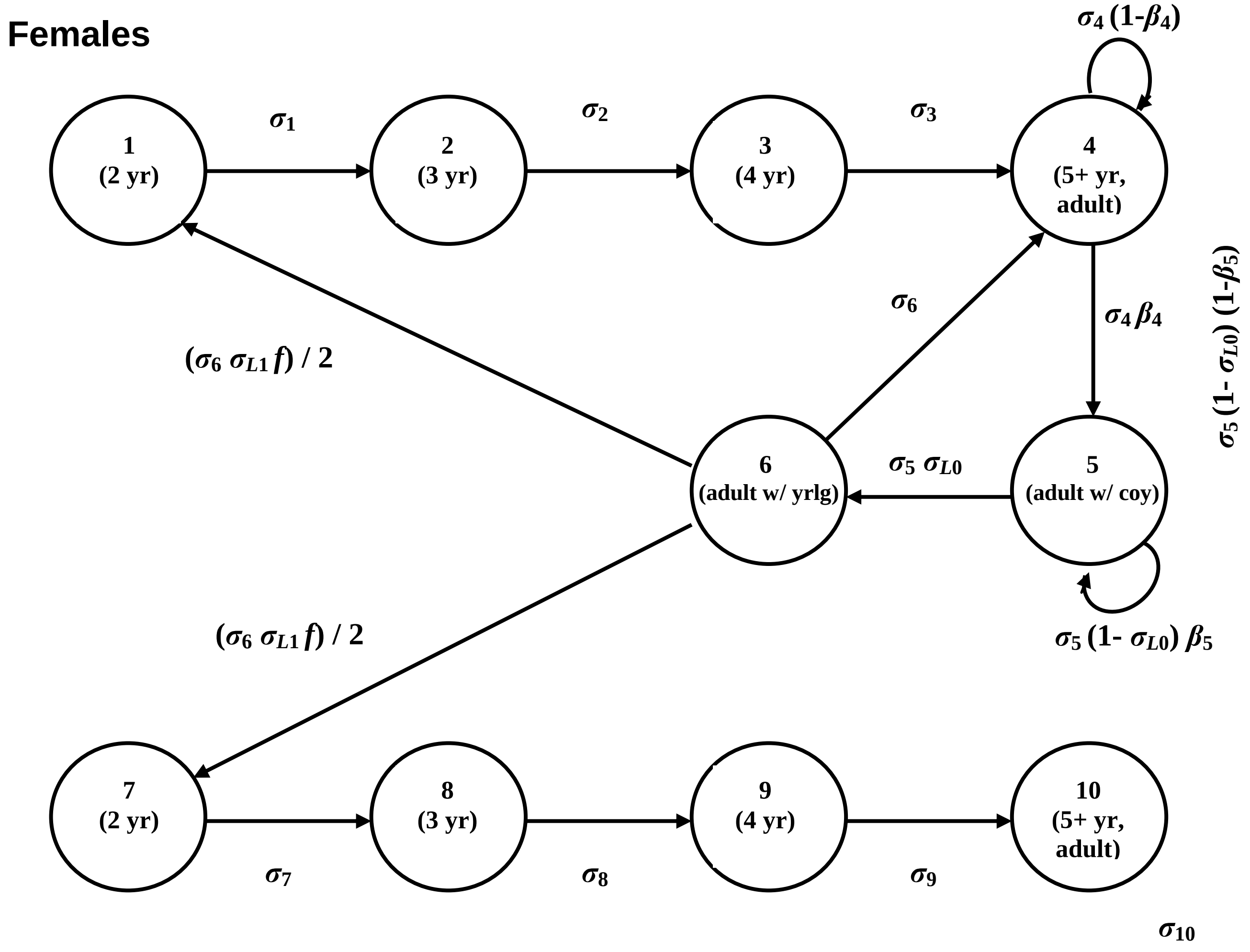

Females
1 (2 yr)
2 (3 yr)
3 (4 yr)
4 (5+ yr, adult)
5 (adult w/ coy)
6 (adult w/ yrlg)
7 (2 yr)
8 (3 yr)
9 (4 yr)
10 (5+ yr, adult)
σ_1
σ_2
σ_3
σ_4 (1-β_4)
$\sigma_4 \beta_4$
σ_5 (1- σ_{L0}) (1-β_5)
σ_5 (1- σ_{L0}) β_5
σ_5 σ_{L0}
σ_6
(σ_6 σ_{L1} f) / 2
(σ_6 σ_{L1} f) / 2
σ_7
σ_8
σ_9
σ_{10}

Figure 3:

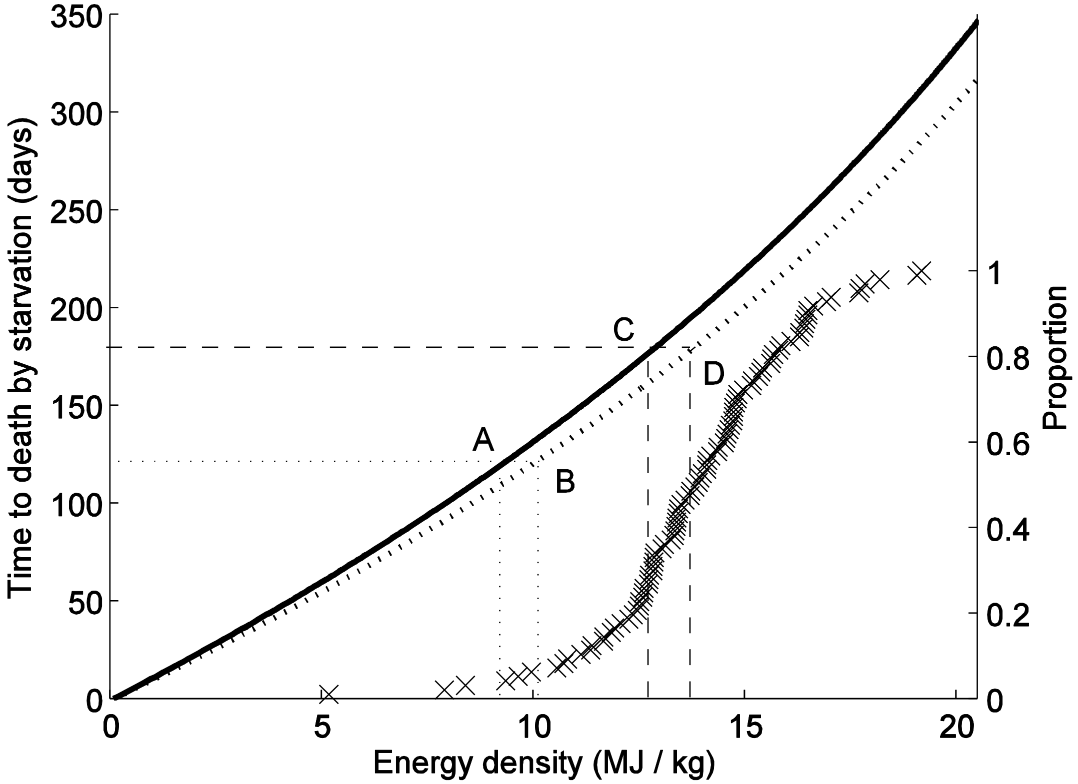
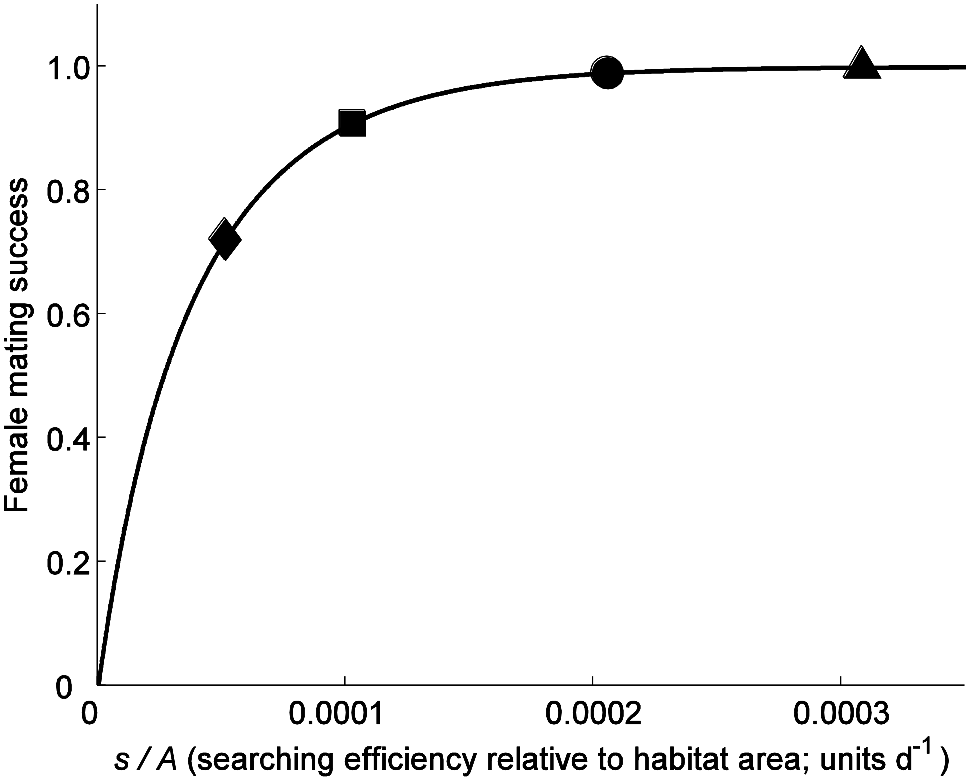

350
300
250
200
150
100
50
0
Time to death by starvation (days)
0
5
10
15
20
Energy density (MJ / kg)
1
0.8
0.6
0.4
0.2
0
Proportion
A
B
C
D

Figure 4:


Female mating success
1.0
0.8
0.6
0.4
0.2
0
0
0.0001
0.0002
0.0003
$s\,/\,A$ (searching efficiency relative to habitat area; units d^{-1})