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And then there was the melting of the ice. He and his people lived on the ice;
ice was their home; ice was their citadel. Since the vast disturbances in the Arctic,
the ice had begun to disappear, and Iorek knew that he had to find an
icebound fastness for his kin, or they would perish.

– Philip Pullman, *The Amber Spyglass*

University of Alberta

MODELLING FUTURE IMPACTS OF CLIMATE CHANGE AND HARVEST ON THE REPRODUCTIVE SUCCESS OF FEMALE POLAR BEARS (*URSUS MARITIMUS*)

by

Péter Kálmán Molnár

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Mathematical and Statistical Biology

Department of Mathematical and Statistical Sciences
Department of Biological Sciences

Edmonton, Alberta
Spring 2009

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Modelling Future Impacts of Climate Change and Harvest on the Reproductive Success of Female Polar Bears (*Ursus maritimus*)** submitted by **Péter Kálmán Molnár** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy**.

Dr. Mark A. Lewis (Co-Supervisor)

Dr. Andrew E. Derocher (Co-Supervisor)

Dr. Subhash R. Lele

Dr. Colleen Cassady St. Clair

Dr. Robert J. Hudson

Dr. Nils Chr. Stenseth

Date: ______________________

To Kálmán Molnár, my Grandfather.

I have known you for too short, but your memory keeps inspiring me.

Abstract

Climate change and human harvest are among the most significant threats to polar bear (*Ursus maritimus*) populations today. Climatic warming and resultant sea ice reductions affect polar bears because they depend on this substrate for most aspects of their life history, including access to seals, their main prey. Harvest is highly sex-selective, and males have been reduced significantly in most Canadian populations, leading to concerns that males might eventually be depleted to a point where many females become unable to mate (a so-called Allee effect). Few studies have attempted quantitative predictions of polar bear population dynamics under climate change, and all predictions are associated with large uncertainty. The conditions that would lead to an Allee effect are similarly unclear, but sex-selective harvest is ongoing. In this thesis I coupled mathematical models with empirical data to understand and anticipate effects of climate change and human harvest on the reproductive success of female polar bears. To predict conditions leading to an Allee effect, I developed a mechanistic model for the polar bear mating system. The model described observed mating dynamics well, predicts the proportion of mated females from population density and operational sex ratio, and specifically outlines conditions for an Allee effect. Female mating success was shown to be a nonlinear function of the operational sex ratio, implying sudden reproductive collapse if males are severely depleted. The threshold operational sex ratio for such an Allee effect depends on population density. To predict effects of climatic warming on female reproduction, I first developed a body composition model that estimates the amount of energy stored in the fat and protein reserves of a polar bear. Based on this model, I developed a dynamic energy budget model that predicts changes in energy stores of both fasting and feeding adults. Metabolic rates of adult polar bears were estimated using the energy budget model, and corresponded closely to theoretically expected and experimentally measured values. The models were then used to predict changes in litter size of pregnant females in western Hudson Bay as a result of predicted losses in sea ice and feeding opportunities, and consequent reductions in female storage energy. Severe declines in litter size can be expected under climatic warming, although the precise rates of change depend on current, to date unobserved, summer feeding rates. Behavioural adaptation towards terrestrial feeding is unlikely to significantly compensate for expected losses in storage energy and resultant reductions in litter size. The results of this thesis are a significant step towards a predictive framework for polar bear populations, and aid optimal population management and proactive direction of conservation efforts.

Acknowledgements

I am deeply grateful to my supervisors Mark Lewis and Andrew Derocher, who took me on as a student when I knew little about ecology, always believed in me, and supported me tirelessly throughout the years. Thank you for your enthusiasm, encouragement and critical insight. It has been a true honour and privilege to work with you and learn from you. A very special thanks also to my committee members Colleen Cassady St. Clair and Subhash Lele who always challenged me to become a better scientist. Marjorie Wonham, mentor and friend, has provided scientific guidance and emotional support at all times – I cannot thank you enough. Chris Jerde, Marty Krkosek, and Hannah McKenzie, friends and PhD partners in crime, thank you for all the discussions and fun times both on and off the whiteboard – I truly enjoyed working with you. To my friends and colleagues at the Lewis and Derocher Labs, thank you so much: Jaime Ashander, Marie Auger-Methe, Caroline Bampfylde, Oliver Barker, Seth Cherry, Andria Dawson, Tomas de Camino Beck, Raluca Eftime, Frédéric Hamelin, Frank Hilker, Amy Hurford, Jon Jacobsen, Yu Jin, Catherine Lambert, Jungmin Lee, Frithjof Lutscher, Justin Marleau, Sarah Medill, Jim Muirhead, John Nagy, Bill Nelson, Erik Noonburg, Mario Pineda-Krch, Alex Potapov, Harshana Rajakaruna, Evan Richardson, Vicki Sahanatien, Carly Strasser, Lindsay Towns, Jeanette Wheeler, Meike Wittman – our interactions have influenced me deeply and were critical to my development as a scientist. Mark Duller, Cecilia Hutchinson, and Caspar Williams, thank you so much for all your help throughout the years, in matters big and small.

Numerous people have provided valuable insight and critical guidance at various stages of the dissertation process: Christian Lydersen, Roger Nisbet, Øystein Wiig – thank you all. I owe gratitude to John Arnould, Stephen Atkinson, Martyn Obbard, Mitchell Taylor, and the late Malcolm Ramsay, who collected and kindly made available the polar bear data critical for this project. It would not have been possible without your support. Sebastian Diehl and Wilfried Gabriel, thank your for your generosity and hospitality during my research stay at the University of Munich.

A very special thanks to my friend and collaborator Tin Klanjscek for a wonderful and productive visit in Croatia, for your enthusiasm, and for our ongoing discussions, often at hours that most people would consider insane. A special thanks also to Norbert Baumann for sparking my interest in mathematics at an early age, and to Peter Gaenssler and Daniel Rost, for fostering it later in my life.

Support and funds for this project were provided by ArcticNet, Canada Research Chair, Canadian Circumpolar Institute, Canadian International Polar Year, Canadian Wildlife Federation, Canadian Wildlife Service, Environment Canada, Manitoba Conservation Sustainable Development Innovations Fund, Natural Sciences and Engineering Research Council, Nunavut Department of Sustainable Development, Nunavut Wildlife Management Board, Ontario Ministry of Natural Resources, Polar Continental Shelf Project, Polar Bears International, University of Alberta, University of Saskatchewan, and World Wildlife Fund Canada.

Outside of academia, I have enjoyed the love and support of many friends, without whom I would not have persisted. You know who you are, thank you all for everything. To Elif, a very special thanks for being supportive beyond measure. Words can never capture what you mean to me. Mom, Dad, Gábor and Évi, thank you for your love and support throughout all these years. Thank you for always believing in me. Without you I would not be the person I am today.

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Chapter 1

1 Introduction

Average global temperatures have increased by 0.74 ºC in the last 100 years, and are predicted to increase by a further 1.1-6.4 ºC in the 21st century (IPCC 2007). Observed and projected effects on plants, wildlife and ecosystems are many, including (but not limited to) changes in physiology, phenology, range-boundaries, abundance and distribution of species, as well as changes to community compositions and interspecific interactions. The effects of climatic warming may be beneficial or detrimental to a species, depending on its life history and ecology (e.g., Hughes 2000; McCarty 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Harley *et al.* 2006; Parmesan 2006; Tylianakis *et al.* 2008; Hegland *et al.* 2009).

Ice-obligate species, such as polar bear (*Ursus maritimus*), walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), and ringed seal (*Pusa hispida*) are among the most vulnerable to climatic warming (Tynan & DeMaster 1997; Laidre *et al.* 2008; Moore & Huntington 2008). Of these, polar bears have become the flagship species for climate change awareness. They are increasingly used by the media as a communication tool for issues of climate change, have become the subject of intense political debate, and public interest in the future of the species is increasing (e.g., Slocum 2004; Engelhaupt 2007; Charles 2008). However, even though the vulnerability of polar bears to climatic warming is well established (e.g., Derocher *et al.* 2004; Stirling & Parkinson 2006; Laidre *et al.* 2008; Wiig *et al.* 2008), scientists have only recently begun to understand how polar bear abundance and distribution may change numerically in a warming climate (e.g., Amstrup *et al.* 2007; Hunter *et al.* 2007; Durner *et al.* 2009). Moreover, even though climate-induced habitat fragmentation and loss is probably the biggest concern for the species (Wiig *et al.* 2008), it is not the only one: in a recent expert survey, conducted among members of the International Union for the Conservation of Nature Species Survival Commission Polar Bear Specialist Group, survey participants named climate change, harvest, and pollution as the three main threats to polar bear populations today (O'Neill *et al.* 2008).

In this introduction, I will first outline current threats to polar bears more specifically, with an emphasis on climate change and harvest, the topics of this dissertation. I will then discuss why modelling approaches are necessary to address current challenges in polar bear conservation, outline previous modelling approaches, and discuss some of their shortcomings. This will provide the motivation and starting point for my dissertation.

1.1 Current Threats to Polar Bears

1.1.1 Polar Bears and Climate Change

The Arctic is warming (Comiso 2003; Steele *et al.* 2008), and profound effects on the sea ice have already been observed. Sea ice thickness is decreasing (Rothrock *et al.* 1999; Comiso 2002; Lindsay & Zhang 2005; Maslanik *et al.* 2007), the perennial sea ice cover is shrinking (Johannessen *et al.* 1999; Comiso 2002; Nghiem *et al.* 2006; Comiso *et al.* 2008), and annual sea ice extents have repeatedly reached record minima in the past decade (Vinnikov *et al.* 1999; Serreze *et al.* 2003; Stroeve *et al.* 2005; Comiso 2006; Comiso *et al.* 2008). The sea ice is already declining at rates faster than expected (Stroeve *et al.* 2007), and further temperature increases and consequent sea ice declines are expected to accelerate in the future (Comiso 2003; Holland *et al.* 2006; Serreze *et al.* 2007). Regional variability and variability in predictive models exist, but the general trend is towards a seasonally ice-free Arctic ocean (Zhang & Walsh 2006; Serreze *et al.* 2007; Parkinson & Cavalieri 2008).

Polar bears inhabit the ice-covered waters of the Arctic and are vulnerable to sea ice loss, because they depend on this substrate for most aspects of their life history. Most importantly, polar bears need sea ice to access their main prey species, ringed seals and bearded seals (Stirling & Archibald 1977; Smith 1980). Locally, other seal species such as harp seals (*Phoca groenlandica*), harbour seals (*Phoca vitulina*), and hooded seals (*Cystophora cristata*), or other marine mammals such as white whales (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and walrus, can complement the diet (Smith &

Sjare 1990; Derocher *et al.* 2002; Iverson *et al.* 2006; Thiemann *et al.* 2008), or may become more important under changing sea ice conditions (Derocher *et al*. 2004; Iverson *et al.* 2006; Thiemann *et al.* 2008). However, in general all marine prey species are expected to become less accessible to polar bears as the sea ice declines. Terrestrial food sources such as blueberries (*Vaccinium uliginosum*; Derocher *et al.* 1993a), seabirds (Russell 1975; Stempniewicz 2006), reindeer (*Rangifer tarandus*; Derocher *et al.* 2000), or even whale carcasses (Bentzen *et al.* 2007; Schliebe *et al.* 2008), 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).

The sea ice is also used for travelling and mating (Ramsay & Stirling 1986; Stirling *et al.* 1993), and to some degree by pregnant females for maternity denning (Amstrup & Gardner 1994). In a warmer climate, areas of open water and ice floe drift rates are expected to increase, making polar bear movement energetically more expensive (Mauritzen *et al.* 2001, 2003). It has also been suggested that pregnancy rates may decline due to an increased difficulty of mate-finding in a more fragmented and dynamic sea ice habitat (Derocher *et al.* 2004). Furthermore, pregnant females may not be able to reach preferred terrestrial den sites (Ramsay & Stirling 1990; Fischbach *et al.* 2007), or may have to cover large distances of open water when returning to their core habitat after exiting maternity dens, regardless of whether dens are chosen on land or on drifting multi-year sea ice (Amstrup & Gardner 1994; Derocher *et al.* 2004). An increased necessity of swimming may further reduce energy stores of already food-stressed females, and could also increase mortality of accompanying cubs, which are less well insulated and cannot withstand prolonged exposure to cold water (Blix & Lentfer 1979). A multitude of other, more subtle, effects of climate warming on polar bears are also thought possible (Derocher *et al.* 2004; Wiig *et al.* 2008), but an extensive review is beyond the scope of this chapter.

The combined effects of decreasing food availability and increasing energetic demands in a warming climate are predicted to result in decreasing polar bear body conditions and a consequent cascade of demographic effects (Stirling & Derocher 1993; Derocher *et al.* 2004; Wiig *et al.* 2008). Pregnant females give birth in maternity dens, where no food is available for a period of at least 4-5 months (Ramsay & Stirling 1988;

Messier *et al.* 1994; Atkinson & Ramsay 1995). The lightest female ever observed to give birth weighed 189 kg at den entry (Derocher *et al.* 1992). Females below such a threshold probably cannot reproduce because they do not have sufficient energy stores to meet the energetic demands of survival, gestation, and early lactation during the 4-5 month fasting period. Although heavier females may reproduce, their reproductive success would still be negatively affected by reduced body condition, because maternal body condition is positively correlated with litter size and litter mass at den emergence, which in turn is positively correlated with cub survival (Derocher & Stirling 1996, 1998). After den exit, cubs are usually nursed for *ca.* 2 years, but increasing food stress may result in early cessation of lactation, further jeopardizing cub survival (Derocher *et al.* 1993b). In contrast, adult survival rates are probably only affected under severe conditions because polar bears can survive extended periods without feeding (Atkinson & Ramsay 1995). Subadults, however, are less proficient in finding food (Stirling & Latour 1978), and may therefore suffer from increased mortality under adverse conditions even if adult survival is unaffected (Wiig *et al.* 2008). Such negative changes in demographic parameters could eventually lead to decreased population growth rates or even population declines.

There is an increasing body of evidence that some of these predicted changes are already occurring. In western Hudson Bay (Figure 1.1), at the southern limit of the species' geographical range, declines in polar bear body condition, reproductive success, juvenile, subadult and senescent-adult survival, as well as population abundance, have been documented, and are thought to result from increased nutritional stress due to a prolonged open-water season during summer and fall (Stirling *et al.* 1999; Regehr *et al.* 2007). Polar bears in the adjacent southern Hudson Bay population and the more northerly southern Beaufort Sea population (Figure 1.1) have shown similar declines in body condition (Obbard *et al.* 2006; Regehr *et al.* 2006). Trends in survival are less clear, possibly due to low sample sizes, but there is some evidence for increases in cub and senescent-adult mortality in both populations (Regehr *et al.* 2006; Obbard *et al.* 2007). Declines in body condition, survival rates, and reproductive parameters, have not been reported for other populations, either because these changes are not yet occurring, or because they remained undetected due to a lack of appropriate time series. However, Stirling & Parkinson (2006) reported increased sightings of polar bears near human settlements in the populations of Foxe Basin, Baffin Bay, and Davis Strait (Figure 1.1) and interpreted these sightings as a result of increased food stress associated with prolonged open water periods. Further, although anecdotal, evidence of adverse effects of climatic warming is provided by reports of cannibalism (Amstrup *et al.* 2006) and incidents of drowning (Monnett & Gleason 2006) in presumably food-stressed adult polar bears (Cherry *et al.* 2009).

Acknowledging the vulnerability of polar bears to climate warming induced habitat loss, the species was listed as "Threatened" under the US *Endangered Species Act* in May 2008 (Federal Register, 2008). The decision made polar bears the first species listed under the Act primarily for reasons of global warming.

1.1.2 Polar Bears and Harvest

Less than four decades ago, over-harvest was considered the biggest threat to polar bear populations (Prestrud & Stirling 1994; Freeman & Wenzel 2006). Since then, conservation measures and hunting regulations have been put into place (Fikkan *et al.* 1993, Prestrud & Stirling 1994), and most populations seem to have recovered from over-harvesting (Aars *et al*. 2006). Today, the hunting of polar bears is completely banned in Norway and Russia, and strongly regulated in the other three polar bear range states Denmark (Greenland), the United States of America, and Canada (Aars *et al*. 2006). The United States only allows a subsistence hunt to Alaska Natives, and has recently also prohibited the import of sport-hunted polar bear trophies through the species' listing as "Threatened" under the *Endangered Species Act*. Greenland and Canada regulate the polar bear harvest through quota systems. Whereas Greenland only allows a subsistence harvest to local hunters, Canada remains the only country where native hunters can sell their quota to guided sports hunts (Aars *et al*. 2006).

In Canada, quotas are determined based on population size estimates, estimated population growth rates and the maximum sustainable yield from simulation models (Taylor *et al.* 1987; Lee & Taylor 1994; Taylor *et al.* 2003; Taylor *et al*. 2008a). A sex-selective harvesting policy is implemented, where hunters are encouraged to maintain a harvest ratio of two males for every female. This selective strategy is aimed at increasing the sustainable yield whilst simultaneously maximizing the economic value of the hunt (Freeman & Wenzel 2006; Taylor *et al*. 2008a). Moreover, it has been argued that the increasing allocation of tags to guided trophy hunts (where up to 80% of animals taken are male) not only provides social, cultural and economic benefits to communities throughout the Canadian Arctic, but may also benefit polar bear conservation through increased appreciation of the economic value of this species and increased incentives for habitat protection (Freeman & Wenzel 2006).

However, a strongly male-biased harvest, and in particular a harvest that is biased towards prime-age large males, can also have a number of negative effects, including decreased fitness of breeding age males (Coltman *et al*. 2003; Darimont *et al*. 2009), increased infanticide (Swenson *et al*. 1997; Wielgus & Bunnell 2000; Whitman *et al*. 2004), or decreased fertilization rates of females (Milner-Gulland *et al*. 2003; Courchamp *et al*. 2008). None of these effects has been assessed in Canadian polar bear populations despite ongoing sex-selective harvest.

To date, the sex ratio has been skewed significantly towards females in most Canadian polar bear populations (Taylor *et al*. 2002; Taylor *et al*. 2006; Regehr *et al*. 2007; Taylor *et al*. 2008b,c). Even though birth rates have remained high so far (Aars *et al*. 2006), concerns have been raised that males could be depleted to a point where many females become unable to find mates (Derocher *et al*. 1997; McLoughlin *et al*. 2005). More generally, concerns have also been raised that harvest levels previously thought appropriate may not be sustainable for polar bear populations increasingly stressed by climatic warming (Wiig 2005; Regehr *et al*. 2007).

1.1.3 Other Threats to Polar Bears

Possibly the biggest threat to polar bear populations today, other than climate change and harvest, is pollution. Polar bears occupy the top of the Arctic food chain and sustain themselves on a high fat diet, which makes them vulnerable to bioaccumulation of toxicants (Norstrom *et al.* 1998). These contaminants may affect the endocrine system (Skaare *et al.* 2001), the immune system (Bernhoft *et al.* 2000), and by extension survival and reproduction (Derocher *et al.* 2003; Sonne *et al.* 2006). Moreover, with climatic warming, exposure of polar bears to contaminants may increase further due to altered atmospheric pathways and sea currents, permafrost melting, and increased shipping traffic in the Arctic (Macdonald *et al.* 2003; Derocher *et al.* 2004; Wiig *et al.* 2008). In general, population level effects of pollution are unknown but may exist in some of the more polluted populations (Derocher 2005).

Additional threats to polar bear populations include oil and gas development in polar bear habitat (Stirling 1990; Amstrup 1993), human-bear conflicts and resultant defence kills (Derocher *et al.* 2004; Wiig *et al.* 2008), and human disturbance, for example, through increasing Arctic tourism (Kaltenborn 2000; Stewart *et al.* 2005). Although current impacts of these factors are minor (Aars *et al.* 2006), they may become more significant in the near future (Derocher *et al.* 2004; Wiig *et al.* 2008). Polar bears are sensitive to oil spills (Hurst & Øritsland 1982; Stirling 1990; Hurst *et al.* 1991), and with increasing industrial development in polar bear habitat it is possible that this will become an additional source of mortality. Human disturbance, be it through tourism or development, may further contribute to stress in polar bears, possibly affecting metabolism, survival, and reproduction (Watts *et al.* 1991; Amstrup 1993; Dyck & Baydack 2004). Finally, the number of defence kills may also increase if food-stressed polar bears increasingly seek out human settlements in search for food (Stirling & Parkinson 2006; Wiig *et al.* 2008).

1.2 Towards an Understanding of the Future of Polar Bears

Much is known about the biology and ecology of polar bears. Long-term research and monitoring programs have resulted in one of the most extensive datasets for any Arctic mammal, and have contributed significantly to our understanding of this species. The population of western Hudson Bay, for example, has been monitored for over 40 years, which has resulted in a wealth of data and peer-reviewed publications on polar bear physiology, reproduction, survival, population dynamics, diet, movement, and habitat use, among others. However, the vast majority of this work is descriptive.

In a changing world, new questions arise. For instance, even though strong negative effects of climatic warming on polar bears are expected (Derocher *et al.* 2004; Stirling & Parkinson 2006; Laidre *et al.* 2008; Wiig *et al.* 2008), there is much uncertainty surrounding the time frame and manner in which polar bear populations will respond. It is difficult to address this issue with historic data alone, because past and predicted environmental conditions are distinctly dissimilar (Wiig *et al.* 2008). Simple extrapolation of observed vital rates or population dynamics is therefore not possible. The implications of male-selective harvesting strategies that continue to alter population compositions cannot be addressed from past observations alone by similar arguments. However, for optimal population management it is essential to proactively address questions such as:

- "How many males are needed in a population to ensure sufficiently high female reproductive success for a viable population?"

or

- "What would happen to a polar bear population if the summer open-water fasting season would be extended by an additional month?"

Formalizing ecological processes in mathematical models, and combining these models with historical data for parameterization (and possibly validation), can provide the basis to answer such questions, and thus for sound ecological risk assessment, optimal population management, and proactive direction of conservation efforts. Relatively few such models exist for ursids in general, and for polar bears in particular. The exception are population models (most often matrix models) that are commonly used to synthesize observed reproductive and survival rates for population risk analyses and to determine harvest quotas (e.g., Bunnell & Tait 1980; Eberhardt 1990; Freedman *et al.* 2003; Schwartz *et al.* 2006; Taylor *et al.* 2008a,b,c). More recently, such models have also been applied to assess polar bear population viability under climate warming and resulting sea ice reductions (Amstrup *et al.* 2007; Hunter *et al.* 2007).

In the following sections, I will briefly summarize how models have been used to address issues of climate change and harvest in polar bears. For both topics, I will briefly discuss shortcomings of current approaches, which will then provide the motivation and starting point for my dissertation. For the sake of completeness, I include a short discussion on models concerning pollution and other threats of polar bear populations, but these will not be pursued further within this dissertation.

1.2.1 Models Addressing Climate Change Impacts on Polar Bears

Based on polar bear life history and ecology, a number of studies have attempted qualitative predictions on the future of polar bears under climatic warming, and some of their predictions are outlined in section 1.1.1 (Stirling & Derocher 1993; Derocher *et al.* 2004; Rosing-Asvid 2006; Wiig *et al.* 2008). These assessments are useful, but cannot provide quantitative information on the manner and time frame in which polar bears will be affected. To date, only two studies have attempted such predictions: Hunter *et al.* (2007) coupled general circulation models with deterministic and stochastic matrix models to obtain population size projections for the southern Beaufort Sea under projections of future sea ice. Amstrup *et al.* (2007) coupled general circulation models with a polar bear carrying capacity model and a Bayesian network model, and projected that approximately two-thirds of the world's polar bear population would be lost by mid-century given current sea ice projections. These studies were part of the assessment conducted for the US Fish and Wildlife Service leading to the listing of polar bears as "Threatened" under the US *Endangered Species Act* (Federal Register, 2008).

Nevertheless, many questions remain unanswered. Both studies are large-scale and focus on projections of population sizes and/or distributions. Population sizes, however, are a direct consequence of survival and reproductive rates. One challenge in predictive population models is therefore to obtain reasonable estimates of survival and reproductive parameters under a variability of climatic conditions (Caswell 2001). If observed and predicted climatic conditions differ substantially, such as for polar bears, this task becomes complicated and uncertainty in population predictions can be large

(Beissinger & Westphal 1998; Coulson *et al.* 2001; Ellner *et al.* 2002; Sutherland 2006). Hunter *et al.* (2007) based their predictions on survival and reproduction estimates obtained from only six years of capture-recapture data. Amstrup *et al.* (2007) opted for a different approach, parameterizing their polar bear carrying capacity model with current population size estimates, and coupling this model with qualitative expert judgement on potential population stressors. Both authors attempted to address issues of uncertainty through extensive sensitivity analyses.

An alternative approach is to consider the effect of climate change on the body condition of individuals, and the relationship between body condition, reproductive success and survival, directly (Beissinger & Westphal 1998). Especially in polar bears, where much of the life history is tied to storing large quantities of energy when hunting and utilizing these stores when fasting (Watts & Hansen 1987; Ramsay & Stirling 1988; Atkinson & Ramsay 1995), this approach seems promising. However, even though reproductive success and survival are directly affected by body condition (cf. section 1.1.1), the functional relationships between climate and individual body condition, and between body condition, survival and reproduction are poorly understood. Energy budget models have the potential to elucidate these relationships (e.g., Ross & Nisbet 1990; Kooijman 2000; Winship *et al.* 2002), and could therefore complement the approaches taken by Hunter *et al.* (2007) and Amstrup *et al.* (2007). A combination of these two approaches, one focusing on the individual level and the processes relating environmental condition, body condition, reproduction and survival to each other, the other focusing on population level consequences of overall reproduction and survival, may not solve the problem of large uncertainties in population viability analyses. Nonetheless, for complex ecological problems, like predicting population responses under climatic warming, such a synthetic approach is recommended and could substantially increase our understanding regarding the future of polar bears (e.g., Berteaux *et al.* 2006; Carroll 2007; McRae *et al.* 2008).

1.2.2 Models Addressing Harvest Impacts on Polar Bears

Harvest quotas in Canada are determined by use of a population simulation program called RISKMAN (Taylor *et al.* 2003; Aars *et al.* 2006). RISKMAN is described as an individual-based model that mainly differs from other population dynamics models in its ability to correctly simulate the three-year reproductive cycle of female polar bears (Taylor *et al.* 2003; McLoughlin *et al.* 2005). The program can track both male and female population sizes, and allows incorporating sex- and age-specific harvest selectivity and vulnerability. However, harvest quotas are solely based on projections of female population size, assuming a harvest ratio of two males for every female. This ratio has been determined by generic model runs incorporating both sexes and requiring that a certain minimum mean age is maintained among males (McLoughlin *et al.* 2005; Taylor *et al.* 2008a).

While the program can track age-structure and population size of both sexes, it does not include an interaction between males and females. It thereby assumes implicitly that female reproductive success is independent of male population density (Taylor *et al.* 2008a). Whether or not this assumption is justified has not been assessed. A sex-selective harvest, however, can alter both relative and absolute densities of adult males and females. Even if a minimum age among males is maintained, female reproductive success may be negatively affected by declining male densities due to an inability of finding a mate (Milner-Gulland *et al.* 2003; Courchamp *et al.* 2008). At what densities such adverse effects on female reproduction would occur is unknown, and cannot be assessed using RISKMAN. Other models are therefore needed that explicitly account for the role of males in the reproductive dynamics of polar bears.

1.2.3 Models Addressing Other Threats to Polar Bears

It is difficult to conclusively determine how pollution affects polar bear populations today, and even more difficult to make predictions into the future (Derocher *et al.* 2004; Wiig *et al.* 2008). However, general bioenergetic modelling of marine mammals suggests a number of negative effects of pollutants on survival and reproductive success that are likely to be amplified in polar bears when they become increasingly food-stressed by climatic warming. Concerns include (but are not limited to) increased concentrations of toxic chemicals in the blood stream, and an increased vertical transfer of toxicants from mothers to cubs (Klanjscek *et al.* 2007).

The effects of increasing pollution levels on the reproductive success and survival of individuals could be assessed within the framework of dynamic energy budget models (Kooijman & Bedaux 1996a; Nisbet *et al.* 2000). This approach is becoming increasingly common in ecotoxicology, and examples for such assessments range from daphnia (Kooijman & Bedaux 1996b) to right whales (*Eubalaena* glacialis; Klanjscek *et al.* 2007). To the best of my knowledge, no such efforts are currently underway for polar bears.

It may even be more difficult to quantify potential future impacts of oil and gas development, tourism, and increasing human-bear interactions, because causal relationships are poorly understood and empirical studies are limited.

1.3 Dissertation Outline

Population abundance is the focus of all current modelling approaches addressing the effects of climate change and harvest on polar bears. Mathematical models addressing the biological processes governing individual reproductive success and survival are lacking, but could be valuable because population abundance is inherently related to reproduction and survival, and we do not yet fully understand how changing environmental conditions or harvest-induced changes in population composition may affect these demographic parameters.

The main questions regarding the future of polar bears under given scenarios of climate change or harvest pertain to polar bear population dynamics under yet unobserved conditions. Hence, appropriate data on reproduction or survival that could aid predictive attempts do not and cannot exist. Predictions by population models that only summarize abundance effects of reproduction and survival, but do not incorporate the processes governing these demographic parameters, must therefore necessarily either extrapolate from present conditions or use expert judgement to make reasonable model assumptions.

Models addressing the biological processes governing reproduction and survival can provide guidance in this regard. If process-oriented models could be formulated that predict reproduction and survival under new conditions, then it would suffice to predict these conditions to obtain predictions for reproduction and survival, and thus population abundance. More specifically, consider, for example, reproduction under climatic warming. It is well-known that reproductive success depends on body condition (Derocher *et al.* 1992; Derocher & Stirling 1996, 1998). If we could formulate models that predict how body condition is affected by climatic warming, and how reproduction is affected by body condition, then we could predict reproduction under climatic warming.

In this dissertation I make advances in this regard. I focus on the reproductive success of females, and on potential negative effects of a male-biased harvest and climatic warming. I formulate process-oriented mechanistic models and couple these with historical data to answer two main questions:

(1) How does the probability of a female finding a mate during the mating season depend on male and female densities? In other words, how would female pregnancy rates be affected by harvest-mediated changes in population composition, and in particular by a continued depletion of males?

(2) How many cubs will a pregnant female produce as a function of her body condition? Furthermore, specific to the population of western Hudson Bay, can we predict how litter sizes would change as a result of climate induced changes in sea ice dynamics and consequent changes in female body condition?

I begin by addressing sex-selective harvest, and the role of males in the population dynamics of polar bears. In Chapter 2, I formulate and parameterize a mechanistic model for the polar bear mating system that predicts the proportion of fertilized females at the end of the mating season, given population density and operational sex ratio (i.e., the ratio between adult males and adult females that are available for mating). I use the model to specifically outline conditions that lead to reduced pregnancy rates due to a lack of males. The model provides managers with the information necessary to develop optimal sex-specific harvesting strategies that account for the role of males in the reproductive dynamics of polar bears.

I then switch focus to address effects of climatic warming on the expected litter size of pregnant females. For this purpose, I first develop and parameterize a body composition model that allows me to estimate the amount of energy stored in the fat and protein reserves of a polar bear, given its length and body mass (Chapter 3). The model also provides me with a means to estimate the metabolic rate of fasting adult polar bears, and allows me to consider polar bears within a dynamic energy budget framework. The model is discussed in light of currently available methods to quantify the nutritional status of mammals in general, and polar bears specifically.

In Chapter 4, I utilize the body composition model from Chapter 3 to determine how litter size depends on the energy stores of pregnant females. I then develop and parameterize a polar bear energy budget model to evaluate how energy stores, and consequently litter sizes, of pregnant females in western Hudson Bay might change under climatic warming.

In the concluding Chapter 5, I summarize my results, discuss them within the larger framework of current modelling approaches towards mate finding and bioenergetics, respectively, and make suggestions for directions of future research.

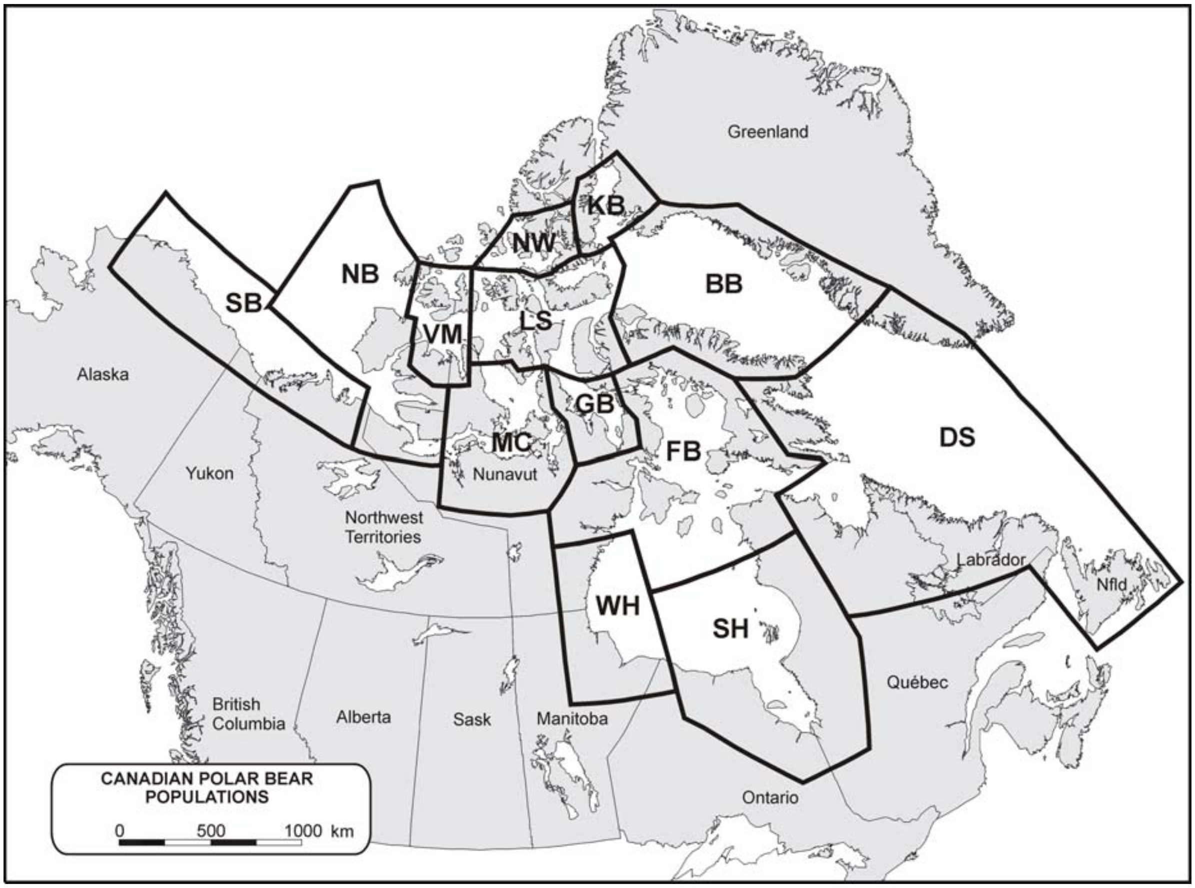

Figure 1.1: Canadian polar bear populations as of 31 December 2004. BB: Baffin Bay; DS: Davis Strait; FB: Foxe Basin; GB: Gulf of Boothia; KB: Kane Basin; LS: Lancaster Sound; MC: M'Clintock Channel; NB: Northern Beaufort Sea; NW: Norwegian Bay; SB: Southern Beaufort Sea; SH: Southern Hudson Bay; VM: Viscount Melville Sound; WH: Western Hudson Bay. The figure is from Aars *et al.* (2006, p. 106).

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Chapter 2[*]

2 Modelling the Mating System of Polar Bears: a Mechanistic Approach to the Allee Effect

2.1 Introduction

Much attention has been devoted to the study of Allee effects in recent years, a phenomenon where individuals benefit from the presence of conspecifics, and suffer from a decrease in some component of fitness at low population sizes or densities (Fowler & Baker 1991; Sæther *et al.* 1996; Stephens *et al.* 1999; Boukal & Berec 2002). While many mechanisms could give rise to an Allee effect (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Berec *et al.* 2007; Courchamp *et al.* 2008), by far the most commonly studied is the difficulty of finding mates at low population densities (e.g., Dennis 1989; McCarthy 1997; South & Kenward 2001; Boukal & Berec 2002). Decreased probabilities of finding a mate at low densities result in decreased reproductive success, and thus a positive relationship between this component of fitness and population density.

The harvest of animal populations can have unforeseen consequences if Allee effects are not recognized (Courchamp *et al.* 1999; Stephens & Sutherland 1999). Allee effects can accelerate population decline, possibly even leading to extinction. Recently, Allee effects, initiated by inappropriate harvesting, have been demonstrated for saiga antelopes (*Saiga tatarica*; Milner-Gulland *et al.* 2003), African wild dogs (*Lycaon pictus*; Courchamp & Macdonald 2001), African elephants (*Loxodonta africana*; Poole 1989), and moose (*Alces alces*; Solberg *et al.* 2002). An Allee effect has also been proposed for the slow recovery and continuing declines of Atlantic cod (*Gadus morhua*; Rowe *et al.* 2004), and possibly other commercially exploited fish stocks (Liermann &

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[*] A version of this chapter has been published as: Molnár, P. K., Derocher, A. E., Lewis, M. A. & Taylor, M. K. 2008. Modelling the mating system of polar bears: a mechanistic approach to the Allee effect. *Proceedings of the Royal Society of London, Series B* **275**: 217-226.

Hilborn 1997). Even the extinction of the passenger pigeon (*Ectopistes migratorius*) involved harvesting and was possibly accelerated by an Allee effect (Halliday 1980).

The potential impact of Allee effects on population persistence makes it crucial to determine the circumstances leading to an Allee effect before such a scenario is reached. Such knowledge would aid the implementation of optimal harvesting strategies or the direction of conservation efforts, particularly for threatened and endangered species existing at low population sizes or densities but not yet showing an Allee effect, such as North Atlantic right whales (*Eubalaena glacialis*; Fujiwara & Caswell 2001), Amur tigers (*Panthera tigris*; Carroll & Miquelle 2006), or polar bears (*Ursus maritimus*). Unlike smaller organisms where Allee effects can sometimes be demonstrated in laboratory populations (e.g., Allee 1931), empirical data on Allee effects cannot be gathered for large free-ranging species before an Allee effect occurs. Thus, predictive methods are needed.

In this chapter I present such a predictive approach for polar bears. These solitary, non-territorial animals (DeMaster & Stirling 1981) occur at low densities and are vulnerable to Allee effects due to low frequencies of potential mating encounters. The unpredictability of the Arctic sea ice, and the consequent unpredictability of the spatial distribution of mates, makes mate-searching an important variable in their reproductive dynamics (Ramsay & Stirling 1986).

A male-biased operational sex ratio (Emlen & Oring 1977) with two to three males for every available female results from a prolonged mother-offspring bond, and ensures high female mating success in unharvested populations (Lentfer *et al.* 1980; Ramsay & Stirling 1986). However, prolonged sex-selective harvest has significantly reduced the numbers of adult males in most Canadian polar bear populations, leading to balanced or even female-biased operational sex ratios (Lee & Taylor 1994; Derocher *et al.* 1997). Nonetheless, management policies continue to encourage hunters to select for males so that at least two-thirds of the harvest is male (Freeman & Wenzel 2006; Taylor *et al.* 2008a). This selective removal of males, and the generally higher vulnerability of males to harvest (Lee & Taylor 1994), has led to concerns that male populations could be depleted to a point where many females become unable to find mates (Derocher *et al.* 1997; McLoughlin *et al.* 2005).

Mating season length and the time allocated to mate-searching and mating limit the number of females each male can locate and fertilize. Consequently, there will be a sex ratio below which female fertilization rates decline due to male scarcity (Beddington 1974; Caughley 1977). Determining this sex ratio, and thus understanding how many males are needed to maintain stable populations, is therefore crucial for the evaluation of current and future harvesting strategies. However, no Allee effect has yet been reported for polar bears, and fertilization rates are not directly monitored. Thus, no empirical data exist on the relationship between fertilization rates and male and female densities, and a modelling approach is needed.

One-sex models can sometimes be used to detect Allee effects in cases where appropriate data exist (Myers *et al.* 1995; Morris 2002). However, they have low predictive power for Allee effects arising from a difficulty of finding mates, and cannot be used to validate management strategies *a priori* (Boukal & Berec 2002), because an individual's success in finding mates is influenced by both population density and population sex ratio (Legendre *et al.* 1999; Bessa-Gomes *et al.* 2004; Rankin & Kokko 2007). Two-sex models are more appropriate because they explicitly address mate shortage. In fact, models that aim to understand the effects of a depleted male population should explicitly consider the mating system (Legendre *et al.* 1999; Engen *et al.* 2003; Bessa-Gomes *et al.* 2004; McLoughlin *et al.* 2005) and accurately fit historical data (Stephens *et al.* 2002; Haefner 2005), particularly when the objective is the prediction of Allee effects (Boukal & Berec 2002). Although two-sex models have been studied, investigations were mostly theoretical (e.g., Caswell & Weeks 1986; Lindström & Kokko 1998; Ranta *et al.* 1999; Bessa-Gomes *et al.* 2004; Rankin & Kokko 2007). The application of two-sex models to biological data remains scarce (but see Stephens *et al.* 2002; Hurford *et al.* 2006).

Recent work highlights the importance to distinguish between a *component* Allee effect, defined as a positive relationship between any component of individual fitness and population density or number, and a *demographic* Allee effect, which is a positive relationship between the *per capita* growth rate and population density or number (Stephens *et al.* 1999). Decreased success in finding mates due to low densities or skewed sex ratios should be considered a component Allee effect, which may or may not translate into a demographic Allee effect (Stephens *et al.* 1999). As a first step in understanding the effects of sex-selective polar bear harvest, my objective is to predict fertilization rates from male and female densities, and thus identify circumstances leading to such a component Allee effect.

For this purpose, I develop a mechanistic model for the mating system of polar bears: I extend the dynamical systems framework of Wells *et al.* (1990) and Veit & Lewis (1996) to track solitary males, solitary females, and breeding pairs through the mating season, including pair formation and separation explicitly. A possible component Allee effect arises naturally through the proportion of females that have not mated by the end of the mating season. Using a maximum likelihood approach, I then estimate model parameters by fitting the predicted pairing dynamics to observed pairing data from the population of Lancaster Sound, Nunavut, Canada (Figure 1.1). Model inputs are the respective densities of sexually active males and females; model output is the proportion of females fertilized by the end of the mating season. This simple, biologically realistic, model can be used to specify the conditions leading to a component Allee effect of reduced fertilization rates due to a lack of males.

I begin by introducing the study population and proceed then to development, parameterization, and analysis of the mating model.

2.2 Study Area, Data Collection and Definitions

I used data collected during the most recent polar bear population inventory of Lancaster Sound, Nunavut, Canada (Taylor *et al.* 2008b). Each year from 1993 to 1997, the population area was systematically searched from early April to early June in a geographically uniform manner, with every bear seen captured. For each bear, age, sex, reproductive status and pairing status was recorded. The sampling season varied slightly between years, with the earliest sampling on April 3, the latest on June 6. Details on the immobilization and handling of bears, as well as an extended description of the study population, can be found in Taylor *et al.* (2008b).

Ages were determined for older bears by counting the annular rings of an extracted vestigial premolar tooth (Calvert & Ramsay 1998), and for younger bears (≤ 1 year) by tooth eruption patterns. I defined males as sexually mature if they were at least 5 years old. Although intense competition for females might prevent young males from mating (Ramsay & Stirling 1986; Palmer *et al.* 1988), most 5 year olds are physically mature (in contrast to the majority of 4 year olds), and would be capable of breeding if an opportunity arose (Rosing-Asvid *et al.* 2002). I regarded females as sexually mature if they were at least 4 years old because 5 year old females can produce cubs after mating the year before (Furnell & Schweinsburg 1984; Aars *et al*. 2006). I considered immature bears and females accompanied by cubs-of-the-year or yearlings as unavailable for mating (Ramsay & Stirling 1986) and excluded them from further analyses. Because most cubs are weaned at 2.5 years of age in the high Arctic, and females can come into oestrus that same season (Lentfer *et al.* 1980; Ramsay & Stirling 1986), I treated females with 2 year olds as available-to-breed and pooled them with females without cubs.

I further classified bears as solitary or paired. A bear was paired if captured with a mature bear of the opposite sex and behaving in a manner that suggested pairing. In instances where several males were associated with a female (10.9% of breeding pairs), I considered the oldest attending male as paired and the other males as solitary. A few individuals were captured twice during the same season (2.9% of males and 2.1% of females). I included second captures in the pairing dynamics analyses, because a bear can change between being solitary and paired throughout the mating season.

2.3 Model Development

2.3.1 The Mating System of Polar Bears

Males locate females by following their tracks (Stirling 1988). Subsequently formed breeding pairs last approximately between one and four weeks (Ramsay & Stirling 1986; Wiig *et al.* 1992), but the length of pair association is poorly documented in general. Similar to other ursids (Boone *et al.* 1998, 2004), polar bears are thought to be induced ovulators (Lønø 1970), and such a long period may be necessary both to induce ovulation in females and to ensure paternity by avoiding sperm competition (Ramsay & Stirling 1986).

Males are thought to be polygynous (Berta & Sumich 1999), locating, defending and fertilizing females one after another. The number of females a male can locate during a mating season is unknown, but probably depends on mating season length, the time for mate location, and the length of pair associations. Furthermore, the ability of males to continue mate-searching after pairs separate may play a role. Mate-searching is demanding, and males often forego feeding during the mating season, focusing on reproduction instead (Cherry *et al.* 2009). Especially younger males, still growing, may be limited in their searching ability by their need to forage.

Ramsay & Stirling (1986) and Wiig *et al.* (1992) suggested that polyandry might occur with females consecutively forming breeding pairs with different males, but the frequency of such events is unknown. However, the maximum time a female will associate with males is restricted by oestrus, which can last up to four weeks (Malyov 1988; Wiig *et al.* 1992).

Mating season length and timing are unclear. Breeding pairs were reported as early as March (Lønø 1970; Lentfer *et al.* 1980), and Rosing-Asvid *et al.* (2002) suggested a mating season extended from early March to early June, with a peak between April and early May. However, levels of serum steroid concentrations in male polar bears suggest a mating season from early April to late May (Palmer *et al.* 1988; Howell-Skalla *et al.* 2002).

2.3.2 Model Assumptions and Structure

I modelled the pairing dynamics of a polar bear population during the mating season using five differential equations that explicitly incorporate pair formation, pair separation, and the ability of males to continue mate-searching after pair separation. I only considered mature males and mature females not accompanied by cubs-of-the-year or yearlings. Females with 2 year old cubs were considered available-to-breed, and I did not distinguish between them and females without dependent offspring:

$$(2.1\text{a}) \qquad \underbrace{\frac{dM}{dt}}_{\substack{\text{Solitary}\\\text{available}\\\text{males}}} = -\underbrace{\sigma M F}_{\substack{\text{Pair}\\\text{formation}}} + \underbrace{\alpha \mu P}_{\substack{\text{Males available}\\\text{after pair separation}}}$$

$$(2.1\text{b}) \qquad \underbrace{\frac{dF}{dt}}_{\substack{\text{Unfertilized}\\\text{females}}} = -\underbrace{\sigma M F}_{\substack{\text{Pair}\\\text{formation}}}$$

$$(2.1\text{c}) \qquad \underbrace{\frac{dP}{dt}}_{\text{Breeding pairs}} = \underbrace{\sigma M F}_{\substack{\text{Pair}\\\text{formation}}} - \underbrace{\mu P}_{\substack{\text{Pair}\\\text{separation}}}$$

$$(2.1\text{d}) \qquad \underbrace{\frac{dM^*}{dt}}_{\substack{\text{Solitary}\\\text{unavailable}\\\text{males}}} = \underbrace{(1-\alpha)\mu P}_{\substack{\text{Males unavailable}\\\text{after pair separation}}}$$

$$(2.1\text{e}) \qquad \underbrace{\frac{dF^*}{dt}}_{\substack{\text{Ferilized}\\\text{females}}} = \underbrace{\mu P}_{\substack{\text{Pair}\\\text{separation}}}$$

$M(t)$, $M^*(t)$, $P(t)$, $F(t)$, and $F^*(t)$ represent the respective densities (at time t) of solitary males searching for mates, solitary males that have ceased searching for mates, breeding pairs, solitary unmated females, and solitary mated females that have become unavailable for mating, respectively. I assumed that all mated females are fertilized.

Adult males and adult females without cubs-of-the-year or yearlings show similar habitat preferences (Stirling *et al.* 1993). I therefore assume them to be randomly distributed in space (within the population boundaries) and well-mixed, and modelled the process of pair formation using the Law of Mass Action, which gives rise to a nonlinear interaction term. The parameter σ represents hereby the rate of pair formation. Pairs were assumed to remain together for μ^{-1} time units, so that pairs dissolve at rate μ. To account for potential variability in the ability of males to focus on mate-searching rather than foraging, I assumed that after pair separation males become unavailable with probability 1-α to fertilize other females. The parameter α is termed male mating ability. $\alpha = 1$ implies that all solitary males search for mates at all times, $\alpha = 0$ represents the limiting case of male monogamy.

I did not model polyandry explicitly, although some females may subsequently associate with different males within a period constrained by oestrus. Such behaviour would reduce the number of solitary males for prolonged periods and could affect population mating success by lowering the chances of other females to mate. However, if mate-searching between consecutive pairings is negligibly short, then polyandry is sufficiently represented through prolonged pair associations, and thus, the parameter μ.

I assumed that all mature males and all mature females that are not accompanied by cubs-of-the-year or yearlings are solitary and available for breeding at time $t_0 = 0$, the beginning of the mating season:

$$M(0) = m_0 \tag{2.2a}$$

$$F(0) = f_0 \tag{2.2b}$$

$$P(0) = M^*(0) = F^*(0) = 0 \quad . \tag{2.2c}$$

Here, m_0 denotes the density of mature males, and f_0 the density of mature females not accompanied by cubs-of-the-year or yearlings. I assumed that m_0 and f_0 remain constant throughout the mating season, as implied by equations (2.1) and (2.2):

$$M(t) + P(t) + M^*(t) = m_0 \tag{2.3a}$$

$$F(t) + P(t) + F^*(t) = f_0 \quad . \tag{2.3b}$$

The mating season was assumed to last T time units. Female mating success was defined as the proportion of females fertilized by the end of the mating season, including females that may still be paired at that time. Female mating success is therefore given by $1 - F(T) / f_0$.

I explored a range of additional models to accommodate uncertainties in mate-searching behaviour, including a model with a rest stage for polygynous males after mating, and a model that explicitly included another period of mate-searching between consecutive pairings for polyandrous females. Because these more complex models were not supported significantly better by the data, I use the simple model (2.1) throughout.

2.3.3 Parameter Estimation

The densities of available males and females at the beginning of the mating season were estimated as:

(2.4a) m_0 = # mature males / habitat area

(2.4b) f_0 = # mature females not accompanied by cubs-of-the-year or yearlings / habitat area

The respective male and female numbers were estimated using sex-specific population size estimates (Taylor *et al.* 2008b) and the standing age and reproductive stage structure in captures, which were assumed to be representative of the population (Table 2.1). Habitat area was estimated as the total marine area within population boundaries using a geographic information system (ArcGIS 9.1, Environmental Systems Research Institute, Redlands, California, USA). The geographic population boundaries were previously established using mark-recapture movement data (Taylor & Lee 1995), DNA analysis (Paetkau *et al.* 1999), and cluster analysis of radio-telemetry data (Bethke *et al.* 1996; Taylor *et al.* 2001). The ratio m_0 / f_0 will henceforth be referred to as the operational sex ratio.

The parameters σ and μ were estimated using maximum likelihood, fitting the predicted to the observed pairing dynamics. The maximum likelihood function was adapted to the sampling design, and is based on the respective proportions of males, females and pairs in daily samples. The maximum likelihood function and its derivation are presented in section 2.3.4. For the purpose of parameter estimation, I pooled the pairing data by day-of-the-year, assuming that mating season timing and associated pairing dynamics do not differ between years; annual variation is unlikely because photoperiod probably regulates the reproductive cycle of polar bears (Palmer *et al.* 1988). For simplicity, I fixed April 2 as the start of the mating season, t_0, one day before the earliest sample. Although this is consistent with estimates of early April as the start (Palmer *et al.* 1988), an earlier beginning of the mating season is possible (Rosing-Asvid *et al.* 2002). I explored sensitivity of model parameter estimates and mating success predictions to this simplifying assumption by allowing pair formations before April 2 and estimating an additional free parameter, the density of pairs already formed on April 2, $P(0) = p_0$, through maximum likelihood. However, this only slightly changed the maximum likelihood estimates for σ and μ (by less than 5% and less than 3%, respectively), so that mating success predictions were not affected significantly. The simplifying assumption regarding t_0 therefore seems appropriate. It is not necessary to fix mating season length for the estimation of σ and μ. However, to estimate female mating success, $1 - F(T) / f_0$, I set $T = 60$ days, which corresponds to an end of the mating season on May 31 (Howell-Skalla *et al.* 2002; Rosing-Asvid *et al.* 2002).

As the pairing dynamics were insensitive to α, I was unable to estimate this parameter from data. Instead, I assumed maximal male mating ability and fixed $\alpha = 1$ for model fitting because older males dominate the pairing dynamics in this high density population. This assumption did not significantly affect the maximum likelihood estimates of σ and μ (e.g., by about 6% and 13%, respectively, when using $\alpha = 0$ instead of $\alpha = 1$). However, reduced male mating abilities could negatively affect female mating success under different initial conditions, such as female-biased operational sex ratios. This is explored in the sensitivity analyses of section 2.5.

2.3.4 Derivation of the Maximum Likelihood Function for the Pairing Dynamics Model

In this section, I describe the maximum likelihood approach used to estimate the free parameters σ and μ.

To estimate σ and μ, I needed to fit the predicted pairing dynamics to the observed pairing data. Typical methods of fitting ordinary differential equations to data involve the method of least squares (Haefner 2005). In the present case, this would be appropriate if time series on male, female, and pair densities throughout the mating season were available. However, such data do not exist, so I developed a method that is based on the proportion of males, females, and breeding pairs in daily samples, and uses a multinomial maximum likelihood function:

The model described by equations (2.1) and (2.2) predicts the density of breeding pairs $P(t)$ and the respective densities of males and females that are available for mating ($M(t)$ and $F(t)$) and of those that are not ($M^*(t)$ and $F^*(t)$) at any given time t. In the field, it is not possible to distinguish between bears that are available for mating, and those that are not. Therefore, I summarized model predictions to give the total densities of solitary males and solitary females at time t as $M(t)+M^*(t)$ and $F(t)+F^*(t)$, respectively. At any given time t during a survey, a solitary male, a solitary female or a breeding pair could be caught from a sampling population whose density is predicted as $M(t)+M^*(t)+F(t)+F^*(t)+P(t)$. This formulation for sampling population density acknowledges that (consistently with model formulation (2.1)) a breeding pair is only counted as one capture, even though it consists of two bears. The respective proportions of solitary males, solitary females and breeding pairs in this sampling population at time t are therefore predicted as

$$\text{(2.5a)} \qquad p_{\mathrm{M}}(t) = \frac{M(t)+M^*(t)}{M(t)+M^*(t)+F(t)+F^*(t)+P(t)} = \frac{M(t)+M^*(t)}{m_0+f_0-P(t)}$$

$$\text{(2.5b)} \qquad p_{\mathrm{F}}(t) = \frac{F(t)+F^*(t)}{M(t)+M^*(t)+F(t)+F^*(t)+P(t)} = \frac{F(t)+F^*(t)}{m_0+f_0-P(t)}$$

$$\text{(2.5c)} \qquad p_{\mathrm{P}}(t) = \frac{P(t)}{M(t)+M^*(t)+F(t)+F^*(t)+P(t)} = \frac{P(t)}{m_0+f_0-P(t)}$$

Each bear can change between being solitary and paired throughout the mating season, so that captures should be regarded as sampling with replacement. Thus, assuming all captures to be independent from each other, the probability of catching exactly $m(t)$ males, $f(t)$ females and $p(t)$ pairs on a given sampling day t with a given total of $c(t) = m(t)+f(t)+p(t)$ captures, is multinomially distributed and predicted as

$$(2.6) \qquad \Pr\big(m(t), f(t), p(t) \,\big|\, c(t)\big) = \frac{c(t)!}{m(t)!\,f(t)!\,p(t)!}\big(p_{\mathrm{M}}(t)\big)^{m(t)}\big(p_{\mathrm{F}}(t)\big)^{f(t)}\big(p_{\mathrm{P}}(t)\big)^{p(t)} \;,$$

where the probabilities of catching a male, a female, or a breeding pair, $p_{\mathrm{M}}(t)$, $p_{\mathrm{F}}(t)$, and $p_{\mathrm{P}}(t)$, are given by equations (2.5a)-(2.5c). Given $c(t_{\mathrm{i}}) = m(t_{\mathrm{i}})+f(t_{\mathrm{i}})+p(t_{\mathrm{i}})$ captures on day-of-the-year t_{i}, the negative log-likelihood function for pair formation rate, σ, and pair dissolution rate, μ, is given by

$$(2.7) \quad -l\left(\sigma, \mu \,\middle|\, m(t_1), f(t_1), p(t_1), \ldots, m(t_{\mathrm{n}}), f(t_{\mathrm{n}}), p(t_{\mathrm{n}})\right) = -\ln\left(\prod_{\mathrm{i}=1}^{\mathrm{n}} \Pr\big(m(t_{\mathrm{i}}), f(t_{\mathrm{i}}), p(t_{\mathrm{i}}) \,\big|\, c(t_{\mathrm{i}})\big)\right)$$

where t_1 and t_{n} represent the first and last days of sampling respectively. By minimizing this function, I obtained the maximum likelihood estimates for σ and μ (Table 2.1).

2.4 Results and Model Analysis

Of 261 mature males and 220 mature available females sampled, 64 males and females were paired (24.5% and 29.1% respectively). Breeding pairs were observed between April 5 and May 28. Pairing activity peaked around mid-April followed by a slow decline in the proportions of paired males and females until the end of May (Figure 2.1). In April, 33.8% of sampled males and 40.7% of sampled females were paired, in contrast to May, when only 15.3% of males and 17.9% of females were paired.

The model captures these pairing dynamics well. After early pair formations, a broad peak in the proportions of paired males and females is predicted due to prolonged pair associations. A gradual decline in the proportion of breeding pairs follows as pairs separate and fewer unfertilized females are available for pairing (Figure 2.2). Pair formation rate was estimated as σ = 2.05 km^2 h^{-1} (bootstrapped 95% confidence interval: 1.27-3.42 km^2 h^{-1}), length of pair association as μ^{-1} = 17.5 days (bootstrapped 95% confidence interval: 14.1-21.6 days; Table 2.1). Opportunistic field observations of pair association lengths in grizzly and polar bears range from at least 7 to at least 22 days (Herrero & Hammer 1977; Ramsay & Stirling 1986, Wiig *et al.* 1992; A. E. Derocher & M. K. Taylor, unpublished data; I. Stirling, pers. comm.), giving additional confidence in this parameter estimate.

Using these parameter estimates, the model predicts female mating success from male and female densities, m_0 and f_0, male mating ability, α, and mating season length, T. Figure 2.3 summarizes these predictions with contour lines giving mating success as a function of male and female densities, assuming maximal male mating ability ($\alpha = 1$) and mating season length $T = 60$ days. No component Allee effect due to male scarcity was predicted for the Lancaster Sound population, with 99% of females fertilized by May 31 (bootstrapped 95% confidence interval: 94.5-100.0%; Figure 2.3). This estimate closely corresponds to the observed litter production rate of 95.4% for older adult females (age ≥7 years) in Lancaster Sound, i.e., for females where litter production rates are least affected by failed pregnancies (Taylor *et al.* 2008b).

However, female mating success is a strongly nonlinear function of the operational sex ratio, m_0 / f_0. Therefore, once mating success starts declining due to male scarcity, a small additional loss of males will result in a strong reduction of female mating success, suggesting rapid reproductive collapse. Figure 2.4 illustrates this relationship for five representative densities (Aars *et al.* 2006), varying the operational sex ratio, but keeping the overall density of breeding males and females, m_0+f_0, constant.

Furthermore, female mating success depends not only on the operational sex ratio, but also on the overall density of available breeders, m_0+f_0 (Figure 2.4a). As density decreases, an increasing proportion of males is required to maintain a constant level of female mating success. For example, while $m_0 / f_0 = 0.67$ is sufficient to achieve 95% mating success at the estimated density of available breeders in Lancaster Sound, $m_0 / f_0 = 1.55$ is needed at half that density, and $m_0 / f_0 = 4.43$ at one-third that density. Moreover, 95% mating success cannot be achieved with realistic operational sex ratios at one-quarter that density (Figure 2.4a). The latter two examples illustrate the possibility of a component Allee effect of reduced female mating success at low densities even at the natural operational sex ratio of two to three males per available female. In contrast, although relatively fewer males are required to maintain mating success at higher densities, a potential reproductive collapse resulting from male scarcity would also be faster and more sudden at higher densities owing to the increasing nonlinearity between mating success and operational sex ratio (Figure 2.4a).

The nonlinear relationship between female mating success and operational sex ratio arises regardless of the magnitude of the model parameters pair formation rate (σ), length of pair association (μ^{-1}), male mating ability (α), and mating season length (T) (Figures 2.4-2.7). Similarly, female mating success, and thus the threshold operational sex ratio below which mating success declines, is density-dependent regardless of model parameters. However, the density-dependence of female mating success becomes weaker as pair formation rates increase, with mating success becoming less dependent on the overall density $m_0 + f_0$, and only dependent on the operational sex ratio m_0 / f_0. For instance, using $\sigma = 2.05$ km^2 h^{-1}, $m_0 / f_0 = 0.67$ is expected to yield 95% female mating success at the estimated density of available breeders in Lancaster Sound, but $m_0 / f_0 = 4.43$ is required at one-third that density. By contrast, assuming $\sigma = 20$ km^2 h^{-1}, 95% mating success would be achieved with $m_0 / f_0 = 0.26$ and $m_0 / f_0 = 0.34$ at the two densities, respectively (Figure 2.4). In fact, as σ increases further, the threshold operational sex ratio below which female mating success declines, approaches $m_0 / f_0 \approx 0.29 = \mu^{-1} T^{-1}$, regardless of density. In this limiting case of negligible mate searching, limitations on female mating success arise from the fact that each male can only mate with an average of $T / \mu^{-1} \approx 3.43$ females due to restrictions imposed by pair association length and mating season length.

All model parameters influence quantitative predictions of female mating success. Increasing pair formation rate, increasing male mating ability, decreasing length of pair association, and increasing mating season length all increase mating success. Mating success is most sensitive to pair formation rate, particularly at low densities, and somewhat sensitive to male mating ability, which becomes increasingly important at higher densities combined with balanced to female-biased operational sex ratios. By contrast, length of pair association (and thus the prevalence of polyandry) and mating season length have little influence on mating success. A detailed sensitivity analysis is provided in the next section.

2.5 Sensitivity Analyses of Female Mating Success

In this section I explore the sensitivity of female mating success ($1 - F(T) / f_0$) to changes in the model parameters pair formation rate (σ), male mating ability (α), length of pair association (μ^{-1}), and mating season length (T). For this purpose, I vary each parameter while holding all others constant, and give female mating success for all possible combinations of male and female densities, m_0 and f_0. Pair formation rate is varied by an order of magnitude from $\sigma = 0.2$ km^2 h^{-1} to $\sigma = 20$ km^2 h^{-1}, to account for a possible underestimation of σ due to a lack of pairing data from March. Pair association length is varied from $\mu^{-1} = 10.5$ days to $\mu^{-1} = 24.5$ days, which likely encompasses the natural range of pair association lengths (Ramsay & Stirling 1986; Malyov 1988; Wiig *et al.* 1992). No data on male mating ability exist, so I explore the full range by varying α from 0 to 1. Mating season length is varied from $T = 53$ days to $T = 67$ days.

2.5.1 Pair Formation Rate (σ)

Female mating success is most sensitive to σ, particularly at low densities. For instance, applying $\sigma = 2.05$ km^2 h^{-1} to three hypothetical populations with operational sex ratio $m_0 / f_0 = 1.08$ and densities ranging from 0.99 to 1.97 bears per 1000 km^2 (densities one-quarter to one-half as high as in Lancaster Sound), a component Allee effect due to difficulties in finding mates is predicted for all scenarios with female mating success ranging from 72% to 91%. In contrast, increasing pair formation rate to $\sigma = 20$ km^2 h^{-1} ensures 100% mating success in all three populations. High pair formation rates ensure high mating success regardless of density for all but very female-biased operational sex ratios (Figures 2.4 and 2.5a). In contrast, female mating success is greatly reduced if σ is decreased to $\sigma = 0.2$ km^2 h^{-1}. In this case, the same three population scenarios would only yield 13% to 24% female mating success (Figure 2.5b).

Mating success is less sensitive to σ at high densities because high densities ensure high encounter rates between males and females by themselves (cf. the interaction terms in equations (2.1a)-(2.1c)). In fact, increasing the density of available breeders while keeping searching efficiency (and thus σ) constant is equivalent to increasing searching efficiency (and thus σ) while keeping density constant.

2.5.2 Male Mating Ability (α)

Male mating ability can also have strong effects on female mating success, however, under different conditions. While pair formation rate (and thus mate searching efficiency) is the most important factor determining mating success at low densities, and becomes less important as density increases (Figure 2.4), male mating ability has little effect at low densities (Figure 2.6a). For instance, increasing σ = 2.05 km^2 h^{-1} to σ = 20 km^2 h^{-1} raises predicted mating success from 59% to 100% at m_0 / f_0 = 1.08 and density $m_0 + f_0$ = 0.66 bears per 1000 km^2 (one-sixth the estimated density in Lancaster Sound), but decreasing α = 1 to α = 0 reduces mating success only from 59% to 51%.

In contrast to σ, the importance of α increases with increasing density, where pronounced effects on mating success can be found at balanced to female-biased operational sex ratios (Figure 2.6a). At higher densities males and females can easily find each other, but at female-biased sex ratios the ability of males to mate with several females becomes crucial. If, for example, the male population in Lancaster Sound would be reduced to half its size (from 489 to 245 mature males), while the number of mature available females is kept at 451 (i.e., m_0 / f_0 = 0.54), then 85% mating success is predicted with α = 1, but only 52% mating success with α = 0, a difference of 147 females (Figure 2.6b).

As expected, male mating ability has little effect on female mating success under male-biased operational sex ratios, regardless of population density (Figure 2.6a).

2.5.3 Length of Pair Association (μ^{-1}) and Mating Season Length (T)

Length of pair association and mating season length have little influence on female mating success, regardless of density (Figures 2.7 and 2.8). Especially the latter is reassuring, because it implies that my choice of T = 60 days does not affect my conclusions regarding mating success, as long as the mating season ends around late-May, as previously suggested (Howell-Skalla *et al.* 2002; Rosing-Asvid *et al.* 2002) and also supported by the fact that no breeding pairs were observed in my data after May 28 (Figure 2.1).

2.6 Discussion

Intensive sex-selective harvest of Canadian polar bear populations has led to concerns that a lack of males might eventually lead to reduced fertilization rates and subsequent population declines (Derocher *et al.* 1997; McLoughlin *et al.* 2005). However, until now no means existed to assess how many males are needed to maintain stable populations. Due to the limited range of densities and sex ratios in natural populations, infrequent population inventories, and because fertilization rates are not routinely measured, no data exist to describe the relationship between female mating success and male and female densities empirically. Therefore, I developed a mechanistic model that predicts mating success from male and female densities, and thus describes the circumstances leading to a component Allee effect of reduced female mating success due to male scarcity. The model provides managers with the information necessary to develop optimal sex-specific harvesting strategies that account for the role of males in the reproductive dynamics of polar bears.

My approach of modelling the mating dynamics to predict female mating success differs from most previously proposed two-sex models, which usually focus on between generation dynamics and assume a phenomenological birth function like the harmonic mean (Caswell & Weeks 1986; Lindström & Kokko 1998; Ranta *et al.* 1999), or phenomenologically describe mating success as a function of the operational sex ratio

(Rankin & Kokko 2007). In contrast, I used a mechanistic process model that describes the pairing dynamics of the mating season explicitly, focusing on the biological processes underlying mating success. Because my objective is the prediction of Allee effects, and predictions can be highly sensitive to model structure (Pascual *et al.* 1997; Wood & Thomas 1999; Stephens *et al.* 2002), such a mechanistic modelling approach is preferable over heuristic or semi-mechanistic models that include the Allee effect *a priori*, or phenomenologically describe mating success as a function of male and female abundances, particularly in the absence of data to parameterize and validate proposed functions (Boukal & Berec 2002). A similar approach was taken by Wells *et al.* (1990) and Veit & Lewis (1996), who also suggested second-order reproductive kinetics. However, my study not only extended their framework to the mating biology of polar bears, it is also the first to compare the predicted pairing dynamics to observed pairing data, and thus seek empirical validation for the proposed model structure. This step is crucial for predictive models, which should not only emphasize realism, but also accurately fit historical data (Stephens *et al.* 2002; Haefner 2005).

The model explicitly incorporates pair formation and separation, the physical ability of males to locate and mate with several females, and mating season length, which all influence female mating success. Mate-searching is an important variable in the reproductive dynamics of polar bears (Ramsay & Stirling 1986), and is implicitly incorporated through the rate of pair formation, which is simply the encounter rate between males and females multiplied by the probability of pair formation upon encounter (i.e., the degree of mate choice in the population). The sensitivity of mating success to pair formation rate supports the significance of efficient mate-searching for the mating dynamics of polar bears and further suggests a similarly important role of mate choice (Møller & Legendre 2001).

Regardless of parameter values, some qualitative predictions with profound management implications arise from the model. First, the threshold operational sex ratio, below which a component Allee effect of reduced female mating success is expected, is not constant, but depends on the overall density of available breeders. The proportion of males needed to achieve high mating success increases with decreasing density, so that low density populations might experience a component Allee effect even at the natural operational sex ratio of two to three males per available female. This density-dependence arises from the need to search for mates, and differs from findings in harem-breeding animals such as many ungulates, where the threshold operational sex ratio is relatively constant, and depends on the physiological capacity of males to inseminate females (Ginsberg & Milner-Gulland 1994; Mysterud *et al.* 2002). Mate-searching is not an important component in the mating dynamics of harem breeders, so that these findings are consistent with my prediction that mating success becomes solely dependent on the operational sex ratio under high searching efficiencies.

Second, female mating success is a nonlinear function of the operational sex ratio, implying sudden and rapid reproductive collapse, if males are depleted below sustainable limits. Owing to this nonlinearity, already female-biased sex ratios, infrequent population inventories, and the difficulty to determine the threshold operational sex ratio due to its density-dependence, I recommend a precautionary harvesting approach. Currently observed high litter production rates despite reduced male numbers (Aars *et al.* 2006) should not be taken as evidence that populations are secure.

A cautionary example is given by the saiga antelope, where similar patterns as predicted here were observed. Despite heavy sex-selective poaching and a continuing depletion of adult males, female fertilization rates remained unaffected in this ungulate for a long time, but eventually collapsed in a sudden and nonlinear fashion when males were depleted below a critical threshold (Milner-Gulland *et al.* 2003).

The Lancaster Sound polar bear population with estimated 489 mature males and 451 mature available females seems relatively secure: 99% female mating success is predicted, with only 349 males required to fertilize 95% of females (assuming $\alpha = 1$). However, consider, for instance, a population reduction to one-third this density (163 males and 150 females). Then the current operational sex ratio of 1.08 yields only 81% mating success, and 278 males would be needed to fertilize 95% of females. In other words, the current operational sex ratio would lead to a component Allee effect, again illustrating the density-dependence of mating success.

Quantitative predictions of mating success require relatively accurate parameter estimates, particularly of pair formation rate, the most sensitive model parameter. There is, however, uncertainty in my pair formation rate estimate due to the lack of pairing data from March. An early mating season start combined with large variability in the timing of female oestrus would lead to an underestimation of pair formation rate due to lower densities of available females at any given time. Without data on pairings from March, the timing of oestrus, or male and female encounter rates, this matter cannot be explored further. However, underestimated pair formation rates would result in underestimated female mating success, making all my predictions conservative.

It is also possible that I have overestimated pair formation rate by overestimating habitat area and thus underestimating densities, if bears aggregate due to habitat preferences (Stirling *et al.* 1993). However, such an overestimation would not affect mating success predictions in Lancaster Sound, because the same densities were used for parameter estimation and predictions. The matter would only become important if model parameters were used to predict mating success in other populations. Such predictions would require accurate estimates of both pair formation rate and male and female densities in these populations. Extrapolation of the results presented here to other populations should therefore be treated with caution.

In contrast to searching efficiency, female mating success is insensitive to male mating ability at low densities, where the long time necessary for mate location makes it irrelevant whether males continue mate-searching after breeding pair dissolutions. However, strong negative effects of low male mating abilities were found at higher densities combined with balanced to female-biased operational sex ratios, where males and females easily find each other, but the ability of males to mate with several females becomes crucial. Because sex-selective harvest can also reduce mean male age (Taylor *et al.* 2008a), and male mating ability is probably age-dependent, a component Allee effect could be initiated even at high densities with the estimated operational sex ratios maintained.

The simplifying assumptions of constant male and female densities, m_0 and f_0, throughout the mating season, as well as treating all but one male in multiple male breeding groups as solitary, are unlikely to affect my results. Variation in m_0 and f_0 may occur, for instance, if originally unavailable females lose their litters and come into oestrus, or if individuals are lost to harvest or natural mortality. However, such changes are probably small relative to total male and female numbers, and would not significantly affect the pairing dynamics. Similarly, only few females were associated with several males when sampled. Moreover, because my objective is the prediction of Allee effects due to male scarcity, it is unnecessary to model multiple male breeding groups explicitly: multiple male breeding groups probably become less frequent as male densities decrease.

In conclusion, I have modelled the mating system of polar bears to identify circumstances leading to a component Allee effect of reduced female mating success. The model is intentionally simple, predicting mating success from male and female densities using only four parameters, with predictions insensitive to two of them. It incorporates, however, key biological mechanisms of the mating system. The model should next be coupled with a population dynamics model like RISKMAN (Taylor *et al.* 2003; Aars *et al.* 2006) to explore whether and how a component Allee effect translates into a demographic Allee effect. Such a synthetic approach of simultaneously considering the mating dynamics along with population level consequences of resultant reproductive success would provide the necessary information to evaluate and possibly improve current harvesting strategies. The model should also be evaluated with data from other polar bear populations to assess and possibly improve the parameter estimates presented here. Owing to the sensitivity of model predictions to pair formation rate and male mating ability, particular emphasis should be given to determining these parameters. Despite the lack of data on mating success, pairing data as utilized here are routinely collected during mark-recapture studies and can be used for model parameterization or validation

Although I have focused on the prediction of Allee effects in polar bears, my model is general enough to be applicable to other species, and it can easily be modified to incorporate characteristics of other mating systems. Here the key quantity remains the estimation of pair formation rates, that is, of encounter rates between males and females discounted for mate choice. If pairing data of the form used here are not available or unfeasible to collect, encounter rates could alternatively be estimated through different means like intensive radiotelemetry programs (Kovacs & Powell 2003), or separately modelled using movement speeds (Hutchinson & Waser 2007).

Parameter	Definition	Estimate	Units	Method of estimation
Population size estimates				
---	No. of mature males	489	bears	Mark-recapture
---	No. of mature females not accompanied by cubs-of-the-year or yearlings	451	bears	Mark-recapture
---	Habitat area	238862	km^2	Total marine area within population boundaries
Model parameter estimates				
m_0	Density of males available for mating at mating season start	2.05	bears / 1000 km^2	# mature males / habitat area
f_0	Density of females available for mating at mating season start	1.89	bears / 1000km^2	# mature females not accompanied by cubs-of-the-year or yearlings / habitat area
m_0 / f_0	Operational sex ratio	1.08	---	---
σ	Pair formation rate	2.05 (1.27; 3.42)	km^2 h^{-1}	Maximum likelihood
μ^{-1}	Length of pair association	17.5 (14.1;21.6)	days	Maximum likelihood
α	Male mating ability	1	---	Fixed for parameter estimation and to estimate female mating success (assumption of maximal mating ability)
t_0	Mating season start	April 2	---	1 day before the first day of sampling
T	Mating season length	60	days	Fixed to estimate female mating success

Table 2.1: Population size and model parameter estimates for the Lancaster Sound polar bear population. Brackets below the maximum likelihood estimates for σ and μ^{-1} show bootstrapped 95% confidence intervals. For details regarding the methods of estimation, see main text.

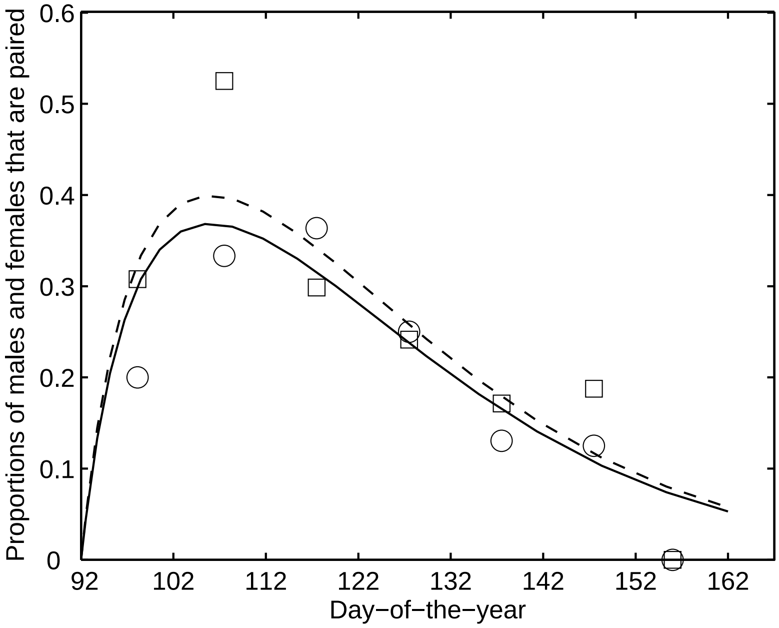

Figure 2.1: Observed and predicted proportions of mature males (observed: circles; predicted: solid line) and mature females not accompanied by cubs-of-the-year or yearlings (observed: squares; predicted: dashed line) paired on a given day during the mating season in Lancaster Sound. Data are pooled by day-of-the-year across the study period, and (for illustrative purposes only) over 10 day intervals, starting on the first sampling day. Initial conditions were 489 mature males and 451 mature females not accompanied by cubs-of-the-year or yearlings. Parameters were estimated using maximum likelihood (σ = 2.05 km^2 h^{-1}, μ^{-1} = 17.5 days), assuming maximal male mating ability (α = 1), and using t_0 = April 2 as the first day of the mating season.

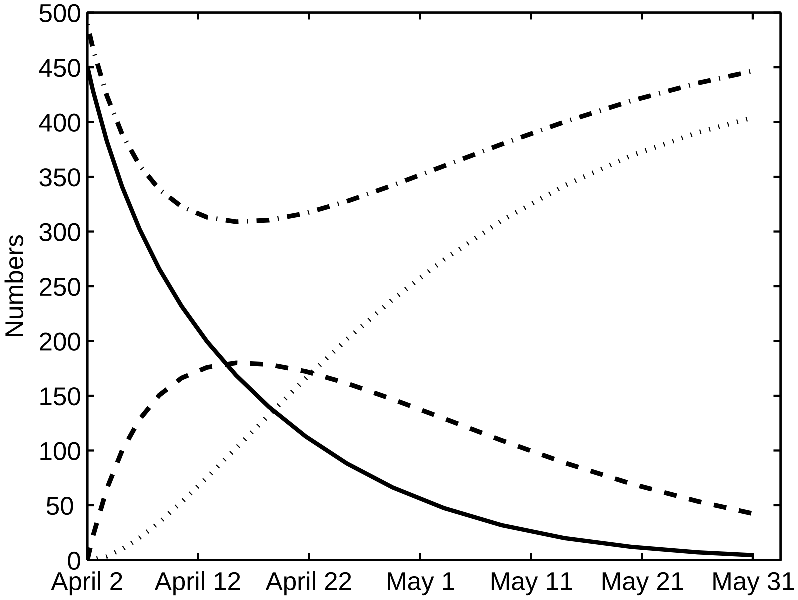

Figure 2.2: Simulated pairing dynamics during the mating season in Lancaster Sound, showing the predicted numbers of solitary males (dot-dashed line), breeding pairs (dashed line), solitary unfertilized (solid line) and solitary fertilized females (dotted line) as a function of time.

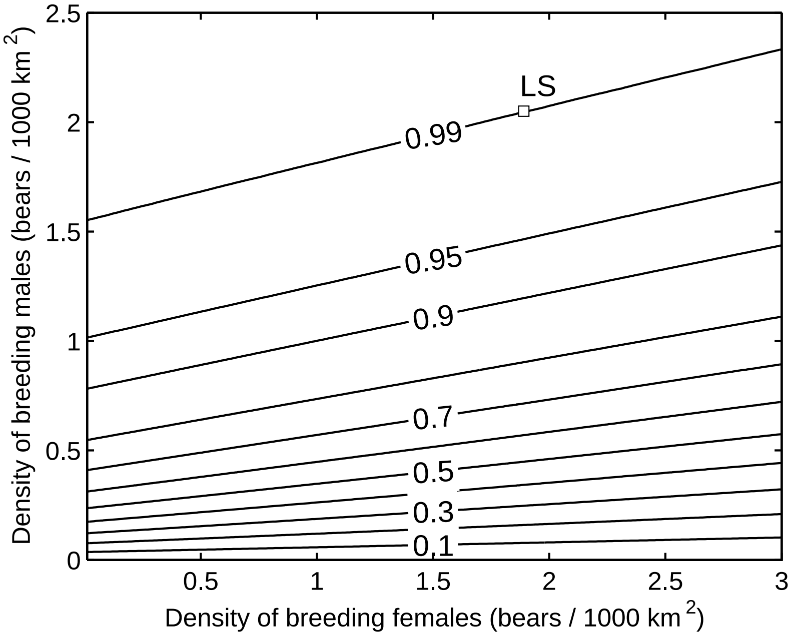

Figure 2.3: Contour lines giving female mating success as a function of male and female densities, using the maximum likelihood parameter estimates from Lancaster Sound (σ = 2.05 km^2 h^{-1}, μ^{-1} = 17.5 days), and assuming maximal male mating ability (α = 1) and T = 60 days as mating season length. The square indicates predicted mating success in Lancaster Sound (LS) according to the estimated male and female densities.

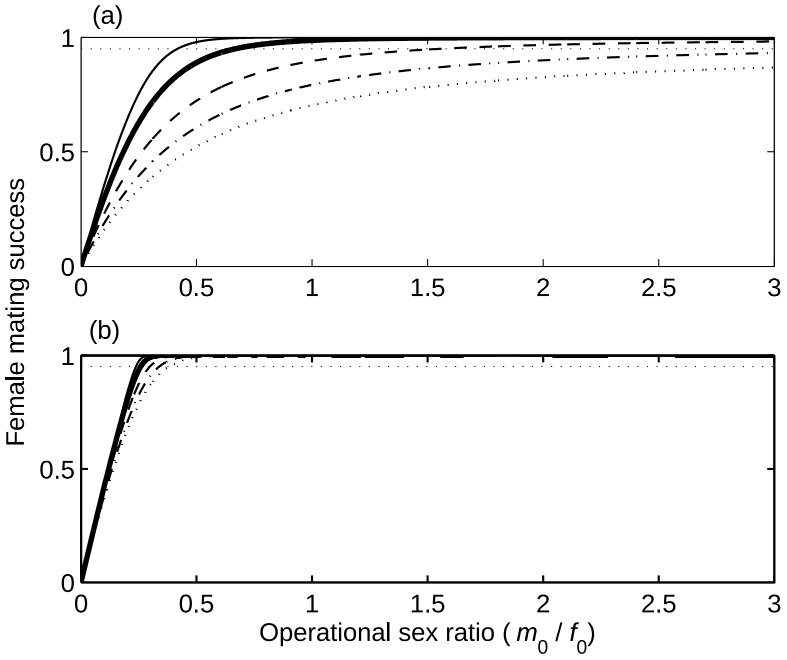

Figure 2.4: Female mating success as a function of operational sex ratio, m_0 / f_0, with overall density of breeding males and females, $m_0 + f_0$, held constant. Five representative densities are shown as follows: the estimated density in Lancaster Sound (solid thick line; 3.94 bears per 1000 km^2); as well as densities double that high (solid thin line; 7.88 bears per 1000 km^2); one-half as high (dashed line; 1.97 bears per 1000 km^2); one-third as high (dot-dashed line; 1.31 bears per 1000 km^2); and one-quarter as high (dotted line; 0.99 bears per 1000 km^2). The horizontal dotted line represents 95% mating success. (a) uses the maximum likelihood parameter estimates from Lancaster Sound (σ = 2.05 km^2 h^{-1}, μ^{-1} = 17.5 days); (b) uses σ = 20 km^2 h^{-1}, μ^{-1} = 17.5 days. Both (a) and (b) assume maximal male mating ability (α = 1) and T = 60 days as mating season length.

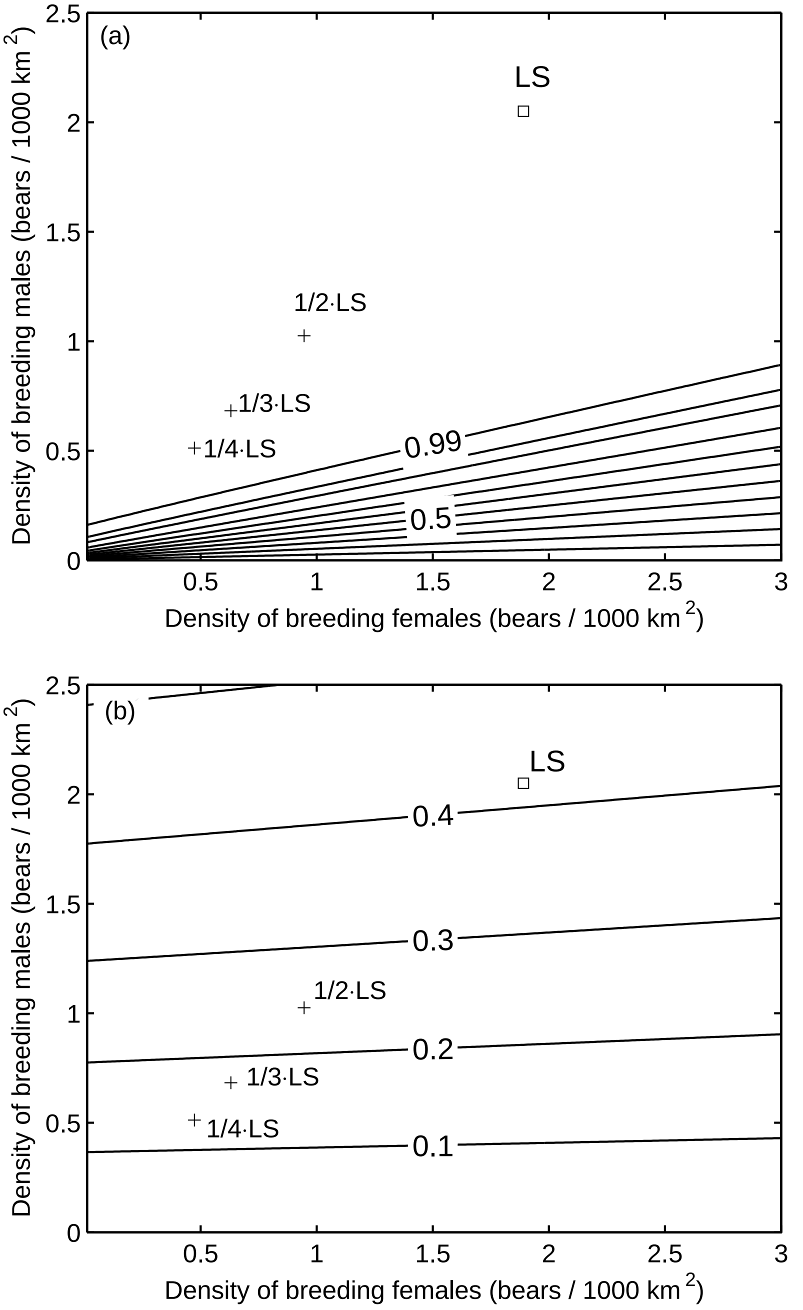

Figure 2.5: Contour lines giving female mating success as a function of male and female densities. The estimated male and female density of Lancaster Sound (LS) is indicated by a square. Three other hypothetical populations with operational sex ratio as in Lancaster Sound ($m_0/f_0 = 1.08$), but densities one-half, one-third, and one-quarter as high, are indicated by crosses. (a) uses $\sigma = 20$ km^2 h^{-1}, (b) uses $\sigma = 0.2$ km^2 h^{-1}. Both (a) and (b) use the maximum likelihood estimate from Lancaster Sound for pair dissolution rate ($\mu^{-1} = 17.5$ days), and assume maximal male mating ability ($\alpha = 1$) and $T = 60$ days as mating season length.

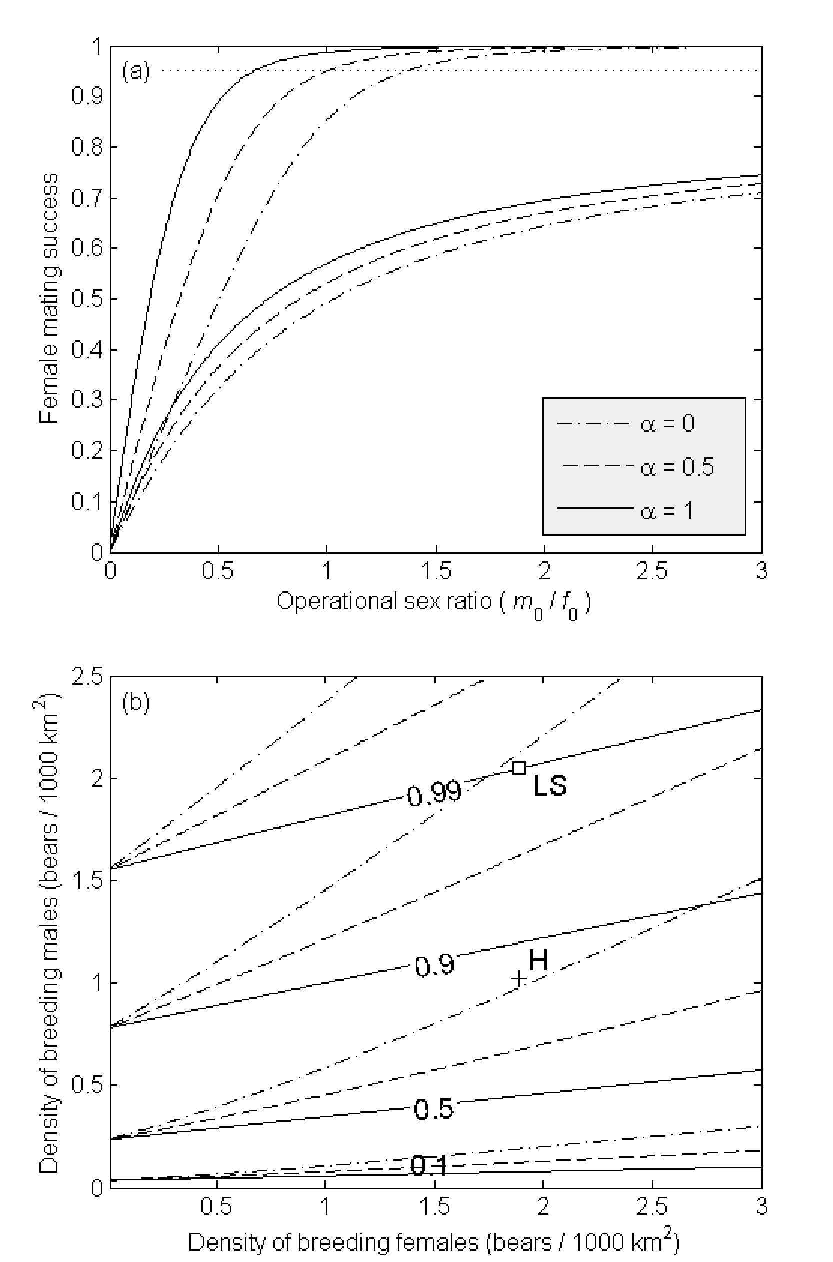

Figure 2.6: Sensitivity of female mating success to male mating ability, α. Parameters are: σ = 2.05 km^2 h^{-1}; μ^{-1} = 17.5 days; T = 60 days. α is varied: α = 1 (solid lines), α = 0.5 (dashed lines), α = 0 (dot-dashed lines). (a) Female mating success as a function of operational sex ratio, m_0 / f_0, with overall density of breeding males and females, $m_0 + f_0$, held constant. Two densities are shown for each parameter set: the estimated density in Lancaster Sound (3.94 bears per 1000 km^2; three lines at top left), and a density one-sixth as high (0.66 bears per 1000 km^2; three lines at bottom right). The horizontal dotted line represents 95% mating success. (b) Contour lines giving female mating success as a function of male and female densities. The estimated male and female density of Lancaster Sound (LS) is indicated by a square. A hypothetical population (H) with the estimated female density of Lancaster Sound, but half the male density is shown by a cross (see text for details).

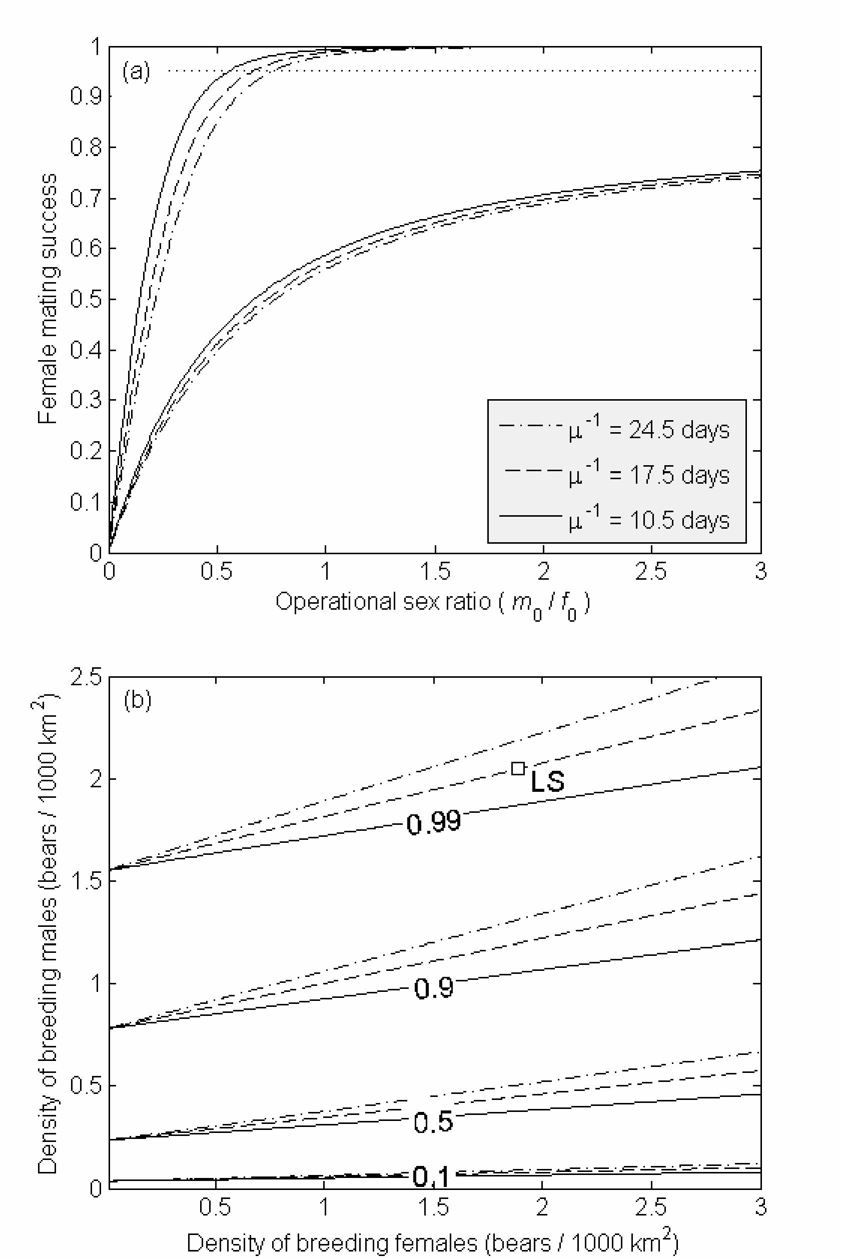

Figure 2.7: Sensitivity of female mating success to length of pair association, μ^{-1}. Parameters are: $\sigma = 2.05$ km^2 h^{-1}; $\alpha = 1$; $T = 60$ days. μ^{-1} is varied: $\mu^{-1} = 10.5$ days (solid lines), $\mu^{-1} = 17.5$ days (dashed lines), $\mu^{-1} = 24.5$ days (dot-dashed lines). (a) Female mating success as a function of operational sex ratio, m_0 / f_0, with overall density of breeding males and females, $m_0 + f_0$, held constant. Two densities are shown for each parameter set: the estimated density in Lancaster Sound (3.94 bears per 1000 km^2; three lines at top left), and a density one-sixth as high (0.66 bears per 1000 km^2; three lines at bottom right). The horizontal dotted line represents 95% mating success. (b) Contour lines giving female mating success as a function of male and female densities. The estimated male and female density of Lancaster Sound (LS) is indicated by a square.

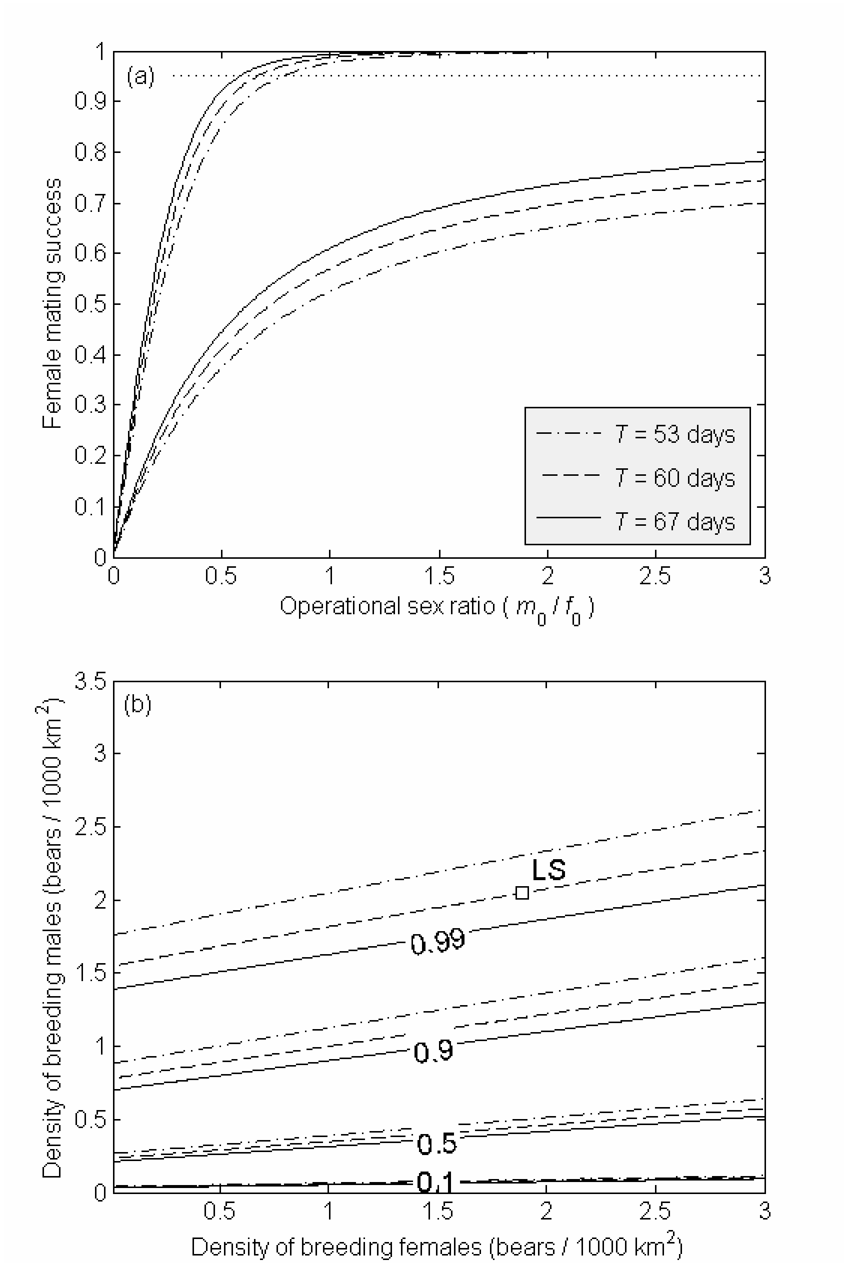

Figure 2.8: Sensitivity of female mating success to mating season length, *T*. Parameters are: $\sigma = 2.05$ km^2 h^{-1}; $\mu^{-1} = 17.5$ days; $\alpha = 1$. *T* is varied: *T*=67 days (solid lines), *T*=60 days (dashed lines), *T*=53 days (dot-dashed lines). (a) Female mating success as a function of operational sex ratio, m_0 / f_0, with overall density of breeding males and females, $m_0 + f_0$, held constant. Two densities are shown for each parameter set: the estimated density in Lancaster Sound (3.94 bears per 1000 km^2; three lines at top left), and a density one-sixth as high (0.66 bears per 1000 km^2; three lines at bottom right). The horizontal dotted line represents 95% mating success. (b) Contour lines giving female mating success as a function of male and female densities. The estimated male and female density of Lancaster Sound (LS) is indicated by a square.

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Chapter 3*

3 Estimating Energy Stores and Metabolic Rates of Polar Bears from Body Mass and Body Length

3.1 Introduction

Individuals of many species experience fluctuations in body condition as a result of fluctuations in energy intake and expenditure (e.g., Kingsley *et al.* 1983; Watts & Hansen 1987; Robin *et al.* 1988; Ryg *et al.* 1990; Boswell *et al.* 1994; Fietz & Ganzhorn 1999). When energy intake exceeds expenditure, individuals allocate the surplus to storage, which can then be used during periods of food scarcity to fuel physical processes such as maintenance, growth, or reproduction. Many factors influence energy intake and expenditure, including behaviour, physiology, and resource availability (Kooijman 2000). Resource availability often varies in space and time, and may also be affected by environmental changes such as habitat destruction, habitat restoration, or climate change. Changes in food intake resulting from such fluctuations and trends will first affect the physical condition of individuals, which may then lead to changes in survival and/or reproductive success and ultimately affect population dynamics. Monitoring the body condition of individuals is therefore critical to early detection of population trends, especially for species experiencing a fluctuating or changing food supply.

Polar bears (*Ursus maritimus*) are well-known for large seasonal fluctuations in food supply and body condition, their dependence on stored energy for reproduction and survival, and their vulnerability to climatic warming (Ramsay & Stirling 1988; Stirling & Øritsland 1995; Derocher & Stirling 1996; Derocher *et al.* 2004; Wiig *et al.* 2008).

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* A version of this chapter has been submitted for publication to *Journal of Experimental Biology* as: Molnár, P. K., Klanjscek, T., Derocher, A. E., Obbard, M. E. & Lewis, M. A. Estimating energy stores and metabolic rates of polar bears from body mass and body length.

Pregnant females, for example, can fast up to 8 months during gestation and early lactation (Atkinson & Ramsay 1995). During this time all energy for survival, gestation, and lactation must be drawn from fat and nutrient stores, and insufficient energy stores can negatively affect reproductive success (Atkinson & Ramsay 1995; Derocher *et al.* 2004). Furthermore, in the southern portions of the species' geographical range, bears are forced ashore in summer when the sea ice melts. Little or no food is available on land and all bears rely on stored energy for survival during a 4-5 month fasting season (Ramsay & Hobson 1991; Derocher *et al.* 1993). Body condition thus becomes a key variable in polar bear population dynamics.

Several indices exist to quantify polar bear body condition, including a subjective fatness index used in the field to classify bears on a scale from 1 to 5 (Stirling *et al.* 2008), an index based on standardized residuals from regressing body mass against straight line body length (Cattet *et al.* 2002; Cattet & Obbard 2005), and the Quetelet index defined as body mass divided by squared body length (Stirling *et al.* 1999). Although some of these indices correlate with more direct measurements of body condition, such as the percent lipid content of adipose tissue (Stirling *et al.* 2008), or the combined mass of fat and skeletal muscle (Cattet *et al.* 2002), they cannot provide the amount of stored energy. Such knowledge is, however, necessary to quantify the reproductive potential of a female or to determine whether a bear has sufficient energy stores to survive the fasting season.

Two methods are available to quantify the body composition of living bears: isotopic water dilution and bioelectrical impedance analysis (Cattet *et al.* 2002). Water dilution is expensive, requires prolonged immobilization of animals, and is impractical for large-scale field studies. Impedance analysis is less time-consuming but has many error sources and requires extensive training to obtain accurate measurements (Farley & Robbins 1994; Hilderbrand *et al.* 1998).

In this chapter, I develop a simple, non-invasive method to quantify the nutritional status of live-caught polar bears. My method relies on the concept that all tissue may be characterized as either structure or storage (Kooijman 2000). Storage encompasses all materials that can be used as an energy source for growth, maintenance and reproduction (e.g., non-structural lipids and proteins), plus body water and ash associated with these materials. Structure consists of any remaining tissue, body water and ash, and cannot be utilized for energy even under extreme starvation (e.g., bones, brain, lungs, etc.). Some tissue, such as muscle, belongs partially to structure and partially to storage: muscle mass is accumulated when feeding and catabolized when fasting (Arnould & Ramsay 1994; Atkinson & Ramsay 1995; Atkinson *et al.* 1996a; Cattet *et al.* 2002), but some muscle is retained even when an animal is starving.

Within this framework, I develop and parameterize a body composition model that can be used to estimate structural mass, storage mass, storage composition and storage energy content of individual polar bears. Structural mass is hereby estimated from straight line body length, a morphometric measurement easily obtained in the field and readily available for all handled polar bears. Storage mass and storage energy are estimated from straight line body length and total body mass. I also apply the body composition model to estimate the metabolic rates of fasting adult polar bears from consecutive measurements of straight line body length and total body mass only.

The model is presented and parameterized specifically for polar bears, but could be easily modified to other mammals.

3.2 Model Development

To describe body composition, I differentiated between structure and storage and assumed constant chemical composition of both compartments, i.e., strong homeostasis (Kooijman 2000, pp. 30). I further assumed isomorphic growth, i.e., the conservation of structural shape through the lifetime of an individual (Kooijman, 2000). The definitions of structure and storage together with strong homeostasis imply that structural mass only changes with growth and remains constant otherwise, whereas storage mass fluctuates with food intake and energy expenditure.

I first show how structural mass relates to straight line body length, defined as the dorsal straight-line distance from the tip of the nose to the end of the last tail vertebra when the bear is lying in a sternally recumbent position. Storage mass is then given by the difference between total body mass and structural mass, and storage energy can be estimated from storage mass by accounting for storage composition. Straight line body length was chosen as a predictor variable for structural mass because this measure of length is minimally affected by nutritional status and, furthermore, strongly correlates with skeletal mass, which is a major part of structure (Cattet *et al.* 2002). State variables used in the model are summarized in Table 3.1.

Total body mass of a polar bear, M, is the sum of its structural mass, M_{STR}, and its storage mass, M_{STO} (units: kg):

$$(3.1) \qquad M = M_{\mathrm{STR}} + M_{\mathrm{STO}} \ .$$

Structural mass is the product of structural volume, V_{STR} (units: m^3), and structural density, ρ_{STR} (units: kg m^{-3}). Due to the assumption of isomorphic growth, V_{STR} is proportional to cubed straight line body length (Kooijman 2000). The relationship between structural mass and straight line body length is therefore

$$(3.2) \qquad M_{\mathrm{STR}} = \rho_{\mathrm{STR}} \, V_{\mathrm{STR}} = \rho_{\mathrm{STR}} \, k \, L^3 \ ,$$

where k is a dimensionless parameter, accounting for the irregular shape of the animal.

To relate storage mass to storage energy, I needed to account for storage composition. Ignoring glycogen, a short-term energy source (Schmidt-Nielsen 1997), I assumed that storage consists of fat, protein, ash, and water (Farley & Robbins 1994; Hilderbrand *et al.* 1998). Storage mass then equals the sum of the masses of each storage constituent:

$$(3.3) \qquad M_{\mathrm{STO}} = M_{\mathrm{STO\text{-}F}} + M_{\mathrm{STO\text{-}P}} + M_{\mathrm{STO\text{-}A}} + M_{\mathrm{STO\text{-}W}} \ .$$

Consistently with the strong homeostasis assumption, all four storage components are accumulated when feeding and depleted when fasting, even though only fat and protein are energy sources (Arnould & Ramsay 1994; Atkinson & Ramsay 1995; Atkinson *et al.* 1996a).

Summarizing protein, ash and water in storage as non-structural lean (i.e., fat-free) tissue, I write

$$(3.4)\qquad M_{\text{STO}} = M_{\text{STO-F}} + M_{\text{STO-L}} \ ,$$

where $M_{\text{STO-L}}$ represents the mass of non-structural lean tissue, which by definition equals the sum of $M_{\text{STO-P}}$, $M_{\text{STO-A}}$ and $M_{\text{STO-W}}$. The relationships between $M_{\text{STO-L}}$ and $M_{\text{STO-P}}$, $M_{\text{STO-A}}$, and $M_{\text{STO-W}}$ are

$$(3.5a)\qquad M_{\text{STO-P}} = M_{\text{STO-L}} \cdot (1-\eta_{\text{W}}) \cdot \eta_{\text{P}}$$

$$(3.5b)\qquad M_{\text{STO-A}} = M_{\text{STO-L}} \cdot (1-\eta_{\text{W}}) \cdot (1-\eta_{\text{P}})$$

$$(3.5c)\qquad M_{\text{STO-W}} = M_{\text{STO-L}} \cdot \eta_{\text{W}} \quad ,$$

where η_{W} represents the proportion of lean body mass that is water, and η_{P} the proportion of dry lean body mass that is protein.

Because I aim to convert storage mass into energetic content, and only protein provides an energy source from non-structural lean tissue, I use equation (3.5a) to rewrite equation (3.4) as

$$(3.6)\qquad M_{\text{STO}} = M_{\text{STO-F}} + \frac{M_{\text{STO-P}}}{(1-\eta_{\text{W}})\eta_{\text{P}}} \ .$$

Substituting the energy densities of fat, ε_{F}, and protein, ε_{P} (units: MJ kg^{-1}), I rewrite equation (3.6) as

$$(3.7)\qquad M_{\text{STO}} = \frac{E_{\text{F}}}{\varepsilon_{\text{F}}} + \frac{E_{\text{P}}}{(1-\eta_{\text{W}})\eta_{\text{P}}\,\varepsilon_{\text{P}}} \ ,$$

where E_{F} and E_{P} are the respective amounts of energy (units: MJ) in the fat and protein stores of an animal.

The total energy content of storage, E, equals the sum of energy in the fat and protein stores (i.e., $E = E_{\mathrm{F}} + E_{\mathrm{P}}$). I define γ as the proportion of total storage energy that is stored in body fat and write:

$$(3.8a) \qquad E_{\mathrm{F}} = \gamma\, E$$

$$(3.8b) \qquad E_{\mathrm{P}} = (1-\gamma)E \ .$$

Combining equations (3.7) and (3.8), I obtain the relationship between storage mass and storage energy:

$$(3.9) \qquad M_{\mathrm{STO}} = E\left(\frac{\gamma}{\varepsilon_{\mathrm{F}}} + \frac{1-\gamma}{(1-\eta_{\mathrm{W}})\eta_{\mathrm{P}}\,\varepsilon_{\mathrm{P}}}\right) .$$

Inserting equations (3.2) and (3.9) into equation (3.1) yields the relationship between total body mass, straight line body length, and storage energy:

$$(3.10) \qquad M = \rho_{\mathrm{STR}}\, k\, L^3 + E\left(\frac{\gamma}{\varepsilon_{\mathrm{F}}} + \frac{1-\gamma}{(1-\eta_{\mathrm{W}})\eta_{\mathrm{P}}\,\varepsilon_{\mathrm{P}}}\right) .$$

Solving equation (3.10) for E gives storage energy as a function of total body mass and straight line body length:

$$(3.11) \qquad E = \alpha \cdot \left(M - \rho_{\mathrm{STR}}\, k\, L^3\right) \ ,$$

where, for brevity, I write

$$(3.12) \qquad \alpha = \left(\frac{\gamma}{\varepsilon_{\mathrm{F}}} + \frac{1-\gamma}{(1-\eta_{\mathrm{W}})\eta_{\mathrm{P}}\,\varepsilon_{\mathrm{P}}}\right)^{-1} .$$

Moreover, storage composition can also be specified, and the masses of all storage components can be estimated. Combining equations (3.5), (3.8) and (3.9) gives the proportions of storage mass that are fat, protein, ash, and water (see Appendix A for derivation):

$$\text{(3.13a)} \qquad \frac{M_{\text{STO-F}}}{M_{\text{STO}}} = \alpha \frac{\gamma}{\varepsilon_{\text{F}}}$$

$$\text{(3.13b)} \qquad \frac{M_{\text{STO-P}}}{M_{\text{STO}}} = \alpha \frac{1-\gamma}{\varepsilon_{\text{P}}}$$

$$\text{(3.13c)} \qquad \frac{M_{\text{STO-A}}}{M_{\text{STO}}} = \alpha \frac{(1-\eta_{\text{P}})(1-\gamma)}{\eta_{\text{P}}\, \varepsilon_{\text{P}}}$$

$$\text{(3.13d)} \qquad \frac{M_{\text{STO-W}}}{M_{\text{STO}}} = \alpha \frac{\eta_{\text{W}}(1-\gamma)}{(1-\eta_{\text{W}})\, \eta_{\text{P}}\, \varepsilon_{\text{P}}} \quad .$$

3.3 Model Parameterization

The model contains seven parameters (Table 3.2), two of which (ρ_{STR} and k) relate straight line body length to structural mass. The remaining five convert storage mass into energetic content. I used data from starved polar bears as well as literature data on bear body composition for model parameterization. These data will be introduced more specifically when used. All bears were handled under approval of research permits that followed guidelines of the Canadian Council on Animal Care. Data on two starving bears were collected by government agencies as part of animal control actions for public safety. Statistical analyses were performed in SYSTAT 10 (Systat Software, Inc., Chicago, Illinois, USA). Results were considered significant at $P \leq 0.05$. Means are presented ± 1 SE.

I did not have to estimate the parameters ρ_{STR} and k separately, because only their product, $\rho_{\text{STR}} \cdot k$, determines the relationship between straight line body length and structural mass (cf. equation (3.2)). To estimate $\rho_{\text{STR}} \cdot k$, I used body mass and length of two starving adult polar bears: a female (total body mass: 89.8 kg; straight line body length: 1.81 m; age ≤ 10 years; origin: Deline, Northwest Territories, Canada), and a male (total body mass: 163.3 kg; straight line body length: 2.23 m; age: 7 years; origin: Barrow, Alaska, United States). Both bears were in extremely poor condition, with empty stomachs, empty intestinal tracts, and no subcutaneous body fat. They were described as lethargic and the male was hardly able to stand. I assumed that these bears had no (or only negligible amounts of) storage energy left and set $E = 0$. Body mass then equals structural mass and equation (3.10) can be written as

$$\rho_{\mathrm{STR}}\, k = \frac{M}{L^3} \quad . \tag{3.14}$$

Inserting straight line body lengths and total body masses into equation (3.14) yielded $\rho_{\mathrm{STR}} \cdot k = 15.14$ kg m^{-3} for the female, and $\rho_{\mathrm{STR}} \cdot k = 14.73$ kg m^{-3} for the male. In all further calculations, I used the mean estimate $\rho_{\mathrm{STR}} \cdot k = 14.94$ kg m^{-3} (the low sample size used to estimate $\rho_{\mathrm{STR}} \cdot k$ does not present a major concern, and this will be addressed in sections 3.6 and 3.8).

The body composition parameters η_{W} and η_{P} have been estimated for black bears and brown bears as $\eta_{\mathrm{W}} = 0.734$ and $\eta_{\mathrm{P}} = 0.835$, and were remarkably constant among individuals (Farley & Robbins 1994). No estimates exist for polar bears, so I adopted these estimates for model parameterization in accordance with previous polar bear body composition studies (Atkinson & Ramsay 1995; Atkinson *et al.* 1996a). The energy densities of fat and protein were set as $\varepsilon_{\mathrm{F}} = 39.3$ MJ kg^{-1} and $\varepsilon_{\mathrm{P}} = 18.0$ MJ kg^{-1} (Schmidt-Nielsen 1997).

To estimate the remaining parameter, γ, I rearranged equation (3.10) as

$$\gamma = \frac{M_{\text{STO-F}}\, \varepsilon_{\mathrm{F}}}{\left(M - \rho_{\mathrm{STR}}\, k\, L^3 - M_{\text{STO-F}}\right)\left(\left(1-\eta_{\mathrm{W}}\right)\eta_{\mathrm{P}}\, \varepsilon_{\mathrm{P}}\right) + M_{\text{STO-F}}\, \varepsilon_{\mathrm{F}}} \quad . \tag{3.15}$$

I parameterized equation (3.15) using data from Tables 1 and 2 in Arnould & Ramsay (1994) and Table 1 in Atkinson *et al.* (1996), who measured straight line body length, total body mass and total fat mass of adult females (n = 9), cubs-of-the-year (n = 7), yearlings ($n = 7$), subadult males ($n = 5$) and adult males ($n = 5$). Both studies determined body masses (± 0.5 kg) by weighing immobilized bears with an electronic load cell and estimated total body fat using isotopic water dilution. Each bear was sampled twice, between 17 and 88 days apart. One cub-of-the-year and one adult male were in exceptionally poor condition, with body fat constituting only 1.4% and 1.7% of their respective body mass. I excluded both bears from analyses because patterns of fat and protein utilization likely change under extreme starvation, with potentially large effects on storage composition and, consequently, γ. Straight line body lengths and adult female body fat were unreported in the respective tables so I obtained these data directly from the authors (Arnould 1990).

In polar bears, only a small fraction of body fat is structural [i.e., only in cell membranes, the brain, and small depots in the eye sockets and foot pads (Pond *et al.* 1992)]. I therefore simplified body composition in all further calculations by assuming that all body fat belongs to storage. Fat measurements in Arnould & Ramsay (1994) and Atkinson *et al.* (1996a) thus provided estimates of storage fat masses ($M_{\mathrm{STO\text{-}F}}$). Inserting these estimates, total body masses and straight line body lengths into equation (3.15) gave two estimates of γ for each bear, which I averaged to obtain a single estimate for each individual.

Sex- and age-class had a significant effect on storage composition (Kruskal-Wallis, $H = 14.61$, $P = 0.006$), with mean γ highest in adult females ($\gamma = 0.943 \pm 0.014$), followed by yearlings ($\gamma = 0.941 \pm 0.006$), subadult males ($\gamma = 0.935 \pm 0.004$), cubs-of-the-year ($\gamma = 0.899 \pm 0.011$), and adult males ($\gamma = 0.885 \pm 0.007$; Figure 3.1). Differences in storage composition may reflect sex- and age-related differences in morphology (Derocher *et al.* 2005; Thiemann *et al.* 2006; Stirling *et al.* 2008) and energy utilization (Atkinson *et al.* 1996a,b), and significantly affect storage energy predictions (cf. sensitivity analysis in section 3.6). I therefore parameterized the body composition model separately for all five sex- and age-classes, using the respective mean estimates of γ.

A statistical comparison between observed fat masses (Arnould & Ramsay 1994; Atkinson *et al.* 1996a) and model predictions for storage fat masses (equation (3.13a)) supported the use of sex- and age-class specific estimates of γ: regressing observations against predictions and simultaneously testing for unit slope and zero intercept (Mayer *et* *al.* 1994) yielded a significant difference between observed and predicted fat masses when using the across sex- and age-class average of γ, $\bar{\gamma} = 0.925$ ($F_{2,60} = 11.81$, $P < 0.001$). No such difference was found when using sex- and age-class specific means ($F_{2,60} = 0.65$, $P = 0.524$).

3.4 Results: Body Composition Model

The parameterized body composition model provides the following predictive equations for structural mass, storage mass, and storage energy of a polar bear from its straight line body length and total body mass:

Structural mass can be estimated from straight line body length (cf. equation (3.2)):

$$(3.16) \qquad M_{\text{STR}} = 14.94 L^3 \ .$$

Storage mass is the difference between total body mass and structural mass (cf. equation (3.1)), and can be estimated from

$$(3.17) \qquad M_{\text{STO}} = M - 14.94 L^3 \ .$$

Storage composition was estimated from equations (3.13) and differed between sex- and age-classes (Table 3.3). Relative fat content of storage was highest in adult females, followed by yearlings, subadult males, cubs-of-the-year, and adult males. The pattern was reversed for protein, ash, and water.

Storage energy can be estimated from total body mass and straight line body length (cf. equation (3.11)). Predictive equations for storage energy are presented separately for cubs-of-the-year (C), yearlings (Y), adult females (AF), subadult males (SM) and adult males (AM), thereby accounting for differences in storage composition:

(3.18a) $E_{\mathrm{C}} = 20.77M - 310.30L^3$

(3.18b) $E_{\mathrm{Y}} = 25.84M - 386.05L^3$

(3.18c) $E_{\mathrm{AF}} = 26.14M - 390.53L^3$

(3.18d) $E_{\mathrm{SM}} = 24.97M - 373.05L^3$

(3.18e) $E_{\mathrm{AM}} = 19.50\,M - 291.33L^3$.

Although equations (3.18a-e) are structurally the same, their coefficients differ due to sex- and age-class specific differences in storage composition (Table 3.3). For example, comparing an adult female to an adult male of equal body mass and length, I predict about 1.34 times more storage energy for the female (equations (3.18c) and (3.18e)) due to the higher relative fat content of storage. In contrast, the relationship between storage energy, total body mass and straight line body length differs little between yearlings, adult females, and subadult males (equations (3.18b-d)), or between cubs-of-the-year and adult males (equations (3.18a) and (3.18e)), reflecting similarities in storage composition (Table 3.3).

Figure 3.2 shows model predictions of storage energy from straight line body length and total body mass. The zero-isoclines ($E = 0$) represent starved bears, where energy stores are exhausted and all tissue belongs to structure (i.e., $M = 14.94L^3$). I limit illustrations to the usual range of straight line body lengths for each sex- and age-class, and to bears with total body mass at most four times structural mass (i.e., $M \leq 59.76L^3$), an approximate upper bound to total body mass. At this limit, body fat constitutes 47.0% and 32.9% of total body mass for adult females and adult males respectively (from equations (3.1) and (3.13a)), which is close to the maximal relative body fat contents observed (females: 49%, Atkinson & Ramsay 1995; males: 32%, Atkinson *et al.* 1996a). However, all limits were chosen for illustrative purposes only and equations (3.18) could be used beyond the depicted ranges.

3.5 Model Application: Estimating Metabolic Rates

In this section, I show how the body composition model can be used to estimate the metabolic rate of a fasting, resting, non-growing and non-reproducing polar bear in a thermoneutral state, using straight line body length and consecutive measurements of total body mass only. Such bears expend storage energy only for somatic maintenance, and storage energy decreases with a rate of change proportional to the mass of tissue that requires maintenance (Kooijman 2000). Maintenance requirements for body fat are negligible relative to those of lean tissue (Aarseth *et al.* 1999; Boyd 2002), so that the rate of change in storage energy is given by the following differential equation:

$$(3.19) \qquad \frac{dE}{dt} = -m \cdot \left(M - M_{\text{STO-F}}\right) ,$$

where metabolic rate, *m*, is the energy required per unit time to maintain a unit mass of lean tissue.

Using equations (3.1), (3.2), (3.11) and (3.13a) to convert storage energy (*E*) and storage fat mass ($M_{\text{STO-F}}$) into functions of total body mass (*M*) and straight line body length (*L*), and solving the resulting differential equation, gives total body mass as a function of time *t* (see Appendix B for details):

$$(3.20) \qquad M(t) = C \exp\left(-\frac{m(1-\varphi)}{\alpha} t \right) - \frac{\varphi}{1-\varphi} \rho_{\text{STR}}\, k\, L^3 ,$$

where $\varphi = (\alpha\gamma) / \varepsilon_{\text{F}}$ represents the proportion of storage mass that is fat (cf. equation (3.13a)).

Given two measurements of body mass T time units apart, $M(0) = M_0$ and $M(T) = M_1$, equation (3.20) can be solved to obtain the integration constant

$$C = M_0 + \frac{\varphi}{1-\varphi}\rho_{\mathrm{STR}}\, k\, L^3 \tag{3.21}$$

and an estimate for metabolic rate

$$m = -\frac{\alpha}{(1-\varphi)T} \cdot \ln\left(\frac{(1-\varphi)M_1 + \varphi\, \rho_{\mathrm{STR}}\, k\, L^3}{(1-\varphi)M_0 + \varphi\, \rho_{\mathrm{STR}}\, k\, L^3} \right) . \tag{3.22}$$

If more than two measurements of body mass are available, a non-linear regression of body mass against time, using equation (3.20), will yield estimates of both C and m.

3.6 Sensitivity Analyses

Small sample sizes for model parameterization may have resulted in low accuracy in determining the parameters $\rho_{\mathrm{STR}} \cdot k$ and γ. To understand how deviations in these parameters affect storage energy predictions, I varied them one at a time, while holding the other constant at either $\overline{\rho_{\mathrm{STR}} k}$ = 14.94 kg m^{-3} or at $\overline{\gamma}$ = 0.925 (the across sex- and age-class average of γ). I then calculated $\left(E - \overline{E}\right)/\,\overline{E}$, the resultant proportional change in storage energy E relative to $\overline{E}$, the storage energy of an individual of equal body mass and length, whose structural mass and storage composition are specified by $\overline{\rho_{\mathrm{STR}} k}$ = 14.94 kg m^{-3} and $\overline{\gamma}$ = 0.925, respectively.

The proportional change in storage energy $\left(E - \overline{E}\right)/\,\overline{E}$ between two individuals of equal body length, body mass and structural mass (specified by $\overline{\rho_{\mathrm{STR}} k}$), but differing storage composition (specified by γ and $\overline{\gamma}$, respectively) is given by

$$(3.23)\qquad \frac{E-\overline{E}}{\overline{E}}=\left(\frac{\gamma}{\varepsilon_{\mathrm{F}}}+\frac{1-\gamma}{(1-\eta_{\mathrm{W}})\eta_{\mathrm{P}}\,\varepsilon_{\mathrm{P}}}\right)^{-1}\left(\frac{\overline{\gamma}}{\varepsilon_{\mathrm{F}}}+\frac{1-\overline{\gamma}}{(1-\eta_{\mathrm{W}})\eta_{\mathrm{P}}\,\varepsilon_{\mathrm{P}}}\right)-1\ ,$$

whereas for equal storage composition (specified by $\overline{\gamma}$), but differing structural mass (specified by $\rho_{\mathrm{STR}}\cdot k$ and $\overline{\rho_{\mathrm{STR}}k}$, respectively), I obtain

$$(3.24)\qquad \frac{E-\overline{E}}{\overline{E}}=-p\cdot\left(\frac{M}{\overline{\rho_{\mathrm{STR}}\,k}\,L^{3}}-1\right)^{-1}\ ,$$

where $p=\left(\rho_{\mathrm{STR}}k-\overline{\rho_{\mathrm{STR}}\,k}\right)/\,\overline{\rho_{\mathrm{STR}}\,k}$ represents the proportional increase or decrease in $\rho_{\mathrm{STR}}\cdot k$ relative to $\overline{\rho_{\mathrm{STR}}k}$.

Storage energy E is sensitive to storage composition and increases monotonically with γ (Figure 3.3a). For instance, an average adult male (γ = 0.885) has 17.5% less storage energy than an individual of equal body mass, length and structure, but with $\gamma=\overline{\gamma}$. An average adult female (γ = 0.943) of equal mass, length and structure has 10.6% more storage energy than the reference individual with $\gamma=\overline{\gamma}$ (Figure 3.3a). The sensitivity of storage energy to γ, and thus storage composition, reflects the differing energy densities of body fat and lean tissue, emphasizing the importance of body fat for energy storage and the need to specify γ as accurately as possible.

Model predictions of storage energy are generally less sensitive to $\rho_{\mathrm{STR}}\cdot k$ (Figure 3.3b). However, unlike in γ, sensitivity is dependent on the ratio between total body mass (M) and structural mass as specified by $\overline{\rho_{\mathrm{STR}}k}$ and L (cf. equation (3.24)). Sensitivity of storage energy to $\rho_{\mathrm{STR}}\cdot k$ is low for obese bears, increases with decreasing storage mass and is greatest for starving bears. For instance, a 15% increase in $\rho_{\mathrm{STR}}\cdot k$ results in a 15% decrease of storage energy for a bear whose total body mass is twice its structural mass, but only a 5% decrease in bears with total body mass four times their structural mass.

It is unlikely that I underestimated $\rho_{\mathrm{STR}}\cdot k$ by more than 15%. Lean bears with non-zero storage energy ($E \neq 0$) have been observed whose body mass to cubed straight line body length ratio, M / L^3, equals approximately 1.15 times the current estimate of $\rho_{\mathrm{STR}} \cdot k$ (A. E. Derocher, unpublished data; cf. also the leanest adult male in Atkinson *et al.* (1996a), where $M / L^3 = 17.16$ kg m^{-3}). These bears likely provide an approximate upper bound for $\rho_{\mathrm{STR}} \cdot k$ (cf. equation (3.14)), so I limited sensitivity analyses to perturbations of $\rho_{\mathrm{STR}} \cdot k$ not exceeding 15%.

3.7 Model Validation

Full model validation is not possible because insufficient independent body composition data exist to test model predictions. However, some tests of model consistency for derived variables are possible using straight line body lengths and total body masses only. For this purpose, I obtained straight line body lengths and total body masses of 970 polar bears from western Hudson Bay (all sex- and age-classes; *n*=505) and southern Hudson Bay (cubs-of-the-year, yearlings, subadult and adult females; *n*=465). The geographical location of these populations is shown in Figure 1.1. For detailed population descriptions see Stirling *et al.* (1999) and Obbard *et al.* (2006). Data were collected in 1989-96 in western Hudson Bay and in 1984-86 and 2000-05 in southern Hudson Bay. Total body masses were determined by spring scale for cubs-of-the-year in spring (± 0.25 kg) and with a spring-loaded scale or electronic load cell otherwise (± 0.5 kg). Females ≥4 and males ≥7 years old were considered adults because polar bears in western Hudson Bay complete structural growth at about 4 (females) and 6.5 (males) years of age, respectively (Derocher & Stirling 1998). 2-3 year old females and 2-6 year old males were considered subadults. The data were made available from the Canadian National Polar Bear Database maintained by Environment Canada, and all capture and handling procedures were approved annually by the Animal Care Committees of the Canadian Wildlife Service and Ontario Ministry of Natural Resources.

I performed the following tests for model consistency. First, no bear should be lighter than its predicted structural mass. Second, estimated body compositions were compared against published body composition data. Third, estimates for storage mass and energy density were examined relative to qualitative expectations from polar bear physiology and life history. Fourth, metabolic rates were estimated for fasting adult males and compared to expected metabolic rates.

3.7.1 Structural Mass and Body Composition

One implication of differentiating between structure and storage is that no bear should be lighter than its structural mass. My model fulfilled this requirement for all bears regardless of sex, age, or population (Figure 3.4). Furthermore, all bears were lighter than four times their structural mass, which I have considered an approximate upper bound to total body mass. Total body mass of subadult and adult females ranged from 114% to 366% of their structural mass, with a similar range for cubs-of-the-year (117-339%), yearlings (120-317%), and subadult and adult males (115-321%). These ranges correspond to bears with body fat constituting 7.7-45.6% of their total body mass (adult females), 6.9-33.4% (cubs-of-the-year), 10.3-42.4% (yearlings) and 5.7-30.2% (adult males), respectively (from equations (3.1) and (3.13a)). Upper estimates of relative body fat content correspond closely to previously observed maximal values for both adult females (49%, Atkinson & Ramsay 1995) and adult males (32%, Atkinson *et al.* 1996a).

3.7.2 Storage Mass and Energy Density

Average storage mass was smallest in cubs-of-the-year and increased proportionally with structural mass (Figures 3.5a,b), probably reflecting size-dependent energy acquisition and utilization (Stirling & Øritsland 1995; Kooijman 2000). Males cease growth later than females, and their asymptotic length exceeds that of females (Derocher & Stirling 1998). Mean structural mass is therefore largest in adult males, and so is mean storage mass (Figure 3.5a).

Energy density is often used as a measure of body condition, and is defined as the ratio between storage energy and mass (or volume) of tissue that requires energy for somatic maintenance (Kooijman 2000; Klanjscek *et al.* 2007). Using the previous assumption of negligible maintenance requirements for body fat, energy density is given by the ratio between storage energy and lean body mass, $E / (M - M_{\mathrm{STO\text{-}F}})$. Despite lower mean storage mass, mean energy density of adult females exceeds that of adult males (Figure 3.5c) due to a proportionally higher fat content of storage (Table 3.3). Differences in body composition as specified here are supported by Thiemann *et al.*'s (2006) and Stirling *et al.*'s (2008) findings that female adipose tissue generally contains a higher percentage of lipids than male adipose tissue.

Variability in storage mass and energy density is large for all sex- and age-classes, reflecting large seasonal fluctuations in food supply and consequent body condition (Watts & Hansen 1987; Ramsay & Stirling 1988; Stirling & Øritsland 1995), as well as within-class differences in age and reproductive status. Storage mass, for instance, is most variable in adult males (Figure 3.5a), probably because males continue to accumulate body mass until about 13 years old (Derocher & Wiig 2002), while structural growth is completed by about 6.5 years of age. In contrast, variability in energy density is largest in adult females (Figure 3.5c), where the accumulation of body fat before pregnancy, an extended reproductive fast, and subsequent lactation demands result in large fluctuations in body condition during a three-year reproductive cycle (Ramsay & Stirling 1988; Arnould & Ramsay 1994; Atkinson & Ramsay 1995).

3.7.3 Metabolic Rates

Some adult males (n=13, ages ≥ 8 years) were measured and weighed twice during the fasting season in western Hudson Bay. Measurements for each bear were between 14 and 91 days apart, and obtained between late-July and early-November. Fasting adult males in western Hudson Bay move little (Derocher & Stirling 1990), are in thermoneutral state due to mild summer and fall temperatures (Best 1982), and have completed structural growth (Derocher & Stirling 1998). I therefore assumed that energy is solely expended for somatic maintenance, and used equation (3.22) to estimate metabolic rates (m) from straight line body lengths and changes in total body mass. Metabolic rate estimates ranged from 0.050 to 0.175 MJ per kg lean body mass per day (mean: 0.089 ± 0.011 MJ kg^{-1} d^{-1}).

Metabolic rates of these bears should by definition correspond closely to their basal metabolic rates (Bligh & Johnson 1973). However, a direct comparison between my metabolic rate estimates and those predicted by Kleiber (1975) is difficult. I estimated the rate of energy expenditure relative to a unit mass lean tissue, whereas Kleiber's law predicts the rate of energy expenditure relative to a unit body mass, regardless of body composition. To compare my results with Kleiber's predictions, I rescaled metabolic rate estimates for each bear by multiplying m with the proportion of total body mass that is lean tissue, $(M - M_{\text{STO-F}}) / M$, to obtain the observed rate of energy expenditure relative to a unit body mass, m^*.

Estimates of m^* ranged from 58% to 212% of the values predicted by Kleiber's equation, with 62% of estimates lower than predicted (mean: 107% ± 9%). These results compare favourably with previous measurements of polar bear resting metabolic rates: Watts *et al.* (1987, 1991) estimated the average metabolic rate of three adult females and two subadult males under simulated denning conditions as 73% ± 8.5% and 107% of the values predicted by Kleiber, respectively. Atkinson & Ramsay (1995) gave mean metabolic rates of pregnant and lactating females in maternity dens as 107% ± 5% relative to Kleiber's predictions. The relatively low metabolic rates observed in this and previous studies may be attributable to an ability to reduce metabolism under food scarcity (Watts & Hansen 1987). Metabolic rates ranging from 137% to 212% of Kleiber's predictions (4 of 13 males) suggest increased energy expenditure due to movement, but these values still fall within predicted values for field metabolic rates (Nagy *et al.* 1999).

3.8 Discussion

Structural mass, storage mass, and storage energy of a polar bear can all be estimated from its straight line body length and total body mass, using the body composition model presented here. My method provides considerably more information on the nutritional status of polar bears than currently available methods, including the various body condition indices (Cattet *et al.* 2002; Stirling *et al.* 1999; Stirling *et al.* 2008), isotopic water dilution, and bioelectrical impedance analysis (Farley & Robbins 1994; Hilderbrand *et al.* 1998). The subjective fatness index, Cattet *et al.*'s (2002) body condition index and the Quetelet index cannot estimate storage mass, storage composition, or storage energy. Water dilution and bioelectrical impedance can estimate the energetic content of body fat, but will underestimate total storage energy because body fat constitutes only part of storage. The energetic content of non-structural lean tissue cannot be estimated by these two techniques without supplemental use of a body composition model, because they cannot differentiate between structural and non-structural lean tissue.

My method also provides several practical advantages over isotopic water dilution and bioelectric impedance analysis. Unlike impedance analysis it does not require extensive training to collect the necessary data and is not affected by error sources like depth of anaesthesia, limb and electrode positioning, or previous injuries of the bear (Farley & Robbins 1994; Hilderbrand *et al.* 1998). Unlike water dilution my method is quick, inexpensive, non-invasive, and does not require laboratory analyses. However, the parameterization of my model relied heavily on body composition data obtained by isotopic water dilution and new data would help to validate and refine the model. I therefore recommend my method as a supplement to these techniques.

Currently, handled polar bears are routinely classified on a subjective fatness scale from 1 to 5 as a measure of their body condition (Stirling *et al.* 2008). Despite its simplicity, and a demonstrated correlation with the relative lipid content of adipose tissue, this method has limitations: it carries no information on storage energy and its resolution is low, with over 50% of sampled polar bears rated as average ('3') and over 90% rated between '2' and '4' (Stirling *et al.* 2008). Furthermore, this technique is also vulnerable to misclassifications and inconsistencies from intra- and inter-observer variability. For instance, assuming equal body composition, two bears of equal mass and length should always receive the same fatness rating, a condition that was frequently violated in my study populations for all sex- and age-classes, and particularly for cubs-of-the-year and yearlings (Figure 3.4). In contrast, the method presented here is unaffected by observer variability and provides high resolution by estimating storage energy as a continuous function of body mass and length.

The present model is limited by the low sample size of bears that was available for model parameterization. Although the model performed well for a variety of life history and physiological traits, model analysis revealed high sensitivity of storage energy predictions to the storage composition parameter γ. This sensitivity is not a model artefact but reflects the differing energy densities of body fat and lean tissue. It therefore emphasizes the necessity to estimate γ as accurately as possible. Many factors could affect storage composition, including season, age, or reproductive status of females, but I had insufficient data to determine covariates for γ other than the proposed sex- and age-classes. Model refinements should therefore be attempted as more data become available.

The sample size of 2 starved bears to estimate the structural mass coefficient $\rho_{\mathrm{STR}} \cdot k$ does not present a major concern for storage energy predictions. The coefficient $\rho_{\mathrm{STR}} \cdot k$ usually varies little within species (Kooijman 2000; cf. also the individual estimates for the two starving bears in section 3.3), and sensitivity of storage energy to $\rho_{\mathrm{STR}} \cdot k$ is generally low (Figure 3.3). Furthermore, model predictions of structural mass using the current estimate of $\rho_{\mathrm{STR}} \cdot k$ proved robust for 970 polar bears of all sex- and age-classes from two populations, with no bear lighter than its predicted structural mass (Figure 3.4). The sensitivity of storage energy to $\rho_{\mathrm{STR}} \cdot k$ for very lean bears does not affect the usefulness of my model because few bears reach such poor body condition (e.g., 94.7% of sampled polar bears were heavier than 1.5 times estimated structural mass).

Information on energy stores, provided by the body composition model, can be invaluable in broad-scale ecological studies to link resource availability, individual body condition, demographic parameters and population status. For example, rising air temperatures in Hudson Bay have led to a progressively earlier spring sea ice break-up (Gagnon & Gough 2005), shortening the on-ice feeding period and prolonging the on-shore fasting season for polar bears (Stirling *et al.* 1999). Concurrent declines in body length, body condition, reproductive success, survival and abundance in the western Hudson Bay population are thought to result from nutritional stress associated with the increased fasting period (Regehr *et al.* 2007; Stirling *et al.* 1999). Further negative changes are expected under continued climatic warming (Derocher *et al.* 2004; Stirling & Parkinson 2006), but the time frame and manner are unclear. The body composition model could not only be used to better assess trends in individual body condition than would be possible with traditional body condition indices, but also form the foundation for models that link changes in the environment to changes in survival, growth, and reproduction. I have already shown how the model can be applied to estimate the metabolic rates of fasting adult males. By extension, it would be possible to estimate time to starvation (Zonneveld & Kooijman 1989) and thus the maximum fasting season length a bear can survive on its energy stores. In Chapter 4, I will extend my analyses to show how the expected litter size of pregnant females can be predicted from their energy density, and thus from fasting season length. This approach could be further developed within the framework of dynamic energy budget theory to quantify how changes in resource availability and food intake translate into changes in body condition, growth, reproductive success, and survival (Kooijman 2000). Projected climatic warming scenarios (e.g., Holland *et al.* 2006; Stroeve *et al.* 2007) and resulting predictions of future resource availability could therefore be mechanistically linked to projections of polar bear population dynamics, using the body composition model in combination with physiologically structured population models (de Roos & Persson 2001).

Although the model in its current form is polar bear specific, the concepts of structure and storage are universal, and similar body composition models could easily be developed for any species. In fact, the model in its present form could be used for other species, as long as the assumptions of strong homeostasis, isomorphic growth, and storage consisting of fat, protein, ash, and water, are fulfilled. However, an appropriate species-specific measure of length must be determined that can serve as a predictor variable for structural mass. Furthermore, re-parameterization would be necessary, and care must be taken with regard to two assumptions assumed to hold for polar bears. First, I assumed that starved animals have no storage energy left. In general, it is not true that starvation occurs when all storage energy has been depleted. Rather, starvation can occur in many species (including humans) when ample energy stores remain, but the energy flow from storage is insufficient to cover the costs of somatic maintenance (Castellini & Rea 1992). Second, I assumed that in polar bears all body fat belongs to storage. In some species (e.g., seals, whales) a significant portion of lipids is structural, so that in these cases additional methods must be developed to estimate the proportion of body fat that is structural (e.g., Klanjscek *et al.* 2007).

The present modelling approach allows a more accurate quantification of body condition than presently possible and improves our understanding of individual bioenergetics. The approach could provide a link between energy flow in the environment, individual body condition and population dynamics, not just in polar bears, but in many species that rely on stored energy for aspects of their life history.

State variable	Definition	Units
Measurable state variables		
L	Straight line body length	m
M	Total body mass	kg
Derived state variables		
M_{STR}	Mass of structure	kg
M_{STO}	Mass of storage	kg
$M_{\mathrm{STO\text{-}F}}$	Mass of body fat in storage	kg
$M_{\mathrm{STO\text{-}P}}$	Mass of protein in storage	kg
$M_{\mathrm{STO\text{-}A}}$	Mass of ash in storage	kg
$M_{\mathrm{STO\text{-}W}}$	Mass of body water in storage	kg
$M_{\mathrm{STO\text{-}L}}$	Mass of non-structural lean (i.e., fat-free) tissue (= $M_{\mathrm{STO\text{-}P}} + M_{\mathrm{STO\text{-}A}} + M_{\mathrm{STO\text{-}W}}$)	kg
V_{STR}	Volume of structure	m^3
E	Total energy content of storage	MJ
E_{F}	Energy in storage fat	MJ
E_{P}	Energy in storage protein	MJ

Table 3.1: State variables used in the body composition model.

Parameter	Definition	Estimate (mean ± SE)	Units	Source
ρ_{STR}	Density of structure	---	kg m^{-3}	This chapter (only the product $\rho_{\mathrm{STR}} \cdot k$ is estimated)
k	Shape parameter relating structural volume to straight line body length	---	---	
$\rho_{\mathrm{STR}} \cdot k$	---	14.94	kg m^{-3}	
γ	Proportion of total storage energy that is stored in body fat	0.899 ± 0.011 [a] 0.941 ± 0.006 [b] 0.943 ± 0.014 [c] 0.935 ± 0.004 [d] 0.885 ± 0.007 [e]	---	This chapter – using data from Arnould & Ramsay (1994), Atkinson *et al.* 1996a)
ε_{F}	Energy density of fat	39.3	MJ kg^{-1}	Schmidt-Nielsen 1997
ε_{P}	Energy density of protein	18.0	MJ kg^{-1}	Schmidt-Nielsen 1997
η_{W}	Proportion of lean body mass that is water	0.734	---	Farley & Robbins 1994
η_{P}	Proportion of dry lean body mass that is protein	0.835 ± 0.016	---	Farley & Robbins 1994

[a] cubs-of-the-year, [b] yearlings, [c] adult females, [d] subadult males, [e] adult males

Table 3.2: Parameter estimates for the body composition model.

	Estimated percentage of storage mass that is			
	Fat	Protein	Ash	Water
Cubs-of-the-year	47.5	11.7	2.3	38.5
Yearlings	61.9	8.5	1.7	28.0
Adult females	62.7	8.3	1.6	27.4
Subadult males	59.4	9.0	1.8	29.8
Adult males	43.9	12.5	2.5	41.2

Table 3.3: Estimated storage composition of polar bears.

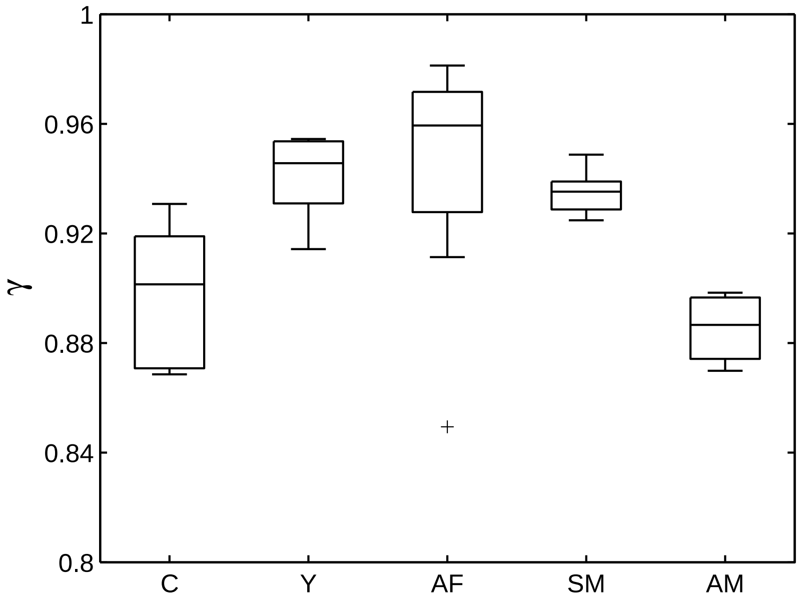


Figure 3.1: Estimates of the proportion of storage energy that is stored in body fat (γ) for 6 cub-of-the-year (C), 7 yearling (Y), 9 adult female (AF), 5 subadult male (SM) and 4 adult male (AM) polar bears from Arnould & Ramsay (1994) and Atkinson *et al.* (1996a). Each box plot shows the median, the upper and lower quartiles, and whiskers which extend to include data no more than 1.5 times the interquartile range away from the quartiles. Data beyond the whiskers are marked by crosses.

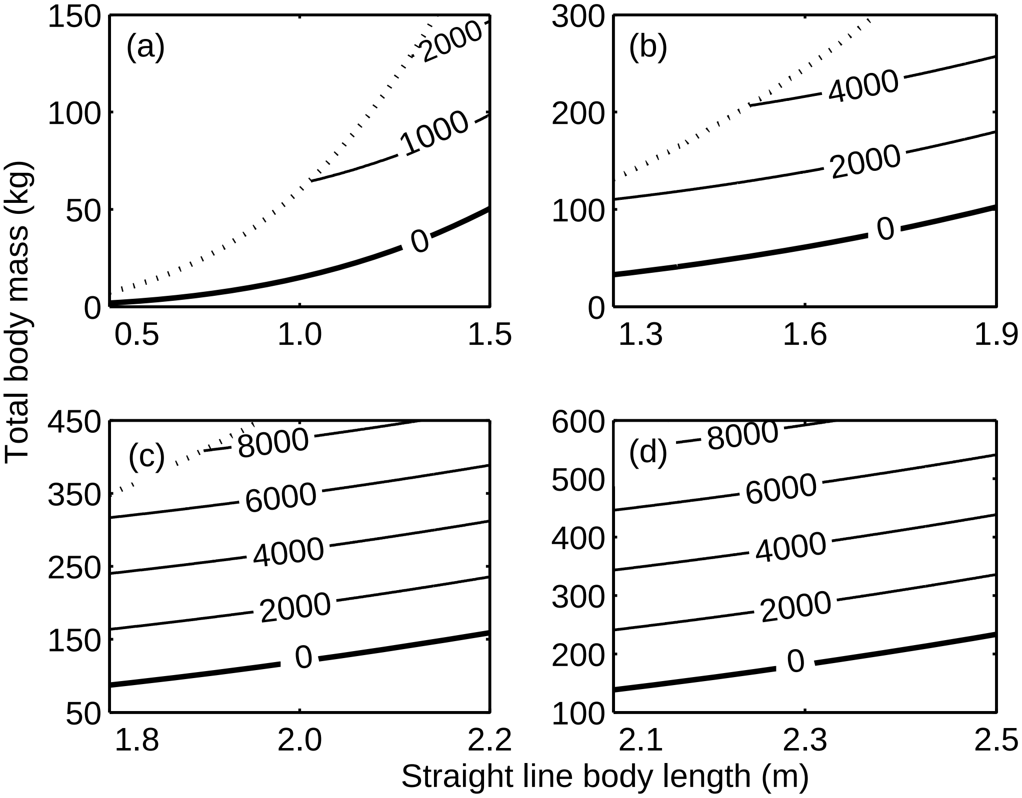


Figure 3.2: Contour lines showing model predictions (equations (3.18)) for polar bear storage energy, *E* (units: MJ), from straight line body length and total body mass for (a) cubs-of-the-year, (b) yearlings, (c) adult females, and (d) adult males. Thick solid lines correspond to starved bears, dotted lines to bears whose total body mass is four times structural mass, an approximate upper bound to total body mass.

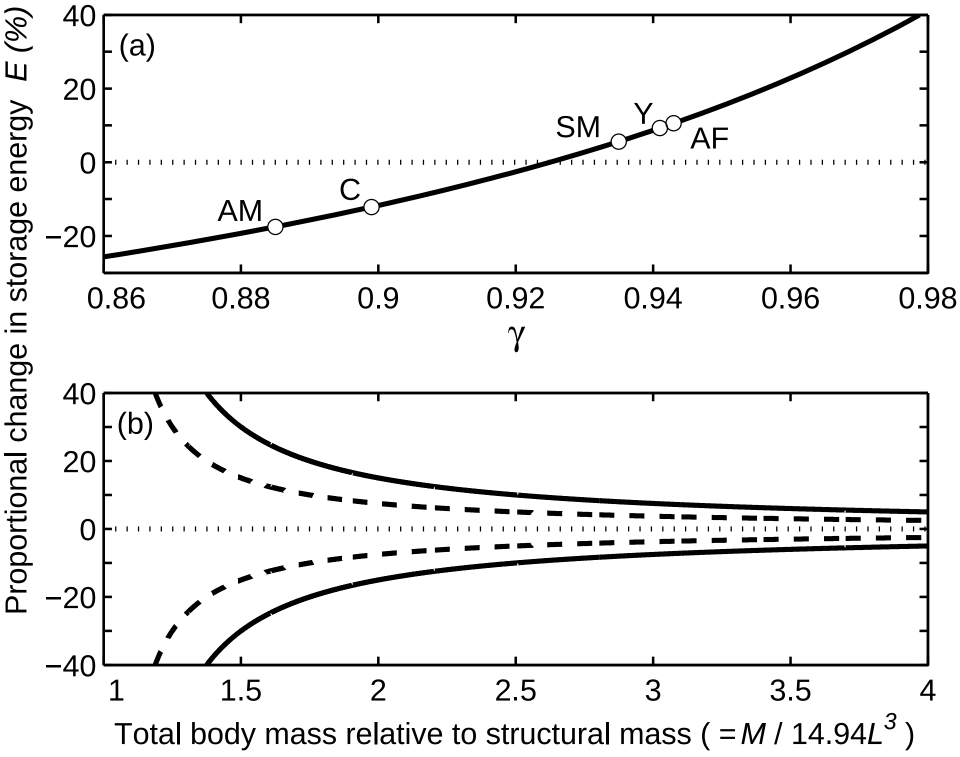
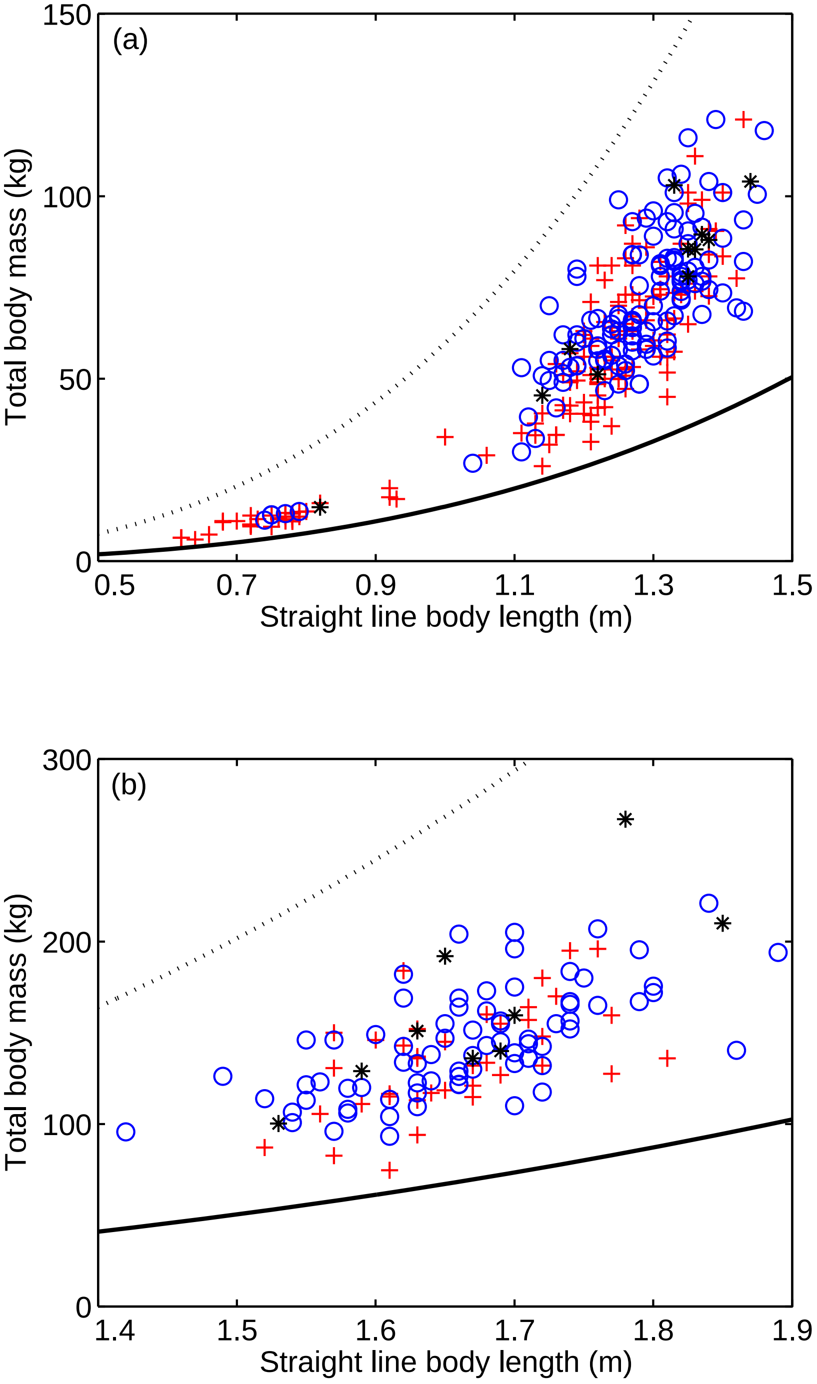


Figure 3.3: Proportional change in storage energy E relative to $\overline{E}$, the storage energy of an individual of equal body mass and length with $\overline{\rho_{\mathrm{STR}} k}$ = 14.94 kg m^{-3} and $\overline{\gamma}$=0.925, (a) when varying γ but holding $\rho_{\mathrm{STR}} k = \overline{\rho_{\mathrm{STR}} k}$ constant, and (b) as a function of total body mass relative to structural mass for a 7.5% decrease or increase (upper and lower dashed lines, respectively) and a 15% decrease or increase (upper and lower solid lines, respectively) in $\rho_{\mathrm{STR}} \cdot k$ (holding $\gamma = \overline{\gamma}$ constant). Circles in (a) represent sex- and age-class specific means of γ for cubs-of-the-year (C), yearlings (Y), adult females (AF), subadult males (SM), and adult males (AM).


(a)
Total body mass (kg)
0
50
100
150
0.5
0.7
0.9
1.1
1.3
1.5
Straight line body length (m)
(b)
Total body mass (kg)
0
100
200
300
1.4
1.5
1.6
1.7
1.8
1.9
Straight line body length (m)

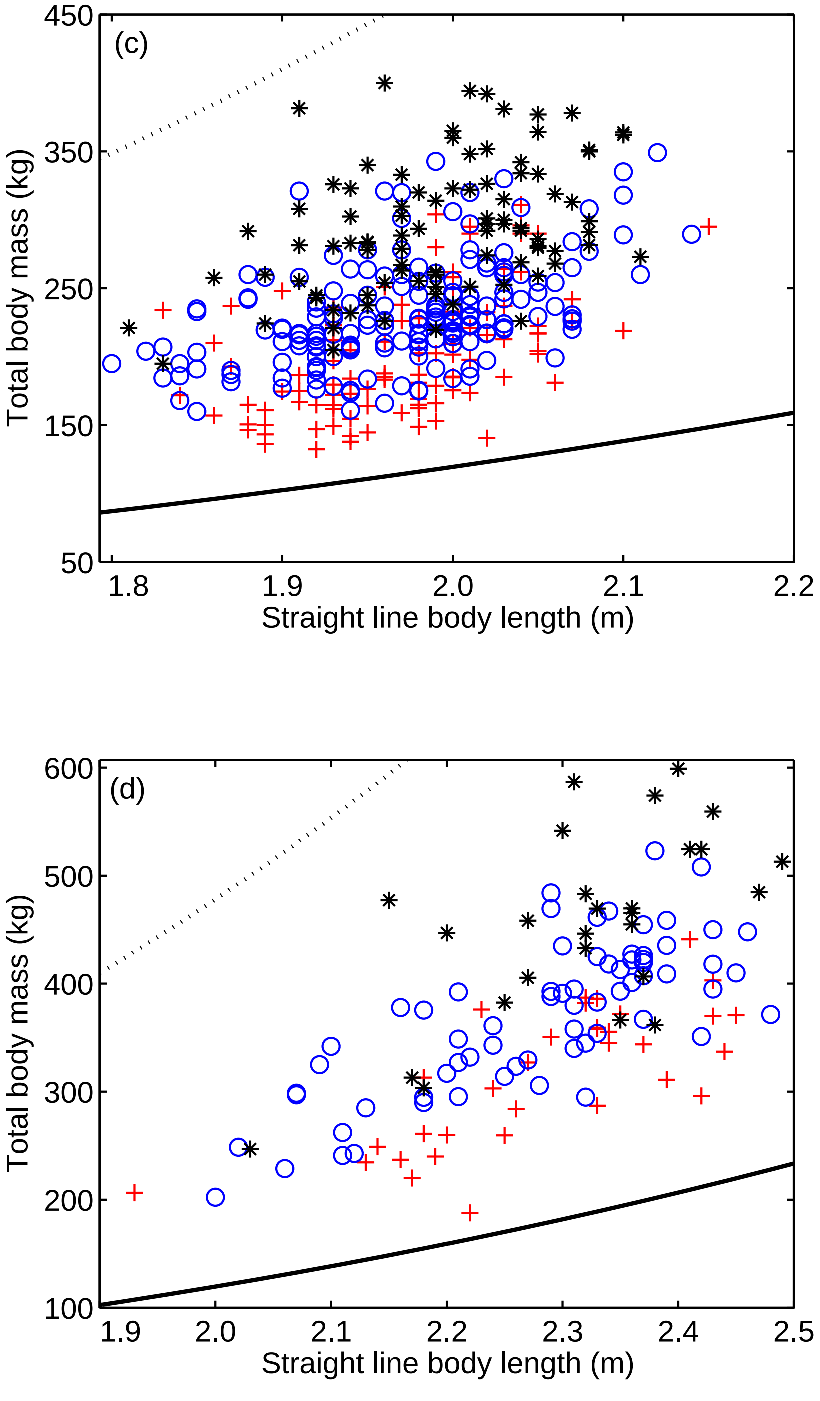


Figure 3.4: Straight line body lengths and total body masses of polar bears in western and southern Hudson Bay. (a) Cubs-of-the-year, (b) yearlings, (c) subadult and adult females, (d) subadult and adult males. Red crosses are bears classified as '1' or '2' on the subjective fatness scale (Stirling *et al.* 2008), blue circles are bears classified as '3', black stars are bears classified as '4' or '5'. Solid lines show predicted structural mass as a function of straight line body length, dotted lines show an approximate upper bound to total body mass, taken as four times structural mass.

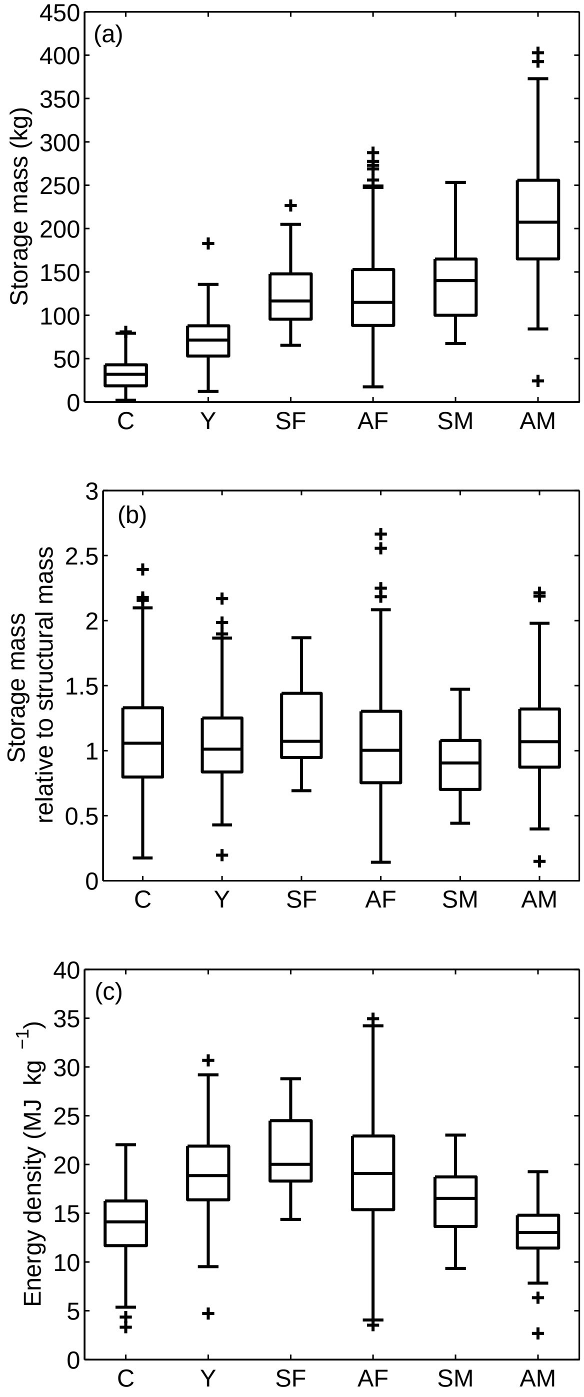


Figure 3.5: Estimated (a) storage mass, (b) storage mass relative to structural mass, and (c) energy density of cub-of-the-year (C), yearling (Y), subadult female (SF), adult female (AF), subadult male (SM) and adult male (AM) polar bears from western and southern Hudson Bay. Each box plot shows the median, the upper and lower quartiles, and whiskers which extend to include data no more than 1.5 times the interquartile range away from the quartiles. Data beyond the whiskers are marked by crosses.

3.9 References

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Chapter 4

4 Energy-Restrictions on Litter Size – Predicting Climate Change Effects on Polar Bear Reproduction in Western Hudson Bay

4.1 Introduction

There is no doubt that climate change is occurring, and climatologists have provided a number of predictive models for changes in temperature, precipitation, sea ice conditions, permafrost, glacial extent, and other issues (IPCC 2007). In contrast, ecologists still face considerable challenges to obtain quantitative predictions for the consequent effects on ecosystems, largely due to limited data and insufficiently understood causal chains (Berteaux *et al.* 2006; Krebs & Berteaux 2006; Sutherland 2006). It is, however, clear that ecosystems are already affected, and qualitative predictions for future changes abound (e.g., McCarty 2001; Root *et al.* 2003; Harley *et al.* 2006; Moore & Huntington 2008). Quantitative predictions have also been attempted (e.g., Sæther *et al.* 2000; Humphries *et al.* 2002; Thomas *et al.* 2004; Jenouvrier *et al.* 2009), but associated uncertainties are often large (Berteaux *et al.* 2006; Krebs & Berteaux 2006; Sutherland 2006).

Ecosystems may be affected at the species level, for instance, through changes in physiology, phenology, range-boundaries, abundance, and distribution, or at higher levels of organization through changes in community composition or interspecific interactions (e.g., Hughes 2000; McCarty 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006; Tylianakis *et al.* 2008; Hegland *et al.* 2009). Among the most vulnerable to climate change are ice-obligate Arctic species including polar bears (*Ursus maritimus*), walrus (*Odobenus rosmarus*), ringed seals (*Pusa hispida*), and bearded seals (*Erignathus barbatus*) (Tynan & DeMaster 1997; Laidre *et al.* 2008; Moore & Huntington 2008). These species are of special concern due to the rapid disappearance of their habitat and the high rate of warming observed and predicted at these latitudes (ACIA 2005). However, they should also be among the most amenable to quantitative predictions due to low species diversity, relatively simple food webs, and a limited range of interspecific interactions (Hobson & Welch 1992).

The future of polar bears under climatic warming is subject to considerable research (e.g., Stirling & Derocher 1993; Derocher *et al.* 2004; Stirling & Parkinson 2006; Amstrup *et al.* 2007; Wiig *et al.* 2008; Durner *et al.* 2009), in part because they constitute an umbrella species for Arctic ecosystems. Polar bears at the southern limit of the species' geographical range are considered the most vulnerable to climatic warming (Stirling & Derocher 1993; Derocher *et al.* 2004; Stirling & Parkinson 2006; Wiig *et al.* 2008). At these latitudes the sea ice melts completely each summer, forcing all bears ashore (Stirling & Parkinson 2006; Durner *et al.* 2009). On land, little or no food is available and bears rely on their energy stores for survival, and in the case of adult females for reproduction also (Ramsay & Hobson 1991; Derocher *et al.* 1993a,b; Atkinson & Ramsay 1995). In recent years, spring sea ice break-up has been occurring progressively earlier, and fall freeze-up progressively later (Gough *et al.* 2004; Gagnon & Gough 2005; Stirling & Parkinson 2006), thereby shortening the feeding period and lengthening the fasting season of polar bears in this so-called Seasonal Sea Ice Ecoregion (Stirling *et al.* 1999; Thiemann *et al.* 2008; Durner *et al.* 2009). Concurrent declines in polar bear body condition, reproduction, survival, and abundance have been documented for the western Hudson Bay population (Figure 1.1), and are thought to result from increasing food stress (Stirling *et al.* 1999; Regehr *et al.* 2007). Similar changes may be occurring in the other four populations of the Seasonal Sea Ice Ecoregion, southern Hudson Bay, Foxe Basin, Davis Strait, and Baffin Bay (Stirling & Parkinson 2006; Obbard *et al.* 2006, 2007; Durner *et al.* 2009; Figure 1.1), but trends are less clear, possibly due to lower monitoring efforts. With continued climatic warming, further negative impacts on polar bear populations are expected (Derocher *et al.* 2004; Stirling & Parkinson 2006; Wiig *et al.* 2008), but the manner and time frame are uncertain.

Quantitative predictions of polar bear population dynamics under climate change are difficult because predicted environmental conditions differ significantly from historic observations (Wiig *et al.* 2008). Consequently, little data exist to guide our attempts, and the only studies to attempt such predictions were limited by the need to extrapolate from present conditions (Hunter *et al.* 2007), the reliance on expert judgement (O'Neill *et al.* 2008), or both (Amstrup *et al.* 2007). Hunter *et al.* (2007), for example, used six years of capture-recapture data to estimate polar bear survival and reproduction as a function sea ice extent. They then used these estimates in matrix models (Caswell 2001) to predict population abundance in the southern Beaufort Sea (Figure 1.1) under climate change, but uncertainty was large due to the limited range of sea ice conditions considered when estimating demographic parameters. Furthermore, their analyses and predictions are restricted to the southern Beaufort Sea, and replication would be difficult in most other populations due to a lack of appropriate data. Amstrup *et al.* (2007) attempted a global approach using a polar bear carrying capacity model. However, a lack of appropriate data linking environmental conditions to polar bear population dynamics forced the authors to rely on expert judgement throughout most of their study (cf. section 1.2.1 for more details). Amstrup *et al.* (2007) suggested potential extirpation of polar bears in the Seasonal Sea Ice Ecoregion within the next 45-100 years, but uncertainty was high, spatial and temporal resolution low, and transitional dynamics unclear. Regional variability in population response has not been addressed but may be important due to regional variation in climate and sea ice predictions (Derocher *et al.* 2004; Wiig *et al.* 2008). Neither study has attempted to develop mechanistic models for the relationship between sea ice dynamics, reproduction and survival.

The biggest limitation in both Hunter *et al.*'s (2007) and Amstrup *et al.*'s (2007) approach was the lack of empirical data describing changes in vital rates as a function of sea ice conditions resembling those predicted. Given this lack of empirical data, and consequent limitations on our ability to predict polar bear population dynamics under climate change, an approach that explicitly links sea ice dynamics to demographic parameters reproduction and survival could be useful. Female reproductive success, for example, is directly affected by body condition, and more specifically, by energy stores (Derocher *et al.* 1992, 1993b; Atkinson & Ramsay 1995; Derocher & Stirling 1994, 1996, 1998a). Body condition, in turn, is negatively affected by reduced sea ice through reduced feeding opportunities and increased energy expenditure (Stirling *et al.* 1999; Derocher *et al.* 2004; Wiig *et al.* 2008). In fact, most predicted effects of climatic warming on polar bears are energy-associated (Derocher *et al.* 2004; Wiig *et al.* 2008; cf. section 1.1.1). A mechanistic understanding of the relationship between environmental conditions, body condition, energetics, reproduction and survival could therefore improve our predictive abilities (Berteaux *et al.* 2006; Krebs & Berteaux 2006) for polar bears and complement the phenomenological population-level approaches taken by Hunter *et al.* (2007) and Amstrup *et al.* (2007).

Dynamic energy budget models explicitly track energy intake and expenditure within an organism and have the potential to predict reproductive output and survival under changing environmental conditions and associated energy intake (Gurney *et al.* 1990; Nisbet *et al.* 2000; Kooijman 2000). To date, they have been applied to invertebrates, fish, amphibians, reptiles, and birds (Kooijman 2000, and references therein). More recently, they have also been extended to include whales (Klanjscek *et al.* 2007). Dynamic energy budget models are preferable over traditional static energy budget models (e.g., Lockyer 1981; Winship *et al.* 2002) for predicting individual responses to changing environmental condition, because they explicitly consider allocation rules and priorities between somatic maintenance, reproduction, and growth, crucial to the understanding of responses to food limitation (McCauley *et al.* 1990; Noonburg *et al.* 1998; Kooijman 2000). In Chapter 3, I provided a body composition model that allows estimation of the energy stores of a polar bear, and thus provides the basis to move this species into a dynamic energy budget framework. I have already shown how the body composition model can be applied to estimate the metabolic rate of fasting adult polar bears (Chapter 3, section 3.5). In this chapter I extend my analyses to reproduction, considering energy-restrictions and consequent climate change effects on litter size of pregnant females in western Hudson Bay.

To understand whether and how climatic warming and a resultant prolonged summer fasting season may affect the litter size of pregnant females, I use a 4-step approach. The methods of each step depend on the results of the previous step, so for convenience I give a brief outline of the approach here, before I proceed to describe the methods in detail. Following the temporal sequence linking sea ice break-up date to litter size, I address each of the following steps, although the order of analyses differs slightly: First, I explore how female energy stores would be affected by earlier on-shore arrival. Second, from energy stores at on-shore arrival I estimate energy stores at den entry. Third, from energy stores at den entry I estimate expected mean litter size at den emergence. Fourth, I evaluate whether terrestrial feeding could compensate for losses in storage energy and litter size due to a prolonged open-water season.

More specifically, the analyses are as follows: To provide context, I begin with a brief overview of the reproductive biology of female polar bears (section 4.2), and introduce the study population (section 4.3). Then, using logistic regression models, I analyze data on pregnant females with known litter size to test the hypotheses that litter size can be predicted from maternal age, storage energy, energy density, or a combination of these state variables (section 4.4). I establish that maternal energy density at den entry is a good predictor variable for litter size, and best among the state variables considered. I therefore use this regression model to calculate the expected mean litter size of pregnant females as a function of energy density at den entry (section 4.4). Having established energy density as a predictor variable, I develop an energy budget model and consider two on-ice feeding scenarios to estimate how the energy density of pregnant females would change if they were forced ashore earlier in summer due to earlier sea ice break-up (section 4.5). Coupling the results of section 4.5 (expected energy density at den entry as a function of on-shore arrival date) with the results of section 4.4 (expected mean litter size as a function of energy density at den entry), I obtain predictions for the expected mean litter size of pregnant females in western Hudson Bay as a function of on-shore arrival date (section 4.5). Finally, I use the energy budget model to calculate terrestrial feeding rates necessary to compensate for losses in energy density and consequently litter size due to earlier on-shore arrival (section 4.5).

4.2 The Reproductive Biology of Polar Bears

Polar bears mate during a relatively distinct spring mating season (Chapter 2, section 2.3.1). Implantation of blastocysts, however, is delayed until fall, when pregnant females enter maternity dens (Ramsay & Stirling 1988; Derocher *et al.* 1992). Gestation is short, probably around 60 days (Derocher *et al.* 1992; Lunn *et al.* 2004). At birth, cubs are altricial, blind, and small, weighing approximately 600 g (Ramsay & Dunbrack 1986). Litter size can range from one to three cubs (Ramsay & Stirling 1988). Post-partum, females remain in the den, nursing their cubs for another 2-4 months (Amstrup & Gardner 1994; Messier *et al.* 1994; Atkinson & Ramsay 1995). Food is unavailable to females while denning. Energetic expenses of survival, gestation, and lactation are met from fat and protein stores accumulated during the previous hunting season (Atkinson & Ramsay 1995). At den emergence, cubs usually weigh 7-15 kg. Cubs normally stay with their mothers until about 2.5 years old and are sustained on both solid food and milk (Stirling 1974; Derocher *et al.* 1993b). Solitary, independent 1.5 year olds have been observed, but the reasons for early weaning are poorly understood (Ramsay & Stirling 1988; Derocher & Stirling 1996). Females do not enter oestrus while accompanied by dependent offspring, resulting in an average interbreeding interval of about three years (Lentfer *et al.* 1980; Ramsay & Stirling 1988). Females reach sexual maturity at about 4 years of age (Lentfer *et al.* 1980; Ramsay & Stirling 1988). Whether or not reproductive senescence occurs in females is debated (Derocher & Stirling 1994).

In this chapter, I only consider reproduction to den emergence. The other components of reproduction could also be addressed within the dynamic energy budget framework provided in this chapter, but such analyses are beyond the scope of this dissertation, and currently not possible due to a lack of appropriate data. However, I will return to the topic in the concluding discussion of Chapter 5, when I outline key data requirements necessary for such a comprehensive approach.

4.3 Study Population

The polar bear population of western Hudson Bay is a relatively discrete subpopulation: overlap in distribution with the adjacent populations of Foxe Basin and southern Hudson Bay (Figure 1.1) occurs during winter and spring when bears are hunting on the sea ice (Stirling *et al.* 2004; Crompton *et al.* 2008), but high fidelity to coastal areas during the open-water season allows the delineation of relatively distinct populations (Derocher & Stirling 1990; Taylor & Lee 1995; Stirling *et al.* 1999; Stirling *et al.* 2004).

The life cycle of polar bears in western Hudson Bay is dominated by sea ice availability. Hudson Bay is covered by annual sea ice for approximately 8 months a year, and is ice-free for the remainder (Gough *et al.* 2004). Sea ice break-up begins around mid-May, and polar bears come ashore between late-July and late-August, depending on ice conditions (Stirling *et al.* 1999). On shore, bears concentrate in a relatively small area located between the Churchill and Nelson rivers, Manitoba, Canada (Derocher *et al.* 1990; Regehr *et al.* 2007). Here, adult males predominantly occupy coastal beaches, while adult females are found in inland areas (Derocher *et al.* 1990; Clark & Stirling 1998). Freeze-up usually occurs during November, when all bears except pregnant females return to the sea ice (Stirling *et al.* 1999). Pregnant females remain in the denning area to give birth. They emerge from their dens late-February, and leave the coast by mid- to late-March (Lunn *et al.* 2004).

Although dates of sea ice break-up and freeze-up vary between years, there is a clear trend towards a progressively earlier spring break-up due to rising air temperatures in Hudson Bay: break-up now occurs on average approximately three weeks earlier than it did 30 years ago, and polar bear on-shore arrival has shifted accordingly (Stirling *et al.* 1999, Gagnon & Gough 2005, Stirling & Parkinson 2006). Along with these changes in sea ice availability, declines in polar bear body condition, reproduction, and survival have been documented (Stirling *et al.* 1999; Regehr *et al.* 2007), resulting in a population decline from about 1200 to about 935 bears (Lunn *et al.* 1997; Regehr *et al.* 2007).

4.4 Determinants for Litter Size at Den Emergence

I begin by analyzing data on pregnant females with known litter sizes to determine appropriate predictive variables for litter size. I establish statistical relationships, which are then used in section 4.5 to evaluate how climatic warming induced early on-shore arrival may affect litter size of pregnant females.

4.4.1 Methods

Pregnant females (n = 40) were captured between early-August and late-October from 1980 to 1995 in the western Hudson Bay denning area. All females were recaptured the following spring (late-February to late-March) when leaving the maternity den with newborn cubs-of-the-year. At both occasions, straight line body length, L, and axillary girth, G, were recorded for each female. Straight line body lengths were measured to the nearest cm as the dorsal straight-line distance from the tip of the nose to the end of the last tail vertebra, while the bears were lying in a sternally recumbent position. Within individuals straight line body lengths generally varied little between fall and spring, with length measurements on average 2 cm (SE: 0.52 cm) larger in fall when compared to spring. These differences are attributed to measurement error and are negligible for my purposes. I therefore used the average straight line body length of each female in all further calculations. Axillary girths were measured to the nearest cm as the circumference around the chest at the axilla. Some bears (n = 12) were weighed (± 0.5 kg) using an electronic load cell suspended from a tripod. For all other bears I estimated total body mass, M, from straight line body length and axillary girth, using a morphometric equation developed for the adjacent southern Hudson Bay population in 1984-86 (Cattet & Obbard 2005):

$$(4.1) \qquad M = e^{-9.03} \cdot L^{1.29} \cdot G^{1.60} \quad .$$

Ages were determined by counting the annular rings of an extracted vestigial premolar tooth (Calvert & Ramsay 1998). All females produced at least one cub, and litter sizes were recorded at den emergence. For more details on the capture procedure see Derocher & Stirling (1994), where parts of the data used here were already reported, albeit in a different context. The data were made available from the Canadian National Polar Bear Database maintained by Environment Canada. All state variables and their abbreviations used here and below are summarized in Table 4.1.

To link female body condition at den entry to litter size at den emergence, I assumed a mean maternity den entry date of October 1 (Derocher *et al.* 1992; Lunn *et al.* 2004). I scaled body masses of all females from first capture to this date, using the mass loss curve derived in section 3.5 (equations (3.20) and (3.21)), restated here for convenience:

$$M(t_1) = \left(M_0 + \frac{\varphi}{1-\varphi} \rho_{\mathrm{STR}}\, k\, L^3 \right) \exp\left(-\frac{m(1-\varphi)}{\alpha} (t_1 - t_0) \right) - \frac{\varphi}{1-\varphi} \rho_{\mathrm{STR}}\, k\, L^3 \quad . \tag{4.2}$$

Here, M_0 is body mass at capture date t_0, φ is the proportion of storage mass that is fat, α is a constant that converts storage mass into storage energy, and $\rho_{\mathrm{STR}} \cdot k$ is a composite proportionality constant needed to estimate structural mass from straight line body length. Metabolic rate, m, is defined as energy required per unit time to maintain a unit mass of lean tissue (cf. section 3.5). I set $\varphi = 0.627$, $\alpha = 26.14$ MJ kg^{-1}, and $\rho_{\mathrm{STR}} \cdot k = 14.94$ kg m^{-3}, as estimated for adult females in Chapter 3. I further use the mean metabolic rate of adult males, $m = 0.089$ MJ kg^{-1} d^{-1} (section 3.7.3), because m refers only to the somatic maintenance rate of lean tissue and sex-specific differences in body composition are already accounted for through the parameters φ and α. The validity of equation (4.2) depends on the assumption that a polar bear is fasting, resting, neither growing nor reproducing, and in a thermoneutral state (section 3.5). Adult females in western Hudson Bay typically feed little or not at all during the summer and fall fasting period (Ramsay & Hobson 1991; Derocher *et al.* 1993a; Hobson *et al.* 2009), move little (Lunn *et al.* 2004; Parks *et al*. 2006), have completed structural growth (Derocher & Stirling 1998b), and are in a thermoneutral state due to mild temperatures (Best 1982). Gestation begins between mid-September and mid-October and lasts approximately 60 days (Derocher *et al.* 1992). However, cubs weigh only about 600 g at birth (Ramsay & Dunbrack 1986), so that the energetic costs of gestation are negligible relative to those of somatic maintenance. Consequently, equation (4.2) remains valid, even if in some females gestation may already have begun by October 1.

Earlier work has attempted to describe litter size at den emergence as a function of maternal body mass at den entry (Derocher & Stirling 1994), but reproductive success is more directly determined by available storage energy (Ross & Nisbet 1990; Atkinson & Ramsay 1995; Kooijman 2000; Lika & Nisbet 2000). I therefore converted estimated body masses at den entry into storage energy at den entry, *E*, using equation (3.18c), which is restated here:

$$E = 26.14M - 390.53L^3 \quad . \tag{4.3}$$

Energy density, defined as the ratio between storage energy and lean body mass, *E* / *LBM* (section 3.7.2), relates available storage energy to the mass of tissue that requires energy for somatic maintenance. Because females in a maternity den expend energy on both reproduction (determined by available storage energy) and somatic maintenance (determined by lean body mass), energy density may be a better predictor for litter size at den emergence than storage energy alone. I therefore also estimated energy density at den entry using the following equation (see Appendix C for derivation):

$$\frac{E}{LBM} = \frac{26.14M - 390.53L^3}{0.373M + 9.37L^3} \quad . \tag{4.4}$$

I then used multinomial logistic regression (Agresti 1996) to determine the probabilities of having one, two, or three cubs at den emergence, p_1, p_2, and p_3, as a function of maternal storage energy and maternal energy density at den entry, respectively. Age was previously suggested as another covariate for reproductive success (Ramsay & Stirling 1988; Derocher & Stirling 1994; Derocher & Stirling 1995). I therefore considered three additional multinomial logistic regression models, using maternal age at den entry as a predictor variable for litter size, either by itself, or in combination with storage energy or energy density, respectively (Table 4.2). Strictly speaking, litter size is an ordinal rather than a nominal variable. However, ordinal regression models require that the proportional odds assumption is fulfilled, which states that the slope parameter in each logit-regression simultaneously performed by the ordinal model is the same (Agresti 1996). This rather restrictive assumption is probably violated in the litter size data for at least some of the regression models considered (cf., for example, the relatively clear energy density threshold between triplet and twin production, but the large overlap between females producing twins and females producing singletons,

Figure 4.1b). Multinomial regression avoids this assumption, and estimates only one additional parameter in the case of three possible outcomes considered here (one, two, or three cubs). I therefore chose to use the more flexible multinomial regression models throughout. Likelihood ratio tests were used to determine the significance of predictor variables in each regression model, and Akaike's Information Criterion adjusted for small sample size, $\mathrm{AIC_c}$ (Burnham & Anderson 2002), to select the regression model that best described the data. The model with the smallest $\mathrm{AIC_c}$ value was considered best, while models with $\mathrm{AIC_c}$ values within 2 units of the best model were considered equally good. I also calculated $\mathrm{AIC_c}$ weights, which represent the relative likelihood of each model, given the data (Burnham & Anderson 2002).

Females with insufficient energy stores to meet the energetic demands of survival, gestation, and lactation during denning do not enter maternity dens, or abort early (Derocher *et al.* 1992). However, only females that produce at least one cub remain in the denning area until early spring, so I had no data to determine the probability of producing zero cubs, p_0, from the multinomial regression models described above. Instead, to fully describe litter size as a function of the covariates age, storage energy, or energy density, I made the simplifying assumption that females do not reproduce if either their storage energy or their energy density (depending on the model considered) is below a minimum threshold on den entry date October 1. Furthermore, I assumed that sexually mature females above this threshold always reproduce. The assumption of such a minimum threshold for reproduction is supported by dynamic energy budget theory (e.g., Ross & Nisbet 1990; Noonburg *et al.* 1998; Lika & Nisbet 2000). Formally, I set

$$(4.5) \qquad p_0(\bar{x}) = \begin{cases} 1 & \text{if} \quad \bar{x} < \bar{x}_{\min} \\ 0 & \text{if} \quad \bar{x} \geq \bar{x}_{\min} \end{cases} ,$$

where $\bar{x}$ represents the covariates in each regression model, and $\bar{x}_{\min}$ represents the corresponding minimum thresholds for reproduction. Sexual maturity was set at 4 years of age (Ramsay and Stirling 1988). The minimum storage energy and energy density thresholds were set as the lowest values ever observed (scaled to October 1, using equations (4.1)-(4.4)) for a female that produced at least one cub (Derocher *et al.* 2004).

Using the derived probabilities of having zero, one, two, or three cubs, I calculated expected mean litter size at den emergence as a function of the covariates $\bar{x}$ in each regression model:

$$X(\bar{x}) = \begin{cases} 0 & \text{if} \quad \bar{x} < \bar{x}_{\min} \\ p_1(\bar{x}) + 2p_2(\bar{x}) + 3p_3(\bar{x}) & \text{if} \quad \bar{x} \geq \bar{x}_{\min} \end{cases} \quad . \tag{4.6}$$

Statistical analyses were performed in SYSTAT 10 (Systat Software, Inc., Chicago, Illinois, USA). Results were considered significant at $P \leq 0.05$. Means are presented ± 1 SE.

4.4.2 Results

7 of 40 (17.5%) females produced singletons, 27 (67.5%) produced twins, and 6 (15.0%) produced triplets. Maternal age at den entry ranged from 5.8 to 21.8 years (mean: 12.4 ± 0.8 years). Maternal storage energy and energy density at den entry ranged from 3106 to 6798 MJ (mean: 4663 ± 142 MJ) and from 20.2 to 30.8 MJ per kg lean body mass (mean: 25.6 ± 0.4 MJ kg^{-1}), respectively. Both storage energy (Likelihood ratio test, $P = 0.0031$) and energy density (Likelihood ratio test, $P = 0.0001$) were good predictor variables of litter size at den emergence. However, the regression models using energy density as a covariate were significantly better in describing the data than the models that used storage energy (Table 4.2). No significant effect of maternal age on litter size was found, either by itself (Likelihood ratio test, $P = 0.168$), or in combination with storage energy (Likelihood ratio test, $P = 0.760$) or energy density (Likelihood ratio test, $P = 0.746$).

The regression model that was best supported by the data utilized only maternal energy density at den entry as a predictor variable for litter size (Tables 4.2 and 4.3). The minimum October 1 energy density ever observed for a female known to produce at least one cub was 20.0 MJ kg^{-1}. Combining equation (4.5) with the regression model

(Table 4.3), I obtain the following probabilities for producing singletons, twins, or triplets, as a function of energy density at den entry (Figure 4.1a):

$$(4.7a) \qquad p_1(E/LBM) = \frac{\exp(38.82 - 1.44 \cdot E/LBM)}{1 + \exp(38.82 - 1.44 \cdot E/LBM) + \exp(35.55 - 1.25 \cdot E/LBM)}$$

$$(4.7b) \qquad p_2(E/LBM) = \frac{\exp(35.55 - 1.25 \cdot E/LBM)}{1 + \exp(38.82 - 1.44 \cdot E/LBM) + \exp(35.55 - 1.25 \cdot E/LBM)}$$

$$(4.7c) \qquad p_3(E/LBM) = \frac{1}{1 + \exp(38.82 - 1.44 \cdot E/LBM) + \exp(35.55 - 1.25 \cdot E/LBM)} \quad ,$$

if $E / LBM \geq 20.0$ MJ kg^{-1}, whereas for $E / LBM < 20.0$ MJ kg^{-1}, the probability of not reproducing is set as one (i.e., $p_0 = 1$, and $p_1 = p_2 = p_3 = 0$).

Expected mean litter size as a function of energy density at den entry is therefore (Figure 4.1b):

$$(4.8a) \qquad X(E/LBM) = \frac{\exp(38.82 - 1.44 \cdot E/LBM) + 2 \cdot \exp(35.55 - 1.25 \cdot E/LBM) + 3}{1 + \exp(38.82 - 1.44 \cdot E/LBM) + \exp(35.55 - 1.25 \cdot E/LBM)} \quad ,$$

if $E / LBM \geq 20.0$ MJ kg^{-1}, and

$$(4.8b) \qquad X(E/LBM) = 0 \quad ,$$

if $E / LBM < 20.0$ MJ kg^{-1} .

Among the 40 pregnant females considered here, expected mean litter sizes ranged from 1.62 to 2.94 cubs for females with the lowest ($E / LBM = 20.2$ MJ kg^{-1}) and highest ($E / LBM = 30.8$ MJ kg^{-1}) energy density at den entry, respectively. Expected mean litter size increases monotonically with energy density – first moderately, and then sharply for females with energy density > 27 MJ kg^{-1}. This pattern reflects (a) the large overlap in energy density of females producing singletons and twins, and (b) that only females with energy density > 26.5 MJ kg^{-1} produced triplets (Figure 4.1b). The overlap in energy density between females producing singletons or twins suggests that while energy density is a good predictor of litter size, other factors not accounted for may also influence litter size. For example, some of the females that were observed with a single cub may have had enough storage energy to produce twins (Figure 4.1b), but may have been limited by the number of fertilized eggs (Rosing-Asvid *et al.* 2002; Van de Velde *et al.* 2003) or may have lost a cub before, or shortly after, den emergence. Alternatively, reproductive strategies may differ between females, with some females opting to produce fewer but heavier cubs (Derocher & Stirling 1998a).

4.5 Effects of Early Sea Ice Break-Up on Litter Size

4.5.1 Methods

My analyses in the previous section showed that maternal energy density at den entry is a good predictor variable for litter size at den emergence, and best among the state variables considered. Because energy density at den entry is affected by both length of the pre-denning fasting season and body condition at on-shore arrival, I proceeded to evaluate how litter size would be expected to change if polar bears in western Hudson Bay were forced ashore earlier as a result of early sea ice break-up. I further evaluated whether females could compensate for energy density losses and reductions in litter size through feeding on terrestrial resources.

Effects of Early Sea Ice Break-up on Litter Size

Between 1991 and 1998, polar bears in western Hudson Bay came ashore on average around August 1 (Stirling *et al.* 1999). To evaluate the effects of early sea ice break-up on expected litter size, I first set this date as reference on-shore arrival date and define August 1 as $t_0 = 0$. I then considered an adult female of straight line body length L, coming ashore on August 1 with body mass $M(0) = M_A$. Using these initial conditions with equations (4.2) and (4.4), I calculated this female's expected energy density at den entry date t_1 (October 1), and obtained her expected mean litter size from equation (4.8).

I repeated these calculations for all possible combinations of body lengths and body masses, and obtained a reference prediction matrix for expected mean litter size as a function of straight line body length, L, and body mass on ashore date August 1, M_A. I restricted analyses to females between $L = 1.8$ m and $L = 2.2$ m, which corresponds to the range of adult female straight line body lengths observed. Further, I did not allow females to be lighter than their structural mass (i.e., $M \geq 14.94 \cdot L^3$) or heavier than four times their structural mass (i.e., $M \leq 59.76 \cdot L^3$; cf. section 3.7.1). In addition, analyses were confined to body masses ≤ 450 kg, which approximately corresponds to the heaviest female ever observed (Ramsay & Stirling 1988).

Next, I estimated how energy densities at den entry, and thus expected litter sizes, would change if early sea ice break-up would force the bears ashore t days before August 1. Early sea ice break-up affects polar bears in two ways. First, the summer fasting season is lengthened; second, the on-ice feeding period is shortened (Stirling *et al.* 1999; Derocher *et al.* 2004; Stirling & Parkinson 2006). However, no on-ice data exist on polar bear body condition for the summer months preceding on-shore arrival, and on-ice feeding rates are not documented for the population of western Hudson Bay. In particular, it is unclear when these bears accumulate most of their storage energy. This lack of data makes it difficult to quantify how polar bear body condition, and thus energy density at den entry, would be affected by early sea ice break-up. I therefore considered two scenarios. First, bears might accumulate most of their storage energy early in the season and feed at reduced rates during the summer months preceding on-shore arrival, simply maintaining their body mass. For this case I assumed that early sea ice break-up would only result in prolonged fasting, but not in poorer body condition when coming ashore. I termed this the "Early Feeding Scenario". Second, on-ice feeding rates might be high during the months of June and July, comparable to those documented for the central Canadian High Arctic (Stirling & Øritsland 1995). In this case, much of a bear's storage energy is accumulated late in the season, so that females forced ashore early would fast t additional days before entering a maternity den and come ashore in poorer body condition. I termed this the "Late Feeding Scenario".

In both scenarios the calculations were as follows: I first considered an adult female of straight line body length L coming ashore on August 1 with body mass $M(0) = M_A$.

Using these initial conditions, I projected backwards in time to estimate her body mass t days before August 1, writing $M(-t) = M_E$ and $M(-t) = M_L$ for the Early and Late Feeding Scenarios, respectively. In the Early Feeding Scenario, I assumed that body mass t days before August 1 equals body mass on August 1, so that $M_E = M_A$. In the Late Feeding Scenario, I accounted for additional missed feeding opportunities and estimated M_L using an energy budget model that tracks changes in storage energy and body mass due to feeding, somatic maintenance and movement. Hereby, I assumed feeding rates as reported by Stirling & Øritsland (1995) for the central Canadian High Arctic. The energy budget model and its parameterization are presented in Appendix D, parameter values are summarized in Table 4.4. Under this approach, a female with estimated body mass $M(-t) = M_L$ (t days before August 1) would come ashore with body mass $M(0) = M_A$ if she could remain on the sea ice, hunting until August 1. I then used M_E and M_L, respectively, as starting body masses for a fasting season that is initiated t days earlier. I again estimated the female's energy density at den entry (October 1) using equations (4.2) and (4.4), and obtained the new expected mean litter size from equation (4.8). I repeated this procedure for all possible combinations of straight line body lengths, L, and body masses on August 1, M_A. I thereby obtained new prediction matrices for expected mean litter size of females that would have body mass M_A if they came ashore on August 1, but came ashore t days before August 1 instead. Comparing these matrices with the reference prediction matrix of females coming ashore on August 1 gave the respective effects of prolonged fasting (Early Feeding Scenario) and prolonged fasting combined with decreased feeding (Late Feeding Scenario) on litter size. These calculations can be done for any ashore date t_0-t, and I illustrate my results for a medium early ashore date, July 1, and an extreme early ashore date, June 1. The logic of these calculations is illustrated in Figure 4.2 for ashore date July 1 and both the Early and the Late Feeding Scenario.

Compensatory Terrestrial Feeding

I also assessed the plausibility of the hypothesis that polar bears could compensate for losses in body mass (and resultant reductions in litter size) due to early sea ice break-up through feeding on terrestrial resources as periodically suggested (e.g., Dyck *et al.* 2007; Rockwell & Gormezano 2009).

For this purpose, I again considered an adult female of straight line body length, L, coming ashore on August 1 with body mass $M(0) = M_\mathrm{A}$. Using these initial conditions in equation (4.2), I calculated her expected body mass at den entry (October 1), $M(t_1) = M_\mathrm{D}$. I considered M_D the target mass for such a female to be reached by October 1, even if she were forced ashore early, to avoid any negative effects of prolonged fasting on reproduction. I then considered an early ashore date t days before August 1, and projected mass M_A backwards in time under the Early and Late Feeding Scenarios to a fasting season starting mass of $M(-t) = M_\mathrm{E}$ and $M(-t) = M_\mathrm{L}$, respectively. Using these initial conditions, I calculated for both scenarios the daily terrestrial feeding rate β_LAND necessary to reach the target mass M_D on October 1 (cf. illustration in Figure 4.2). Hereby, I attempted to remain conservative and accounted for somatic maintenance, but assumed no energy expenditure towards movement or foraging. This assumption, while probably unrealistic due to the relative inefficiency of polar bear movement (Øritsland *et al.* 1976; Hurst *et al.* 1982) and a high risk of hyperthermia in active polar bears (Øritsland 1970; Best 1982), also makes my results comparable to recent energetic studies, which have made similar assumptions (Rockwell & Gormezano 2009). The necessary feeding rate β_LAND can then be calculated from

$$(4.9) \qquad \beta_\mathrm{LAND} = \delta^{-1}\Phi \cdot \frac{E_\mathrm{D} - E(-t)\cdot \exp(-\Phi\cdot(t_1+t))}{1-\exp(-\Phi\cdot(t_1+t))} + \delta^{-1}\Psi \quad ,$$

(see Appendix E for derivation). Here, E_D is the target storage energy at den entry, corresponding to the target mass $M(t_1) = M_\mathrm{D}$, and $E(-t)$ is the storage energy corresponding to the on-shore arrival masses $M(-t) = M_\mathrm{E}$ or $M(-t) = M_\mathrm{L}$, respectively. Φ and Ψ are short for $\Phi = m\cdot\alpha^{-1}(1-\varphi)$ and $\Psi = m\cdot\rho_\mathrm{STR}\cdot k\cdot L^3$. The parameter δ represents digestive efficiency, and was set as $\delta = 0.917$ for all calculations, corresponding to the digestive efficiency for a mixed diet (Best 1985). Repeating this procedure for all possible combinations of body length, L, and body mass at on-shore arrival August 1, M_A, I obtained matrices giving terrestrial feeding rates necessary to compensate for mass losses (and resultant reductions in expected litter size) due to coming ashore t days before August 1. As above, these calculations can be done for any ashore date t_0-t, and I illustrate my results for a medium early ashore date, July 1, and an extreme early ashore date, June 1.

Predictions for Western Hudson Bay: Data Collection and Analyses

The analyses above yield expected mean litter sizes and compensatory summer feeding rates as a function of ashore date t_0-t for all possible combinations of straight line body length and total body mass. While these analyses are instructive, I also attempted to link these general predictions to observed females body conditions to obtain more specific predictions of changes in expected litter size under early sea ice break-up for the population of western Hudson Bay.

For this purpose, I obtained straight line body lengths and body masses of adult females without dependent offspring ($n = 28$; 4.8-22.8 years old), caught non-selectively during the summer fasting seasons of 1989 to 1996 in the western Hudson Bay denning area. Straight line body lengths and ages were determined as described in section 4.4.1. All bears were weighed (± 0.5 kg) using an electronic load cell suspended from a tripod. None of these females was re-caught the following spring, so I could not assess litter size at den emergence. The data were made available from the Canadian National Polar Bear Database maintained by Environment Canada.

Using the mass loss curve (4.2) I scaled body masses of all females to August 1, and repeated the calculations outlined above for each individual, estimating their energy stores before August 1 under both the Early and Late Feeding Scenario, and using these estimates to calculate expected mean litter sizes under earlier on-shore arrival. I considered on-shore arrival dates ranging from June 1 to August 1. I also calculated individual probabilities for producing zero, one, two, or three cubs for each ashore date under both feeding scenarios (equation (4.7)). For each ashore date and feeding scenario, I then summed the probabilities for zero, one, two, or three cubs, over all females and normalized by sample size to obtain the expected proportions of females producing zero, one, two, or three cubs. I summarized predictions by calculating expected mean litter sizes for this sample of females as a function of on-shore arrival date. I finished by calculating individual and average summer feeding rates necessary to compensate for mass losses (and resultant reductions in litter size) due to coming ashore t days before August 1, again considering both feeding scenarios.

4.5.2 Results

Effects of Early Sea Ice Break-up on Litter Size

Expected mean litter size depends on straight line body length, date of on-shore arrival, and body mass on that date (Figure 4.3). For a female of a given straight line body length and a fixed date of on-shore arrival, expected mean litter size increases monotonically with body mass on that date. In contrast, given a certain body mass at on-shore arrival, expected mean litter size decreases monotonically with increasing body length, because larger females need to utilize more storage energy for somatic maintenance and can therefore invest less into reproduction. For instance, a female weighing 300 kg on August 1 is expected to produce 2.9 cubs if her straight line body length is 1.8 m, 1.7 cubs if her body length is 2.0 m, and not at all if her body length is 2.2 m. Females whose total body mass is less than 2.37 times their structural mass on August 1 are not expected to produce cubs, because their energy density is expected to be below the threshold for successful reproduction (20 MJ kg^{-1}) at den entry (Figure 4.3a). All changes in expected mean litter size are highly nonlinear as a function of straight line body length and total body mass due to the nonlinearity of equation (4.8).

For all combinations of body lengths and body masses, expected litter size decreases substantially with early on-shore arrival in both the Early and the Late Feeding Scenarios (Figures 4.3b-e). Relative reductions in litter size are unevenly distributed across body lengths and masses due to the nonlinearity of the litter size response curve (4.8) (Figures 4.3b-e). Females that would have produced triplets if they had remained hunting on the sea ice until August 1 suffer from the largest relative decline in expected mean litter size, due to the relatively sharp energy density threshold between triplet and twin production (Figure 4.1b). The lower body mass threshold separating successful and unsuccessful reproduction rises with advancing ashore date. For instance, considering the Early Feeding Scenario and on-shore arrival July 1, successful reproduction is predicted only for females whose total body mass would be more than 2.54 times their structural mass on August 1 if they had remained hunting on the sea ice (Figure 4.3b). Considering an early on-shore arrival date June 1, this threshold rises to 2.70 times structural mass (Figure 4.3c). Under the Late Feeding Scenario, the thresholds are approximately 2.86 and 3.36 times structural mass for early ashore dates July 1 and June 1, respectively (Figures 4.3d,e).

To link these general predictions for changes in expected litter size under early sea ice break-up to observed female body conditions, I now consider the 28 solitary females caught in the western Hudson Bay denning area. For these females, estimated energy densities at standardized on-shore arrival date August 1 ranged from 13.8 to 31.4 MJ per kg lean body mass (mean: 24.4 ± 0.80MJ kg^{-1}). Estimated energy densities standardized to den entry (October 1) ranged from 9.2 to 28.3 MJ per kg lean body mass (mean: 20.7 ± 0.86 MJ kg^{-1}). The expected proportions of females producing zero, one, two, or three cubs were $p_0 = 0.393$, $p_1 = 0.138$, $p_2 = 0.440$, and $p_3 = 0.030$ (Figure 4.4a). Expected mean litter size was therefore 1.11 (95% CI: 0.75-1.45; Figure 4.4b). In the literature, mean litter sizes are usually reported as the total number of cubs relative to the number of females that are accompanied by cubs (Ramsay & Stirling 1988; Derocher & Stirling 1995). That is, mean litter sizes are reported conditional on successful reproduction to den emergence. For this sample of females, expected mean litter size conditional on successful reproduction to den emergence was 1.82 (95% CI: 1.73-1.92; Figure 4.4b), which is close to the observed mean litter size of 1.84 reported for this area between 1980 and 1992 (Derocher 1999).

Assuming that these females are representative of the population, the following predictions are obtained for changes in litter size in western Hudson Bay as a function of on-shore arrival date. Mean litter sizes are expected to decline continuously with advancing ashore date in both the Early and Late Feeding Scenario. Under the Early Feeding Scenario, expected mean litter size (including females that are not expected to reproduce) declines from 1.11 for coming ashore on August 1, to 0.81 for coming ashore on July 1, and to 0.49 for coming ashore on June 1 (Figure 4.4b). The proportion of females producing twins and triplets is also expected to decline monotonically. In contrast, the proportion of females producing singletons would remain relatively steady (ranging from 0.08 for on-shore arrival June 1 to 0.14 for on-shore arrival July 27) because some females move from having twins to having singletons, while others move from having singletons to not reproducing. The proportion of non-reproducing females is expected to increase monotonically from 0.39 for on-shore arrival August 1, to 0.54 for on-shore arrival July 1, and to 0.71 for on-shore arrival June 1 (Figure 4.4a). Under the Late Feeding Scenario, the decline in mean litter size would be more dramatic, with an expected mean litter size of 0.25 for on-shore arrival July 1, and no female reproducing for on-shore arrival before June 7 (Figure 4.4d). Similarly to the Early Feeding Scenario, the proportion of non-reproducing females is expected to increase monotonically with advancing ashore date, albeit much faster: for ashore date July 1, the expected proportion of females not reproducing is 0.86, and for on-shore arrival before June 7 reproduction would become impossible (Figure 4.4c).

Compensatory Terrestrial Feeding

On-land feeding rates necessary to compensate for mass losses (and resultant reductions in litter size) due to an increased fasting season length and missed on-ice feeding opportunities (the latter only in the Late Feeding Scenario) depend on on-shore arrival date, straight line body length, and total body mass. For on-shore arrival on July 1, necessary feeding rates range from 2.96 to 8.41 MJ d^{-1} for the Early Feeding Scenario, and from 16.44 to 18.08 MJ d^{-1} for the Late Feeding Scenario; for on-shore arrival June 1, necessary feeding rates range from 4.39 to 12.48 MJ d^{-1}, and from 24.48 to 26.59 MJ d^{-1} for the Early and Late Feeding Scenarios, respectively (Figure 4.5). It should, however, be noted that feeding rates as reported by Stirling & Øritsland (1995) for the central

Canadian High Arctic probably overestimate feeding rates of at least some polar bears in western Hudson Bay, at least for the months of June and July. Assuming these feeding rates, movement rates from Parks *et al.* (2006), and the energy budget model presented here (Appendix D), at least one of the 28 solitary adult females cannot be projected backwards as far as June 1, because her total body mass would fall below her structural mass on dates before June 14 (i.e., storage energy would become negative, implying that the female would have been dead). Superficially, this inconsistency might be explained by individual variation in feeding rate, movement rate, or energy utilization. However, several other females also come close to their structural mass when projected backwards to June 1 (Figure 4.5d), indicating that either their feeding rates were also overestimated, or alternatively, that energy utilization was underestimated. Given the available data, this question cannot be resolved. In this regard, the Late Feeding Scenario likely provides the most extreme outcome possible.

Finally, I considered compensatory summer feeding rates for the sample of 28 solitary adult females. Average estimates for necessary summer feeding rates increase nonlinearly with advancing ashore date in both the Early and Late Feeding Scenarios (Figure 4.6a). For instance, coming ashore on July 1, these females would need to consume on average 5.35 MJ d^{-1} (range: 4.11-7.16 MJ d^{-1}) in the Early, and 17.30 MJ d^{-1} (range: 16.74- 17.80MJ d^{-1}) in the Late Feeding Scenario, to compensate for mass losses due to early on-shore arrival. If they came ashore on June 1, average compensatory summer feeding rates increase to 7.94 MJ d^{-1} (range: 6.10-10.63 MJ d^{-1}) in the Early, and to 25.80 MJ d^{-1} (range: 24.94-26.40 MJ d^{-1}) in the Late Feeding Scenario, respectively. The observed nonlinearity in daily feeding rates reflects that coming ashore early by t days also means that summer feeding can be spread out over t additional days. In contrast, *total* compensatory energy intake between the day of on-shore arrival and den entry increases near linearly with advancing ashore date. For each additional day spent on land before August 1, females would need to consume 15.9 MJ under the Early Feeding Scenario, and 51.6 MJ under the Late Feeding Scenario, to compensate for mass losses due to prolonged fasting and decreased on-ice feeding (Figure 4.6b).

4.6 Discussion

Quantitative predictions of population dynamics under climate change are possible if (a) predictions for future environmental conditions are available, (b) the relationship between future conditions and demographic parameters survival and reproduction 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*), this approach has been successful because appropriate data on reproduction and survival under environmental conditions similar to those predicted exist (Jenouvrier *et al.* 2009). In contrast, this approach is difficult for polar bears because historic and predicted environmental conditions differ substantially (Wiig *et al.* 2008), and the functional relationship between survival, reproduction and future conditions is in consequence largely unknown.

The only study to attempt such a synthetic population viability approach in polar bears was by Hunter *et al.* (2007), who predicted the dynamics of the southern Beaufort Sea polar bear population under climate change. The authors were, however, forced to estimate the relationship between sea ice condition, survival, and reproduction, from only six years of capture-recapture data. Their analyses, while laudable, suffer from large uncertainty and wide prediction intervals due to this rather crudely defined relationship. Furthermore, their results cannot be applied to other polar bear populations, where predicted environmental conditions differ, and little or no data exist to quantify the relationship between predicted sea ice conditions and demographic parameters. Rather than estimating demographic parameters from limited data and attempting extrapolation, I suggest using independent predictions of survival and reproduction under future environmental conditions. For energy-determined components of survival and reproduction, such predictions can be obtained from mechanistic dynamic energy budget models, as shown here for the litter size of pregnant females. I have focused on the western Hudson Bay population for model parameterization and predictions, but the approach is general and could be applied to any polar bear population. Reproductive output could be predicted from local sea ice conditions or predictions due to the mechanistic nature of the model, even if no regional data on litter sizes exist.

The prediction of polar bear reproduction under climatic warming hinges on a clear understanding of the causal chain linking changes in sea ice condition to changes in reproduction (Jonzén *et al.* 2005; Krebs & Berteaux 2006). For polar bear populations in the Seasonal Sea Ice Ecoregion this chain is reasonably well understood, and can be described as follows (Stirling *et al.* 1999; Derocher *et al.* 2004; Stirling & Parkinson 2006): Progressively earlier spring sea ice break-up shortens the time polar bears can hunt for seals. With advancing on-shore arrival polar bears are thus expected to come ashore in progressively poorer body condition. A prolonged fasting season further reduces energy stores until gestation begins in fall, thereby negatively affecting litter size, litter mass, and subsequent cub survival. Polar bears may be able to compensate for some losses in body mass and energy stores through terrestrial feeding, but the extent to which this is possible is unclear. In the absence of data describing reproduction as a function of on-shore arrival date, quantitative prediction is impossible without a modelling framework that addresses each of these steps explicitly (Berteaux *et al.* 2006; Krebs & Berteaux 2006; Sutherland 2006). I have presented such a framework in this chapter, and applied it to predict changes in litter size as a function of on-shore arrival date for the population of western Hudson Bay.

Following the causal chain outlined above, I addressed four different questions:

(i) How would female body mass at on-shore arrival be affected by on-shore arrival date?
(ii) Given on-shore arrival date and body mass on this date, can we estimate body mass at den entry?
(iii) Given body mass at den entry, can we predict litter size at den emergence?
(iv) How much terrestrial feeding would be necessary to compensate for losses in body mass (and resultant reductions in litter size) due to early on-shore arrival?

Each of these questions was treated within a common dynamic energy budget framework that synthesized current knowledge on polar bear physiology, behaviour, and feeding, supplemented by new data analyses presented in this thesis. However, data availability for model parameterization differed between each step, resulting in varying degrees of uncertainty. The model therefore also pinpointed data gaps that prevented more accurate predictions of polar bear reproduction under progressively earlier on-shore arrival.

Mass loss of pregnant females between on-shore arrival and den entry (question (ii)), and litter size at den emergence as a function of energy density at den entry (question (iii)) relate to polar bear physiology. These components are likely associated with the smallest relative error, because sufficient data was available to parameterize a body composition model for adult females (Chapter 3), a mass loss curve for fasting adult polar bears (sections 3.5 and 4.4.1), and a logistic regression curve for expected mean litter size at den emergence (section 4.4). It would be possible to improve these components, most notably through additional body composition data as discussed in sections 3.6 and 3.8, and the inclusion of non-reproducing females in the logistic regression models to relax the assumption of an absolute minimum energy density threshold for reproduction (section 4.4). However, given that this threshold was parameterized using the lowest energy density ever observed for a female producing cubs, any bias in predicted litter size reductions would be towards overestimating litter sizes, rendering my predictions conservative.

The largest uncertainty in model predictions of litter sizes under early sea ice break-up stems from the fact that female body masses are not documented for the months preceding on-shore arrival. Consequently, it is unclear at what body masses pregnant females would come ashore if forced ashore earlier (question (i)). On-ice female body mass data would therefore substantially improve our ability to predict changes in reproduction under climatic warming, and could be collected with relatively little effort. In the absence of such data, I attempted to estimate June and July body masses by assuming two on-ice feeding scenarios, which probably represent the most extreme outcomes possible. The Early Feeding Scenario only accounts for prolonged fasting, and thus probably overestimates adult female body masses at early on-shore arrival. In contrast, the Late Feeding Scenario also accounts for missed feeding opportunities by assuming feeding rates as reported for the central Canadian High Arctic (Stirling 1974; Stirling & Øritsland 1995). These feeding rates likely overestimate feeding rates of adult females in western Hudson Bay (section 4.5.2), so that body masses at early on-shore arrival are probably underestimated in this scenario.

Regardless of the feeding scenario considered, substantial declines in mean litter size are predicted for the population of western Hudson Bay with advancing spring sea ice break-up (Figure 4.4). In recent years, adult females were forced to leave the sea ice approximately 1-2 weeks earlier than during the 1990s (A. E. Derocher, unpublished data), and changes in litter size corresponding to those predicted here (Figure 4.4) have already been observed. Females with triplets are now rarely seen, and the proportion of females with twins has also declined (A. E. Derocher, unpublished data). However, precise numbers that could be used for model validation do not exist. Further negative changes are expected with advancing sea ice break-up (Figure 4.4), but the rate of these changes can only be approximated by the two on-ice feeding scenarios described here. More accurate predictions must await data collection of on-ice female body masses or on-ice feeding rates.

Nevertheless, my analyses indicate that the viability of the western Hudson Bay polar bear population may be significantly affected by the ability of females to successfully reproduce despite nutritional stress imposed by a prolonged open-water season. Assuming that the 28 females considered here are representative of the population, and further assuming the Late Feeding Scenario and that spring sea ice break-up continues to advance at a linear rate of -0.75 days year^{-1} (Stirling & Parkinson 2006), more than 80% of pregnant females are expected to be unable to reproduce in a given season within 12-21 years. Under the same assumptions, complete cessation of reproduction is expected to occur within 55-65 years (Figure 4.4c). Even in the Early Feeding Scenario more than two-thirds of pregnant females are expected to have insufficient storage energy for successful parturition in a given season within 55-65 years, again assuming linear sea ice break-up advance (Figure 4.4a). Given that predicted changes in sea ice dynamics are nonlinear, with a trend towards accelerated melting (e.g., Holland *et al.* 2006; Stroeve *et al.* 2007), and given that I have not considered carry-over effects of low female body condition between consecutive years of low sea ice (Stirling & Parkinson 2006), these numbers likely constitute an optimistic projection. These predictions should, however, be treated in light of the assumption that female energy densities in western Hudson Bay were sufficiently represented by the sample of 28 females. The assumption seems justified, because predicted mean litter size for this sample of females closely matched the population average (section 4.5.2). Nevertheless, future studies should attempt to validate my predictions using larger and more recent samples. For monitoring purposes, I recommend recording mean litter sizes relative to all solitary females rather than relative to females that produce at least one cub, as is often done (Ramsay & Stirling 1988; Derocher & Stirling 1995), because the latter statistic is insensitive to changes in litter size due to early on-shore arrival (Figures 4.4b,d).

Terrestrial feeding may slow projected declines in reproductive success somewhat, but is unlikely to significantly compensate for losses in body mass and consequent losses in litter size due to earlier on-shore arrival. For instance, considering the Early Feeding Scenario and an on-shore arrival date July 1, each female would need to consume on average *ca.* 500 MJ before den entry to compensate for mass losses due to prolonged fasting. Under the Late Feeding Scenario, each female's energy requirement increases to *ca.* 1600 MJ. Based on the energy content of blueberry (*Vaccinium uliginosum*; Usui *et al.* 1994), these numbers translate into approximately 333 kg and 1065 kg of blueberries [after correcting digestive efficiency to $\delta = 0.627$; Pritchard & Robbins (1990)], or, using the energy content and digestive efficiency of goose (*Anser caerulescens*) eggs (Rockwell & Gormezano 2009) into 521 and 1670 required eggs per adult female, respectively. These estimates are all highly conservative due to my assumption that terrestrial foraging does not require energy additional to somatic maintenance. Given that even polar bears that currently feed on berries during the on-shore fasting season gain little energy from this supplementary food source (Hobson *et al.* 2009), and given that other food sources such as goose eggs are limited relative to polar bear population size (e.g., only about 200,000 eggs in the entire snow goose colony of the western Hudson Bay denning area (Rockwell & Gormezano 2009) relative to a current polar bear population of approximately 935 animals), sufficient compensatory feeding is highly unlikely despite reported plasticity in polar bear feeding behaviour (Russell 1975; Derocher *et al.* 1993a).

A shift towards earlier blastocyst implantation and maternity den entry may be an alternative means to avoid reductions in litter size due to a prolonged pre-denning fasting season. Such climate-induced changes in phenology have been observed in a variety of taxa, including insects, birds, and amphibians (McCarty 2001; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006). However, it is doubtful whether polar bears could successfully adopt such a strategy. Earlier den entry and parturition would result in earlier den emergence, creating a mismatch between food requirements of newly emerged family groups and peak food availability. Seals are difficult to catch in winter and are most accessible from late-March onwards when they haul out onto the sea ice for pupping and moulting (Stirling & McEwan 1975; Kingsley & Stirling 1991; Stirling & Øritsland 1995). Such an asynchrony between reproductive timing and resource availability could increase cub and adult mortality (Thomas *et al.* 2001), further jeopardizing the viability of polar bear populations. It is possible, that in a warmer climate seals become more accessible early in the season (Stirling & Smith 2004; Rosing-Asvid 2006), or that seal populations increase due to increased primary productivity (Arrigo *et al.* 2008), thereby at least temporarily alleviating some of the food stress in polar bears. However, climate change associated declines in seal pup recruitment are already observed in Hudson Bay (Ferguson *et al.* 2005; Stirling 2005), so that predictions of future seal population declines seem likely (Learmonth *et al.* 2006; Kovacs & Lydersen 2008). Precise assessment of the energetic consequences of such changes in phenology or prey availability are beyond the scope of this dissertation, but could also be attempted within the dynamic energy budget framework presented here.

Future studies should attempt to further develop the modelling framework presented here to include the entire reproductive cycle of polar bears. Many reproductive components are probably determined by storage energy and could thus be negatively affected in food-stressed females. Low storage energy may result in low milk production (Derocher *et al.* 1993b), which may slow cub growth, or even increase cub mortality (Arnould & Ramsay 1994). Slower cub growth may, in turn, result in delayed sexual maturity (Derocher & Stirling 1998b). As food stress increases, females may cease to lactate entirely, unable to maintain milk production during a mother-offspring bond that can last up to 2.5 years (Derocher *et al.* 1993b). Parameterizing a full dynamic energy budget model is data-intensive (Gurney *et al.* 1990; Nisbet *et al.* 2004), and not possible given the currently available data. However, in Chapter 5, I will outline how such models could be developed and discuss key data requirements necessary for model parameterization.

The model presented here, as well as future dynamic energy budget models considering survival or other components of reproduction, could be integrated within matrix models (Klanjscek *et al.* 2006) to evaluate population level effects of predicted changes in demographic parameters. Matrix models, such as the one developed by Hunter *et al.* (2007), predict changes in population abundance due to changes in reproduction and survival, whereas the individual-level approach taken here predicts changes in demographic parameters in response to environmental conditions. The two approaches are therefore complementary, and could be used together to predict polar bear population responses to climatic warming. Other detrimental but non-energy related effects of climate change on both reproduction (e.g., an increased chance of maternity den collapse and family group mortality due to increased precipitation; Clarkson & Irish 1991) and survival (e.g., an increased chance of drowning; Monnett & Gleason 2006) could also be included in such a comprehensive framework.

Abbreviation	Definition	Units
State variables		
L	Straight line body length	m
G	Axillary girth	m
M	Total body mass	kg
LBM	Lean body mass	kg
E	Total energy content of storage	MJ
E / LBM	Energy density (= storage energy relative to lean body mass)	MJ kg^{-1}
Estimated reproductive quantities		
X	Expected mean litter size	---
p_i	Probability of producing i cubs ($i = 0, 1, 2, 3$)	---

Table 4.1: State variables and estimated reproductive output variables.

Model covariates	No. of parameters estimated	AIC_c	ΔAIC_c	AIC_c weight
E / LBM	4	59.80	0	0.877
E / LBM , Age	6	64.62	4.82	0.079
E	4	65.99	6.19	0.040
E , Age	6	70.84	11.04	0.004
Age	4	74.30	14.50	0.001

Table 4.2: Multinomial logistic regression models for litter size at den emergence. Possible covariates are maternal storage energy at den entry (E), maternal energy density at den entry (E / LBM), and maternal age at den entry (Age). Models are ranked by their AIC_c value. ΔAIC_c is the difference between each model's AIC_c value and the AIC_c value of the best supported model.

Comparison	Variable	Parameter estimate ± SE	95% CI
Singletons / Triplets	(Intercept)	38.82 ± 14.21	(16.29 ; 75.47)
	E / LBM	-1.44 ± 0.52	(-2.77 ; -0.61)
Twins / Triplets	(Intercept)	35.55 ± 13.53	(14.86 ; 71.38)
	E / LBM	-1.25 ± 0.49	(-2.54 ; -0.50)

Table 4.3: Estimated coefficients in the best multinomial logistic regression model that describes litter size at den emergence as a function of maternal energy density at den entry. The column "Comparison" refers to the two separate binary regressions simultaneously performed by multinomial regression: one regression compares females producing singletons against females producing triplets, the other compares females producing twins against females producing triplets.

Parameter	Definition	Estimate	Units	Source[*]
Body composition				
φ	Proportion of storage mass that is fat	0.627	---	Chapter 3
α	Constant that converts storage mass into storage energy	26.14	MJ kg^{-1}	Chapter 3
$\rho_{STR}\cdot k$	Proportionality constant relating structural mass to straight line body length	14.94	kg m^{-3}	Chapter 3
Somatic maintenance				
m	Energy required per unit time to maintain a unit mass of lean tissue	0.089	MJ kg^{-1} d^{-1}	Chapter 3
Movement				
a	Proportionality constant accounting for postural effect	0	MJ d^{-1}	Appendix D, data from (1), (2)
b	Allometric exponent	Not estimated	---	---
c	Incremental cost of locomotion	0.0018	MJ km^{-1}	Appendix D, data from (1), (2)
d	Allometric exponent	0.684	---	(3)
v	Average on-ice velocity	5.6	km d^{-1}	(4)
Feeding				
β	On-ice feeding rate (Late Feeding Scenario only)	59.1	MJ d^{-1}	Appendix D, data from (5)-(7)
δ	Digestive efficiency for a mixed diet	0.917	---	(8)

Table 4.4: Energy budget model parameters for adult female polar bears hunting on the sea ice in western Hudson Bay during the months of June and July. [*]Data sources: (1) Øritsland *et al.* (1976); (2) Hurst *et al.* (1982); (3) Taylor *et al.* (1982); (4) Parks *et al.* (2006); (5) Stirling & Øritsland (1995); (6) Stirling (1974); (7) Stirling & McEwan (1975); (8) Best (1985).

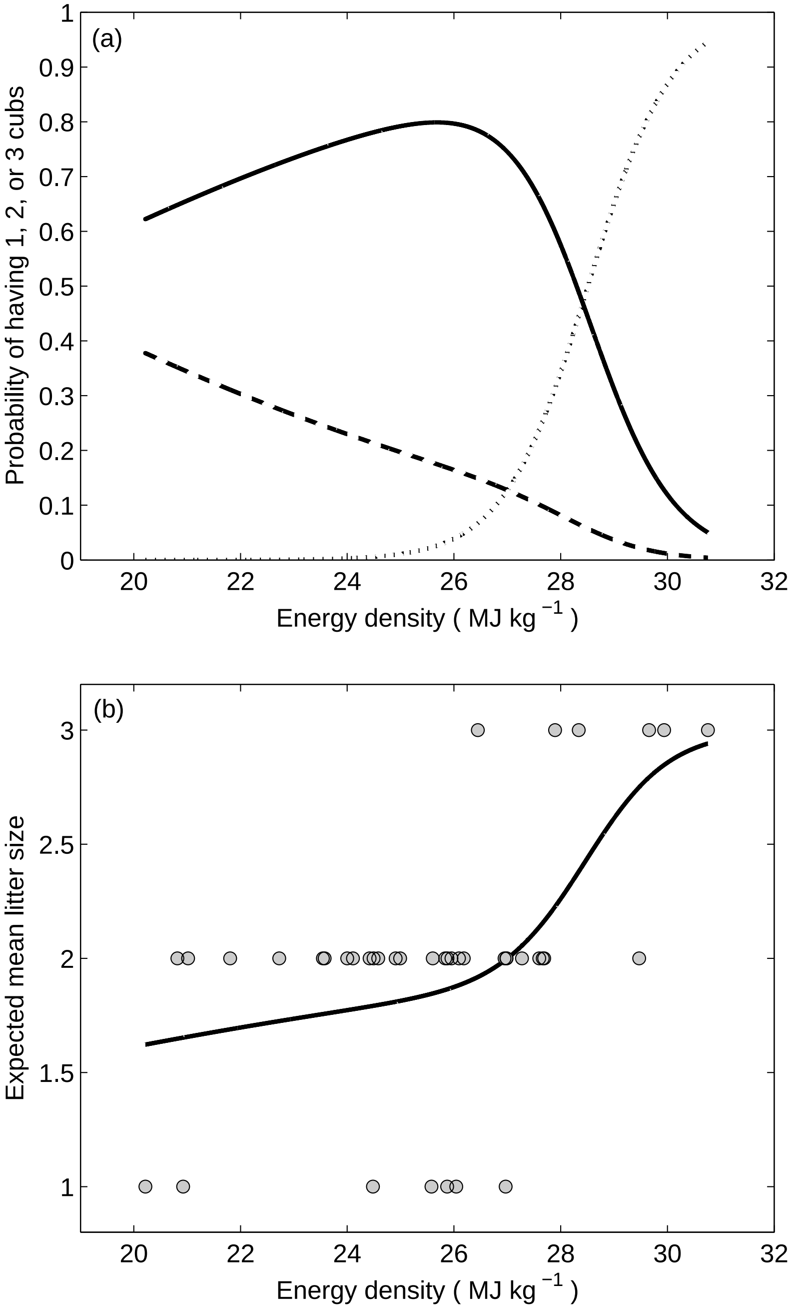


Figure 4.1: (a) Estimated probabilities for a pregnant female polar bear to produce one (dashed line), two (solid line), or three cubs (dotted line) as a function of maternal energy density at den entry, as determined by multinomial logistic regression. (b) Expected mean litter size as a function of maternal energy density at den entry, as determined by multinomial logistic regression. Data are observed litter sizes at den emergence as a function of maternal energy density at den entry.

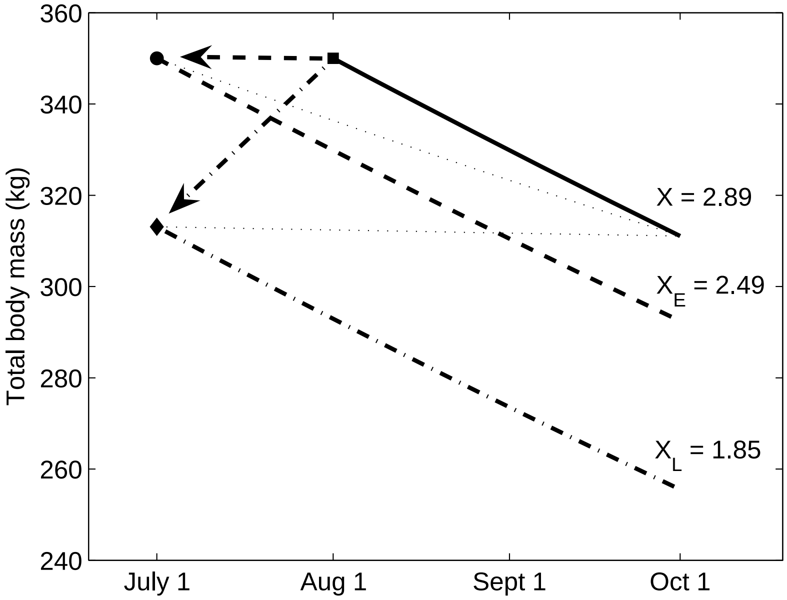
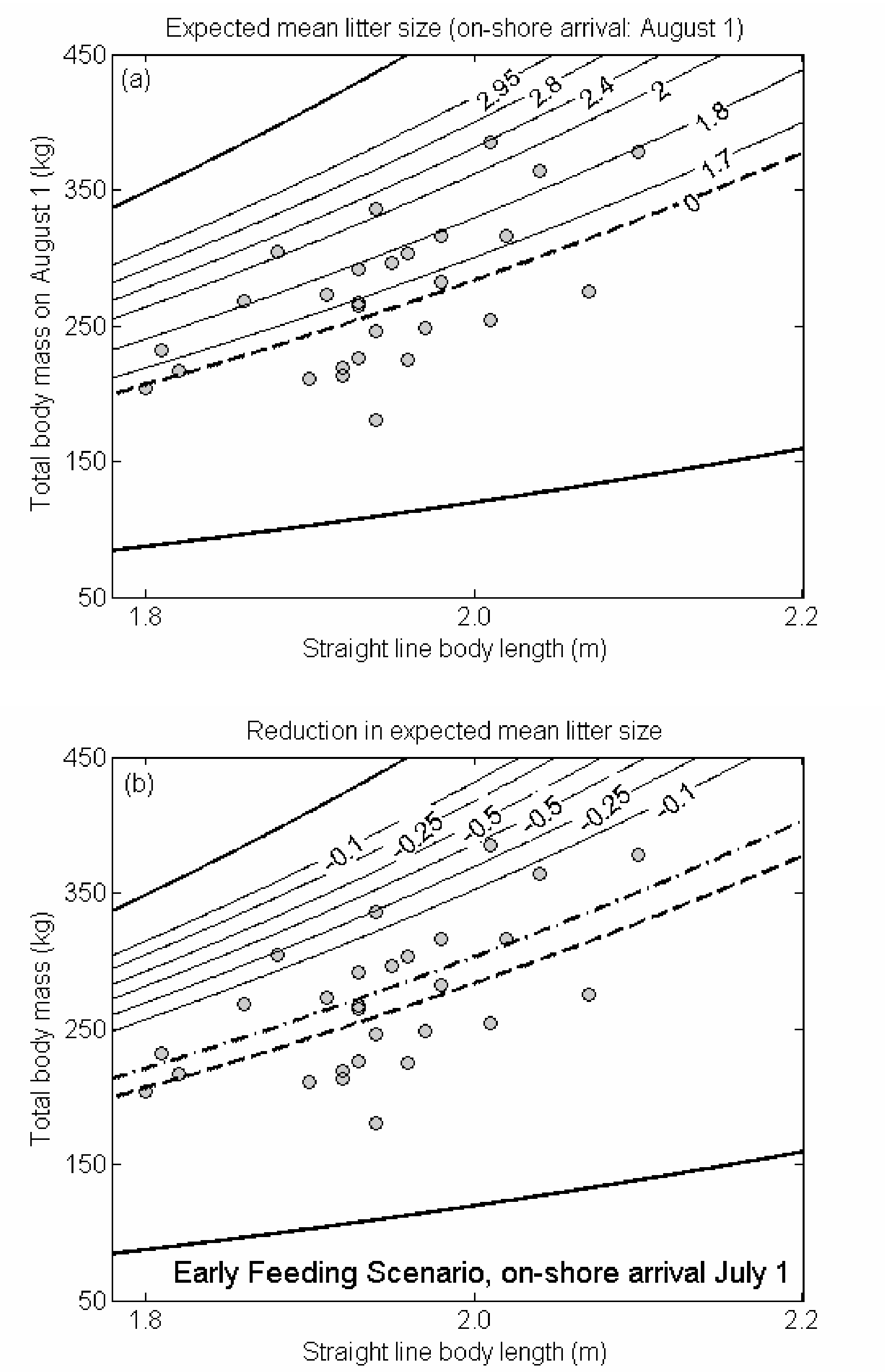
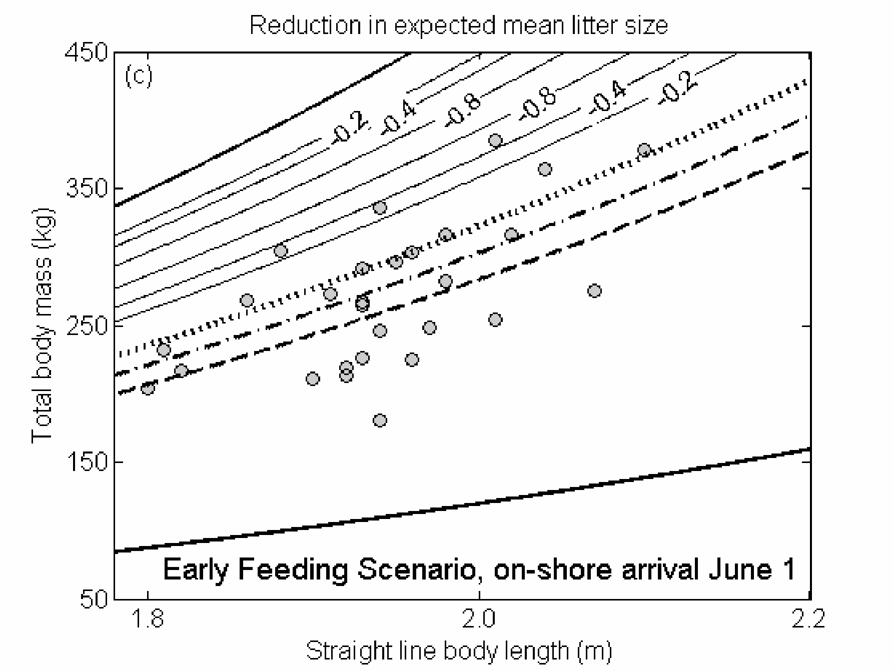
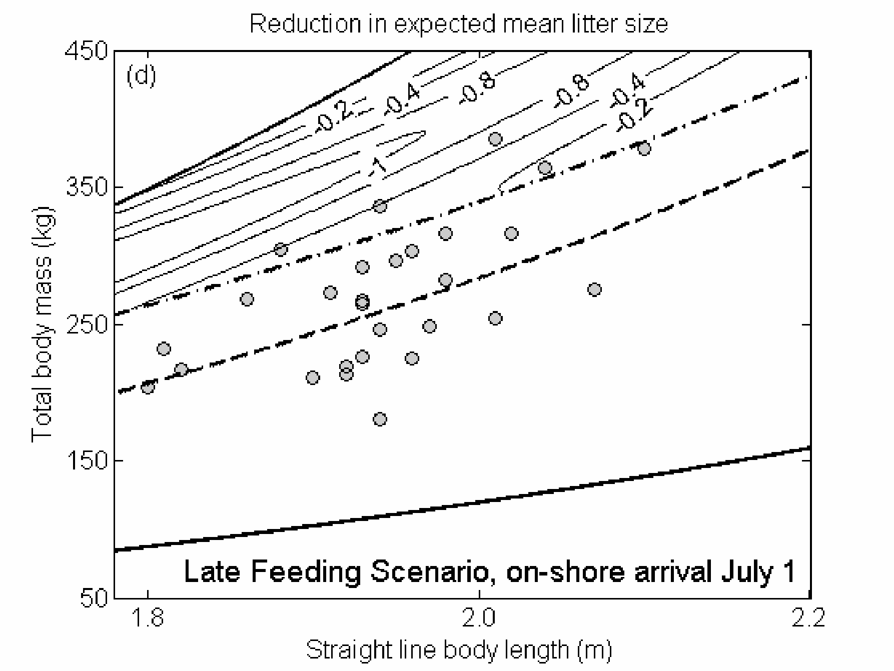


Figure 4.2: The logic of my analyses for changes in expected mean litter size under early sea ice break-up, illustrated for a female with straight line body length L = 1.9 m coming ashore on August 1 with body mass M_A = 350 kg (solid square). Given these initial conditions, body mass at den entry (October 1) is estimated as 311.1 kg (solid line), which results in an expected mean litter size of X = 2.89. Mass is then projected backwards in time from August 1 to an early ashore date (arrows). In this example, an early on-shore arrival of July 1 is considered, and fasting starts with a body mass of M_E = M_A = 350 kg in the Early Feeding Scenario (solid circle), and with a body mass of M_L = 313.1 kg in the Late Feeding Scenario (solid diamond). Mass loss due to fasting results in body masses of 292.4 kg and 255.5 kg on October 1, and expected mean litter sizes of X_E = 2.49 and X_L = 1.85, for the Early (dashed line) and Late (dot-dashed line) Feeding Scenarios, respectively. I also calculate the daily terrestrial energy intake necessary to compensate for mass losses and losses in litter size due to coming ashore on July 1 rather than August 1. If the female can acquire this energy, mass loss (dotted lines) would be slowed enough to reach the target mass 311.1 kg on October 1 (i.e., her den entry body mass if she had come ashore on August 1).


Expected mean litter size (on-shore arrival: August 1)
(a)
2.95
2.8
2.4
2
1.8
1.7
0
Total body mass on August 1 (kg)
Straight line body length (m)
450
350
250
150
50
1.8
2.0
2.2
Reduction in expected mean litter size
(b)
-0.1
-0.25
-0.5
-0.5
-0.25
-0.1
Total body mass (kg)
Straight line body length (m)
Early Feeding Scenario, on-shore arrival July 1
450
350
250
150
50
1.8
2.0
2.2


Reduction in expected mean litter size
(c)
-0.2
-0.4
-0.8
-0.8
-0.4
-0.2
Early Feeding Scenario, on-shore arrival June 1
Total body mass (kg)
450
350
250
150
50
1.8
2.0
2.2
Straight line body length (m)


Reduction in expected mean litter size
(d)
-0.2
-0.4
-0.8
-1
-0.8
-0.4
-0.2
Late Feeding Scenario, on-shore arrival July 1
Total body mass (kg)
450
350
250
150
50
1.8
2.0
2.2
Straight line body length (m)

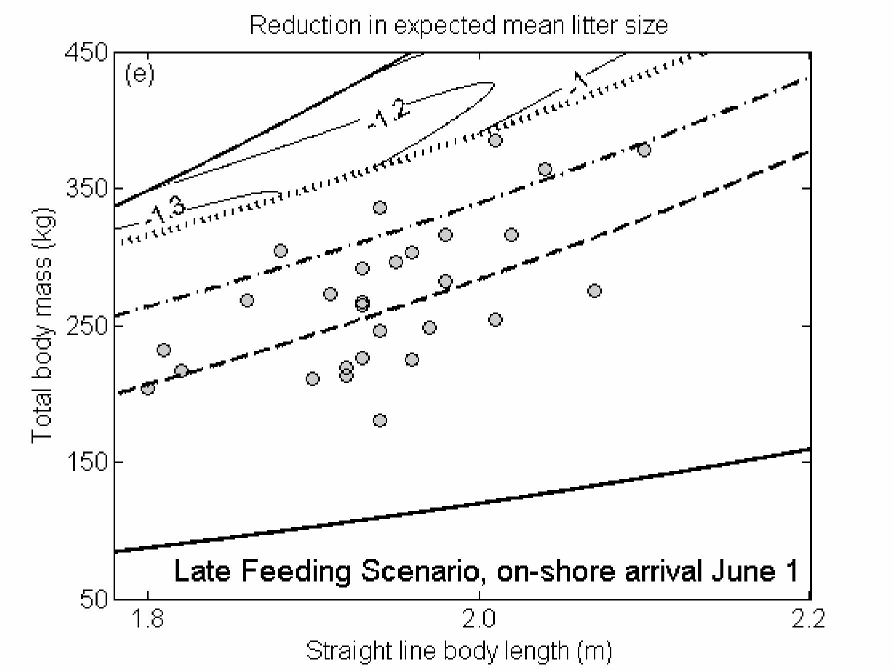


Figure 4.3: (a) Contour lines showing expected mean litter size of females coming ashore on August 1 with straight line body length *L* and total body mass M_A. Females with body masses below the dashed line on August 1 are not expected to produce cubs because their energy density will be below the threshold for successful reproduction at den entry (20 MJ kg^{-1}). (b-e) Expected reductions in mean litter size due to early on-shore arrival. All reductions are shown as a function of straight line body length *L* and the body mass M_A a female would have on August 1 if she remained on the sea ice hunting. Females between the dashed and dot-dashed lines are expected to reproduce if coming ashore on August 1, but not if coming ashore on July 1. Females between the dot-dashed and dotted lines are expected to reproduce if coming ashore on July 1, but not if coming ashore on June 1. Upper and lower solid lines in all panels encompass the range of body masses possible, with the lower line set as structural body mass, the upper line as four times structural mass (section 3.7.1). Data in all panels are body masses and straight line body lengths of 28 solitary females handled during the on-land fasting season in western Hudson Bay, with body masses scaled to August 1.

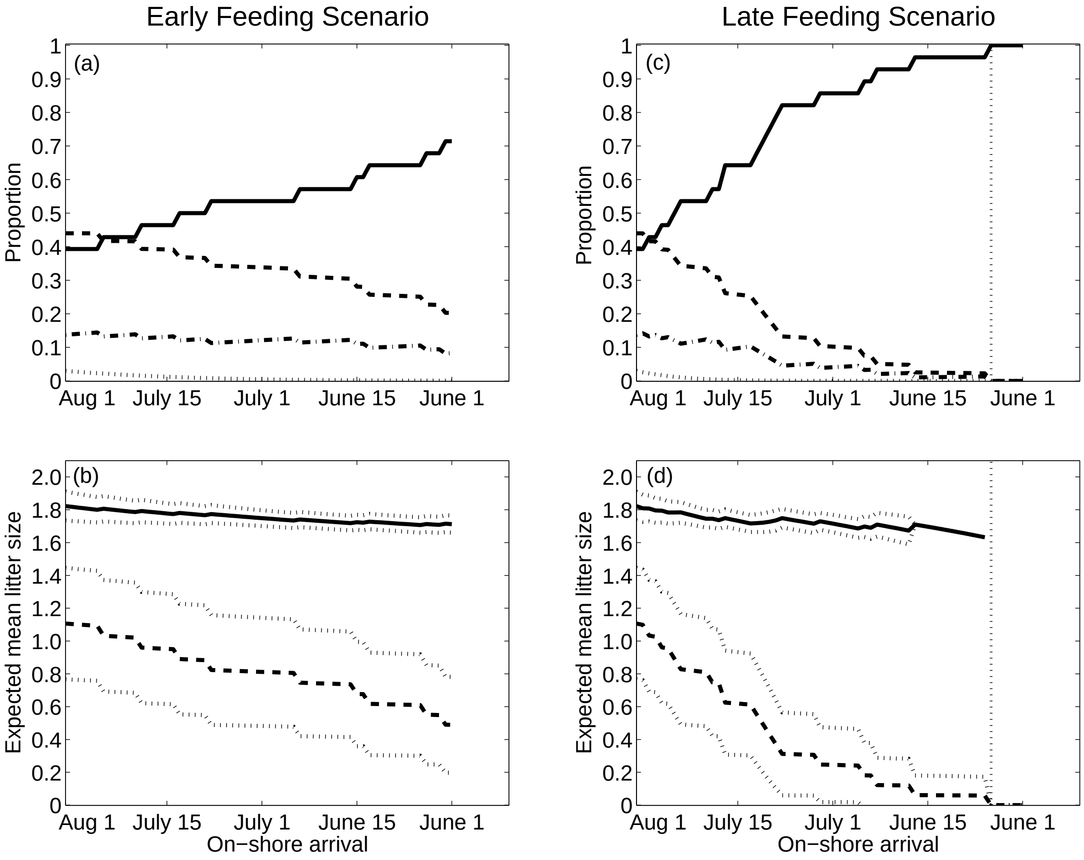


Figure 4.4: Projections of reproduction assuming early on-shore arrival, calculated for the sample of 28 solitary females handled in western Hudson Bay. (a) Expected proportion of females producing zero (solid line), one (dot-dashed line), two (dashed line), or three (dotted line) cubs under the Early Feeding Scenario as a function of on-shore arrival date; (b) Overall expected mean litter size (dashed line) and expected mean litter size conditional on producing at least one cub (solid line) under the Early Feeding Scenario as a function of on-shore arrival date. Dotted lines are 95% confidence intervals; (c) Same as (a), but for the Late Feeding Scenario; (d) Same as (b), but for the Late Feeding Scenario.

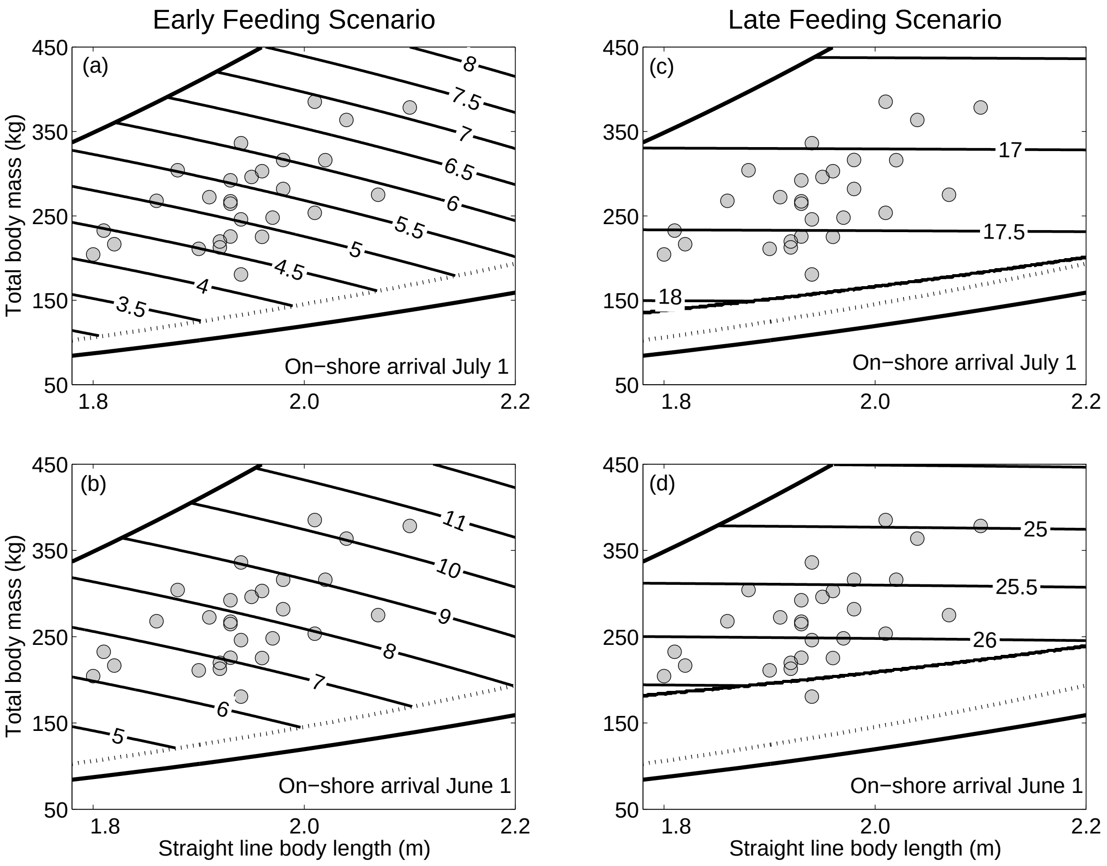


Figure 4.5: Contour lines showing terrestrial feeding rates (MJ d^{-1}) necessary to compensate for mass losses (and resultant reductions in litter size) due to coming ashore before August 1. (a) and (b) show the Early Feeding Scenario, (c) and (d) the Late Feeding Scenario for on-shore arrival dates July 1 and June 1, respectively. All feeding rates are shown as a function of straight line body length L and the body mass M_A a female would have on August 1 if she remained on the sea ice hunting. Upper and lower solid lines in all panels encompass the range of body masses possible, with the lower line set as structural body mass, the upper line as four times structural mass (section 3.7.1). Females with body masses M_A below the dotted lines are not considered because they are expected to starve before den entry. Females with body masses M_A below the dashed line (Late Feeding Scenarios only) are not considered because projecting them backwards using the assumed feeding rates results in nonsensical values (i.e., the female could not have lived on July 1 or June 1, respectively. In other words, if she came ashore with body mass M_A below the dashed line, then she must have eaten less than assumed). Data in all panels are body masses and straight line body lengths of 28 solitary females handled during the on-land fasting season in western Hudson Bay, with body masses scaled to August 1.

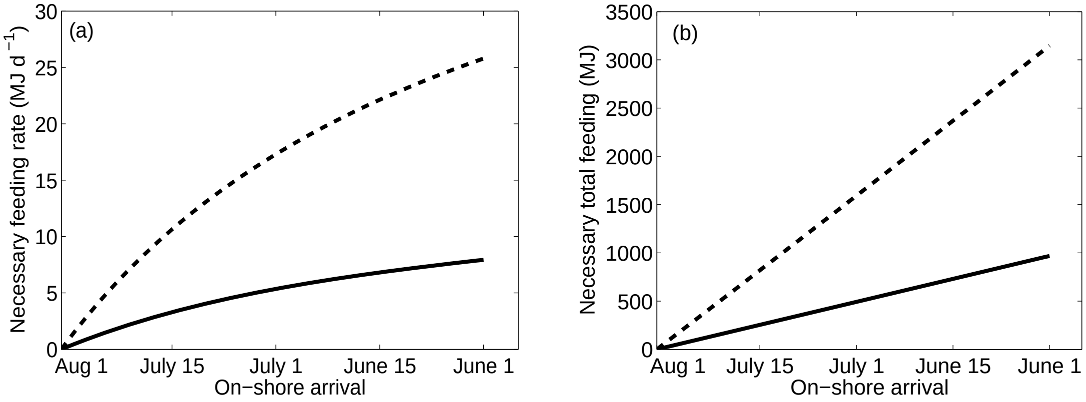


Figure 4.6: Terrestrial feeding necessary to compensate for mass losses (and resultant reductions in litter size) if coming ashore before August 1, as calculated for the sample of 28 solitary females handled in western Hudson Bay. (a) Average terrestrial feeding rate necessary for compensation (MJ d^{-1}). (b) Average total terrestrial feeding necessary for compensation between on-shore arrival and den entry (MJ). In both (a) and (b), solid lines represent the Early Feeding Scenario, dashed lines the Late Feeding Scenario.

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Chapter 5

5 Synthesis, Future Directions, and Concluding Remarks

To date, most predictions on the future of polar bears (*Ursus maritimus*) under climatic warming or various harvest scenarios are either qualitative or based on extrapolation from current conditions (e.g., Stirling & Derocher 1993; Stirling *et al.* 1999; Derocher *et al.* 2004; Aars *et al.* 2006; Rosing-Asvid 2006; Stirling & Parkinson 2006; Dyck *et al.* 2007; Laidre *et al.* 2008; Moore & Huntington 2008; Wiig *et al.* 2008). While these and other studies are useful for providing insights into complex interactions between ecological dynamics, climatic variables, and anthropogenic influences, any predictions obtained by such extrapolation must be treated with caution. Predicted conditions often fall outside observed ranges, so that nonlinear dynamics and process uncertainty can easily result in spurious predictions (Pascual *et al.* 1997; Berteaux *et al.* 2006; Sutherland 2006). This kind of problem is illustrated by the failure of demographers to accurately predict human population growth (Sutherland 2006), or by the large uncertainty involved in climate envelope modelling, used to predict species distributions under climate change (Pearson & Dawson 2003; Heikkinen *et al.* 2006; Pearson *et al.* 2006). Thomas *et al.* (2004), for instance, predict a 0% species extinction risk for the ice biome, in apparent contradiction to qualitative and quantitative analyses predicting substantial extinction, or at least extirpation, risks (Derocher *et al.* 2004; Amstrup *et al.* 2007; Hunter *et al.* 2007; Fuglei & Ims 2008; Kovacs & Lydersen 2008; Moore & Huntington 2008; Ragen *et al.* 2008; Jenouvrier *et al.* 2009). Another example illustrating the limitations of extrapolation, specifically for polar bears, is given by Derocher *et al.* (2004). Based on linear advances in spring sea ice break-up, they calculate that most females in western Hudson Bay would be unable to give birth by 2100. They contrast this estimate with alternative calculations, based on observed linear declines in average female body mass, which imply that unsuccessful parturition for most females would occur by 2012.

Population viability analyses, routinely used to determine harvest quotas of polar bears (e.g., Taylor *et al.* 2006, 2008a,b), and more recently to predict polar bear population dynamics under climate change (Hunter *et al.* 2007), are reasonable advances, but have similar problems (Sutherland 2006): in such population viability analyses, population sizes or extinction risks are predicted from, sometimes sophisticated, phenomenological population models, which assume that future vital rates are accurately represented by existing estimates, or that changes in vital rates in response to density-dependence or environmental trends can be accurately predicted from present conditions. Yet, common problems of population viability analyses (not limited to polar bear modelling) include that vital rate estimates are often based on short datasets, models are poorly (if at all) validated, and density-dependence and environmental trends are seldom accounted for (Beissinger & Westphal 1998; Ludwig 1999; Coulson *et al.* 2001; Ellner *et al.* 2002; Sutherland 2006). Taylor *et al.* (2006, 2008a,b), for instance, do not include the possibility of environmental change and do not account for density-dependence, neither positive nor negative, when determining harvest quotas in polar bears. Hunter *et al.* (2007) include environmental trends in their prediction of polar bear population abundance, but are forced to assume a future stochastic series of "good" and "bad years" (based on general circulation models for future sea ice conditions), where vital rates would correspond to estimates from three "good" and two "bad" years observed between 2001 and 2005.

O'Neill *et al.* (2008) used expert opinion to project polar bear range and abundance under climate change. The authors argue that in the absence of sufficient quantitative population data, "expert opinion is currently the only means available to investigate the impacts of climate change on polar bears in a wider Arctic setting, or in regions where detailed population studies do not exist". I disagree with this statement. Indeed, throughout this dissertation, I have advocated the development of process-oriented mechanistic models, and I have shown how such models can be used to predict individual responses to changing environmental conditions, or to harvest-mediated changes in population composition. The models developed in the previous chapters are complementary to the population models developed by Hunter *et al.* (2007) and Taylor *et al.* (1987, 2003, 2008a,b,c), as discussed in detail in sections 2.6 and 4.6, and taken together, they provide the next step towards a predictive framework of polar bear populations.

To predict potential negative impacts of a highly sex-selective polar bear harvest on female reproduction, I developed a mechanistic model for the polar bear mating system in Chapter 2. The model was parameterized using pairing data from Lancaster Sound, Nunavut, Canada, and described the observed pairing dynamics well. Due to its mechanistic nature, the model can be used to predict the proportion of fertilized females at the end of the mating season, given population density and operational sex ratio. It was shown that female mating success is a nonlinear function of the operational sex ratio, so that a sudden reproductive collapse could occur if males are severely depleted. Furthermore, I demonstrated that the operational sex ratio where such an Allee effect is expected to occur depends on population density. If coupled with a population dynamics model, the results of this chapter could be used by managers to improve current harvesting strategies by appropriately accounting for Allee effects and the role of males in the mating dynamics of polar bears.

To predict effects of climatic warming on polar bear reproduction, I considered polar bears within a dynamic energy budget framework. To do so, I developed and parameterized a body composition model for polar bears that differentiates between structure and storage of an animal (Chapter 3). The model provides equations that can be used to estimate structural mass, storage mass, and storage energy of a polar bear from its straight line body length and total body mass. The model was also used to estimate metabolic rates of fasting adult polar bears. Estimates of metabolic rate corresponded closely to theoretically expected and experimentally measured metabolic rates. Aside from being the fundamental tool for future dynamic energy budget modelling of polar bears, the model also provides a simple, non-invasive means to assess the nutritional status of polar bears, providing considerably more information than currently available methods.

In Chapter 4, I used the methods developed in Chapter 3, supplemented by a more comprehensive polar bear energy budget model, to predict how the litter size of pregnant females in western Hudson Bay would change under climatic warming and a resulting prolonged pre-denning fasting period. I have shown that severe declines in litter size can be expected under climatic warming, but the precise rates of change could only be approximated due to a lack of body condition and feeding data. I have shown that behavioural adaptation towards terrestrial feeding may slow projected declines somewhat, but is unlikely to significantly compensate for expected losses in body mass and resultant reductions in litter size.

In the following concluding discussion, I take a broader perspective and show how the methods and results of this dissertation fit into the larger framework of current approaches towards the modelling of Allee effects and bioenergetics, respectively, emphasizing how my contributions have advanced our understanding both in terms of modelling and polar bear ecology, and concluding each section with an outline of how future research could proceed from here.

5.1 Mate Location, Mate Choice, and Allee Effects

Models of Allee effects have recently become popular in ecology and conservation biology due to an increasing recognition of the fundamental importance of Allee effects to population management (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Liermann & Hilborn 2001). Allee effects may be of concern to the conservation of rare species, impede the success of reintroductions, and affect harvesting strategies (Spencer & Collie 1997; Sinclair *et al.* 1998; Stephens & Sutherland 1999; Courchamp *et al.* 2006; Deredec & Courchamp 2007). Alternatively, they may also be beneficial to management, facilitating the control of invasive species and pest outbreaks (May 1977; Fagan *et al.* 2002; Liebhold & Bascompte 2003; Taylor & Hastings 2005). A number of studies have considered Allee effects, a variety of models have been developed, and excellent reviews have been provided elsewhere (e.g., Fowler & Baker 1991; Courchamp *et al.* 1999; Stephens & Sutherland 1999; Liermann & Hilborn 2001; Boukal & Berec 2002; Taylor & Hastings 2005; Berec *et al.* 2007; Courchamp *et al.* 2008). Rather than reiterating these reviews, I will discuss how my approach fits into this larger framework, how it can be used beyond polar bear ecology to predict Allee effects, and how it could be coupled with movement models in a larger, more synthetic, framework to aid parameter estimation.

Most Allee effect models focus on population dynamics, and thus demographic Allee effects. Fewer consider the mechanisms causing Allee effects explicitly, and even fewer provide guidance regarding parameter estimation (Boukal & Berec 2002; Courchamp *et al.* 2008). The problem can be illustrated using what is probably the simplest population model incorporating an Allee effect:

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right)\left(\frac{N}{K_0}-1\right), \tag{5.1}$$

where N represents population size or density, r the intrinsic rate of population growth, K the carrying capacity, and K_0 an 'Allee effect threshold' (Courchamp *et al.* 1999; Kot 2001). This model is a simple extension of the logistic (Pearl-Verhulst) model, so that populations below K_0 decay to extinction, while those above approach carrying capacity. Even if it would be possible to satisfactorily describe the population dynamics of a species with an Allee effect by such a deterministic one-sex model, the question remains how to estimate the critical population size K_0. Direct estimation of K_0 is impossible unless population growth data can be obtained for a range of low densities. Low detection probabilities at low densities make this task problematic in free-ranging animals, and direct quantification of K_0 is by definition impossible for species that currently occur at high enough densities to show positive population growth in all subpopulations. The detection of Allee effects has been notoriously difficult for similar reasons (Kuussaari *et al.* 1998; Stephens *et al.* 1999; Liermann & Hilborn 2001; Dennis 2002; Morris 2002).

Recognizing the need to explicitly consider the biological mechanisms leading to Allee effects, Stephens *et al.* (1999) suggested the distinction between component and demographic Allee effects (cf. Chapter 2). This notion has been highly influential, and among others renewed the interest in mechanistic models that explicitly incorporate the mating system and both sexes to address mate shortage (e.g., Møller & Legendre 2001, Bessa-Gomes *et al.* 2004; Eskola & Parvinen 2007). For instance, given male (n_m) and female (n_f) numbers, the expected proportion of fertilized females, c, has been commonly expressed as

$$(5.2) \qquad c = \frac{\min(n_f, hn_m)}{n_f} \ ,$$

where h represents the average harem size of a male. For $h = 1$, this formulation represents a monogamous mating system with perfect mate finding. For $h > 1$, we have polygyny (Legendre *et al.* 1999; Bessa-Gomes *et al.* 2004). Møller & Legendre (2001) and Bessa-Gomes *et al.* (2004), for example, used equation (5.2) in stochastic population models to explore how a component Allee effect of reduced female mating success could arise as a result of mating system, sex ratio, and mate choice. Their analyses were strategic, and do not attempt parameterization for a particular species. Given that equation (5.2) does not allow for mate searching, their analyses are most applicable to harem breeding animals, where sperm limitation usually determines the value of the parameter h (Ginsberg & Milner-Gulland 1994; Mysterud *et al.* 2002; Milner-Gulland *et al.* 2003). Accordingly, these studies predict Allee effects as a function of sex ratio and population size only, regardless of population density (Møller & Legendre 2001; Bessa-Gomes *et al.* 2004).

Legendre *et al.* (1999) considered a generalized version of equation (5.2),

$$(5.3) \qquad c = \frac{\gamma \cdot \min(n_f, hn_m)}{n_f} \ ,$$

where the parameter γ ($0 < \gamma \leq 1$) accounts for other factors affecting fertilization, such as mate finding and competition for mates. However, again, short of fitting equation (5.3) to mating success data at various densities, no methods were suggested to estimate γ.

In contrast to these simpler descriptions, I have provided a mechanistic modelling framework that explicitly considers the mating season dynamics (Chapter 2). The female mating success, defined in section 2.3.2 in terms of the dynamical variable $F(t)$, the density of unfertilized females at time t, is simply $1 - F(T) / f_0$, where T indicates the length of the mating season. This definition of mating success contrasts with the above definition, c, found in equations (5.2) and (5.3). The advantages of the mechanistic modelling approach are threefold. First, unlike population models that use a phenomenological Allee effect term (such as model (5.1)), no *a priori* assumption about the existence or form of a potential Allee effect needs to be made. Allee effects arise as a natural consequence of the mating system. Second, my approach considers both sex ratio and sex-specific densities, and thereby unmasked an interaction of these quantities on female mating success – an effect that to my knowledge has not been documented, and cannot be shown from models that only consider population density (e.g., model (5.1)) or sex ratio (e.g., model (5.2)). Third, and maybe most importantly, it permitted the estimation of parameters determining female mating success. I was therefore able to predict conditions that would lead to a component Allee effect of reduced female mating success due to male scarcity, despite a complete absence of data relating female mating success to sex ratio and sex-specific densities. It is noteworthy, in this regard, that my model only uses four parameters, and female mating success is insensitive to two of those. My approach is therefore equally parameter-sparse as many commonly used Allee effect models (e.g., model (5.3)).

The modelling framework provided in Chapter 2 is not limited to the ecology of polar bears. It is simple and flexible enough to allow generalization to any given mating system. Regarding the prediction of Allee effects for a given species, the biggest challenge remains the estimation of the pair formation rate parameter σ, defined in section 2.3.2. Pairing dynamics data available for some polar bear populations were the result of long-term population studies, and may not be available for many species. Nevertheless, mate-finding Allee effects may be important in species that occur at low densities, including (but certainly not limited to) primates, wolves (*Canis lupus*), tigers (*Panthera tigris*), and whales (Cetacea), and should be considered in management decisions, even if Allee effects are currently unobserved (Swart *et al.* 1993; Fujiwara & Caswell 2001; Carroll & Miquelle 2006; Hurford *et al.* 2006; Courchamp *et al.* 2008). If logistical or other reasons prevent the collection of pairing dynamics data, alternative methods can be developed to estimate σ. Pair formation rate is the product of the encounter rate between males and females and the probability of pair formation upon encounter (i.e., mate choice). Encounter rate, however, can be estimated independently from movement patterns, movement speed, and detection distance (e.g., Dennis 1989; Viswanathan *et al.* 1996; McCarthy 1997; Kiørboe & Bagøien 2005; Hutchinson & Waser 2007).

Possibly one of the simplest models for animal encounter arises from the so-called "ideal gas" model, where encounter rates are estimated in analogy to molecular collision rates in an ideal gas (Maxwell 1860). For instance, assuming that individuals are randomly distributed and move independently from each other at constant speed v in randomly oriented straight lines, an individual male's encounter rate with females, σ_{M}, occurring at density F becomes:

$$(5.4) \qquad \sigma_{\mathrm{M}} = \frac{4v}{\pi} \cdot 2d_m \cdot F \ ,$$

where d_m is the male's detection distance, i.e., the radius of a circle within which a female will be detected (Waser 1976). This approach can be extended to include non-random distributions, varying movement speeds, and directed searching (Hutchinson & Waser 2007). It has a long history in ecology, and has, for example, been used to evaluate population densities from line transects (Skellam 1958), the effect of human harvest on mammalian populations (Rowcliffe *et al.* 2003), predation in zooplankton communities (Gerritsen and Strickler 1977), mating in copepods or turtles (Mosimann 1958; Kiørboe & Bagøien 2005), the evolution of mating systems and anti-infanticidal strategies in primates (van Schaik & Dunbar 1990; Harcourt & Greenberg 2001), and the significance of primate polyspecific associations (Waser 1982; Mitani *et al.* 1991). Given movement patterns, movement speeds, detection distance, and male and female densities, such encounter rate models could be used to estimate pair formation rate in the absence of pairing dynamics data. These estimates could then be used in an appropriate mating system specific version of the mating dynamics model (2.1) to predict Allee effects.

Even in polar bears, such an approach may yield additional insight, and help to validate or refine the parameter estimate of σ, derived in Chapter 2. The sensitivity analyses of section 2.5 identified σ as the key parameter for female mating success.

Future research, aiming to quantify the role of males in polar bear population dynamics, should therefore prioritize development of a better understanding of encounter rates between males and females, as well as mate choice, the two components summarized in σ. Until now, encounter rate models could not be developed for polar bears, because radio collars could only be fitted to adult females (Ferguson *et al.* 2001; Parks *et al.* 2006; Andersen *et al.* 2008). In adult males neck diameter exceeds head diameter so that even tightly fitted collars slip off (Amstrup *et al.* 2001). Consequently, little is known about movement speed and movement patterns of adult males (but see Amstrup *et al.* 2001). However, new technologies, such as ear tag radios, will allow us to investigate male movement, and thus gain a better understanding of mate location and pair formation. Intensive tracking programs may even allow a direct estimation of encounter rates, as has been attempted in some black bear (*Ursus americanus*) populations (Kovacs & Powell 2003).

Quantifying mate choice should be given equal attention, but is not easy given the logistic difficulty of directly observing breeding behaviour. Commonly chosen routes involve DNA fingerprinting for paternity analyses (Craighead *et al.* 1995; Schenk & Kovacs 1995; Kovacs & Powell 2003) or the analysis of male age-structure in breeding pairs (A. E. Derocher, unpublished data), but it is not clear how such data would translate into the probability of a female accepting a mate. For example, in high density populations with frequent encounters between males and females, a paternity bias towards older males may arise from female mate choice, male contest competition, or low mating ability in younger males (as defined in section 2.3.2). Paternity analyses or breeding group age-structure analyses from low male-density populations near or below an Allee effect threshold, such as Viscount Melville Sound or M'Clintock Channel (Taylor *et al.* 2002, 2006; Figure 1.1), may be most instructive in this regard. Observed values could be assessed against a null model for expected male mating success, derived from an age-structured extension of the mating model (2.1), and may help to quantify female mate choice. Even so, this task is not simple because female mate choice may adaptively vary as a function of male densities, sex ratios, and expected mating success (Kokko & Mappes 2005). Nevertheless, such analyses could illuminate additional demographic effects of a harvest that is not only sex-selective, but also primarily targets older and larger males, and thus evaluate the sensibility of this policy (Milner *et al.* 2007).

Additional effort should be devoted towards a more accurate description of polar bear distribution and density during the mating season. While the analyses in Chapter 2 in principle would allow extrapolation to other populations, in practice this is currently problematic, because the provided estimate of pair formation rate σ is confounded by uncertainty in population density. Population size in Lancaster Sound was documented, but distribution was not, so that I had to make the simplifying assumption that the population is evenly distributed over the entire marine area within the population boundaries. This assumption may be reasonable if polar bears, like some grizzly bears (Dahle & Swenson 2003), increase their home ranges during the mating season, but it remains a hypothesis that needs to be tested. Quantitative predictions for Lancaster Sound are not affected by this assumption (cf. section 2.6), but the numeric value of σ may be. This needs to be taken into account when using my results to predict Allee effects in other populations.

From a practical perspective, future studies should explore all additional means to better estimate σ, thereby increasing the predictive value of the model presented here. Such studies should include independent estimates for encounter rate, mate choice, and density, but should also attempt replication of the approach presented in Chapter 2 using pairing dynamics data from other well-studied populations (prime candidates for this are the southern Beaufort Sea, Gulf of Boothia, and Svalbard populations).

From a theoretical perspective, the model is applicable for increasing our understanding of the mechanisms causing mate-finding Allee effects. Many extensions utilizing the present framework are conceivable, including generalization to other mating systems (Emlen & Oring 1977; Clutton-Brock 1989; Gerber 2006), and extensions to include a non-homogeneous landscape (Lima & Zollner 1996) or habitat fragmentation (Lamont *et al.* 1993; Amarasekare 1998). Stochastic versions of the mating dynamics model may also be considered, and compared with existing stochastic models of mate searching (e.g., Dennis 1989). Unlike the mating model (2.1), such models usually do not account for dynamic changes in available male and female densities throughout the mating season. However, my analyses showed that a significant proportion of animals was paired at peak mating season (Figures 2.1 and 2.2), and thus unavailable for mating, resulting in dynamic changes in mate location efficiency of searching individuals. Combining stochastic mate searching models with the present mating dynamics model therefore merits investigation, and may provide new insights.

5.2 Energy Budget Models and Polar Bears

Energy budget models have been suggested for elucidating the effects of climate change on reproduction (Berteaux *et al.* 2006). They have been successfully applied to study the energetic consequences of climate-associated mismatches between reproductive timing and resource availability in birds (Thomas *et al.* 2001). Detailed mammalian studies linking climate change to individual energetics and consequent reproductive success are currently lacking (Berteaux *et al.* 2006), but other effects of climate change on mammalian energetics have been studied (e.g., Humphries *et al.* 2002).

Energy budget models can generally be separated into two classes (*sensu* Kooijman 2009): static energy budget models (SEBs) and dynamic energy budget models (DEBs). Probably due to their simplicity, SEBs are still more popular in ecoenergetic studies, and all previous polar bear energy budget models fall into this category (Best 1977; Stirling & Øritsland 1995). SEBs, however, have a number of limitations. They are mostly descriptive, often relying on allometric curves to generalize energy use across size classes both within and across species (e.g., Kleiber 1975; Nagy *et al.* 1999). Parameters in allometric curves are usually difficult to interpret, which has, for example, led to the ongoing debate about the "proper" scaling exponent in Kleiber's equation (Glazier 2005). Furthermore, the unexplained variability in measured energy use relative to expected energy use is often large and reduces the predictive value of many allometric curves (Nagy 2005; Glazier 2006). Such variability may be largely due to a variety of physiological processes subsumed under measured respiration rates (van der Meer 2006; Kooijman 2009). Kleiber's allometric curve, for example, is often used to predict basal metabolic rate, but is based on respiration rates (Kleiber 1975). Respiration rates, however, can include substantial energy expenditure towards growth, even if growth is apparently negligible during measurements (Parry 1983; van der Meer 2006; Kooijman 2009). Allometric curves for field metabolic rate, on the other hand, do not attempt to separate between energy allocated to somatic maintenance, activity, thermoregulation, reproduction, and growth (Nagy 1987, 1994, 2005; Nagy *et al.* 1999). These curves are useful in estimating an individual's food requirement to meet all metabolic expenses, but cannot predict how reproduction and growth would be compromised under food limitation. The same is true for more complex SEBs that distinguish between the energetic requirements of various physiological processes, but do not specify allocation priorities under food stress (e.g., Lockyer 1981; Ryg & Øritsland 1991; Markussen *et al.* 1992; Winship *et al.* 2002).

In contrast to SEBs, dynamic energy budget models explicitly specify allocation rules and priorities between somatic maintenance, thermoregulation, reproduction, and growth (Nisbet *et al.* 2000; van der Meer 2006; Kooijman 2009). Because of this property, they can predict reproductive output and survival under changing environmental conditions and associated energy intake (Gurney *et al.* 1990; Nisbet *et al.* 2000; Kooijman 2009), and are particularly useful to understand an individual's response to food limitation (Zonneveld & Kooijman 1989; McCauley *et al.* 1990; Noonburg *et al.* 1998; Kooijman 2009). DEBs have been applied across all levels of biological organization (Nisbet *et al.* 2000), and have practical applications in a range of fields, including ecotoxicology, pest control, and optimal harvesting (van der Meer 2006). Furthermore, a number of remarkable theoretical successes have been achieved with DEBs, including mechanistic explanations for interspecific body-size scaling relationships, such as Kleiber's allometric curve for respiration rates and the von Bertalanffy growth rate (Nisbet *et al.* 2000; Kooijman 2001). However, DEBs have also been criticized for being complex and parameter-rich, and therefore associated with large uncertainty if used for predictions (Lawton 1991; Brown *et al.* 2004). In response to this criticism, some more recent DEB studies have attempted to reduce complexity by only partially specifying physiological processes mechanistically (i.e., those processes where good parameter estimates and information on functional relationships were available), and estimating other functional relationships empirically (Shertzer & Ellner 2002; Nisbet *et al.* 2004).

In this dissertation I have adopted a similar mechanistic/empirical approach. Rather than modelling gestation explicitly (e.g., Klanjscek *et al.* 2007), I have empirically estimated the expected litter size of pregnant females as a function of energy density at den entry (section 4.4). To obtain predictions for changes in litter size due to a climatic warming induced earlier sea ice break-up and consequent earlier on-shore arrival, I have connected this empirical relationship with a simplified DEB that only incorporates somatic maintenance, movement, and feeding, and was used to estimate body mass and storage energy of pregnant females before current on-shore arrival (Chapter 4). The largest uncertainty in model predictions does, in fact, not stem from uncertainty in polar bear physiology and corresponding DEB parameter estimates, but rather from a lack of data describing on-ice feeding rates and on-ice body condition. Even though a large number of publications have identified climatic warming and a resulting prolonged open-water season as the biggest threat to the western Hudson Bay polar bear population (e.g., Stirling *et al.* 1999; Derocher *et al.* 2004; Stirling *et al.* 2004; Stirling & Parkinson 2006; Regehr *et al.* 2007; Wiig *et al.* 2008), little data exist to quantify how earlier on-shore arrival would affect polar bear body condition. This, however, could at least be approximated if the body condition of polar bears before on-shore arrival, or alternatively on-ice feeding rates, were known. If we are to move from qualitative to quantitative predictions regarding the future of this and other polar bear populations, the collection of such data should become a research priority.

In this dissertation I have provided the first DEB for polar bears, and believe there is much opportunity for further developments in this area. Most expected negative effects of climatic warming on polar bears are energy-associated, either through increased energy expenditure or through decreased feeding opportunities (Derocher *et al.* 2004; Wiig *et al.* 2008; cf. section 1.1.1). Changes in individual growth, reproduction, and survival, in response to changes in energy uptake and expenditure, can be predicted from DEBs, provided that sufficient physiological data can be gathered to specify allocation rules and parameterize model terms (Gurney *et al.* 1990; McCauley *et al.* 1990; Noonburg *et al.* 1998; Nisbet *et al.* 2000; Kooijman *et al.* 2008; Kooijman 2009). This makes DEBs an ideal tool to explore and predict the effects of climatic warming on polar bears.

In addition to feeding, somatic maintenance, and movement, already incorporated in the polar bear DEB presented in Appendix D and used in Chapter 4, a fully specified DEB would also have to include growth and reproduction, and potentially thermoregulation. The development of such DEBs may be relatively straightforward, and much guidance can be obtained from the literature (e.g., Kooijman 2009, as well as issue 56(2), and forthcoming issues 62(1) and 62(2) of *Journal of Sea Research*, which are entirely devoted to DEBs). Although most previously developed DEBs are for invertebrates, an extension to right whales (*Eubalaena glacialis*) has recently been attempted (Klanjscek *et al.* 2007), and a similar approach may be possible for polar bears. Much more difficult than model development is model parameterization because energy fluxes within an individual can usually only be observed indirectly (Nisbet *et al.* 2000; van der Meer 2006; van der Veer *et al.* 2006; Kooijman *et al.* 2008). However, we do have a basis from which to start. Long-term research on polar bears has resulted in large amounts of physiological data, and missing pieces can either be inferred from existing field data, or could be addressed with directed studies. A fully developed polar bear DEB is beyond the scope of this dissertation, but to offer a starting point for future research I will address some key data requirements. Further guidance can be obtained from three recent excellent publications on this matter (van der Meer 2006; van der Veer *et al.* 2006; Kooijman *et al.* 2008).

Somatic Maintenance

Basal metabolic rates of polar bears have been measured in simulated denning studies (Watts *et al.* 1987, 1991). These data are hard to interpret within a DEB framework and difficult to extrapolate to other individuals, because metabolic rates are reported relative to total body mass. However, polar bears experience large fluctuations in body mass, and most changes are due to metabolically inactive body fat (Watts & Hansen 1987; cf. also section 3.7.1). Structure and storage must therefore be considered separately when estimating somatic maintenance. Reinterpretation of the metabolic rates reported by Watts *et al.* (1987, 1991) would be necessary, but this is currently impossible, because these studies do not report straight line body lengths. The relative contributions of lean tissue and body fat to total body mass can therefore not be assessed, and somatic maintenance rates cannot be inferred from the metabolic rates reported by Watts *et al.* (1987, 1991).

I have provided somatic maintenance rate estimates in Chapter 3, and these estimates can be extrapolated to other polar bears using the body composition model (cf. section 4.4.1). In fact, extrapolation is even possible to growing cubs because somatic maintenance rates and costs of growth are explicitly separated in the DEB framework (Nisbet *et al.* 2000; Kooijman 2009). By contrast, if mass-specific allometric curves were used to predict metabolic rates in growing cubs, it would be necessary to take metabolic rates as proportional to $M^{0.83}$ rather than to $M^{0.75}$ (Oftedal 1984; Blaxter 1989; Arnould & Ramsay 1994). This example nicely illustrates one of the weaknesses of SEBs (and strengths of DEBs) discussed above.

It should, however, be noted that my estimates of somatic maintenance rate were based on a relatively small sample size and so was my parameterization of the body composition model. Validation and possible refinements of both the body composition model and somatic maintenance rate estimates should be attempted as more data become available (cf. Chapter 3). For the latter, as well as for all other DEB components discussed below, longitudinal data is preferable over population cross-sections because individual-based processes are considered.

Movement

The energetic cost of polar bear locomotion has been measured in various treadmill studies, and has been reported to be twice as high as in other mammals (Øritsland *et al.* 1976; Hurst *et al.* 1982a,b; Watts *et al.* 1991). The interpretation of results is somewhat debatable due to statistical problems in some of these publications. For instance, Hurst *et al.* (1982b) postulate a linear relationship between cost of locomotion and body mass in polar bears, in apparent contradiction to findings in other species (Taylor *et al.* 1970, 1982). However, Hurst *et al.*'s (1982) conclusions rest on five linear regressions that are based on two data points each, one of which is theoretical (cf. their Figure 1). Furthermore, it is unclear whether polar bear locomotion can indeed be as inefficient as found in treadmill studies (Øritsland *et al.* 1976; Hurst *et al.* 1982a,b), given that polar bears are highly mobile with home ranges of up to 500,000 km^2 (Ferguson *et al.* 1999; Mauritzen *et al.* 2001). Further treadmill studies may provide new insight and could be useful, even though average movement costs are small compared to those of somatic maintenance, because polar bears may have to migrate increasingly longer distances in a habitat that is becoming more dynamic and increasingly fragmented due to climatic warming (Mauritzen *et al.* 2003; Durner *et al.* 2009).

Thermoregulation

Thermoregulation in polar bears is reasonably well understood (Scholander *et al.* 1950; Øritsland 1970; Blix & Lentfer 1979; Best 1982), and the data presented in these studies is likely sufficient to parameterize this model component if needed. However, Best (1982) concluded that the thermoneutral zone of adult polar bears may include temperatures as low as -39.5 °C with winds up to 7 m sec^{-1}. Furthermore, polar bears actively seek out shelter dens during the coldest months of winter (Messier *et al.* 1994; Ferguson *et al.* 2000). Thermoregulatory costs may therefore be negligible at least in adult bears, and will probably become even less important in a warming climate. It may therefore even be unnecessary to include thermoregulation in a polar bear DEB, and a better understanding of this component is likely least crucial for model development.

Growth

The allocation of energy to growth is probably the least understood component in the energy budget of polar bears. It may also be the most difficult to develop and parameterize in a dynamic energy budget model, because energy allocation to growth depends on energy intake (Ross & Nisbet 1990; Lika & Nisbet 2000; Kooijman 2009), and may also be size-dependent (Shertzer & Ellner 2002; Nisbet *et al.* 2004).

Cross-sectional von Bertalanffy growth curves exist for a number of polar bear populations (Kingsley 1979; Derocher & Stirling 1998a; Derocher & Wiig 2002), but these are of limited use in quantifying individual energy allocation to growth: Fits of the von Bertalanffy growth curve to age-dependent mass data (Kingsley 1979; Derocher & Wiig 2002) cannot be used for DEB development, because changes in body mass include changes to structure and storage. These changes need to be separated explicitly, because growth only relates to changes in structure (Nisbet *et al.* 2000; Kooijman 2009). Structure can be approximated through straight line body length (Chapter 3), and fits of the von Bertalanffy growth curve to age-dependent population averages of straight line body length exist (Derocher & Stirling 1998a; Derocher & Wiig 2002). However, these also provide little guidance in DEB development because growth depends on energy intake, and the link between energy intake and reported growth curves is missing. Furthermore, for DEB development and parameterization, it is problematic to use population average growth curves, such as the ones reported by Kingsley (1979), Derocher & Stirling (1998a), and Derocher & Wiig (2002), because important variability in individual energy intake and expenditure may be lost, leading to potentially flawed models of little predictive value (Gurney *et al.* 1990; McCauley *et al.* 1990).

Determining the rules of energy allocation to growth, and parameterizing this model component, ideally requires repeated length measurements of individual bears with known energy intake and expenditure over relatively short periods. Furthermore, in an ideal world, energy intake could be varied experimentally to understand changes in energy allocation under food limitation (Ross & Nisbet 1990; Gurney *et al.* 1990; McCauley *et al.* 1990; Noonburg *et al.* 1998; Nisbet *et al.* 2004; Kooijman *et al.* 2008). It is unlikely that we will be able to collect such data from field studies only, because of the logistic difficulty to sample individual bears repeatedly over relatively short periods, while simultaneously tracking their energy intake. Data from polar bears in zoos may be ideal to fill this gap. Energy intake is known, and changes in body length could at least be approximated. Straight line body lengths may be difficult to measure due to the necessity of immobilization, but other length measurements approximating structural mass, such as head length or zygomatic breadth (Derocher & Stirling 1998a), may be considered after re-parameterizing the predictive equation for structural mass (3.2) appropriately.

Growth data from zoos should be complemented by repeated measures of cub growth under food limitation: such data are unlikely to be available from zoos, but could be obtained with relatively little effort during the on-shore fasting period in populations like western Hudson Bay. The milk energy intake of cubs could hereby be measured through isotope dilution methods (Arnould & Ramsay 1994), or approximated through changes in maternal energy stores (Chapter 3 and Appendix D).

Reproduction

Reproduction in mammals consists of two sequential components: gestation, followed by lactation. In Chapter 4, I have already treated gestation, and section 4.6 discusses how current estimates of litter size at den emergence as a function of energy density at den entry could be improved.

In contrast to the short gestation period, lactation normally lasts up to 2.5 years (Ramsay & Stirling 1988; Derocher *et al.* 1993), and constitutes the energetically most expensive component of reproduction (Gittleman & Thompson 1988; Oftedal 1993). During this period, milk transfer may depend on maternal body condition, cub demand, and cub age. Cub demand, in turn, may be influenced by cub body condition, cub growth, and the amount of solid food consumed (Lee *et al.* 1991; Derocher *et al.* 1993; Oftedal 1993; Arnould & Ramsay 1994). Although it is fairly easy to formulate lactation within a DEB (e.g., Klanjscek *et al.* 2007), relatively large amounts of data are required for model parameterization due to the number of factors involved. Currently, only a single study has measured milk transfer in polar bears (Arnould & Ramsay 1994), and samples were restricted to the on-shore fasting period. However, milk composition data indicate that lactation patterns may be different when feeding (Derocher *et al.* 1993), so that more comprehensive data covering the on-ice feeding period are needed.

A second, to date poorly understood, component of lactation is weaning. In western Hudson Bay, for example, about 55% of handled 1.5 year old cubs were independent of their mothers during the 1980s (Ramsay & Stirling 1988). Since then, the proportion of independent yearlings has significantly declined (Stirling *et al.* 1999). The reasons for early weaning and observed changes are unclear (Ramsay & Stirling 1988; Derocher & Stirling 1996; Stirling *et al.* 1999). Cessation of lactation has been reported for food-stressed females (Derocher *et al.* 1993), which may imply a storage energy (or energy density) threshold below which lactation stops. The existence of such a threshold would be supported by DEB theory (Ross & Nisbet 1990; Lika & Nisbet 2000), and would have implications for lactational performance in females food-stressed by climatic warming. Analysis of lactation patterns (presence/absence) during the on-shore fasting period in relation to maternal energy stores could resolve this question, and merits investigation.

Feeding

Recent studies have provided much insight into the diet composition of polar bears (Derocher *et al.* 2002; Iverson *et al.* 2006; Thiemann *et al.* 2008). However, despite reduced feeding opportunities constituting probably the most significant negative effect of climatic warming on polar bears, we know little about their feeding ecology. Only a handful of studies document kill frequency and meal size, and most observations are limited to Radstock Bay on Devon Island, Nunavut, during the months of April, May, and July (Stirling 1974; Stirling & Archibald 1977; Stirling & Latour 1978; Smith 1980 Stirling & Øritsland 1995). Spatial variability in diet composition exists (Iverson *et al.* 2006; Thiemann *et al.* 2008), and kill frequencies are probably equally variable, both spatially and temporally. Applicability of existing data to other polar bear populations is therefore limited (cf. also discussion in sections 4.5.2 and 4.6 regarding applicability to the western Hudson Bay population).

However, feeding frequency and meal size directly determine storage energy, which, in turn, directly influences survival and reproduction (cf. section 1.1.1, and Chapters 3 and 4). To move towards a quantitative understanding of possible climate change effects on polar bear body condition, and consequent effects on reproduction and survival, it is therefore essential to obtain more comprehensive feeding data. Particular emphasis should hereby be placed on spring and fall feeding, that is, the periods most likely to experience large changes in sea ice dynamics under climate change (Stirling *et al.* 1999; Stirling & Parkinson 2006; Wiig *et al.* 2008).

In sum, regarding the energy budget of polar bears, current knowledge is best with respect to somatic maintenance, movement, and thermoregulation. Much is known about reproduction, but directed study is needed to fill some of the data gaps required for DEB development. Furthermore, most publications concerning the reproduction of polar bears describe components of reproduction relative to total body mass (e.g., Ramsay & Stirling 1988; Derocher *et al.* 1992, 1993; Derocher & Stirling 1994, 1995, 1996, 1998b). In Chapter 3, I have shown that it is necessary to consider both body length and body mass to be able to differentiate between structure and storage. Because reproduction is determined by storage energy or energy density rather than total body mass (Ross & Nisbet 1990; Atkinson & Ramsay 1995; Lika & Nisbet 2000; Kooijman 2009), it may be instructive to revisit these data using the methods developed in this dissertation.

Least is known about growth and feeding, so that further research on these components, along with reproduction, is key for a better understanding of polar bear energy budgets and DEB development. Fortunately, it is not necessary to measure all components independently. DEB theory allows estimating some energy fluxes, if reasonable confidence exists in the other model components, because energy needs to be conserved (Nisbet *et al.* 2004; Klanjscek *et al.* 2007; Kooijman *et al.* 2008; Kooijman 2009). For instance, energy intake could be inferred from repeated measurements of body mass and length, if a dynamic energy budget model describing all physiological energy allocation rules could be developed. This approach was used in Chapter 3 to estimate the somatic maintenance rate of adult male polar bears. Finally, I want to reemphasize the need to collect more body composition data using isotopic water dilution or bioelectric impedance, as discussed in section 3.8, because storage composition may, for example, depend on season. Such differences would influence storage energy estimates, and thus, DEB parameterization and predictions.

Development of a full polar bear DEB may not be simple, but much can be gained from it: beyond serving as a predictive tool for changes in reproduction, growth, and survival under climate change, DEBs could also be used to analyze and predict the effects of pollution on polar bear reproduction, growth, and survival (Kooijman & Bedaux 1996;

Nisbet *et al.* 2000; Klanjscek *et al.* 2007), or to assess the potential for behavioural and plastic adaptations to a changing environment (Lika & Nisbet 2000; cf. also Chapter 4 on compensatory terrestrial feeding). DEBs could also serve to synthesize current knowledge on polar bear physiology, behaviour, and feeding, under a common framework, thereby identifying knowledge gaps and directing future research (Hilborn & Mangel 1997; Haefner 2005). First steps towards such a synthetic approach were already taken here and in Chapters 3 and 4. Finally, DEBs could be coupled with population dynamics models, or even ecosystem models, to link biological levels of organization (Nisbet *et al.* 2000; Kooijman 2001; Klanjscek *et al.* 2006). DEBs may therefore not only be complementary to current polar bear population dynamics modelling (Hunter *et al.* 2007), but could also provide the next step towards a more comprehensive understanding of the Arctic ecosystem, and the role of polar bears therein.

5.3 Concluding Remarks

The application of models in polar bear biology is still in its infancy despite more than four decades of (mostly empirical) research. However, models can be useful to test our understanding of the mechanisms operating in a system, to identify data gaps and direct future research, to predict responses to not yet encountered situations, and to guide decision-making processes and species management (Hilborn & Mangel 1997; Haefner 2005). Good empirical data and conceptual knowledge remain essential, and are key for model development and parameterization, especially if the models are used for prediction or management.

In this dissertation I have used empirical data, statistical inference, and biological modelling to predict the future of polar bears under yet unobserved conditions. My work is among the first to apply such a synthetic approach to this species, and a step towards a comprehensive framework. However, many open questions remain, and new challenges will undoubtedly arise in a rapidly changing world. In the face of these challenges, it will be essential that we utilize all information and tools available to us (Simmonds & Isaac 2007). In particular, coordinated and collaborative efforts between field biologists, modellers, and managers, as well as multi-disciplinary approaches, are urgently needed and will hopefully become standard rather than the exception in coming years of research.

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Appendix A

Derivation of the Storage Composition of Polar Bears (Equation (3.13))

Here I provide the derivation of equations (3.13), which specify the storage composition of a polar bear.

A.1 Fat and Protein (Equations (3.13a) and (3.13b))

To estimate the respective proportions of storage mass that are fat and protein, I rewrite the masses of storage fat ($M_{\text{STO-F}}$) and storage protein ($M_{\text{STO-P}}$) using the energetic content of each compartment (E_{F} and E_{P}) and the energy densities of fat and protein (ε_{F} and ε_{P}):

$$\text{(A.1a)} \qquad M_{\text{STO-F}} = \frac{E_{\text{F}}}{\varepsilon_{\text{F}}}$$

$$\text{(A.1b)} \qquad M_{\text{STO-P}} = \frac{E_{\text{P}}}{\varepsilon_{\text{P}}} \quad .$$

Using equations (3.8a) and (3.8b), I then rewrite equation (A.1) as:

$$\text{(A.2a)} \qquad M_{\text{STO-F}} = \frac{\gamma E}{\varepsilon_{\text{F}}}$$

$$\text{(A.2b)} \qquad M_{\text{STO-P}} = \frac{(1-\gamma)E}{\varepsilon_{\text{P}}} \quad .$$

The respective proportions of storage mass that are fat and protein are therefore given by:

$$\text{(A.3a)} \qquad \frac{M_{\text{STO-F}}}{M_{\text{STO}}} = \frac{\gamma E}{\varepsilon_{\text{F}} M_{\text{STO}}}$$

$$\text{(A.3b)} \qquad \frac{M_{\text{STO-P}}}{M_{\text{STO}}} = \frac{(1-\gamma)E}{\varepsilon_{\text{P}} M_{\text{STO}}} \quad .$$

Substituting $\alpha^{-1}E$ for M_{STO} (equation (3.9)) in equation (A.3) yields equations (3.13a) and (3.13b).

A.2 Ash and Water (Equations (3.13c) and (3.13d))

By combining equation (3.5a) with equations (3.5b) and (3.5c), respectively, I rewrite the respective masses of storage ash ($M_{\text{STO-A}}$) and storage water ($M_{\text{STO-W}}$) as:

$$\text{(A.4a)} \qquad M_{\text{STO-A}} = \frac{1-\eta_{\text{P}}}{\eta_{\text{P}}} M_{\text{STO-P}}$$

$$\text{(A.4b)} \qquad M_{\text{STO-W}} = \frac{\eta_{\text{W}}}{(1-\eta_{\text{W}})\eta_{\text{P}}} M_{\text{STO-P}} \quad .$$

The respective proportions of storage mass that are ash and water are thus given by:

$$\text{(A.5a)} \qquad \frac{M_{\text{STO-A}}}{M_{\text{STO}}} = \frac{1-\eta_{\text{P}}}{\eta_{\text{P}}} \frac{M_{\text{STO-P}}}{M_{\text{STO}}}$$

$$\text{(A.5b)} \qquad \frac{M_{\text{STO-W}}}{M_{\text{STO}}} = \frac{\eta_{\text{W}}}{(1-\eta_{\text{W}})\eta_{\text{P}}} \frac{M_{\text{STO-P}}}{M_{\text{STO}}} \quad .$$

Combining equations (A.5a) and (A.5b) with equation (3.13b) yields equations (3.13c) and (3.13d).

Appendix B

Derivation of the Mass Loss Curve for Fasting Polar Bears (Equation (3.20))

Here I provide the derivation of equation (3.20), which describes total body mass (*M*) as a function of time (*t*) for fasting, resting, non-growing and non-reproducing polar bears in a thermoneutral state.

For such bears the rate of change in storage energy (*E*) was given by differential equation (3.19), which I restate here for convenience:

(B.1) $$\frac{dE}{dt} = -m \cdot \left(M - M_{\text{STO-F}}\right) \quad .$$

Using equation (3.11) to convert storage energy into a function of total body mass and straight line body length, I obtain

(B.2) $$\frac{d\left(\alpha M - \alpha\, \rho_{\text{STR}}\, k\, L^3\right)}{dt} = -m \cdot \left(M - M_{\text{STO-F}}\right) \quad .$$

Acknowledging that for non-growing bears straight line body length is constant, equation (B.2) simplifies to

(B.3) $$\frac{dM}{dt} = -\frac{m \cdot \left(M - M_{\text{STO-F}}\right)}{\alpha} \quad .$$

Storage fat mass ($M_{\text{STO-F}}$) can also be written as a function of total body mass and straight line body length (from equations (3.1), (3.2) and (3.13a)):

$$M_{\text{STO-F}} = \alpha \frac{\gamma}{\varepsilon_{\text{F}}}\left(M - \rho_{\text{STR}}\, k\, L^3\right) \quad . \tag{B.4}$$

Inserting equation (B.4) into equation (B.3) yields the following differential equation describing the rate of change in total body mass:

$$\frac{dM}{dt} = -\frac{m(1-\varphi)}{\alpha} \cdot M - \frac{m\varphi\, \rho_{\text{STR}}\, k\, L^3}{\alpha} \quad , \tag{B.5}$$

where, for brevity, I write $\varphi = (\alpha\gamma) / \varepsilon_{\text{F}}$, representing the proportion of storage mass that is fat (cf. equation (3.13a)).

Solving equation (B.5), a first-order non-homogeneous linear differential equation, gives total body mass M as a function of time t as described by equation (3.20).

Appendix C

Estimating Energy Density from Straight Line Body Length and Total Body Mass (Derivation of Equation (4.4))

Here I provide the derivation of equation (4.4), which is used to estimate the energy density (E / LBM) of adult female polar bears from their straight line body length (L) and total body mass (M).

Lean body mass is given by the difference between total body mass and storage fat mass ($M_{\mathrm{STO\text{-}F}}$) due to the assumption of all body fat belonging to storage (section 3.3):

$$\text{(C.1)} \qquad LBM = M - M_{\mathrm{STO\text{-}F}} \quad .$$

Rewriting storage fat mass as a function of total body mass and straight line body length (equation (B.4)), equation (C.1) becomes

$$\text{(C.2)} \qquad LBM = M - \varphi \left(M - \rho_{\mathrm{STR}}\, k\, L^3\right) \quad ,$$

where $\varphi = (\alpha\gamma) / \varepsilon_{\mathrm{F}}$ represents the proportion of storage mass that is fat.

Rearranging equation (C.2) gives

$$\text{(C.3)} \qquad LBM = (1-\varphi)M + \varphi\, \rho_{\mathrm{STR}}\, k\, L^3 \quad ,$$

and inserting the parameter estimates $\varphi = 0.627$ and $\rho_{\mathrm{STR}} \cdot k = 14.94$ kg m^{-3} (Tables 3.2 and 3.3) into equation (C.3) gives

$$\text{(C.4)} \qquad LBM = 0.373\, M + 9.37\, L^3 \quad .$$

By combining equations (C.4) and (4.3) I obtain equation (4.4).

Appendix D

A Polar Bear Energy Budget Model

Here, I present a dynamic energy budget model for polar bears that tracks changes in storage energy due to feeding, somatic maintenance and movement. The model is used in Chapter 4 to estimate body mass, storage energy, and energy density of adult females prior to on-shore arrival, given straight line body length and body mass at on-shore arrival. The model is developed in section D.1 and parameterized in section D.2.

D.1 Derivation of the Energy Budget Model

All tissue of a polar bear may be characterized as structure or storage. Assuming strong homeostasis, structural mass remains constant in a fully grown bear, whereas storage mass fluctuates with energy intake and expenditure (Chapter 3, section 3.2). Storage energy is accumulated through feeding, and can in theory be utilized for somatic maintenance, activity, thermoregulation, reproduction, and growth (Kooijman 2000). Here, I only considered adult females without dependent offspring during summer and fall, so that no energy is allocated to growth, reproduction, or thermoregulation. The rate of change in storage energy E can therefore be written as

$$(\text{D.1}) \qquad \frac{dE}{dt} = F_{\mathrm{IE}} - F_{\mathrm{EM}} - F_{\mathrm{EA}} \quad ,$$

where F_{IE} represents the influx of energy from the environment through food acquisition and assimilation, and F_{EM} and F_{EA} represent the respective rates at which storage energy is utilized for somatic maintenance and activity.

Somatic maintenance depends on body composition because maintenance requirements of body fat are negligible relative to those of lean tissue (Aarseth *et al.* 1999; Boyd 2002). In accordance with Chapter 3 (section 3.5), I therefore assumed that somatic maintenance rate F_{EM} is proportional to lean body mass, *LBM*. I rewrite lean body mass as a function of storage energy *E* and straight line body length *L* by combining equations (C.3) and (3.11) to obtain

$$\text{(D.2)} \qquad LBM = \alpha^{-1}(1-\varphi)\cdot E + \rho_{\mathrm{STR}}\, k\, L^3 \ .$$

Somatic maintenance rate F_{EM} therefore becomes

$$\text{(D.3)} \qquad F_{\mathrm{EM}} = m \cdot \left(\alpha^{-1}(1-\varphi)\cdot E + \rho_{\mathrm{STR}}\, k\, L^3\right) ,$$

where metabolic rate, *m*, is the energy required per unit time to maintain a unit mass of lean tissue. This formulation is equivalent to the one provided for somatic maintenance in section 3.5 (equation (3.19)), but is tracking storage energy rather than total body mass, which becomes more convenient in the context of a fully formulated dynamic energy budget model.

In contrast to somatic maintenance, energy costs of activity depend on total body mass, because both lean tissue and body fat need to be moved. Energy consumption during movement can be described by an allometric equation of the form

$$\text{(D.4)} \qquad F_{\mathrm{EA}} = aM^{b} + cM^{d} \cdot v \ ,$$

where *v* represents velocity (Taylor *et al.* 1970; Fedak & Seeherman 1979; Taylor *et al.* 1982). The first part of this sum, aM^{b}, represents the metabolic costs of maintaining posture during locomotion (Schmidt-Nielsen 1972; Wunder 1975). The second part, $cM^{d}\cdot v$, reflects the positive linear relationship between energy consumption and velocity. This linearity has been demonstrated for a wide variety of animals (Taylor *et al.* 1970; Fedak & Seeherman 1979; Taylor *et al.* 1982), including polar bears for the range of velocities encountered in the wild (Øritsland *et al.* 1976; Hurst *et al.* 1982).

Feeding rates are often modelled as size-dependent within the dynamic energy budget framework (Kooijman 2000; Nisbet *et al.* 2000), but no evidence exists for size-dependent feeding in adult polar bears. Therefore, in absence of any evidence to the contrary, I opted for the most parsimonious model, assuming size-independent and constant feeding at rate *β*. After accounting for digestive efficiency *δ*, the rate of energy influx becomes:

$$F_{\mathrm{IE}} = \delta\beta \ . \tag{D.5}$$

In sum, the dynamics of storage energy can be written as:

$$\underbrace{\frac{dE}{dt}}_{\substack{\text{Rate of change}\\ \text{in storage energy}}} = \underbrace{\delta\beta}_{\text{Feeding}} - \underbrace{m \cdot \left(\alpha^{-1}(1-\varphi)\cdot E + \rho_{\mathrm{STR}}\, k\, L^3\right)}_{\text{Somatic maintenance}} - \underbrace{\left(aM^b + cM^d \cdot v\right)}_{\text{Activity}} \ . \tag{D.6}$$

The dynamics of total body mass (*M*) and energy density (*E / LBM*) are also fully described by equation (D.6), because storage energy *E* can be converted into these state variables by use of equations (4.3) or (4.4), respectively.

D.2 Parameterizing the Energy Budget Model

Only considering adult females, I set body composition parameters as $\varphi = 0.627$, $\alpha = 26.14$ MJ kg^{-1}, $\rho_{\mathrm{STR}} \cdot k = 14.94$ kg m^{-3}, and metabolic rate as $m = 0.089$ MJ kg^{-1} d^{-1} (section 4.3.1).

Re-examining data on oxygen consumption in treadmill studies of two 4 year old polar bears (Øritsland *et al.* 1976; Hurst *et al.* 1982) provided no evidence for a postural effect, because the y-intercept of the linear regression between oxygen consumption and walking speed was at or below basal metabolic rate (Taylor *et al.* 1970; Schmidt-Nielsen 1972). I therefore assumed that any postural effect in polar bears would be negligible, and set $a = 0$. Polar bears are thought to be inefficient walkers (Øritsland *et al.* 1976; Hurst *et* *al.* 1982), and re-examining the polar bear treadmill data in relation to the interspecies allometric curve provided by Taylor *et al.* (1982) yielded a proportionality constant c = 0.0018 MJ km^{-1}, twice as high as for other species. The treadmill data were insufficient to determine the exponent d specifically for polar bears, so I set $d = 0.684$, in accordance with Taylor *et al.*'s (1982) interspecific allometric curve. Average velocities of solitary females during June and July were set as $v = 5.6$ km d^{-1} (Parks *et al.* 2006).

On ice feeding rates are not documented for polar bears in western Hudson Bay. To approximate energy acquisition by adult females in western Hudson Bay, I assumed a diet consisting only of ringed seals (Thiemann *et al.* 2008), and set capture rates and age-composition of kills by averaging the values reported by Stirling & Øritsland (1995) for the central Canadian High Arctic during the months of June and July. Of the two sets of calorific values reported for individual seals by Stirling & Øritsland (1995), I used the (more conservative) regression values these authors derived from the literature (Stirling & Øritsland, p. 2604). I further corrected energy acquisition downwards, by assuming that 20% of any given kill is not eaten (Stirling 1974; Stirling & McEwan 1975), arriving at an average feeding rate $\beta = 59.1$ MJ d^{-1}. Digestive efficiency was set as $\delta = 0.917$, assuming a mixed diet consisting of both fat and protein (Best 1977, 1985).

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Appendix E

Estimating Compensatory Feeding Rates (Derivation of Equation (4.9))

Here I provide the derivation of equation (4.9), which is used to estimate the daily terrestrial feeding rate β_{LAND} necessary to reach a certain target mass within a specified time period. More generally, this equation can be used to estimate feeding rate if straight line body length, initial and final storage energy (or equivalently, initial and final body mass), and somatic maintenance rate are known, and if no energy is expended towards movement, growth, reproduction, or thermoregulation.

Adult female polar bears in western Hudson Bay move little while on land (Lunn *et al.* 2004; Parks *et al.* 2006), and the resulting movement costs are negligible relative to the energy expended towards somatic maintenance. I therefore considered a simplified energy budget, which assumes no energy allocation towards movement. In an attempt to be conservative, I further assumed that increased terrestrial foraging would not result in increased energy expenditure. The energy budget model (D.6) therefore becomes

$$\text{(E.1)} \qquad \underbrace{\frac{dE}{dt}}_{\substack{\text{Rate of change} \\ \text{in storage energy}}} = \underbrace{\delta\beta_{\mathrm{LAND}}}_{\text{Feeding}} - \underbrace{m\cdot\left(\alpha^{-1}(1-\varphi)\cdot E + \rho_{\mathrm{STR}}\,k\,L^3\right)}_{\text{Somatic maintenance}} \; .$$

Equation (E.1) is a first-order non-homogeneous linear differential equation, which can be solved to give storage energy as a function of time *t*:

(E.2)

$$E(t) = \frac{\delta\beta_{\mathrm{LAND}} - m\,\rho_{\mathrm{STR}}\,k\,L^3}{m\alpha^{-1}(1-\varphi)} + \left(E_0 - \frac{\delta\beta_{\mathrm{LAND}} - m\,\rho_{\mathrm{STR}}\,k\,L^3}{m\alpha^{-1}(1-\varphi)}\right)\cdot \exp\left(-m\alpha^{-1}(1-\varphi)(t-t_0)\right) ,$$

where E_0 is the initial storage energy at time t_0 (i.e., $E(t_0) = E_0$).

Given storage energy at time t_1 (i.e., $E(t_1) = E_1$), feeding rate β_{LAND} can be estimated by solving equation (E.2):

$$\text{(E.3)} \qquad \beta_{\mathrm{LAND}} = \delta^{-1}\Phi \cdot \frac{E_1 - E_0 \cdot \exp\left(-\Phi \cdot \left(t_1 - t_0\right)\right)}{1 - \exp\left(-\Phi \cdot \left(t_1 - t_0\right)\right)} + \delta^{-1}\Psi \ ,$$

where Φ and Ψ are short for

$$\text{(E.4a)} \qquad \Phi = m\,\alpha^{-1}\left(1 - \varphi\right)$$

$$\text{(E.4b)} \qquad \Psi = m\,\rho_{\mathrm{STR}}\,k\,L^3 \quad .$$

E.1 References

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