Polar Bear (*Ursus maritimus*) Foraging Ecology in Spring

by

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Abstract

Polar bears (*Ursus maritimus*) enter a period of intensified feeding in the spring, which allows for the accumulation of energy stores critical to surviving the open water season. Study on polar bear predation has been limited by sample size and spatial extent, and hypotheses on the demographic composition of seal kills and the spatial distribution of polar bears and seals were incongruent. In this thesis, I used a long-term dataset (1985-2011) of seals killed by polar bears (n = 650) and predation attempts at ringed seal (*Pusa hispida*) subnivean lairs (n = 1396) in the Beaufort Sea, Canada, to link the habitats polar bears use and the seals that polar bears kill during hyperphagia. Using DNA and field observations, I determined that polar bears primarily killed ringed seals, but that bearded seals (*Erignathus barbatus*) contributed a significant portion of kill biomass. An increase in seal kill frequency was observed temporally over the spring, associated with the onset of ringed seal whelping. The influence of ringed seal whelping was also observable at inter-annual scales, with total kill frequency positively correlated to years of high ringed seal natality, while adults were killed in higher proportion in years when natality was low. Employing locations of seal kills and attempted hunts at ringed seal subnivean lairs, I examined the habitats in which polar bears hunt and ringed seals whelp. Polar bears selected for active areas of sea ice near the floe edge when hunting seals. Ringed seal whelping areas were located over a range of habitats, and the distribution was correlated with natality. In years of low natality pup kills were observed primarily in shorefast ice close to land, but during years of high natality the distribution widened, and pup kills were observed farther from land and more frequently near active ice areas. Results suggest that during periods of high natality, the habitats in which ringed seals whelp overlaps with areas preferred by polar bears for hunting. The spatial overlap between polar bears and whelping ringed seals likely influences a change in the age-class proportions of kills, as polar bears respond to the availability of vulnerable pups. Finally, I explored the assumptions of common analytical modelling approaches in ecology. I established that including biologically relevant measures, such as the size of kills, provided significant improvement to the models in both fit and interpretation. Measuring only the occurrence of an ecological event, whether temporally or spatially, was found to be insufficient when validated against independent data. The empirical analyses within this dissertation suggest that strong assumptions of ecological models may not always hold. Collecting biologically relevant data in the field, beyond simply recording events, can test model assumptions and validate results, increasing model portability and the relevance of the findings.

Preface

This thesis is an original work by Nicholas William Pilfold. Field methods were in accordance with the Canadian Council on Animal Care guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee (Permit #A5070-01). The data for the thesis was collected in collaboration with Environment Canada. Dr. Ian Stirling and Dennis Andriashek were instrumental in collecting the majority of the field data used for the analyses in this thesis.

To my Father, John William Pilfold.

For introducing me at an early age
to the power and wonder of the scientific method.

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The majority of the data collected in this thesis was not done by me, and without the collection efforts of many others, I would not have a thesis. In particular, Dr. Ian Stirling and Dennis Andriashek collected the majority of the data between 1985-2006. Dr. Andrew Derocher and members of his lab also contributed to the data collection process, especially between 2007-2011. I thank the field efforts of Marie Auger-Méthé, Seth Cherry, Stephen Hamilton, Alysa McCall, Peter Molnár, Jodie Pongracz, Evan Richardson, Vicki Sahanatien, and Greg Thiemann.

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Chapter 1

1 Introduction

1.1 The evolutionary ecology of predation vulnerability

In 1859, Charles Darwin proposed Natural Selection as the "preservation of favourable individual differences and variations, and the destruction of those which are injurious" (Darwin 1859). Perhaps the most vivid illustration of Natural Selection is predation, where a single act by a predator immediately modifies the genetic composition of a prey population. Coevolution between predator and prey can be thought of as an evolutionary arms race, in which adaptations of anti-predation traits in prey spur the evolution of more advanced hunting traits for predators (Dawkins and Krebs 1979). The fitness tradeoff in the arms race is asymmetric, otherwise known as the life-dinner principle: if a predator does not kill, it misses dinner; if a prey animal avoids predation, it lives (Dawkins and Krebs 1979). This asymmetry puts a higher selection pressure on prey, leaving predators in an evolutionary lag. An alternate view to the life-dinner principle is that the asymmetry is owed to the predictable fitness consequence to the prey in an interaction versus the unpredictable fitness consequence to a predator (Brodie and Brodie 1999). A single failed hunting attempt may not predict the outcome of the next attempt for the predator, and most predators modulate the fitness impact of failed captures by preying on several species (Brodie and Brodie 1999). The selection pressure placed on predators by prey is therefore averaged across several prey species, resulting in generalized rather than highly specialized predatory traits.

Cognitive adaptations may play a role in compensating for the evolutionary asymmetry between prey and predator, as well as predatory and life-history tradeoffs, which can limit the evolution of physical traits. Brain size has been linked to the development of social systems (Dunbar 1998;

Shultz and Dunbar 2010), which can help overcome capture difficulties posed by prey (Macdonald 1983). Carnivores engaged in cursorial hunting of large mobile prey are more likely to cooperate, and as a result, possess larger brain sizes than solitary carnivores (Smith *et al.* 2012). Some mammalian predators select for prey with lower brain sizes, and presumably less behavioural flexibility (Shultz and Finlayson 2010), which may have reciprocal effects on the evolution of anti-predator strategy (Møller and Erritzøe 2014). The evolutionary path of predatory traits may rely as much on cognitively identifying weaknesses in a prey species, as adapting physical traits such as strength or speed.

A proposed application of Natural Selection is that predators consistently select the weakest individuals from a prey population (Errington 1946; Mech 1970; Curio 1976). Evidence suggests that as the difficulty of capture increases, predators are more likely to kill substandard or otherwise vulnerable individuals (Temple 1987; Husseman *et al.* 2003). Vulnerability can include physiological conditions that limit anti-predator response, such as reproduction, disease, and age (Magnhagen 1991; Swenson *et al.* 2007; Krumm *et al.* 2010). In some cases, predators will exploit abiotic conditions that accentuate pre-existing prey vulnerabilities. For example, lions (*Panthera leo*) and leopards (*Panthera pardus*) tend to avoid areas of higher prey abundance, and instead prefer habitats that increase prey catch-ability (Hopcraft *et al.* 2005; Balme *et al.* 2007). Additionally, climatic conditions may change the vulnerability of prey, resulting in seasonal prey switching and/or differential kill rates (Post *et al.* 1999; Loveridge *et al.* 2006; Owen-Smith 2008).

In environments with seasonal food shortages, limited periods of food abundance increase the cost of missed feeding opportunities. Therefore, it may be expected that predators in seasonal environments will be more likely to focus on substandard or vulnerable prey to maximize capture rates, especially during seasonal bouts of productivity. Additionally, adaptive physiological mechanisms for storing energy may combine with predation strategy to maximize net energetic gain. Predators can then rely on the stores gained during a heightened feeding period to fast through periods of low prey availability and/or migrate to seasonal refugia.

1.2 Hyperphagia

Hyperphagia is the behaviour of increasing food intake beyond what is required for metabolic maintenance to increase energy stores. Preparation for and recovery from seasonal food shortages is a common driver of hyperphagia, documented in fish (Bull and Metcalfe 1997), birds (Mortensen and Blix 1985), and mammals (Asikainen *et al.* 2005; Barboza *et al.* 2006). Pre-migratory hyperphagia, common to birds, provides the fat stores needed for the metabolic requirements of extended periods of flight (Odum 1960). In addition to seasonal food shortages, annual life phases such as reproduction or moulting can cause fasting (Mrosovsky and Sherry 1980), and hyperphagia can help recover lost stores. Red deer (*Cervus elaphus*) stags enter hyperphagia after the rut, while hinds compensate the energetic demands of lactation with intensified feeding (Mitchell *et al.* 1976; Groot Bruinderink and Hazebroek 1995). During the productive open water season, ringed seals (*Pusa hispida*) recover blubber stores that were expended during reproduction and moulting (Ryg *et al.* 1990; Young and Ferguson 2013).

Hyperphagia can be cued by exogenous factors, but is endogenously controlled for many species living in environments with predictable seasonal change. Exogenous cues can include changes in the availability of a new or existing food supply. Brown bears (*Ursus arctos*) and black bears (*U. americanus*) will shift their diet during autumn hyperphagia, coinciding with the migration of salmon (*Oncorhynchus* spp.), and/or the availability of berries (Welch *et al.* 1997; Hilderbrand *et al.* 1999a; Robbins *et al.* 2007). A diet shift to frugivory plays a role in pre-migratory hyperphagia of many bird species (Bairlein 2004), timed to the availability of fruit with high lipid content

(Herrera 1984). However, some species do not shift diet during hyperphagia, but rather take advantage of an increase in the vulnerability of their primary prey. For example, pre-migration hyperphagia in Whimbrels (*Numenius phaeopus*) depends on the vulnerability of fiddler crabs (*Uca tangeri*), their main prey (Zwarts 1990). As spring progresses and air temperatures warm, fiddler crabs spend more time on the surface of the sand rather than in their boroughs, which allows the intake rate of Whimbrels to increase, providing the energetic stores for migration (Zwarts 1990).

Predictable exogenous factors may spur the evolution of innate endogenous responses that are phenologically matched to resource peaks. For example, migratory birds held in captivity under constant environmental conditions show concurring body mass changes to their wild conspecifics (Bairlein 2004). Temperate and Arctic ungulates fed *ad libitum* voluntarily reduce and increase consumption coinciding with seasonal changes in forage quality and availability (Schwartz *et al.* 1988; Peltier *et al.* 2003; Thompson and Barboza 2013). Additionally, the timing of reproductive activities of predators can be matched to expected seasonal bouts of prey availability, enhancing the survival of predator offspring (Cushing 1969, 1990). Polar bears (*Ursus maritimus*) are an excellent study species to examine hyperphagia, because both exogenous and endogenous factors are involved. Herein, I focus my dissertation on feeding ecology of polar bears in spring, and examine potential influential factors that may regulate this important period.

1.3 Polar bear hyperphagia

Polar bear hyperphagia coincides with females leaving the den with cubs-of-the-year (Ramsay and Andriashek 1986; Messier *et al.* 1994; Amstrup 2003), and is phenologically matched to the reproductive activities of their prey (Stirling and McEwan 1975; Ramsay and Stirling 1988; Hammill and Smith 1991). Polar bears primarily feed on ringed seals, and to a lesser extent bearded seals (*Erignathus barbatus*), both of which reproduce and mate between late March and late May (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1987; Kovacs *et al.* 1996; Thiemann *et al.* 2008). Predation success in winter is thought to be low (Stirling and Øritsland 1995), and evidence suggests polar bears are less active during this period (Messier *et al.* 1992, 1994). As a result, minimum body mass for the year is generally reached in March (Ramsay and Stirling 1988). Polar bears may acquire as much as two-thirds of the energy requirement for the year in spring (Stirling and Øritsland 1995). This intense feeding period provides the energy stores required to survive through the open water season (Watts and Hansen 1987; Ramsay and Stirling 1988), when reduced prey availability can result in the onset of a fasting physiological state similar to hibernation in other bear species (Nelson 1987; Derocher *et al.* 1990; Ramsay *et al.* 1991; Cherry *et al.* 2009). Although the diet can consist of terrestrial species during the open water season (Russell 1975; Derocher *et al.* 1993), the energetic contribution to the overall diet is low (Ramsay and Hobson 1991).

Studies of seals killed in the spring by polar bears suggest hyperphagia is in response to the synchronous birth of ringed seal pups, whom are vulnerable to surface predators (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980; Hammill and Smith 1991). In shorefast sea ice areas, polar bears can be significant predators of ringed seal pups, killing 8-44% of the pup production in an area (Hammill and Smith 1991). As such, the proportion of pups killed by polar bears in spring is sensitive to seal natality. Surveys of ringed seals killed by polar bears between 1971-1975 in the Beaufort Sea and Amundsen Gulf showed a marked decrease in the proportion of pup kills in years with lower ringed seal natality (Stirling and Archibald 1977; Stirling 2002). Reduced availability of ringed seal pups in spring has also been linked to lower body condition and reproductive success in polar bears (Kingsley 1979; Stirling and Lunn 1997).

In addition to pups, studies suggest polar bears primarily prey on younger age-classes in spring, up to two years of age, with adult seals killed less often (Stirling *et al.* 1975; Stirling and Archibald 1977; Smith 1980; Hammill and Smith 1991; Stirling and Øritsland 1995). Vulnerability to predation has been hypothesized to be based on experience, with young seals less wary and more easily caught by polar bears (Stirling and Archibald 1977; Stirling *et al.* 1993). Additionally, adult male ringed seals have been suggested to have a unique anti-predator defense: a pungent sebaceous secretion for scent marking breeding territories (Hardy *et al.* 1991; Ryg *et al.* 1992). Studies noted that hunting polar bears largely ignored ringed seal subnivean lairs marked by rutting males (Smith 1980; Hammill and Smith 1991; Furgal *et al.* 1996). Explanations for this avoidance have included: the meat of rutting male ringed seals is unpalatable to polar bears (Smith 1980; Gjertz and Lydersen 1986; Hammill and Smith 1991); breeding odour serves to confuse the olfactory senses of polar bears during hunting (Smith 1980); or adult males in subnivean lairs are more difficult to catch for polar bears than younger age classes (Hammill and Smith 1991; Furgal *et al.* 1996). However, no study has identified ringed seal kills by sex, therefore the anti-predator benefits of male breeding odour remains untested.

Polar bears primarily use floe edge and moving ice habitat in spring, preferring areas of active ice with leads (Ramsay and Stirling 1986; Stirling *et al.* 1993; Ferguson *et al.* 2000). The floe edge area is high in primary productivity in spring (Stirling 1997; Arrigo and van Dijken 2004; Makabe *et al.* 2010; Perrette *et al.* 2011), and ringed seals and bearded seals are often found in high abundance (Stirling *et al.* 1977; Stirling *et al.* 1982; Harwood and Stirling 1992). It has been suggested that the floe edge area is preferred by polar bears because of the availability seals for hunting (Stirling *et al.* 1975; Stirling and Archibald 1977; Smith 1980). However, a contradiction exists between the hypothesized age-structure of seal kills, and the type of habitat polar bears use for hunting. While subadult seals may be plentiful at the floe edge, the primary prey item, ringed seal pups, are found in stable shorefast ice. Snowdrifts along ridges in the shorefast ice and interisland channels of archipelagos are considered preferred habitat for ringed seal birth lair construction (McLaren 1958; Lydersen and Gjertz 1986; Smith *et al.* 1991). Although it is reported that ringed seal pups may account for >50% of seal kills (Stirling and Archibald 1977; Hammill and Smith 1991; Stirling and Øritsland 1995), Stirling *et al.* (1993) found that only 16% of polar bear tracks were in pupping habitat in spring, while 82% were in moving ice and floe edge habitat.

Three non-exclusive hypotheses may explain the inconsistency between the age-class distribution of seal kills and polar bear spatial distribution: 1) polar bear movement patterns are not reflective of hunting preferences; 2) polar bears do not kill pups as frequently as suggested or 3) ringed seal pups may be born in or near moving ice or floe edge habitat types. Stirling and Archibald (1977) documented few seal kills in floe edge and moving ice habitat, which suggests the abundance of tracks may be unrelated to predation. However, a broad scale habitat selection model for seal kills is nonexistent. Further, research on the age structure of seal kills has been limited in sample size and based primarily on observations in shorefast ice (Stirling and Archibald 1977; Smith 1980; Hammill and Smith 1991). Ringed seal pup kills have been observed with limited or no consumption (Stirling and McEwan 1975; Fig. 1.1), suggesting a low energetic value in early spring and potentially limited influence on polar bear hyperphagia. Finally, anecdotal evidence suggests that ringed seals can breed in the moving pack ice (Fedoseev 1975; Finley *et al.* 1983; Wiig *et al.* 1999), but a broad scale study of ringed seal pupping habitat is absent. In my thesis, I address all three possible hypotheses in an attempt to provide a cohesive link between the habitats polar bears use and the seals they kill during hyperphagia.

1.4 Dissertation outline

The demographic structure of kills can provide insight into intraspecific differences in predation vulnerability, as well as provide the basis to understand the population dynamics between predator and prey. In Chapter 2, I analyse the species, age-class and sex composition of seals killed by polar bears in the spring in the Beaufort Sea, Canada. The results from this chapter provide the basis for estimating the biomass of kills, which becomes an important aspect of the ecological models I employ in later chapters, as well as test assumptions about the type of seals polar bears kill in spring. I illustrate how the demographic composition of kills varies with ringed seal natality, the seasonal link between ringed seal whelping and kill frequency, as well as how age is the primary intraspecific vulnerability of ringed seals to predation.

Understanding how ecological interactions drive spatial patterns is a cornerstone of ecology. In Chapters 3 and 4, I investigate the relationship between predation and the spatial distribution of polar bears and ringed seals. Chapter 3 focuses on the habitat in which polar bears kill seals, using the locations and estimated biomass of seal kills. I validate this analysis by comparing the distribution of polar bear captures to the modelled quality of the habitat. The validation allows for additional ecological hypotheses to be tested, including the role of intraspecific competition in determining species distribution. Despite the acknowledgement that intraspecific interactions likely influence species distribution (Araujo and Luoto 2007; Elith and Leathwick 2009), specific empirical examinations integrated with the results from a Species Distribution Model (SDM) are rare. Additionally, in Chapter 3 I test the habitat-matching assumption of SDMs: density of use is a sufficient indicator of habitat quality (Cassini 2011). Using biomass estimations from Chapter 2, I show how this strong assumption of SDMs is an inaccurate approach for how polar bears select foraging habitat. In Chapter 4, I use polar bear predatory behaviour to identify ringed seal breeding habitat. This analysis is the first broad scale empirical assessment of areas used for whelping by ringed seals, and becomes a central piece of evidence in providing a cohesive link between the habitats polar bears use and the seals they kill during hyperphagia.

In Chapter 5, I investigate the influence of multi-temporal abiotic and biotic factors on the likelihood of a predation event. Using this model, I compare polar bear fasting rates identified from physiological markers in the blood to the expected seal kill rate at the time the polar bear was sampled. The comparison corroborates the predation event model and assesses trends related to climate change. My analyses suggest that the change in fasting rates of polar bears reported by Cherry *et al.* (2009) is due to a complex set of factors including underlying population dynamics of ringed seals, rather than a single scale environmental correlation.

In Chapter 6 I synthesize the results of the dissertation into a new ecological hypothesis to explain polar bear hyperphagia. The evidence supplied by this thesis clarifies how the spatial distribution of polar bears and ringed seals relates to the demographic composition of seals killed during hyperphagia. Additionally, I examine how using relevant biological metrics in ecological modelling can improve the accuracy of the model. I review ways in which biologically relevant metrics may be collected for carnivores and used in SDMs.

Figure 1.1 Ringed seal pup kill observed in the Beaufort Sea, Canada, on April 22, 2010. A polar bear has killed the pup, but left the carcass mostly unconsumed, suggesting a limited energetic value for the kill. Observations such as these raise the possibility that pups may be of limited influence to the overall diet of polar bears during hyperphagia.

Chapter 2[‡]

2 Age and Sex Composition of Seals Killed by Polar Bears in the Eastern Beaufort Sea

2.1 Introduction

Reproduction can incur considerable survival tradeoffs, including increased risk of predation. Mating competition, copulation, and parental care can increase detection of prey by predators, as well as energetically exhaust prey, reducing vigilance against predation (Magnhagen 1991; Sih 1994; Zuk and Kolluru 1998). Sexually dimorphic traits associated with mating success can also increase intraspecific vulnerability to predation, as many predators exhibit sex-selective prey choice (*e.g.* Acharya 1995; Quinn and Kinnison 1999; Sommer 2000). Synchrony in the parturition of prey swamps predators with an abundance of physically weaker and less experienced prey (Ims 1990). As a result, predators are responsive to prey reproductive cycles and the associated vulnerability of reproductive adults and their young.

Polar bears (*Ursus maritimus*) are obligate carnivores, and enter a period of hyperphagia during spring, facilitated by the reproduction and mating cycle of their prey (Stirling and McEwan 1975; Ramsay and Stirling 1988; Hammill and Smith 1991). Polar bears of the Beaufort Sea primarily feed on ringed seals (*Pusa hispida*), and occasionally bearded seals (*Erignathus barbatus*), both of which reproduce and mate between late March and late May

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(Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1987; Kovacs *et al.* 1996; Thiemann *et al.* 2008). Success rates for polar bears hunting in winter are thought to be low (Stirling and Øritsland 1995), and evidence suggests polar bears are less active during this period (Messier *et al.* 1992, 1994). As a result, most polar bears are at or near their minimum body mass for the year in March (Ramsay and Stirling 1988). Hyperphagic behaviour in spring allows polar bears to increase their mass before the onset of the open water season (Ramsay and Stirling 1988), when reduced prey availability can result in the onset of a fasting physiological state similar to hibernation in other bear species (Nelson 1987; Derocher *et al.* 1990; Ramsay *et al.* 1991; Cherry *et al.* 2009).

Previous studies of seals killed in the spring by polar bears suggest the proximate mechanism for prey access for polar bear hyperphagia is the synchronous birth of ringed seal pups, whom are vulnerable to surface predators (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980; Hammill and Smith 1991). In shorefast sea ice areas, polar bears can be significant predators of ringed seal pups, killing up to 44% of the pup production in an area (Hammill and Smith 1991). As such, the proportion of seal pups killed by polar bears in spring is sensitive to seal natality. Although sample sizes were limited, surveys of ringed seals killed by polar bears between 1971-1975 in the Beaufort Sea and Amundsen Gulf showed a marked decrease in the proportion of pup kills in years with lower ringed seal natality, a conclusion that was supported by the simultaneous occurrence of reduced ovulation rates (Stirling and Archibald 1977; Stirling 2002). Lower ringed seal ovulation rates were documented again in 1985-1987 at Sachs Harbour (Kingsley and Byers 1998) and in 2003-2006, at Ulukhaktok (Harwood *et al.* 2012). However, the affect of lower ringed seal natality on polar bear predation and hyperphagia during these periods is unknown.

In addition to the increase of vulnerable pups, adult ringed seals may be at a heightened risk of predation in spring relative to other times of the year.

During the open water season ringed seals are pelagic, and polar bears rarely catch seals without having access to them from sea ice (Stirling and Archibald 1977; Derocher *et al.* 2002) but see Furnell and Oolooyuk (1980). As maximal sea ice extent in the Arctic is reached in March (Fetterer *et al.* 2009), ringed seals in early spring are confined to using self-maintained breathing holes, limiting surfacing options. Due to reproductive activities and mating, ringed seal adults spend nearly 50% of their time out of the water in April and May, much higher than previous months (Kelly *et al.* 2010). Limited surfacing areas and increased time spent near or on the ice platform by adult ringed seals may increase the hunting success rate for polar bears. Adult female ringed seals birth and nurse pups in subnivean lairs (Smith and Stirling 1975; Furgal *et al.* 1996), and it has been hypothesized that killing ringed seal pups at the lair may provide polar bears a secondary opportunity of capturing the adult female (Stirling and McEwan 1975; Smith 1980, 1987; Smith *et al.* 1991), although the success of this tactic is unknown. Diving profiles of adult male ringed seals during the breeding season indicate they spend more time near the surface to mark and guard shared breathing holes (Kelly and Wartzok 1996; Kelly *et al.* 2010). Scent marking by adult males is a conspicuous form of mate signaling (Hardy *et al.* 1991; Ryg *et al.* 1992), and likely increases the chances of detection by polar bears. It has been suggested, however, that the odour of breeding male ringed seals is strong enough to confer an anti-predation benefit from polar bears (Smith 1980; Hammill and Smith 1991; Furgal *et al.* 1996), although this has only been examined with hunting attempts on subnivean liars, not seal kills.

The objectives of this study were to: quantify the composition of species, age, and gender of seals killed by polar bears in spring in the Beaufort Sea; investigate how temporal shifts in ringed seal natality affect kill composition; and, test hypotheses on the intraspecific vulnerabilities of ringed seals to predation. If ringed seal natality rates affect the overall composition of kills by polar bears in a particular year, the proportion of ringed seal pups killed should be greater in years with high rates of ringed seal ovulation. In addition, if reproductive activities increase vulnerability to predation, more adult seals should be killed following the peak of parturition. Furthermore, if the strong and apparently unpleasant smell of adult male ringed seals in spring reduces their attractiveness to predators, it might be predicted that males would be killed less frequently than adult females. Finally, if ringed seal vulnerability increases because of exposure to predation at subnivean lairs, then a positive correlation should exist between the number of observed hunting attempts on lairs and both pup and adult kill rates. Observations of both pup and adult female ringed seal kills should occur at the same location, if polar bears are able to catch a ringed seal mother after killing her pup.

2.2 Materials and methods

Observations of hunts (digs) and seals killed by polar bears were collected between early-April and late-May (range April 3 – May 28) in 1985-1987, 1992-1994, 2000, and 2003-2011. Observations were gathered opportunistically during polar bear inventory and ecology research. The study area was the eastern Beaufort Sea east of 141° W and south of 75° N, and the Amundsen Gulf (Fig. 2.1). Helicopter flights originated from Tuktoyaktuk, Sachs Harbour, Ulukhaktok, Cape Parry, and Norway Island and were limited to within 150 km of the coast. Search effort included surveying active ice near leads and stable shorefast ice areas (Stirling *et al.* 1993).

Digs and kills were identified from the helicopter during tracking of polar bears. Digs were categorized as snowdrifts along pressure ridges that were dug into by polar bears. Kill sites were confirmed by the presence of blood, carcass, remains that have been scavenged, or carcasses that were actively being fed upon by polar bears. Due to logistic restrictions, it was not possible to land and investigate all kill sites, so some were noted only from the air. When possible, sites with remains present were investigated and tissue, jaw, and claw samples from kills were collected. Species, age class, and gender were also noted when possible. In some cases where only blood remained, if the amount of blood was minimal, and it was found near a pressure ridge with a dig nearby, it was assumed to represent the kill of a ringed seal pup (Derocher *et al.* 2002). Observations of white lanugo at the kill site also helped confirm ringed seal pup kills when few remains were present. Seal kills by Arctic fox (*Vulpes lagopus*) were excluded based on the presence of fox tracks and the absence of polar bear tracks.

Tooth histology and claw samples were used to augment seal kill age class observations. Canine seal teeth were extracted from recovered jaws, decalcified, and aged to the year following Stewart *et al.* (1996). To assist with aging, a DFC480 microscope camera (Leica Microsystems, Wetzlar, Germany) was used to take tooth images (Fig. 2.2). Age was determined using between 6 and 8 longitudinal sections per tooth. Claw samples were employed only to categorize a kill as either pup (0+ years), juvenile (1-6 years) or adult≥(7 years), because claw wear precludes accurately aging beyond 10 years (McLaren 1958).

DNA analysis was used to confirm species and identify gender of seal kills. Seal samples were stored at -20º C and included all observation years except 1985-1987. Extracted DNA of 147 seal kill samples were analyzed by Wildlife Genetics International (Nelson, British Columbia). DNA profiles for both species and gender yielded clear results (D. Paetkau, personal comm.). Results of laboratory age and species classifications were compared with field notes to test the strength of *in situ* records. This test assessed the confidence in the use of field observations when laboratory analysis was not available for confirmation.

Seal kill observations were pooled over all years (1985-2011), and pooled by time periods with data from Stirling and Archibald (Stirling and Archibald 1977), associated with high (1971-1973; 2007-2011) or low (1974-1975; 1985-1987; 2003-2006) ringed seal ovulation rates. Differences in the proportion of kills between age classes within species, and between years within age classes, were tested for statistical significance using a Pearson Chi-square. The Marascuilo procedure was used for *post-hoc* analysis, as it allows for the comparison of proportion data of several populations simultaneously, using a Chi-square statistic (Marascuilo 1966). Given that species was not identified in 31% of the 650 seal kill observations, and age-class was not identified in 58% of the observations, multiple imputation methods were considered (Schafer 1997). However, Little's MCAR test was not significant ($\chi^2 = 1.35$, $df = 1$, $P = 0.25$), and pooled input values did not result in a significantly different estimate of the proportions of species or age-class; indicating little bias in using only complete data. Therefore, all proportions are presented using complete data only. Identified kills were also converted to total biomass for comparison following Derocher *et al.* (2002). Mean kill and dig observations per flight day were compared between 1985-1987 and 2003-2006 using *t*-tests, adjusted to seasonal day (April 11-May 10).

Seal kill observations were pooled into five-day intervals ($n = 8$) to test for the presence of within season trends. A Kruskal-Wallis test was used to analyze whether the distribution of kill observations was equal across time intervals. *Post-hoc* pairwise comparisons using Kruskal-Wallis ranks tested whether kill rates at individual time intervals differed.

Linear regression was employed to test for a relationship between the number of digs (independent) and the number of adult or pup ringed seals killed (dependent) each year. The correlation used data from the years 1985-1987, and 2003-2006, because these years had high sampling intensity (range 26-47 days), and dig observations were consistently recorded. Data were pooled ($n = 14$) into observations that occurred early in the sampling season ($\leq$ April 25) and late $\geq$ (April 26). Regression was performed on Box Cox transformed data (Box and Cox 1964; $\lambda = 0.5$), to meet the assumptions of normality (Shapiro-Wilk, $P > 0.05$). All statistical tests were conducted in SPSS 18.0 (IBM, Chicago, Illinois), and 95% confidence intervals are reported with all means, unless otherwise stated. For all significance tests, alpha was set to 0.05.

2.3 Results

Between 1985-2011, 370 helicopter flight days were flown over the Beaufort Sea, during which 650 kills and 1396 digs were recorded. Sampling effort between years varied with 72.9% of total flight days recorded in 1985-1987 and 2003-2006, accounting for 77.2% of the kills and 80.9% of digs.

Of the 650 kills, species was undetermined for 200. Ringed seals accounted for 90.2% (406/450) of kills of known species, while bearded seals accounted for the remaining 9.8% (44/450). DNA analysis agreed with the field assessment of species classification in 94.1% of the cases where both were recorded ($n = 102$). Of 450 samples from known species, age class was determined for 344 ringed seals and 32 bearded seals. For ringed seals, 38.4% (132/344) were pups, 18.0% (62/344) were juveniles and 43.6% (150/344) were adults. Overall, ringed seal pup and adult age classes were killed at a higher proportion than juveniles ($P < 0.001$, $n = 344$). Of the ringed seal adults, 49.6% were≥21 years of age (60/121), with the oldest being a 41 year -old female from Dolphin and Union Strait (Fig. 2.3). The eight oldest ringed seals aged by tooth histology and identified by gender were all female. The oldest male was 30 years of age. Mean age for killed adult male ringed seals was 20.7 ± 1.9 years and 22.6 ± 3.4 years for adult females and did not differ by sex ($t = 1.11$, $df = 62$, $P = 0.27$). For bearded seals, 25.0% (8/32) were pups, 40.6% (13/32) were juveniles and 34.4% (11/32) were adults. Proportions of bearded seal kills did not differ by age class ($P \geq 0.40$), although the number of known age class samples was small ($n = 32$). When identified kills were converted to biomass, ringed seals contributed 67% of the overall prey biomass, while bearded seals contributed 33%. Tooth histology classification of seal ages by adult, juvenile, and pup, agreed with field assessment in 87.9% of the cases where both were reported ($n = 33$). DNA analysis of gender of ringed seal adult kills determined the sex ratio as 0.50 ($n = 78$).

Age class proportions of ringed seal kills from this study along with Stirling and Archibald (Stirling and Archibald 1977), were not distributed evenly between time periods associated with high and low ringed seal ovulation rates ($\chi^2 = 176.8$, $df = 8$, $P < 0.001$, Fig. 2.4). Ringed seal pups were killed at the highest proportion from 2007-2011 as compared to any other time period ($P < 0.01$). Proportions of adult ringed seal kills were lowest in 1971-1973 and 2007-2011 compared to the other periods ($P < 0.001$). In 1985-1987, 2.20 kills/flight day were observed, which was not different than the 1.84 kills/flight day in 2003-2006 ($t = 1.07$, $df = 228$, $P = 0.28$). In 2003-2006, 5.16 digs/flight day were observed and was significantly higher than the 2.36 digs/flight day in 1985-1987 ($t = -2.87$, $df = 228$, $P < 0.01$). Mean estimated age of adult ringed seals killed increased from 17.9 ± 1.8 years between 1985-1994 to 21.6 ± 2.3 years between 2000-2011 ($t = 2.51$, $df = 113$, $P = 0.01$).

Abundances of seal kill observations were not distributed evenly over the season ($H = 47.5$, $df = 7$, $P < 0.001$, Fig. 2.5a). *Post-hoc* analysis revealed kill observations were significantly higher from April 21 – May 5 compared to April 6 – 15 ($P < 0.01$, Fig. 2.5a). Pup and juvenile ringed seal kill observations per day ($n = 40$) did not differ over time ($H_{\text{pup}} = 12.5$, $P_{\text{pup}} = 0.09$; $H_{\text{juv}} = 8.6$, $P_{\text{juv}} = 0.29$; $df = 7$, Fig. 2.5b). Observations of adult ringed seal kills per day varied ($H = 17.8$, $df = 7$, $P = 0.01$), as a *post-hoc* examination revealed that the number of kills observed was higher April 26 – 30 compared to April 6 – 15 ($P < 0.05$, Fig. 2.5b). Temporal correlation between daily observation rates of total kills and adult ringed seal kills was evident (Spearman rank correlation, $r_s = 0.69$, $P < 0.001$, $n = 40$).

There was a positive correlation between the number of digs observed and the number of ringed seal pup kills ($r^2 = 0.30$, $df = 12$, $P = 0.04$, Fig. 2.6a) but no correlation between the number of digs observed and the number of adult ringed seal kills ($r^2 = 0.07$, $df = 12$, $P = 0.37$, Fig. 2.6b). Additionally, there were no observations of a pup and adult ringed seal killed at the same location. The closest proximity of a pup and adult kill was observed on April 29, 2009, when an adult female kill was found 1.76 km from a pup kill.

2.4 Discussion

Extrapolating foraging behaviour of polar bears from opportunistic observations is subject to potential bias. Search effort in this study was not systematic, as kills were found while following polar bear tracks. This resulted in a high representation of the floe edge and moving ice habitats that polar bears show a preference for (Stirling *et al.* 1993), while underrepresenting other habitats, potentially resulting in some bias in kill composition. However, because the objective of the research was to locate as many polar bears as possible, it is likely that the sampling reflected areas where polar bear foraging was successful, reducing the possibility of missing substantial numbers of kills in other habitats. Searching for kills was also dependent on the spatial scope of polar bear ecology and inventory research. Most research flights were flown between the Tuktoyaktuk Peninsula and Herschel Island, or on the western and southern coasts of Banks Island and the western entrance to Amundsen Gulf, with less time spent farther east in the Amundsen Gulf. Additionally, between 2007-2011, research flights were based only from Tuktoyaktuk, resulting in search effort restricted to the southern Beaufort Sea. As depth contours and sea ice conditions vary throughout the eastern Beaufort Sea and Amundsen Gulf, extrapolating from one area may not fully depict foraging behaviour for polar bears across the study region. Nonetheless, I submit that the samples are broadly representative of the seals killed.

Species composition in the diet of polar bears of the Beaufort Sea was similar to that reported in past studies (Stirling and Archibald 1977; Thiemann *et al.* 2008). Polar bears primarily preyed upon ringed seals, with only small numbers of bearded seals being predated which, in part at least, reflects the relative abundance of the two species in the study area (Stirling *et al.* 1982). However, because subadult and adult bearded seals are substantially larger than ringed seals, it appears that the majority are killed by adult male polar bears, though carcasses may be scavenged by younger animals (Stirling and Derocher 1990; Thiemann *et al.* 2008; Thiemann *et al.* 2011). Although the numeric contribution of bearded seals to the kill composition is low, bearded seals contributed approximately one-third of the kill biomass. However, caution is warranted in interpreting the biomass composition to be anything but a rough estimate. The estimate of dietary contribution of bearded seals in this study is higher than from previous estimates using fatty acid analysis (Thiemann *et al.* 2008). As the estimation technique pools juveniles and adults into the same weight class for each species (Derocher *et al.* 2002), the calculation may have upwardly biased bearded seal contribution. Nonetheless, the finding supports polar bear dietary studies in other regions, which have found bearded seals to be an important contributor to the overall biomass intake (Smith 1980; Derocher *et al.* 2002).

Age class composition of ringed seal kills varied temporally, in general association with years of low and high ringed seal ovulation rates. Ringed seal pups were killed at the highest proportion between 2007-2011, when ringed seal ovulation rates were over 90% (Harwood *et al.* 2012). The result suggests that when ringed seal recruitment is high, polar bears kill mostly ringed seal pups in spring. Ringed seal juveniles were killed half as frequently as adults between 1971-2011, which was unexpected given that polar bears focus on younger age classes during predation (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980; Stirling and Øritsland 1995). However, this result may also reflect that the majority of kills were observed in years with lower ringed seal productivity. Juvenile ringed seals were observed to decrease in Inuit open water catches for two to three years immediately following low ringed seal natality (Smith 1987; Kingsley and Byers 1998). These results support the suggestion that the decadal cycle of ringed seal productivity affects the kill composition of polar bears in the spring (Stirling and Lunn 1997; Stirling 2002).

Observations of juvenile ringed seal kills were lower in 2003-2011 than in 1985-1987. The mechanism for the decline is not well understood. Juvenile ringed seals in the study area have been observed to be in worsening body condition over the past two decades (Harwood *et al.* 2012). Coupled with an increase in the average age of adult ringed seal kills, decreases in juvenile representation in the kill composition could be symptomatic of a declining population. However, understanding of juvenile ringed seal behaviour and distribution are still inadequate. Juvenile ringed seals do not restrict themselves to a territory, and will spatially segregate themselves from adults during early spring to take advantage of high quality foraging areas (Crawford *et al.* 2011). This may translate into an unpredictable source of prey for polar bears, and disentangling the predator-prey effects from possible population effects is difficult. As such, it is unwarranted to speculate further on the causes of the observed trends.

Seasonal analysis indicated an increase in the rate of observations of ringed seal adult kills and total kills after the peak ringed seal whelping date. A temporal correlation between these two trends suggests ringed seal adult kills may have driven the increase in total observed kill rates. There are two nonexclusive hypotheses for the increased kill rates of adult seals following whelping. First, reproductive behaviour may increase predation risk for adults. Adult female ringed seals are income breeders (Lydersen 1995; Lydersen and Kovacs 1999), and have a spatially restricted foraging pattern while nursing (Kelly and Quakenbush 1990; Kelly *et al.* 2010). Territorial behaviour in adult male ringed seals peaks post-whelping and less dominant males are excluded from prime-breeding habitat (Smith 1987; Krafft *et al.* 2007). Additionally, both male and female ringed seals spend an increasing amount of time out of the water during reproduction and mating (Kelly *et al.* 2010). The restricted spatial ranges of adults and repeated use of surfacing areas may increase the likelihood of predatory success for a sit-and-wait predator such as the polar bear.

Second, approximately half of the adults killed were ≥21 years, indicating a potential age related mechanism of vulnerability in adults. Although ringed seal life expectancy can range up to 45 years (Lydersen and Gjertz 1987), the proportion of the adult population over 20 years old rarely exceeds 30% in catch statistics (Lydersen and Gjertz 1987; Smith 1987; Chambellant *et al.* 2012). Using smoothed age-frequency estimates from Smith (Smith 1987), ringed seal adults 21 years and older only compose ca. 15% of the adult age class. A high kill composition of pups and older seals supports the controversial theory that as a predator, polar bears may be killing the old and the weak in the prey population (Mech 1970; Curio 1976). For ambush predators, prey selection is largely limited to what avails itself, and therefore dependent on the behaviour of the prey. In years of high ringed seal ovulation, polar bears have access to a large number of vulnerable pups. In low ovulation years, polar bears diets include a higher proportion of older adult ringed seals, whose potentially more limited mobility may increase their vulnerability.

Ringed seal reproduction is energetically demanding, and adults are in a negative energy phase during the spring (Ryg *et al.* 1990; Ryg and Øritsland 1991). Ringed seals of the eastern Beaufort Sea show no signs of reproductive senescence (Smith 1987), but muscular senescence is possible. In Weddell seals (*Leptonychotes weddellii*), muscular senescence is known to occur in older adults, as increasing collagen levels reduce contractile efficiency and sprint capacity (Hindle *et al.* 2009). One potential consequence of muscular senescence during a negative energy phase is the restriction of optimal dive behaviours (Hindle and Horning 2010). The energetic demands of reproduction potentially compound with muscular senescence in older ringed seals to reduce their ability to escape predatory attack. As cause of death is undetermined in this study, it also plausible that some older seals may have died from the stress incurred during reproduction, and polar bears are simply scavenging the carrion.

The finding that adult male and adult female ringed seals were killed in similar proportion is contrary to the prediction that polar bears avoid adult males during spring. Previous studies had noted that hunting polar bears ignored ringed seal subnivean lairs with a strong rutting male scent (Smith 1980; Hammill and Smith 1991; Furgal *et al.* 1996). Explanations for this avoidance included: the meat of rutting male ringed seals is unpalatable to polar bears (Smith 1980; Gjertz and Lydersen 1986; Hammill and Smith 1991); breeding odour serves to confuse the olfactory senses of polar bears during hunting (Smith 1980); or adult males in subnivean lairs are more difficult to catch for polar bears than younger age classes (Hammill and Smith 1991; Furgal *et al.* 1996). Results from this study suggested adult male ringed seals comprised a significant portion of the polar bear diet in spring, and therefore the only hypothesis supported by this study is the last: adult males may be more difficult to catch in stable ice subnivean lairs.

The number of observed attempted hunts on subnivean lairs (digs) was positively correlated with the number of pup kills, but not correlated with the number of adult kills. This observation is consistent with evidence that attacks on subnivean lairs in stable ice are predominately aimed at ringed seal pups (Smith 1980; Gjertz and Lydersen 1986; Hammill and Smith 1991). However, there is a hypothesis that in cases where a pup kill provides limited energetic return, polar bears may attempt to exploit the mother-pup bond, and capture the adult female (Stirling and McEwan 1975; Smith 1980, 1987; Smith *et al.* 1991). Yet, during my study I found no support for such a hunting strategy.

Stirling and McEwan (1975), reported that some of the newborn ringed seal pups killed at lairs are unconsumed, and given pups low energetic value and fat content during nursing, they suggested polar bears may have been hunting the adult females. Given dig success rates can be less than 10%

(Stirling and Archibald 1977), and polar bears are inefficient walkers (Hurst *et al.* 1982), searching and digging for ringed seal pups alone may not result in a net energy gain. Due to the inability to screen out scavenging of kills by other predators, relative consumption rates were not examined. However, despite pups' daily gain in fatty tissue (Lydersen and Hammill 1993a), the number of pup kills I observed per day between mid-April and early May remained relatively constant. Two hypotheses could support these observations. First, the daily increase in the mass of ringed seal pups provides progressively greater thermal insulation, and pups spend more time in the water column as the nursing period progresses (Lydersen and Hammill 1993b). Reduced vulnerability to predation may counteract increased hunting effort by polar bears, explaining the relatively constant kill rate within season. Second, preying on ringed seal pups may be part of a greater overall strategy of polar bear females protecting cubs (< 1 year old) in spring, and lower energetic gains are a consequence of their habitat selection. Habitat selection studies in the Beaufort Sea suggest that female polar bears with cubs select stable, shorefast ice habitat with subnivean lairs, segregating themselves from the rest of the polar bear population (Stirling *et al.* 1993). It is hypothesized that females with cubs avoid adult males (Derocher and Stirling 1990a; Stirling *et al.* 1993) due to risk of infanticide and being killed themselves (Taylor *et al.* 1985; Derocher and Wiig 1999). Adult females with cubs may trade reduced energetic input for protection of young during this period, which could contribute to the high proportion of ringed seal pup kills, despite the pups' limited energetic value.

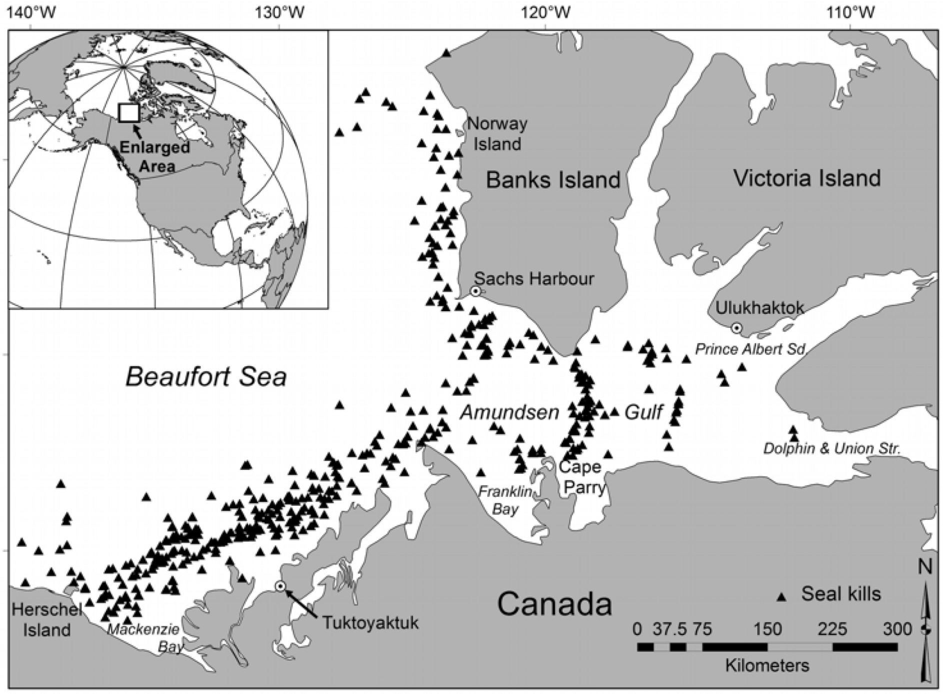
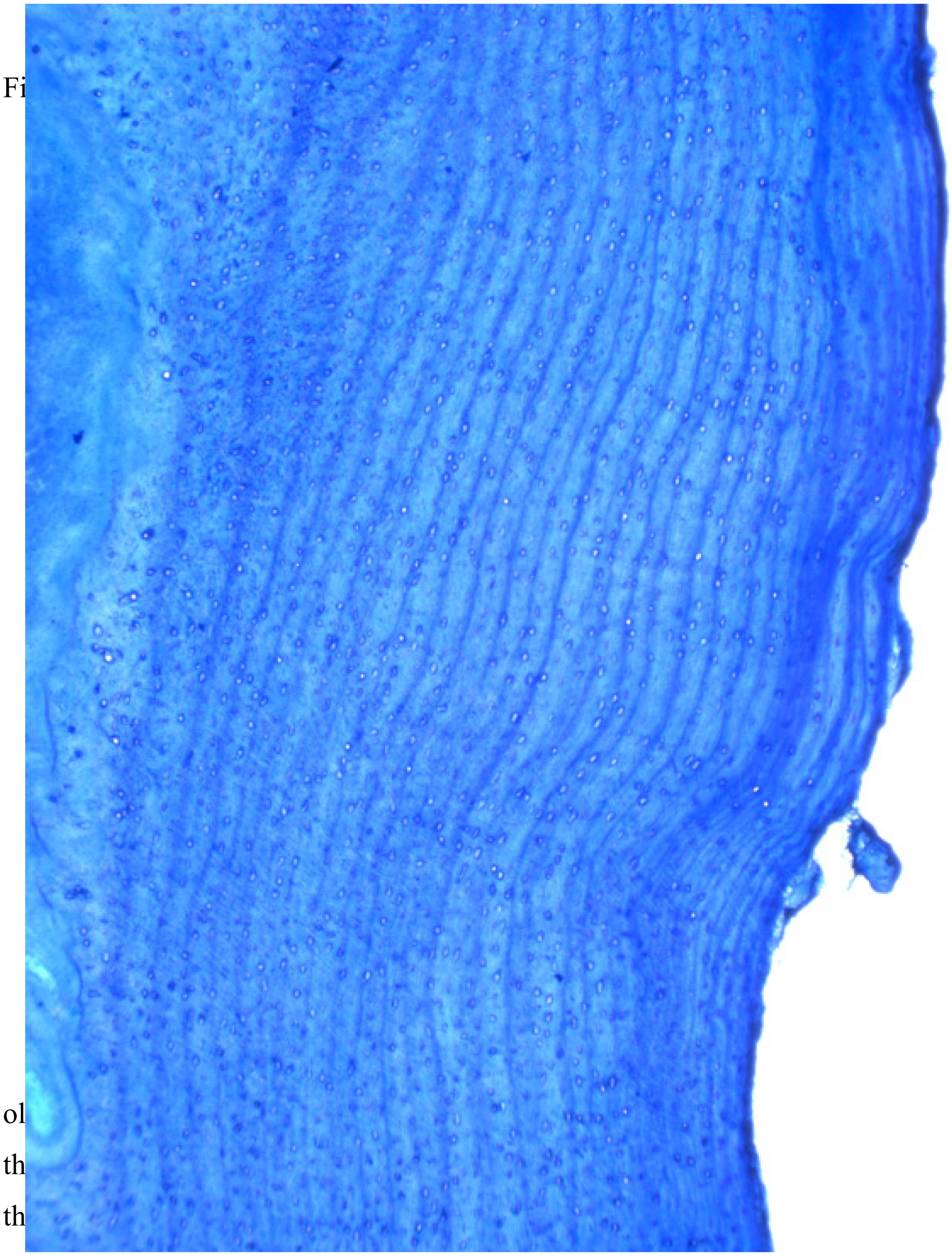


Figure 2.1 Study area in which seals killed by polar bears (▲) were observed between 1985-2011.



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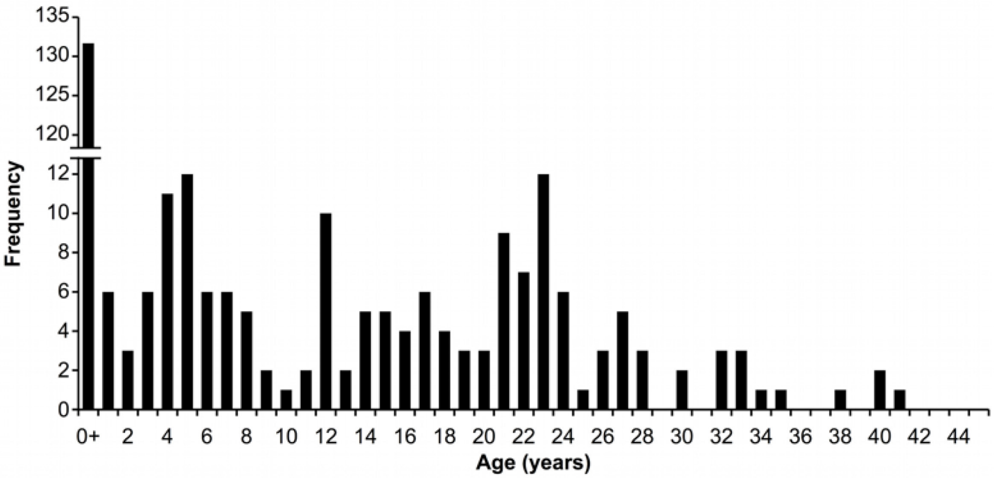

Figure 2.3 Age structure of ringed seals killed by polar bears in spring between 1985-2011, as determined by tooth histology and field observation (pup age class 0+).

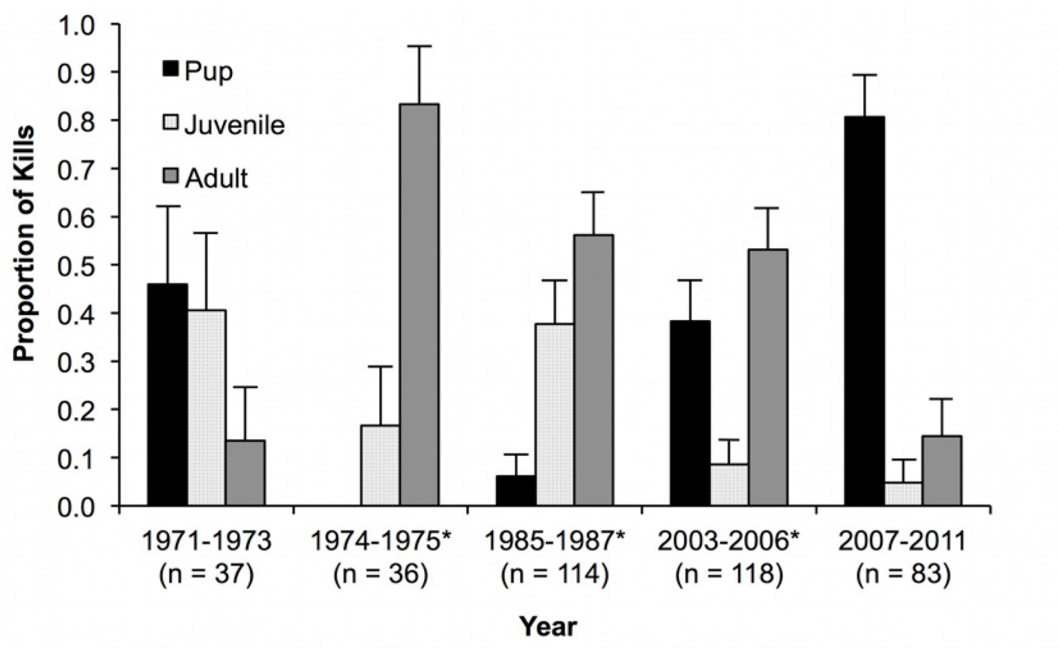

Figure 2.4 Proportions of ringed seals killed by polar bears in the eastern Beaufort Sea between 1971-2011, categorized by pup (0+ years), juvenile (1-6 years) and adult (≥ 7 years) age classes (95% CI shown). Data from 1971-1975 reproduced with permission from Stirling and Archibald 1977. *Years with lower ringed seal reproduction as recorded at Sachs Harbour and Ulukhaktok (Kingsley and Byers 1998; Harwood *et al.* 2000; Harwood *et al.* 2012).

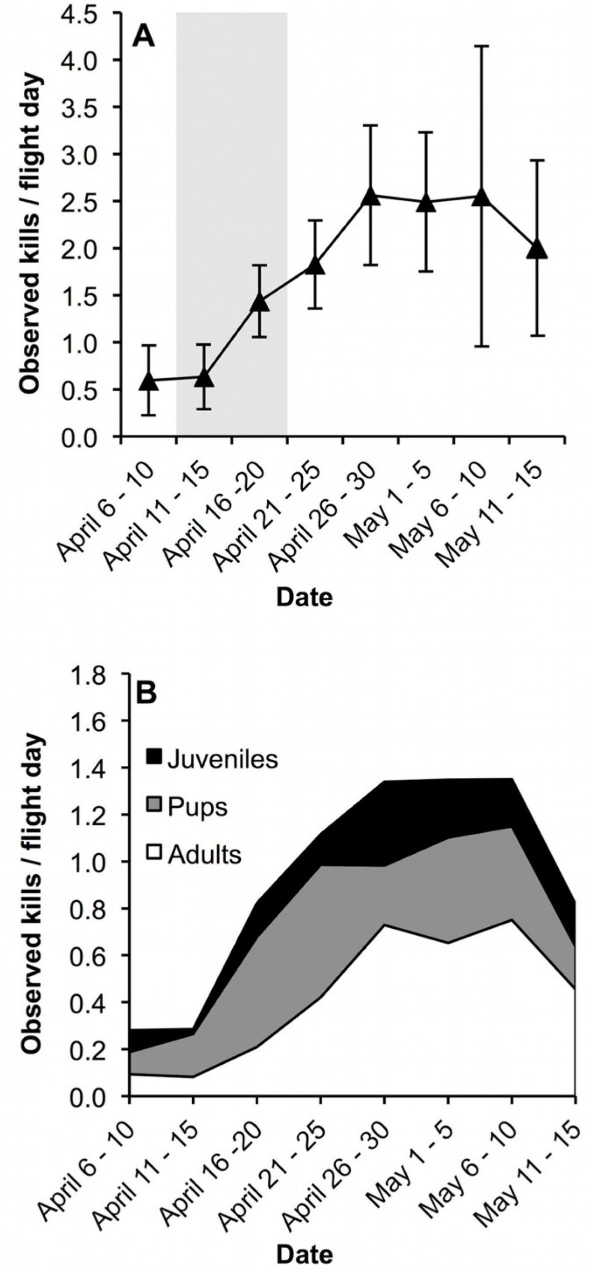

Figure 2.5 Mean number of seal kills observed per five-day period in the eastern Beaufort Sea between 1985-2011. (a) Mean daily number of all kills observed (± SE); error represents combined daily and annual variation in observations. Grey shading indicates peak ringed seal whelping in the Beaufort Sea (Smith 1987). (b) Mean number of ringed seal pup (0+ years), juvenile (1-6 years) and adult (≥ 7 years) kills observed.

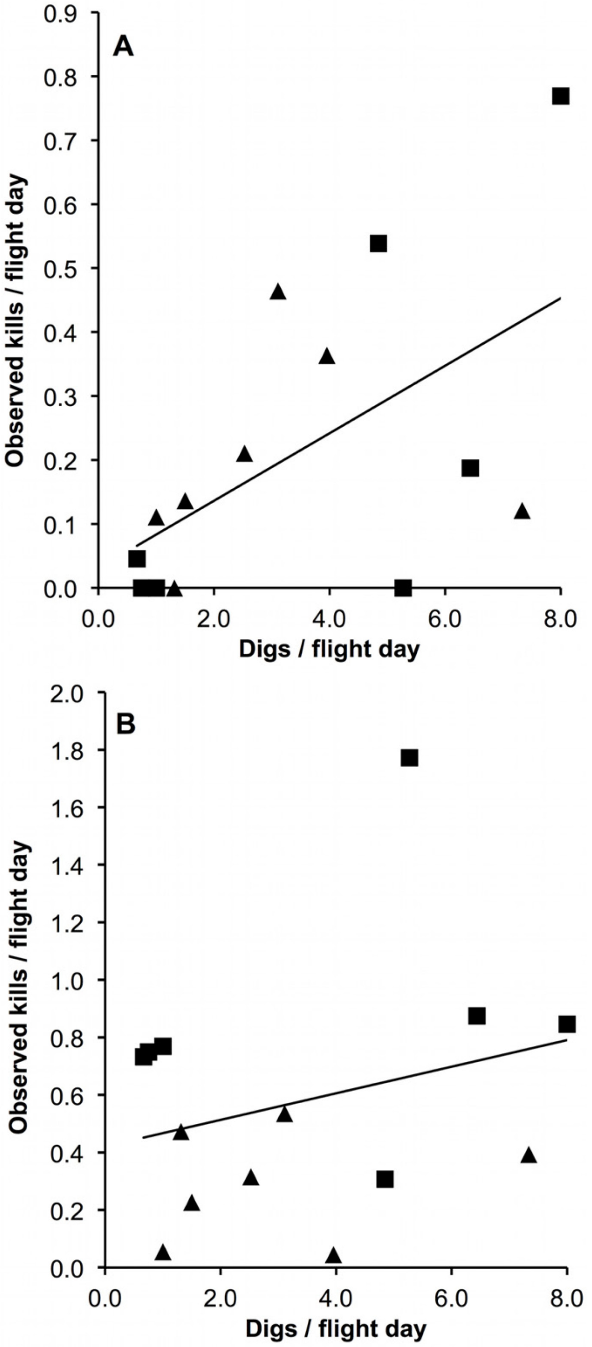

Figure 2.6 Relationship between attempted hunts on subnivean ringed seal lairs (digs) observed per flight day and ringed seal kills. (a) pups (0+ years, $r^2 = 0.30$, $P = 0.04$). (b) adults (≥ 7 years, $P = 0.37$). Observations were pooled ($n = 14$) into early (▲, ≤ April 25) and late season (■, ≥ April 26). Data shown untransformed; see text.

Chapter 3[‡]

3 Influence of Interference Competition on the Distribution of a Non-Territorial Carnivore

3.1 Introduction

Species distribution models (SDMs) typically describe species-environment relationships by correlating a species' occurrence/absence with habitat attributes. Despite the success of SDMs, their application has been criticised for a lack of integration with ecological theory (Austin 2007). In particular, although interspecific and intraspecific competition is widely understood to influence species distribution, SDMs have seen little application to spatial competition theory (Guisan and Thuiller 2005; Elith and Leathwick 2009). Additionally, SDMs can make simplifying assumptions regarding species distributions, the effects of which are often ignored in empirical studies. Here, I investigate the role of intraspecific competition in determining the distribution of an apex predator relative to foraging habitat, while exploring the validity of habitat matching, a key SDM assumption.

SDMs generally assume species follow a habitat-matching rule, in which distribution directly correlates with habitat quality (Cassini 2011). Habitat matching is founded on Parker's 'input matching rule' (Parker 1978), which was derived as a prediction of the ideal free distribution (IFD; Fretwell and Lucas 1970). The IFD suggests that a species should be distributed

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optimally across a landscape if: all individuals have absolute knowledge of and equal access to high quality habitat; and all individuals are competitively equal. However, individuals within a population invariably differ in competitive ability, and dominant individuals can influence the distribution of subordinates through interference competition. Phenomenological and mechanistic spatial distribution models of unequal competitors predict one of two general distributions: a (semi)truncated distribution, where competitively superior individuals dominate high quality habitat and subordinates are either mixed between high and low or relegated to low quality habitat (Sutherland and Parker 1985; Parker and Sutherland 1986; Holmgren 1995); or a mixed distribution appearing no different than if all individuals were competitively equal (van der Meer 1997; Smallegange and van der Meer 2009).

Most empirical studies of unequal-competitor models have supported phenotypically limited truncation, where dominant competitors exclude subordinates from high quality habitat (*e.g.* Monaghan 1980; Milinski *et al.* 1995; Alonso *et al.* 1997). Field tests have predominately examined aggregating avian predators foraging in dense patches of static, spatially predictable prey, over local scales. In these environments spatial truncation of competitors is expected because resource monopolization and aggression are likely (Gyimesi *et al.* 2010). However, many predators forage on mobile, spatially dispersed prey, which can influence predator distribution differently. For example, predatory success can be heterogeneous across space and habitat quality may be associated with areas of prey vulnerability rather than abundance (Hopcraft *et al.* 2005; Balme *et al.* 2007). Further, the importance of interference competition on species distribution is scale dependent (Kneitel and Chase 2004). In spatially heterogeneous competitive environments, local exclusion and regional coexistence between competitors can occur simultaneously (Amarasekare 2003). Yet, a broad scale empirical examination of unequal-competitor models applied to a predator hunting a dispersed and mobile prey is absent.

Polar bears (*Ursus maritimus*) are a sea-ice obligate, non-territorial apex predator preying primarily on ringed seals (*Pusa hispida*), and to a lesser extent much larger bearded seals (*Erignathus barbatus*) (Thiemann *et al.* 2008). Ringed seals and bearded seals exist at low density and with limited spatial predictability (Stirling *et al.* 1982), which may be responsible for the lack of territorial behaviour exhibited by polar bears (Ramsay and Stirling 1986). Polar bears are solitary hunters and non-territoriality allows freedom to aggregate in high quality foraging habitat. Annual home ranges of polar bears can cover a seascape of several thousand square kilometres (Ferguson *et al.* 1999), where a seascape can be defined as a marine area containing a mosaic of habitat patches in which a focal patch is contained (*sensu* Dunning *et al.* 1992). Here, I analysed polar bear distribution relative to foraging habitat in spring to infer the influence of two types of interference: competitive asymmetries in predatory ability and conspecific predation risk.

Habitat suitability is dependent on an individual's capacity to exploit resources, which can be limited by physical capability, experience, and conspecific interference. Adult male polar bears are at least twice the size of other conspecifics (Kingsley 1979), allowing them to kill the largest prey, generally unattainable for other classes of bears (Thiemann *et al.* 2011). Size also affects social dominance in polar bears (Derocher and Stirling 1990b; Derocher *et al.* 2010) and adults will kleptoparasitize subadults (Stirling 1974). Therefore, I hypothesized that polar bear distribution in spring is truncated, with adults dominating the highest quality foraging habitat, and subadults in lower quality habitat to reduce interference competition.

Conspecific predation risk can also influence differentiated habitat selection within species (Ebensperger 1998). In polar bears, adult females with cubs-of-the-year (COY; cubs < 1 year) spatially segregate from adult males (Stirling *et al.* 1993) to reduce the risk of infanticide or being preyed upon themselves (Taylor *et al.* 1985). Additionally, some sea-ice habitats pose a hypothermic risk to young (Blix and Lentfer 1979), and mothers with COY may avoid them. I hypothesized that segregation results in adult females with COY using lower quality foraging habitat relative to the rest of the population.

To test competitive interference in polar bears, foraging habitat quality was modelled using resource selection functions (RSF; Manly *et al.* 2002) applied at a seascape scale. Most RSF applications sample animal locations (*e.g.* telemetry, spoor) as an indication of habitat use, without identifying specific behaviours (Beyer *et al.* 2010). Habitat preference is therefore based on the density of space-use over time, rather than a measured return garnered by the animal during use. I tested whether density of use was sufficient in quantifying forage habitat quality, a key RSF and SDM assumption. I constructed two foraging habitat quality models based on locations of seals killed by polar bears. One model considered each kill location to be equal, and the other model weighted locations based on prey biomass. I compared the models' ability to predict the distribution of polar bears in spring from capture data, assuming polar bears seek out high quality foraging habitat.

3.2 Materials and methods

Observations of seals killed by polar bears, and polar bear captures, were collected between early-April and mid-May (range April 3 – May 17) in 2003-2011. The area included the Beaufort Sea east of 141° W and south of 75° N, as well as Amundsen Gulf (Fig. 3.1a). Helicopter flights originated from Tuktoyaktuk, Sachs Harbour, Ulukhaktok (Holman), Cape Parry, and Norway Island and extended up to 120 km offshore. The area is composed of mostly annual shorefast ice and pack ice. In spring, a recurrent flaw lead of open water forms near the shorefast ice boundary producing an active sea ice zone (*e.g.* Fig. 3.1b), as the lead can change in width with wind and temperature. Comparatively, the sea-ice conditions in the near shore areas are dominated by shorefast ice that is stable, due to its attachment to land and grounded ridges.

Seal kill sites were located opportunistically during polar bear population inventory and ecology research, identified from a helicopter by the presence of blood and/or carcass remains. When possible, kill sites with remains were investigated by landing, and tissue, jaw, and claw samples from kills were collected. Species, sex and age class were determined through a combination of field observation, tooth histology, and DNA analysis (Chapter 2). In some cases where only blood spots remained, if the amount of blood was minimal, and it was found near a pressure ridge with a dug out ringed seal maternal lair, it was assumed to be a ringed seal pup kill (Derocher *et al.* 2002). White lanugo at the kill site also helped confirm ringed seal pup kills when few remains were present. Locations of kills were recorded by GPS.

Polar bears were caught non-selectively by remote injection of Telazol® (Stirling *et al.* 1989) from a helicopter. Gender was identified in the field, while age was identified by counts of tooth annuli from a vestigial premolar in the laboratory (Calvert and Ramsay 1998). Field methods were in accordance with the Canadian Council on Animal Care guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee. Polar bears were categorized into six classes: adult males ($\geq$ 5 years), lone adult females ($\geq$ 5 years), subadult males (< 5 years), subadult females (< 5 years), adult females with COY, and adult females with older cubs (1-2 years). Each captured bear was tagged with a unique ID and marked to prevent recapture in the same year.

Foraging habitat quality was modelled using a fixed-effect exponential RSF, in a "used" versus "available" framework (Manly *et al.* 2002):

$$\hat{w}(x) = \exp\left(\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_n\right)$$

with covariates x_n and coefficients $\hat{\beta}_n$. Used locations were sites where seals had been killed by polar bears. As sea-ice conditions change on a daily basis, available locations were generated for each flight day. Available points were randomly generated locations, constrained to the helicopter flight path at a rate of one point per 50 km travelled. A total of 96,660 km were flown in 2003-

2011 generating 1934 points, but points in open water or on land were removed, resulting in 1736 available points.

Sea-ice covariates used to model habitat quality included: distance from land (km), bathymetry (-m), distance to shorefast ice boundary (km), sea ice concentration locally (%), sea ice concentration regionally (%), floe edge, and ice type classified as new ice, pack ice, and shorefast ice (Table 3.1; Jakobsson *et al.* 2008; Spreen *et al.* 2008; Spreen and Kaleschke 2008). Covariates were chosen to dichotomize the seascape into active and stable sea-ice conditions, which have distinct prey assemblages and hunting environments. Shorefast ice located in shallow near-shore areas is stable, and dominated in the spring by an abundance of vulnerable ringed seal pups (Smith and Stirling 1975). Active sea ice resides in deeper offshore areas, centred on the flaw lead in this area, which usually forms at the edge of the shorefast ice boundary. New ice has recently formed (*e.g.* a refrozen crack) and is also indicative of active ice. In active ice areas, a wider array of prey exists including bearded seals, and juvenile and adult ringed seals (Stirling *et al.* 1982).

Covariates were screened for collinearity, and those with Pearson's correlation coefficient $|r_s| > 0.6$ were not retained in the same model. Shorefast ice and pack ice were correlated ($r_s = 0.78$), and pack ice was removed due to its lack of fit. Covariates were examined for nonlinearity using quadratic and natural log transformations. Natural log transformation of distance from land, bathymetry, and distance to shorefast ice boundary all provided lower log-likelihood scores. Regional sea ice concentration was transformed to a quadratic for model fit.

A weighted binomial logistic regression was employed to determine the coefficients $\hat{\beta}_n$ for the exponential RSF. Sample weighting has been used in RSF studies to correct for GPS bias (Frair *et al.* 2004); but in my case, the weight was not for correcting GPS error nor determined by inverse probability weighting. Instead, the sample weight was the kill biomass, estimated from literature for each seal age-class (Table 3.2). To determine if an observational bias existed in the kill composition as a result of the opportunistic nature of collection, the kill composition was compared to an independent polar bear dietary analysis using fatty acid signature analysis (Thiemann *et al.* 2008). To understand the effect of weighted regression on habitat selection, an unweighted model was built for comparison, using the same data and model selection criteria.

Akaike's Information Criterion for small samples (AIC_c; Burnham and Anderson 2002) was used to select the most parsimonious models for both the unweighted and weighted designs. I determined the top model to be any individual model or group of models with an AIC_c weight (w_i) exceeding 0.90. Overdispersion ($\hat{c}$) was evaluated by dividing the Pearson χ^2 by the degrees of freedom on the global model. Standard error for the weighted model was calculated with the Huber/White sandwich estimator. All models were analysed using GLM in SPSS 18.0 (IBM, Chicago, USA).

A fivefold cross validation was employed to examine the predictive capability of the covariates in the habitat quality models (Boyce *et al.* 2002). Top unweighted and weighted models were then compared in their ability to predict polar bear distribution in spring. Polar bear distribution was evaluated using capture locations, collected over the same period as kills (n = 622). To ensure independence between the seal kill locations used to derive the habitat quality model and polar bear distribution from capture data, captures that occurred at the same location or the same pixel as a seal kill were excluded. After screening, 531 polar bear locations remained.

Top unweighted and weighted models were used to create daily habitat quality maps for each flight day in ArcGIS 10.0 (Esri, Redlands, USA). Habitat quality was determined by the RSF output, with RSF values subdivided into 20% quantiles for each day and mapped at a grain of 6.25 km × 6.25 km (AMSR-E grain). Polar bear capture locations were intersected with daily habitat quality maps for both models. Polar bear distribution relative to habitat quality was evaluated between models using a Pearson χ^2 and Spearman ranks correlation.

Pearson χ^2 was used to compare the proportion of polar bear age and sex classes in high quality foraging habitat. I defined "high quality foraging habitat" as: habitat within the top 20% of the RSF valued study area each day (i.e. habitat quality quantile 5). The Marascuilo procedure was used for *post-hoc* analysis, as it allows for the comparison of proportion data of several populations simultaneously, using a Chi-square statistic (Marascuilo 1966). All tests were completed in SPSS 18.0 (IBM, Chicago, USA). For all significance tests, alpha was set to 0.05, and 95% confidence intervals are reported with all proportions.

3.3 Results

Seal kills (n = 219) included 203 ringed seals (78 adults, 10 juveniles and 115 pups) and 16 bearded seals (7 adults, 3 juveniles and 6 pups). The proportions of ringed seal and bearded seal (92.7% ringed seal; 7.3% bearded seal) were consistent with polar bear diet using fatty acid analysis (Thiemann *et al.* 2008), suggesting limited observational bias. Polar bear captures (n = 531) included: 137 lone adult females, 157 adult males, 48 subadult females, 51 subadult males, 53 adult females with COY, and 85 adult females with older cubs.

The top individual foraging habitat model for both the unweighted and weighted design had an AIC_c weight less than 0.90; therefore the beta coefficients were averaged from the top group of models, such that the total AIC_c weight $\geq$ 0.90 (Appendix A). The global models of the weighted and unweighted design showed no overdispersion ($\hat{c}_W$ = 1.36, $\hat{c}_u$ = 0.98). The covariates of the models had strong predictive capacity according to the fivefold cross validation (r_s = 1.00, P = 0.02). All covariates were included in the final model for both model designs, except local sea ice concentration

(LOC_ICE; Table 3.3). When compared to the unweighted model, the weighted design reversed the floe edge (F_Edge) coefficient from negative to positive, and shorefast ice (Fast_Ice) from positive to negative (Table 3.3).

The proportion of polar bears distributed in 20% quantiles of foraging habitat quality was different between the weighted and unweighted design ($\chi^2 = 19.64$, $df = 4$, $P < 0.001$, Fig. 3.2). Spearman ranks correlation between the numbers of bears in quantiles of increasing habitat quality was positive for the weighted model ($r_s = 0.90$, $P = 0.04$), but non-significant for the unweighted ($P = 0.75$). The weighted design was used to model foraging habitat quality.

Foraging habitat quality was highest close to the shorefast ice boundary (Fig. 3.3a), near floe edges (F_Edge), and in newly formed ice (New_Ice). Similarly, foraging quality was poor near shorelines (Fig. 3.3b), in shallow areas (Fig. 3.3c), and on shorefast ice (Fast_Ice), indicating a preference for hunting in active ice. Preference for active ice was also evident over the entire study area with foraging habitat quality peaking at 85% regional sea ice concentration (Fig. 3.3d).

Proportions of the six classes of polar bears were unequally represented in the high quality foraging habitat ($\chi^2 = 14.71$, $df = 5$, $P = 0.01$, Fig. 4). Proportions of lone adult females, adult males, subadult females, subadult males and females with older cubs in high quality foraging habitat did not significantly differ (Fig. 3.4). However, compared to the rest of the population, a lower proportion of females with COY were in the high quality foraging habitat (Fig. 4).

3.4 Discussion

This study represents the first seascape scale assessment of the phenomenological predictions of unequal-competitor models on an apex mammalian carnivore. While previous small-scale field tests have largely confirmed phenotype-limited truncation in the distribution of unequal competitors, my results suggest a mixed distribution. In addition, while evasion of infanticidal males by females with vulnerable young is a common attribute of mammalian-mating systems, my results suggest that avoidance may lead to the use of lower quality foraging habitat. Finally, I determined that for a large carnivore, kill size, as a proxy for available energy, is as important a metric as kill abundance in modelling the quality of foraging habitat.

Resource selection theory proposes that an animal shows preference if it selects a resource at a higher proportion than its availability in the environment (Johnson 1980), with the underlying hypothesis that preference is motivated by maximizing individual fitness (Railsback *et al.* 2003). In resource selection theory applications, as in other SDMs, it is assumed that the density of animal use is indicative of habitat quality (Cassini 2011). However, the results from my study suggest that density of use alone was an insufficient indicator of habitat quality.

Weighted logistic regression was employed in the habitat model to include a measure of return for a given location of use. When compared to an unweighted modelling approach, the weighted model provided a stronger fit to polar bear distribution and reversed the direction of coefficients for two covariates: floe edge and shorefast ice. The reversal of coefficient direction in these covariates is indicative of the type of vulnerable prey. In stable shorefast ice, ringed seals predominate, and primarily inhabit subnivean lairs (Furgal *et al.* 1996). Hunting attempts at subnivean lairs in spring results mostly in ringed seal pup kills, with adults killed less frequently (Chapter 2). On floe edges in active ice, prey can be larger. Bearded seals mate and give birth to their young on floes of drifting pack ice (Kovacs *et al.* 1996), staying close to lead edges, preferring areas with medium to smaller floes of pack ice (Simpkins *et al.* 2003). Ringed seal juveniles and adults may also be abundant near the shorefast ice boundary (Stirling *et al.* 1982; Frost *et al.* 2004). When each kill was considered equal, the abundance of ringed seal pup kills in shorefast ice areas drove the model to indicate high quality kill habitat. However, the value of a habitat may be unrelated to the frequency of its use (Van Horne 1983); in this case, the number of kills. A bearded seal adult can be more than fifty times the mass of a newborn ringed seal, a substantial difference in the energetic return to a polar bear. Including biomass as a regression weight allowed the model to calculate the trade-off between the abundance and the size of kills. I see potential in using this type of approach to evaluate the biological importance of habitat in resource selection studies, especially when the unit of use has a measurable return to the individual or population.

Female polar bears with COY were observed in lower quality habitat compared to other polar bears, implying a possible trade-off between cub protection and forage quality. Avoidance of infanticidal males is a well-documented phenomenon in many mammalian mating systems (Ebensperger 1998). However, the consequences of avoidance have received limited attention. Notably, female Alaskan brown bears (*U. arctos*) with young cubs ate less salmon (*Onchorhynchus* spp.), and were recorded farther from salmon streams than other classes of bears during hyperphagia (Ben-David *et al.* 2004). Although my results suggest a similar pattern of displacement in female polar bears with COY, the habitat quality model could not account for differences in prey-encounter rates as a function of competitor density. Segregation by females with COY may result in an increased prey-encounter rate due to lower competitor density, which could nullify the impact of a poor quality foraging habitat. However, adult females with older, more mobile cubs are faced with similar energetic challenges, but do not segregate from the population.

Infanticidal risk may not be the only influencing factor in habitat selection by adult females with COY. Selecting for stable sea-ice platforms minimizes the requirement for swimming across open water, reducing the hypothermic risk to small cubs (Blix and Lentfer 1979). Additionally, while ringed seal pups have limited energetic return in early spring, their spatial distribution may be more predictable than other prey sources (Freitas *et al.*

2012). Ringed seal pups are also unfamiliar with surface predators (Stirling and Archibald 1977), and are likely easier targets for a female polar bear hunting with cubs.

Polar bears of unequal competitive ability (adults vs. subadults) did not segregate by habitat quality. I found support that the distribution of unequal competitors may be mixed (van der Meer 1997; Smallegange and van der Meer 2009). Although subadult polar bears experience kleptoparasitism from larger bears (Stirling 1974), and are unable to successfully hunt the largest prey (Thiemann *et al.* 2011), they are found in similar proportion to adults in high quality foraging habitat. This outcome may result because: 1) intraclass interference competition may be stronger than interclass competition; 2) the foraging niche may be partitioned by predatory tactic; and 3) densities of polar bears may be low enough to negate interference competition as a significant cost.

A mixed distribution of unequal competitors, similar in appearance to an IFD, might result if dominant animals have an increased prey encounter rate relative to subordinates regardless of habitat quality (van der Meer 1997). As subadult polar bears are inefficient hunters (Stirling and Latour 1978), and smaller in size, their presence may not negatively affect the prey encounter rate of adults. Further, as time wasting from interference competition is maximized when competitors are equal (Smallegange and van der Meer 2009), subadults and adults may avoid competitors from their own class. This may lead to an intraspecific version of heteromyopia (Murrell and Law 2003), where intraclass competition is stronger than interclass competition and leads to spatial mixing between interclass competitors. As a result, subadults may act as a competition buffer between dominant individuals (van der Meer 1997), while providing kleptoparasitic opportunities for adults. Seals are widely dispersed, found at low density, and are infrequently killed by polar bears (Stirling and Archibald 1977; Stirling *et al.* 1982). Such conditions likely increase the benefit adults garner by stealing prey caught by subadults (Hamilton 2002).

While the advantages of a mixed distribution for adults are clear, the advantage to subadults is intriguing.

Subadults may benefit from entering high quality foraging habitat by scavenging carrion. Given the size of most classes of seals, a single prey item can satiate a polar bear before consumption of the available biomass is complete (Best 1977). Polar bears usually feed only once on a kill, and can leave substantial carrion (Stirling 1974; Stirling and Derocher 1990). Moreover, polar bears require up to 38 hours to fully digest seal biomass, with higher gastrointestinal transit times for biomass with greater proportions of fat (Best 1984). Digestion limitation can regulate interference competition (van Gils and Piersma 2004), because a satiated predator is less likely to compete for a food resource, or defend carrion from scavenging. For example, on very large kills and carrion, polar bears are known to share consumption simultaneously with unrelated and subordinate individuals (Stirling 1974; Miller *et al.* 2006).

Scavenging by subadults may also reflect differential search costs between inexperienced and experienced hunters. Polar bears preferentially consume the fatty tissue of a seal (Stirling 1974), which is efficiently assimilated into their biomass (Best 1984). For an experienced hunter, such as an adult, consuming an entire seal may not be as valuable as consuming only select portions, and then killing again. However, for an inexperienced hunter, such as a subadult, there may be benefit in consuming the remains left by an adult, as search costs for a fresh kill are likely higher.

Holmgren (1995) suggested unequal competitors differing in search efficiency would result in a truncated distribution in a standing stock system. But, the model assumed prey items were monopolized. The impact of scavenging is generally underestimated in predator-prey interactions (Wilson and Wolkovich 2011), and may be important for subordinate or inexperienced individuals. Adult and subadult polar bears may partition the foraging niche through an experience related ‘killer-scavenger’ trade-off. Adults may focus on higher reward hunting opportunities, while subadults, limited by physical size and ability, rely more on carrion. Resource partitioning is thus accomplished through an additional axis of predatory tactic and utilization of prey, allowing for spatial coexistence.

A third possibility is that polar bears exist at densities in which interference competition is negligible. Thiemann *et al.* (2011) determined that the fat of subadults had a narrower range of fatty acid prey signatures than adults, possibly indicating that subadults actively prey on a focal set of seals, depending less on scavenging. As spring is mating season, many dominant adult males may be focused on searching or competing for mates, and less on feeding (Ramsay and Stirling 1986). Adult males focussing on mating may allow subordinate individuals to hunt and feed undetected near dominant competitors. Spring in the Beaufort Sea also represents a pulse in prey resources for polar bears (Chapter 2), and increased prey-encounter rates may minimize interference.

Table 3.1 Covariates used to model foraging habitat quality for a resource selection function of polar bear foraging habitats in spring in the Beaufort Sea, Canada, 2003-2011.

Habitat Covariate	Acronym	Range	Source
Distance to shorefast ice boundary	I_DIST	0.0 - 174.9 km	Canadian Ice Service regional charts (seaward edge of shorefast ice)
Distance from land	L_DIST	1.1 - 116.2 km	
Bathymetry	DEPTH	5.2 - 1450.8 m	IBCAO Bathymetry charts
Local sea ice concentration	LOC_ICE	3 - 100 %	AMSR-E satellite data
Regional sea ice concentration	REG_ICE + REG_ICE^2	70.6 - 99.7 %	AMSR-E satellite data
Flow edge	F_Edge		AMSR-E satellite data
Thick annual shorefast ice	Fast_Ice†		Canadian Ice Service regional charts (polygons coded: 10/4•/8)
Big to vast floes of very close annual pack ice	Pack_Ice†		Canadian Ice Service regional charts (polygons coded: 9+/4•/5 to 6)
Small to big floes of very close new pack ice	New_Ice		Canadian Ice Service regional charts (polygons coded: 9 to 9+/1 to 5/3 to 5)

†Correlated ($|r_s|$ = 0.78), Pack_Ice removed from analysis

Table 3.2 Estimated biomass and converted regression weight for each kill based on species and age class.

Species	Age-class	Est. Biomass (kg)	Regression Weight
Ringed seal	Pup	11	1
	Juvenile/Adult	57	6
Bearded seal	Pup	62	6
	Juvenile/Adult	273	27

Source: Derocher et al. 2002

Table 3.3 Comparison of covariate selection for habitat quality between top models using unweighted and weighted design. Average (β) from averaging top models so that AIC$_c$ $w_i > 0.90$. Selection ratio for each covariate is indicated by exp (β), where values that are greater than 1 indicate selection and values less than 1 indicate avoidance. Bold indicates significant difference ($P < 0.05$) in β values between models. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Model Coefficients	Habitat Covariates								
	L_DIST	I_DIST	DEPTH	LOC_ICE	REG_ICE	REG_ICE^{2}	F_Edge	Fast_Ice	New_Ice
Unweighted									
Average (β)	0.710	-0.228	0.079		0.294	-0.002	-0.134	**0.315**	0.876
Upper CI	0.957	-0.140	0.204		0.639	0.000	0.373	0.646	1.607
Lower CI	0.463	-0.316	-0.046		-0.051	-0.004	-0.641	-0.016	0.145
Exp (β)	2.033***	0.796***	1.082		1.342	0.998	0.875	1.307	2.402*
Weighted									
Average (β)	0.380	-0.256	0.136	0.000	0.338	-0.002	0.409	**-0.214**	0.513
Upper CI	0.502	-0.199	0.206	0.005	0.552	-0.001	0.717	-0.032	0.969
Lower CI	0.258	-0.312	0.066	-0.005	0.123	-0.003	0.101	-0.396	0.057
Exp (β)	1.463***	0.774***	1.145***	1.000	1.402**	0.998**	1.506**	0.808*	1.671*

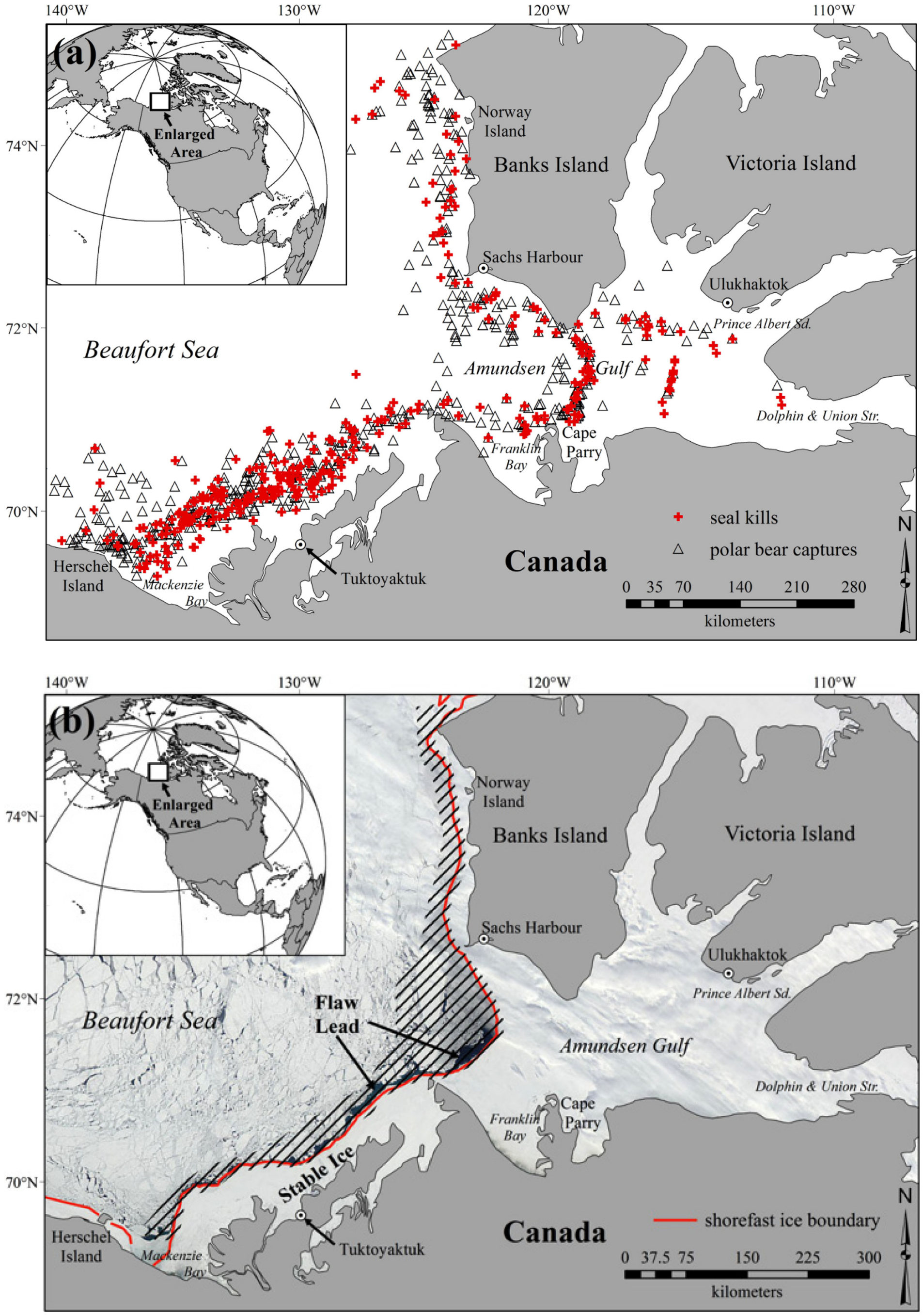

Figure 3.1 Study area. (a) Locations of seals killed by polar bears (✚) and polar bear captures (△). (b) NASA/GSFC Rapid Response image for April 30, 2009, with shorefast ice boundary from Canadian Ice Service. Hatched area indicates active sea ice zone.

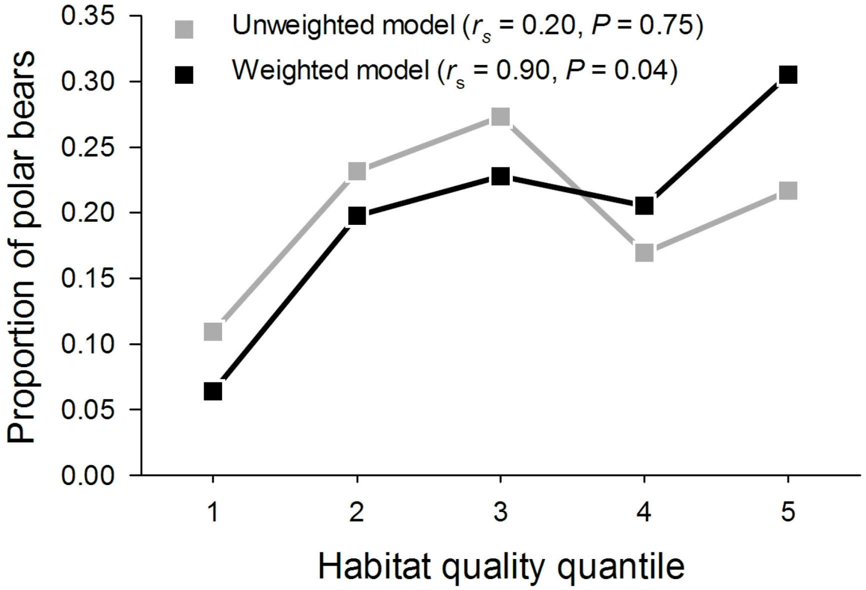

Figure 3.2 Proportions of polar bear capture locations per habitat quality quantile in spring in the Beaufort Sea, Canada, 2003-2011, according to a weighted and unweighted resource selection model design.

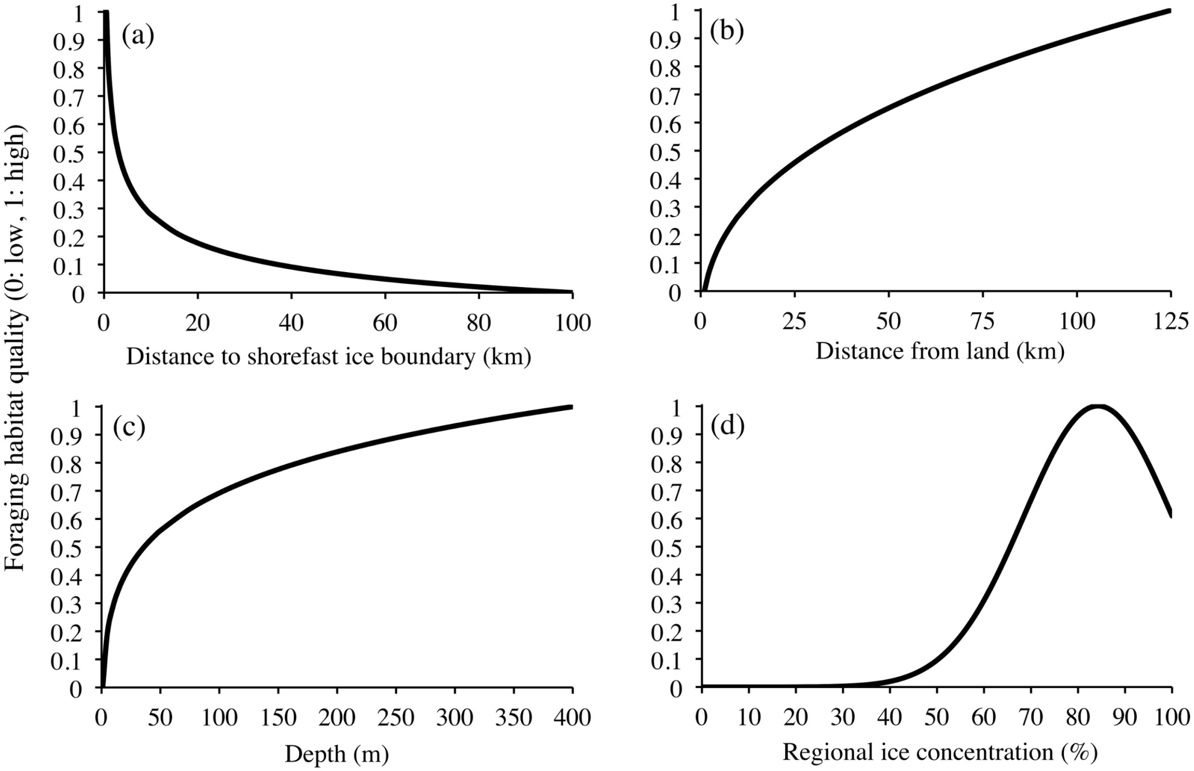

Figure 3.3 Scaled univariate response for the four continuous habitat covariates in the resource selection model of foraging habitat quality, with kills weighted by their estimated biomass. All other covariates were held to their median values when computing the response curve.

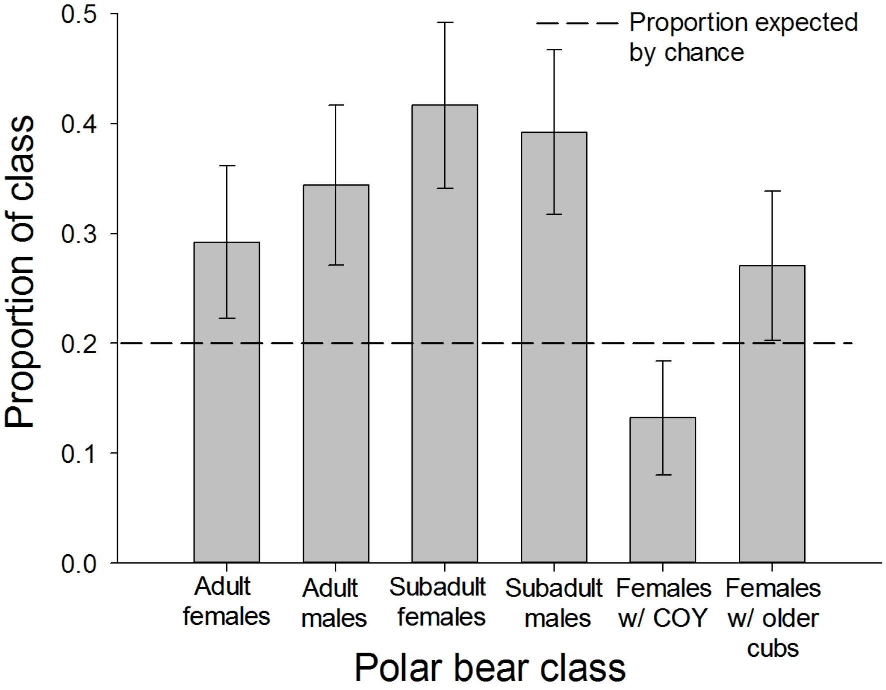

Figure 3.4 Proportion of polar bear classes observed in high quality habitat (top 10% resource selection function valued area each day) in the Beaufort Sea, Canada, 2003-2011.

Chapter 4[‡]

4 Polar Bear Predatory Behaviour Reveals Seascape Distribution of Ringed Seal Lairs

4.1 Introduction

Understanding the spatial distribution and behaviour of species living in remote or extreme environments can be challenging, particularly if the species is cryptic. Direct observation can be biased to areas accessible for study. The advent of Global Positioning System (GPS) transmitters has provided the ability to track animals through environments where direct observation is impractical (Cagnacci *et al.* 2010). However, GPS transmitters are expensive and can fail, limiting sample size (Hebblewhite and Haydon 2010). Additionally, for species with high site fidelity, spatial data may be biased to the scope of transmitter deployment. As an alternative, ecological interactions between cryptic species may leave visible signs that can facilitate detection and provide valuable insight into species distribution.

Predator-prey relationships are spatially dependent, and provide the potential to reveal life-history characteristics of both predator and prey simultaneously. Optimal foraging theory suggests predators should prefer prey and habitats that increase the likelihood of capture (Stephens and Krebs 1986). The kill composition of predators may disclose information on prey condition including reproductive status (Magnhagen 1991) and health (Krumm *et al.* 2010). Except at fine scales (Hopcraft *et al.* 2005; Davidson *et al.* 2012),

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predator habitat selection generally correlates with areas of high prey abundance (Murray *et al.* 1994; Palomares *et al.* 2001; Spong 2002), providing insight into prey distribution. Most studies utilizing prey kills have focused on the behaviour of the predator, rarely assessing the ecology of the prey beyond predation risk. Here, I investigate whether the behaviour of a predator can expand understanding on the broad scale distribution of a cryptic prey.

Polar bears (*Ursus maritimus*) and ringed seals (*Pusa hispida*) form a closely linked, well-documented ecological relationship (Stirling 2002). Ringed seals are the primary prey of polar bears (Stirling and Archibald 1977; Derocher *et al.* 2002; Thiemann *et al.* 2008), and large-scale population estimates suggest the abundance of the two species is correlated (Stirling and Øritsland 1995). The main feeding season for polar bears begins mid-April in response to ringed seal reproduction (Ramsay and Stirling 1988; Hammill and Smith 1991; Stirling and Øritsland 1995; Chapter 2). In the Canadian Beaufort Sea, ringed seal natality fluctuates on a decadal-scale cycle (Smith 1987; Kingsley and Byers 1998; Harwood *et al.* 2000; Harwood *et al.* 2012) and polar bears respond by killing more pups in years with higher reproductive output (Stirling and Archibald 1977; Chapter 2). In addition to reflecting the population dynamics of ringed seals, polar bear predatory behaviour may facilitate insight into ringed seal habitat during periods of low and high natality.

A key component of ringed seal habitat is the subnivean lair. A single ringed seal may have a complex of lairs (Smith and Stirling 1975; Smith and Hammill 1981; Lydersen and Gjertz 1986; Kelly and Quakenbush 1990), which serve two primary functions: parturition and nursing of young, and hauling out or resting (Smith 1987). Lair sites are generally associated with pressure ridges in stable annual ice because snow accumulates on the lee side of the ridge (Smith and Stirling 1975; Furgal *et al.* 1996). Lair construction begins when sufficient ice and overlying snow have accumulated (Smith and Stirling 1975), and lairs are maintained until the end of the breeding season in spring, approximately six weeks after pupping, or until snow melt causes structural collapse (Hammill and Smith 1991; Stirling and Smith 2004). Subnivean lairs provide a protective barrier from predation as well as a warmer microclimate that shelters newborn pups from the cold (Hammill and Smith 1991; Furgal *et al.* 1996). Snowdrifts along ridges in the near-shore fast ice and interisland channels of archipelagos are considered preferred habitat for lair construction (McLaren 1958; Lydersen and Gjertz 1986; Smith *et al.* 1991). Adults defend aquatic territories below the sea ice resulting in competitive exclusion of conspecifics, particularly subadults (Smith and Hammill 1981; Krafft *et al.* 2007). Subnivean lairs have also been observed in pack ice areas (Fedoseev 1975; Finley *et al.* 1983; Wiig *et al.* 1999), but due to the relative inaccessibility of such areas for study, less is known about these lairs, the age structure of the animals that create them, or the relative survival of pups born in such habitat.

When preying on ringed seals inside subnivean lairs, polar bears will identify the lair site by smell, and dig or break-through the roof (Stirling and Archibald 1977; Stirling and Latour 1978; Hammill and Smith 1991). Polar bears hunting at lairs may ignore those occupied by rutting adult males (Smith 1980; Hammill and Smith 1991; Furgal *et al.* 1996), and primarily target pups (Smith 1980; Gjertz and Lydersen 1986; Hammill and Smith 1991; Chapter 2). Previous studies have relied on the use of specially trained dogs to locate lair sites (*e.g.* Smith and Stirling 1975; Lydersen and Gjertz 1986; Hammill and Smith 1991; Furgal *et al.* 1996). Although effective, the technique is labour-intensive, making it difficult to apply at a seascape scale over a single season and across variable habitats. Additionally, ringed seal telemetry studies are predisposed to focusing on lairs in near-shore capture areas, as adults show high site fidelity to breeding areas, and captures occur during the breeding season (Kelly *et al.* 2010). However, hunting attempts by polar bears at subnivean lairs leave a characteristic excavation discernable from the air, allowing for observations across both near-shore and offshore environments.

I used observations of polar bear predatory behaviour made while tracking individual bears to: identify broad scale habitat characteristics of ringed seal subnivean lairs preyed on by polar bears; and determine whether changes to ringed seal natality rates were reflected in differences in the types of habitat in which pups were killed. Resource selection functions (RSF; Manly *et al.* 2002) were employed to determine the relative probability of polar bear predation attempts on ringed seals in subnivean lairs as a function of habitat. Concurrent harvest-based monitoring of ringed seal ovulation rates and pup production in the Canadian Beaufort Sea (www.beaufortseals.com) was utilized as an indicator of the reproductive output of the population. In 2003-2006 ringed seal ovulation rates declined, reaching a 20-year low in 2005, and pup production consequently decreased (Harwood *et al.* 2012). In 2007-2011, all mature harvested females had ovulated, and the proportion of pups in the harvest stabilized (Harwood *et al.* 2012). The habitat type in which observations of pups killed by polar bears was compared between years of low (2003-2006) and high (2007-2011) natality to examine the effect of reproductive output on habitat use.

4.2 Materials and methods

The study area comprised the eastern Beaufort Sea, including Amundsen Gulf, within 150 km of the Canadian coast (Fig. 1). Helicopter flights originated from Tuktoyaktuk, Sachs Harbour, Ulukhaktok (Holman), Cape Parry, and Norway Island. Observations of attempted hunts on ringed seal subnivean lairs by polar bears were collected between April 6 and May 10 in 2004-2006. Observations of ringed seal pup kills were collected between April 6 and May 17 in 2003-2011. The Tuktoyaktuk Peninsula region was defined as the surveyed area east of 141° W, and west of Cape Bathurst (Fig. 4.1).

The study area is composed mainly of thick annual fast ice along the coast and pack ice farther offshore. A characteristic feature of the region is the

Cape Bathurst polynya and related flaw lead system (Stirling 1980; Arrigo and van Dijken 2004). Sea ice conditions near the lead are dynamic, as changing wind patterns alter the width of the lead, and cold temperatures can freeze the open water. In comparison, the sea ice in near-shore areas is dominated by fast ice that is stable, due to its attachment to land and grounded ridges.

Attempted hunts at ringed seal subnivean lairs by polar bears and ringed seal pups killed by polar bears were observed from a helicopter while tracking individual bears. Hunting attempts leave a characteristic excavation in the snow (Fig. 4.2), and are identifiable from the air. Hunting attempts at lairs included both successful kills, which were readily recognizable by patches of red from blood and sometimes parts of the carcass, and unsuccessful attempts where the surrounding snow was clean. As the helicopter did not land on the sea ice to investigate unsuccessful attempts, I was unable to differentiate birth from haul-out lairs for this study.

Ringed seal pup kills were identified either by the presence of blood and/or carcass remains. Kill sites with remains present were investigated when possible and tissue, jaw, and claw samples were collected. Age class was determined through field observation and tooth annuli counts, and species confirmed in the field or with DNA analysis (Chapter 2). In some cases where only blood spots remained at the lair site, if the amount of blood was minimal, it was assumed to be a pup kill (Derocher *et al.* 2002). In some cases, the presence of white lanugo at the kill site helped confirm ringed seal pup kills when few remains were present. Locations of subnivean lairs and pup kills were recorded by GPS.

Sea ice habitat was described using six covariates including: distance from land (km), bathymetry (-m), sea ice backscatter (dB), sea ice heterogeneity, and ice type classified as pack ice and fast ice. Bathymetry was measured using the International Bathymetric Chart of the Arctic Ocean (IBCAO) on a 500 m grid (Jakobsson *et al.* 2012). Sea ice backscatter and sea ice heterogeneity were determined from Envisat-1, a Synthetic Aperture Radar (SAR) satellite. Wide scan satellite images (60 m resolution) were downloaded from the European Space Agency. Differentiation between sea ice types with SAR is best in winter prior to the onset of melt (Barber and Yackel 1999), therefore search results were restricted to March 10 – April 15. As Envisat-1 imagery is on a 35-day orbital cycle, the imagery over the study area was limited to a single mosaic for each season. Before analysis, SAR imagery was orthorectified, speckle filtered and mosaicked using Next ESA SAR Toolbox (Array Systems Computing, Toronto, Canada).

Sea ice backscatter values tend to range between -25 and -5 dB. Higher backscatter values (-12 to -5 dB) are generally indicative of multiyear ice; mid-range values (-16 to -12 dB) are characteristic of deformed first-year ice, while lower ranges (-22 to -16 dB) are characteristic of flat first-year ice (Kwok and Cunningham 1994; Barber and Thomas 1998). Higher backscatter values situated within regions of lower backscatter may indicate ice deformity caused by pressure ridge formation (Haas *et al.* 1999). To differentiate homogeneous regions of sea ice such as flat or extensive rubble against heterogeneous regions caused by pressure ridge deformation, a neighborhood analysis was preformed. A 3 x 3 moving-window was used to analyse the standard deviation in backscatter value of each pixel relative to the neighboring pixels. High standard deviation values indicate edges or abrupt changes, some of which can be caused by the formation of a pressure ridge in otherwise flat sea ice.

Sea ice type categories were determined from bimonthly Canadian Ice Service regional ice charts (www.ice-glaces.ec.gc.ca). Fast ice was categorized as thick (>120 cm) annual fast ice. Pack ice was categorized as big to vast (500 m to 10 km) floes of thick (>120 cm) annual pack ice. These two sea ice categories accounted for 86% of the ice types surveyed, while the remaining sea ice surveyed could not be categorized into a single type.

Relative probability of polar bear predation attempts at subnivean lairs was modelled using a fixed-effect exponential RSF, in a "used" versus "available" framework (Manly *et al.* 2002). Used locations were sites of polar bear hunting attempts on ringed seal subnivean lairs. Available points were random locations, generated daily, and constrained to the helicopter flight path at a rate of one point per 50 km travelled. Total distance flown of 55,256 km in 2004-2006 generated 1106 random points and excluding those in open water or on land resulted in 896 points for modelling.

Akaike's Information Criterion (AIC; Burnham and Anderson 2002) was used to select the most parsimonious model. Overdispersion ($\hat{c}$) was tested by dividing the Pearson χ^2 by the degrees of freedom on the global model. Covariates were examined for nonlinearity using quadratic and natural log transformations. A quadratic transformation of distance from land and a natural log transformation of bathymetry provided lower univariate log-likelihood scores and were used for modelling. Covariates were screened for collinearity using a Pearson's correlation matrix. Covariates with a correlation coefficient of $|r_s| > 0.6$, were not retained in the same model. Fast ice and pack ice were correlated ($r_s = 0.82$), and pack ice was dropped from the candidate models due to its lack of fit. As a result, fast ice preference was referenced against all other sea ice categories. Remaining covariates were tested for multicollinearity, but all variance inflation factors were ≤1.5, suggesting little influence on model output. The resulting top model was used to create habitat maps for sea ice conditions reflecting April 1 of each year (2004-2006), at a grain of 500m, and limited to the range of observations not including outliers (≤100 km from land and ≤600 m depth). RSF values were standardized so the maximum was 1.0.

Habitat characteristics of ringed seal pup kill locations were compared between periods of low and high ringed seal reproductive output using Mann-Whitney for continuous data (Shapiro-Wilk, $P < 0.05$), and a Pearson chi-square for proportional data. The Marascuilo procedure was used for *post-hoc* analysis, as it allows for the comparison of proportion data of several populations simultaneously, using a chi-square statistic (Marascuilo 1966). All models and statistical tests were analysed in SPSS 20.0 (IBM, Chicago, USA) and 95% confidence intervals are reported with all proportions. Medians and ranges are reported for all continuous data. For all significance tests, alpha was set to 0.05.

4.3 Results

Between 2004-2006, 386 polar bear hunting attempts at ringed seal subnivean lairs were recorded by GPS. The top individual resource selection model had an AIC weight of 0.58, and was not significantly different than the next top model (ΔAIC = 1.09). However, the top two models only differed by one covariate, suggesting the inclusion of backscatter heterogeneity (Scatter_SD) in the top model was not justified (Arnold 2010). The global model showed no sign of overdispersion ($\hat{c} = 1.05$).

Polar bear predation attempts on ringed seal lairs were more likely to occur in stable ice environments (Table 4.1). Although the best fit for sea ice backscatter was linear, observations of hunting attempts (use) peaked at -15 dB, while survey observations (available) peaked at -14 dB, indicating a high abundance of deformed annual ice (Fig. 4.3). The relative likelihood of a predation attempt was higher near-shore and in fast ice, with peak relative probability occurring 42 km from shore (Fig. 4.4a). Relative probability also exhibited a rapid increase over shallow depths, and plateaued over deeper depths (Fig. 4.4b). Applying the top model to ice conditions for April 1 in each year (2004-2006) suggested that the eastern Amundsen Gulf had the highest relative probability of hunting attempts on subnivean lairs (Fig. 4.5).

Between 2003-2011, 115 ringed seal pup kills were documented. The earliest seasonal date for a pup kill was recorded on April 12, 2005. Of the pup kills, 50.4% (58/115) were located in fast ice and 41.7% (48/115) in large to giant floes of annual pack ice. Pup kills were located in a median water depth of 26 m (range: 5 m to 513 m) and a median distance of 43 km from land (range: 6 km to 116 km). Most kills in this study were observed in the region off the Tuktoyaktuk Peninsula (98/115) because this area received consistent survey effort from 2003-2011.

Examining pup kills within the Tuktoyaktuk Peninsula region revealed differences in the overall patterns of habitat use between years with lower (2003-2006) and higher (2007-2011) natality. During years of low reproduction, ringed seal pup kills were located closer to land at a median distance of 36 km (range: 6 km to 70 km), as compared to 46 km (range: 19 km to 115 km) in years of high natality ($Z = -2.17$, $df = 97$, $P = 0.03$). The distance from land of the helicopter flight-paths did not change between periods ($\text{median}_{\text{low}} = 35$ km, $\text{median}_{\text{high}} = 33$ km, $P = 0.43$). A higher proportion of pup kills were located in fast ice than in pack ice in years of low natality, but there was no difference in years of high natality (Fig. 4.6), despite flying over fast ice more ($\text{fast}_{\text{low}} = 52\%$, $\text{fast}_{\text{high}} = 64\%$). The proportion of pups killed in fast ice was greater in years of low natality as compared to high ($\chi^2 = 4.46$, $df = 1$, $P = 0.03$). The proportion of pups killed in pack ice was greater in years of high natality as compared to low ($\chi^2 = 5.27$, $df = 1$, $P = 0.02$). The median depth of 21 m (range: 5 m to 140 m) for locations where pups were killed in years of low reproductive output was not significantly different from the median depth of 23 m (range: 7 m to 481 m) in years of high ($Z = 1.13$, $df = 97$, $P = 0.26$). Helicopter flight paths while tracking polar bears were more frequent over deeper water in years of low natality as compared to high ($\text{median}_{\text{low}} = 25$ m, $\text{median}_{\text{high}} = 18$ m, $P < 0.01$).

4.4 Discussion

Cryptic species living in remote environments pose a degree of difficulty to researchers investigating their distribution and behaviour. This study demonstrates how documenting the hunting behaviour of a predator can reveal life-history characteristics of a cryptic prey. Previous studies on ringed seal breeding habitat are dominated by near-shore investigations. Capitalizing on a spatially dependent ecological relationship between polar bears and ringed seals revealed greater habitat variation in subnivean lair distribution than previously appreciated for ringed seals. The highest relative probability of polar bear predation attempts on ringed seal lairs during a period of low natality was in near-shore, annual fast ice, which is consistent with previous reports of ringed seal habitat preferences for lair construction (McLaren 1958; Lydersen and Gjertz 1986; Smith *et al.* 1991). However, while ringed seals are thought to prefer shallower depths (Stirling *et al.* 1982; Kingsley *et al.* 1985; Frost *et al.* 2004; Crawford *et al.* 2011), there was a high relative probability of hunting attempts over deeper depths (Fig. 4b), suggesting wide bathymetric variation in the distribution of ringed seal lairs.

Regional differences in stable sea ice conditions likely accounts for the high relative probability of predation attempts at subnivean lairs over deeper water. Although 82% (160/194) of the predation attempts in the Tuktoyaktuk Peninsula region and on the west side of Banks Island were over waters <100 m deep, 90% (173/192) of the predation attempts in Amundsen Gulf were over depths >100 m. Fast ice in the Tuktoyaktuk Peninsula region and off the west side of Banks Island is exposed to wind and currents from the Beaufort Sea, forming a predictable edge in shallow water, similar to the Alaskan coastline (Mahoney *et al.* 2007a; Mahoney *et al.* 2007b). Conversely, sea ice in Amundsen Gulf is largely protected and stabilized by the high availability of shoreline attachment sites, and fast ice can exist over deeper waters in early spring (Galley *et al.* 2008), as it did in 2004-2006 (Canadian Ice Service). This may explain why distance from land was a more important driver in the RSF model than water depth (Fig. 4.5), as water depth alone was insufficient in explaining the variation in the stable ice conditions ringed seals seek. Ringed seals have a broad diet including benthic, epontic, and pelagic prey (Smith 1987; Siegstad *et al.* 1998; Thiemann *et al.* 2007), suggesting flexibility for foraging in a range of water depths.

Snow depth is thought to be a primary limiting factor in the availability of suitable locations for subnivean lairs (Furgal *et al.* 1996; Hezel *et al.* 2012). Snow accumulation in the Canadian Beaufort Sea is generally too thin to support subnivean lair construction, unless a surface deformity exists that allows for deposition of wind driven snow (Smith and Stirling 1975; Smith *et al.* 1991). Pressure ridges in areas of otherwise flat ice can provide the necessary fine scale habitat features for breeding habitat (Smith 1987). SAR data were employed to differentiate heterogeneous sea ice areas that could represent deformations in flat ice. Sea ice backscatter values for survey flights suggest extensive rafting of the sea ice surface, reflecting the heavy sea ice conditions observed in 2004-2006 (Stirling *et al.* 2008). Highly deformed sea ice may have increased the number of ridges unrelated with subnivean lair habitat, limiting the detection of lairs using backscatter heterogeneity. Polar bears were observed to be attempting hunts in unusual locations in 2004-2006 (Stirling *et al.* 2008) and a higher proportion of bears were in a state of nutritional stress (Cherry *et al.* 2009). Heavy ice conditions and low reproductive output of ringed seals (Harwood *et al.* 2012) may have increased the difficulty of locating subnivean lairs during this period.

Polar bears kill a higher proportion of pups in years of high ringed seal natality (Stirling and Archibald 1977; Chapter 2), suggesting that pup kills may provide insight into fluctuations in ringed seal natality. The results of this study suggest that variation in the spatial distribution of pup kills may also be an indicator of ringed seal natality. In years of high natality, there was no significant difference in the proportion of pup kills in pack ice and fast ice, and correspondingly, kills were observed farther from shore. Given that survey effort was unrelated with changes in pup kill distribution, two nonexclusive hypotheses may explain this pattern: 1) saturation of available breeding habitat in near-shore fast ice may have increased the use of habitats farther from shore and in pack ice by ringed seals for reproduction during years of high natality, and 2) females forced to breed near active sea ice areas may be at an increased risk of losing the pup to polar bear predation than those in stable, near-shore ice.

Habitat suitability is largely a function of the resources available relative to the density of competitors (Fretwell and Lucas 1970). Lower quality habitat may increase in suitability as occupancy of high quality habitat increases. Between periods of low and high natality, ringed seal ovulation rates can change by 50-70% (Stirling *et al.* 1982; Harwood *et al.* 2012), resulting in a marked change in the number of active breeders in the population. Suitable fast ice habitat for subnivean lairs is limited (Furgal *et al.* 1996), and breeding ringed seals defend underwater territories, resulting in a limitation of maximum density (Smith and Hammill 1981; Krafft *et al.* 2007). A large increase in the number of breeding ringed seals in fast ice during high natality may increase the use of pupping habitats farther from shore and in pack ice as females are forced to extend their search for suitable, unoccupied habitat. Anecdotal evidence suggest ringed seals breed in pack ice environments (Fedoseev 1975; Finley *et al.* 1983), giving rise to questions about the facultative use of pack ice near fast ice areas (Smith and Lydersen 1991; Wiig *et al.* 1999). My results suggest that while near-shore fast ice environments appear to be preferred, ringed seals in the Canadian Beaufort Sea will also breed in adjacent pack ice areas, particularly during periods of high natality.

Predator density may also affect the observed spatial distribution of ringed seal pup kills. In spring, polar bears prefer occupying active ice, selecting for regions near floe edges and away from stable fast ice environments (Ramsay and Stirling 1986; Ferguson *et al.* 2000), although this can vary by age-class (Stirling *et al.* 1993; Freitas *et al.* 2012). The selection for active ice reflects polar bear predatory preference, and nearly all demographics of polar bears prefer to occupy and hunt in active ice areas (Chapter 3). High densities of hunting polar bears likely increases the predation pressure on ringed seals in subnivean lairs located in nearby pack ice and fast ice environments. During periods of high natality, ringed seals unable to secure near-shore habitat may be forced to pup in proximity to active ice areas, possibly increasing predation risk. The observed abundance of pup kills farther from stable ice areas is likely influenced by unequal predatory risk, rather than solely proportional to the abundance of ringed seals breeding in pack ice areas. Therefore, the detected habitat shift of ringed seal pup kills may reflect a combination of broadening habitat use as a function of breeder density as well as predation pressure in areas with high densities of polar bears.

Table 4.1 Relative probability indices for habitat covariates of the top resource selection model for attempt hunts on subnivean lairs in the Beaufort Sea, Canada, 2004-2006. Selection ratio for each covariate is indicated by exp (β), where values that are greater than 1 indicate higher relative probability of observing a predation attempt and values less than 1 indicate a lower relative probability. Covariates include distance from land (D_LAND), bathymetry (DEPTH), sea ice backscatter (SCATTER_dB) and sea ice classified as fast ice (Fast_Ice).

Covariate	D_LAND	D_LAND^2	DEPTH	SCATTER _dB	Fast_Ice
β	0.084	-0.001	0.142	-0.139	0.962
Upper CI (β)	0.105	-0.0006	0.252	-0.073	1.241
Lower CI (β)	0.062	-0.0014	0.033	-0.205	0.683
exp (β)	1.088**	0.999**	1.153*	0.870**	2.617**

$^{*}P < 0.01$, $^{**}P < 0.001$

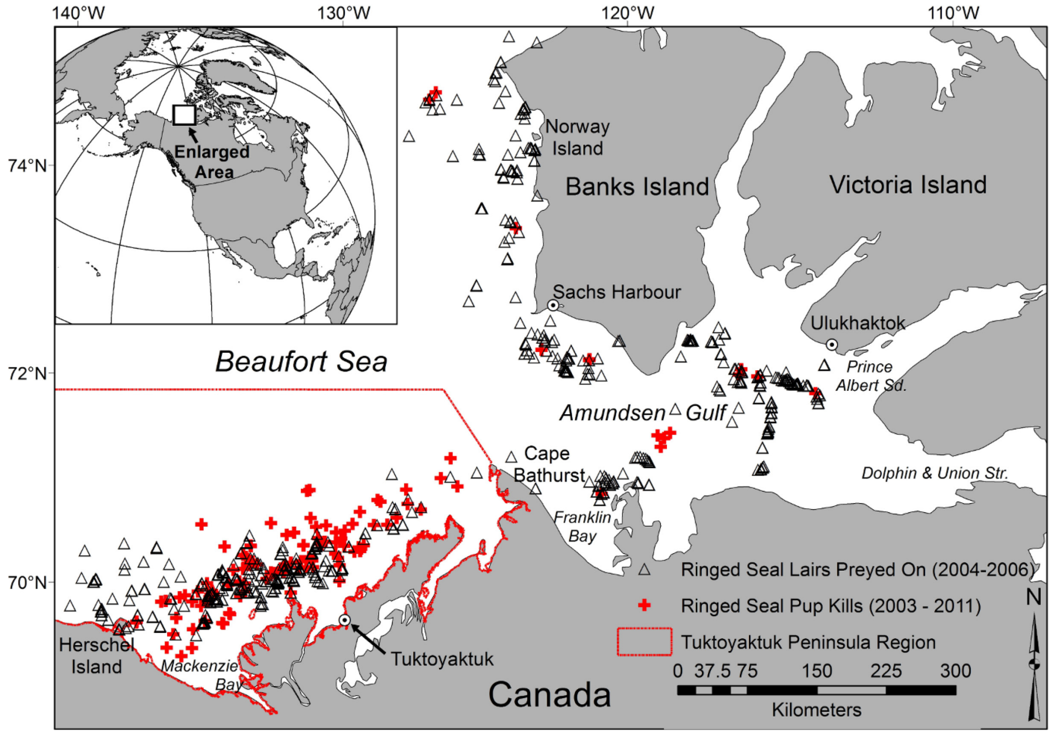

Figure 4.1 Locations of observed ringed seal pups killed by polar bears (✚, 2003-2011) and hunting attempts at ringed seal lairs by polar bears (△, 2004-2006) in the Beaufort Sea, Canada. Red boundary line indicates Tuktoyaktuk Peninsula region used in comparison of ringed seal pupping habitat between low (2003-2006) and high (2007-2011) reproductive periods.

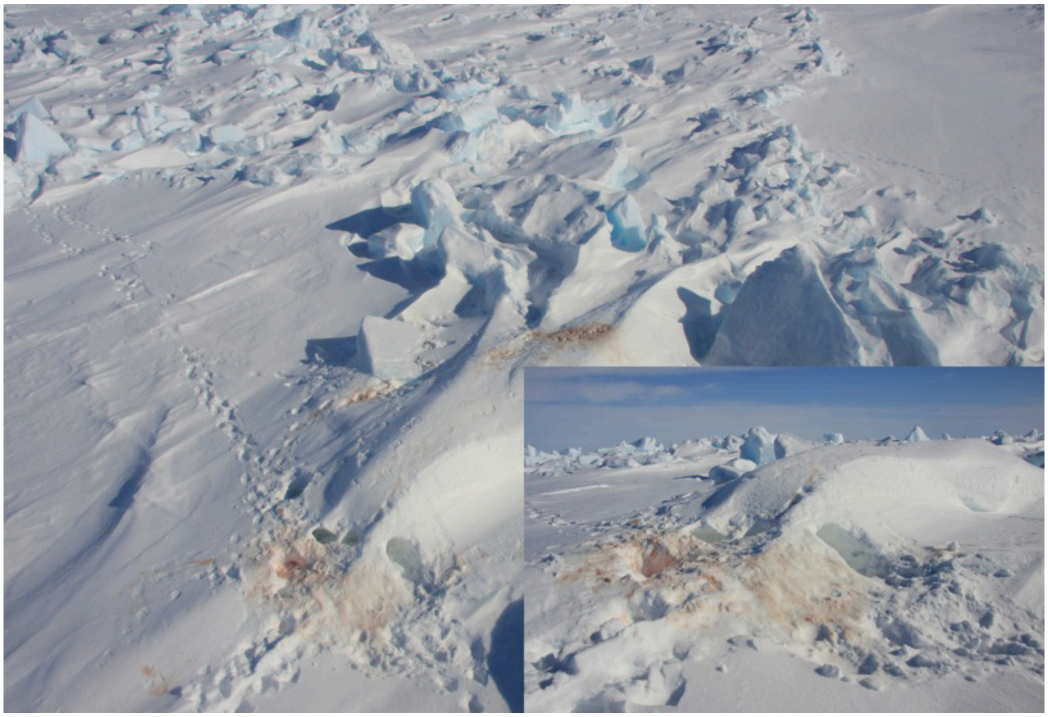

Figure 4.2 An example of an observation of a successful hunting attempt by a polar bear at a subnivean birth lair in the Beaufort Sea, Canada, April 21, 2010.

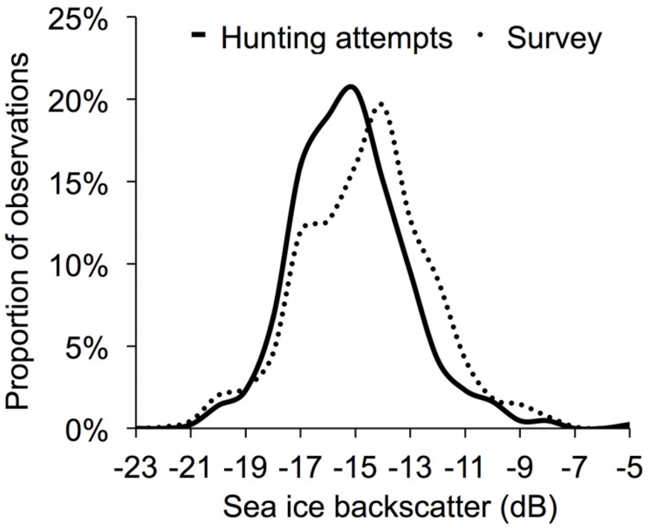

Figure 4.3 Smoothed line distribution of the frequency of sea ice backscatter (dB) values for area surveyed and hunting attempt observations, with distributions peaking in deformed annual ice (Kwok and Cunningham 1994).

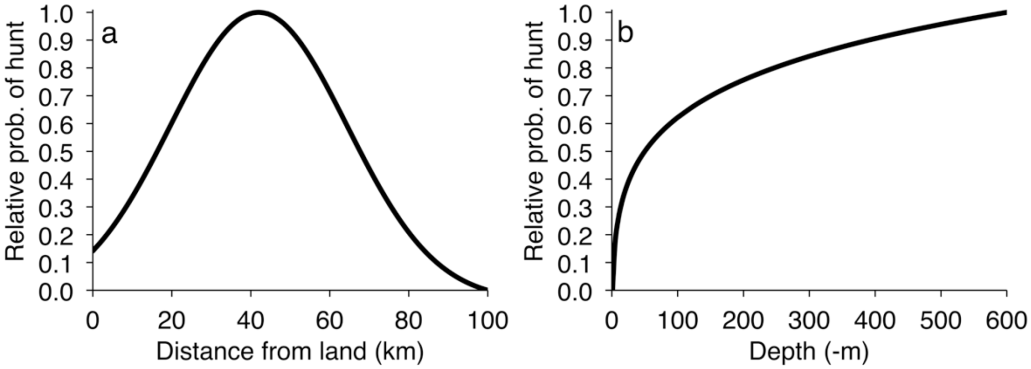

Figure 4.4 Scaled univariate response for distance from land and bathymetry in the resource selection model of polar bear predation attempts on ringed seal subnivean lairs in the Beaufort Sea, Canada. All other covariates were held to their median values when computing the response curve.

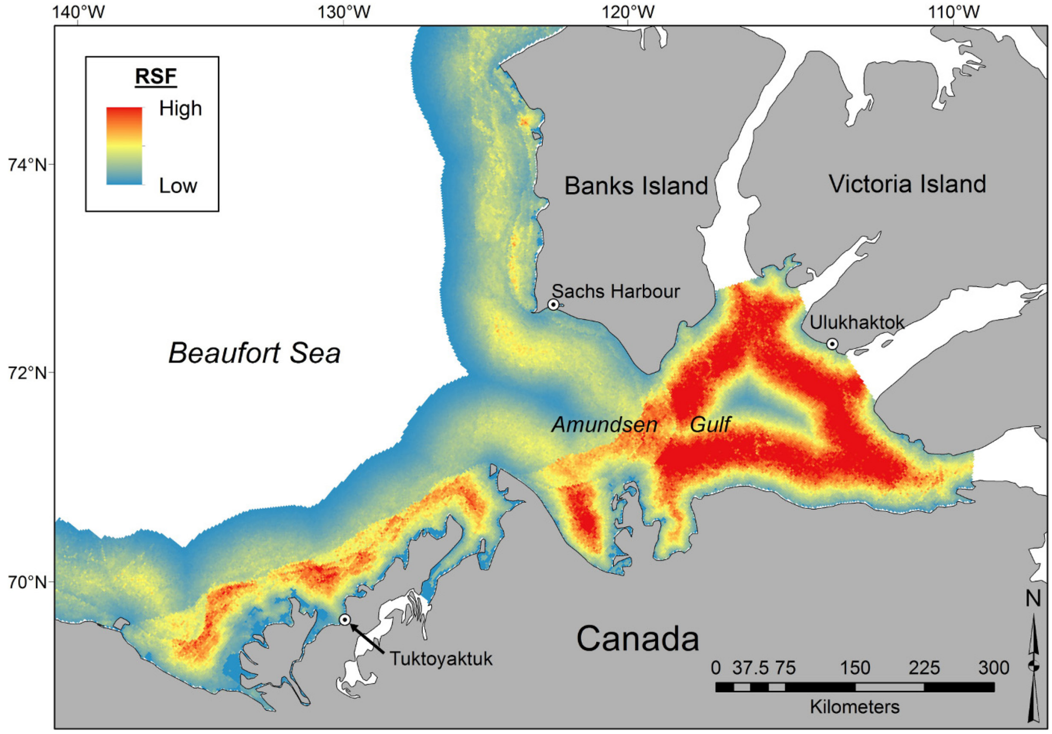

Figure 4.5 Mean relative probability of polar bear hunting attempts on ringed seal subnivean lairs during low reproductive output, reflective of sea ice conditions for April 1 in the Beaufort Sea, Canada, 2004-2006. Output is reflective of quality and spatial repeatability.

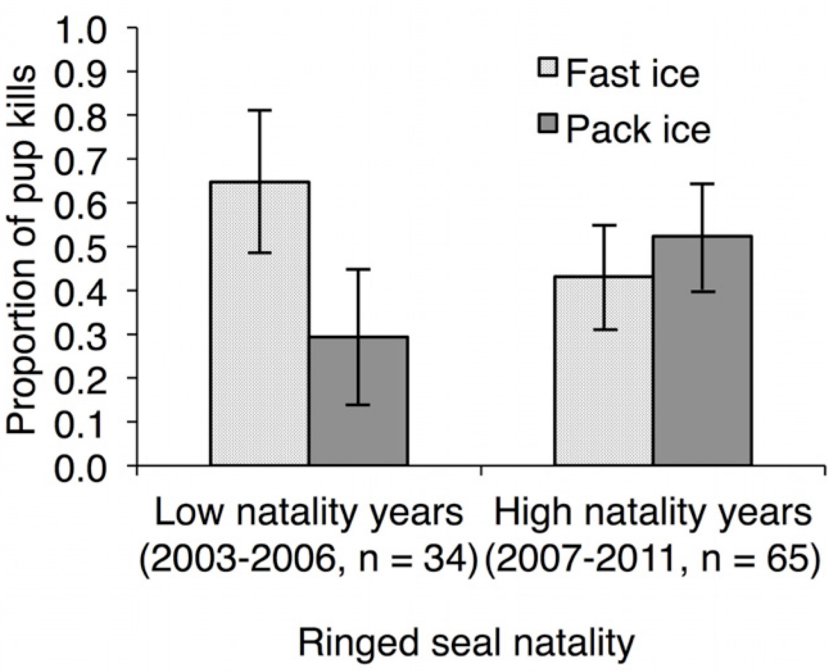

Figure 4.6 Comparison of proportion of ringed seal pup kills observed in fast ice and pack ice in the Tuktoyaktuk Peninsula region, Canada, between years of low and high ringed seal reproductive output, 95% confidence intervals shown.

Chapter 5[‡]

5 Multi-temporal factors influence spring predation for polar bears in a changing climate

5.1 Introduction

Predation is an ecological interaction shaped by biotic factors and modified by abiotic conditions, which can interact on various temporal scales. For large carnivores, a number of studies have demonstrated the influence of climatic oscillations on long-term predator-prey interactions (Post *et al.* 1999; Owen-Smith 2008; Hone *et al.* 2011). A few studies have documented abiotic manipulation of prey vulnerability on finer scales for large carnivores, such as during the hunt itself (*e.g.* Hilborn *et al.* 2012). However, there is a paucity of studies that compare the importance of abiotic and biotic factors functioning at multiple temporal scales on the likelihood of a predation event. This is particularly relevant to examining the role of climate change on predator-prey interactions, where systemic shifts in abiotic conditions may change the composition of food webs (Barton and Schmitz 2009; Woodward *et al.* 2012).

Despite climate change having a suite of abiotic effects (IPCC 2013), experimental and observational studies on predator-prey interactions and climate have generally relied on using single explanatory variables at a single temporal scale for manipulation or comparison (*e.g.* seasonal temperature).

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However, ignoring multiple explanatory factors in climate change studies may overestimate the influence of the assumed driver (Gullett *et al.* 2014). For example, the temporal structure between multiple abiotic factors may moderate the vulnerability of prey to predation (Pincebourde *et al.* 2012). Biotic factors, such as the behaviour of the predator, may be relevant in stabilizing fluctuations in prey population dynamics brought on by climate change (Wilmers *et al.* 2007). Dividing and comparing fine and large scale factors may allow for identification of important factors in predator-prey interactions, and identify ecological linkages that are sensitive to climate change.

Climate change has been recognized as a major driver in reductions in the extent, thickness and duration of sea ice in the Arctic (Stroeve *et al.* 2007), which is the primary habitat of polar bears (*Ursus maritimus*). As the duration of the summer melt season extends, polar bears spend less time hunting seals and more time fasting (Stirling and Derocher 2012). Empirical studies have linked lowered polar bear survival, reproduction and body size to the increase in the number of ice-free days (*e.g.* Regehr *et al.* 2010; Rode *et al.* 2010). Additionally, Cherry *et al.* (2009) reported that fasting rates of polar bears in spring had more than doubled between 1985-86 and 2005-06, suggesting on-ice hunting conditions may also be changing. Climate has been linked to modifying the recruitment of polar bear's primary prey, ringed seals (*Pusa hispida*), and the prey composition of polar bear diets in spring-summer (Ferguson *et al.* 2005; McKinney *et al.* 2013). Although these reports propose that prey availability may change with climate for the polar bear, the extent to which climate influences seal predation is poorly understood.

Here, I employ data on seals killed by polar bears collected in spring between 1985 and 2011 in the Beaufort Sea, Canada, to evaluate the influence of daily and inter-annual scale biotic and abiotic factors on the likelihood of predation events. Polar bears are hyperphagic in spring and may acquire as much as two-thirds of the energy requirement for the year (Stirling and Øritsland 1995), providing fat reserves for survival through periods of low prey access during the summer melt season. At finer temporal scales, the synchronous parturition of ringed seals in spring has been suggested to be an important driver of polar bear hyperphagia (Hammill and Smith 1991; Stirling and Øritsland 1995; Chapter 2). Additionally, spring sea ice is dynamic, peaking in quality for polar bears at regional sea ice concentrations of 80-85% (Durner *et al.* 2009; Chapter 3), and abandoned correlated with dates of 30-50% regional sea ice concentration (Stirling *et al.* 1999; Cherry *et al.* 2013). At a larger temporal scale, the physical structure of sea ice in spring is reflective of climatic conditions over the winter months (Rigor *et al.* 2002), and may influence predation events (Stirling *et al.* 2008). I compared the influence of these and other biotic and abiotic factors on the likelihood of predation events, as well as examined the likelihood of ringed seal pup, juvenile and adult age-class kills to investigate potential intraspecific differences in predation vulnerability of polar bear's primary prey. Finally, to examine the effect of climate change on predation, I integrated the results of my study with findings on fasting rates in polar bears. Cherry et al. (2009) reported that the proportion of polar bears fasting in the spring in the Beaufort Sea had increased from 10% in 1985-86 to 25% in 2005-06. I applied the conditions observed in these periods to the top predation model to examine if the expected kill rate from the model could explain the observed polar bear fasting rates.

5.2 Materials and methods

The study area comprised the eastern Beaufort Sea, including Amundsen Gulf, within 150 km of the Canadian coast (Fig. 5.1). Helicopter flights originated from Tuktoyaktuk, Sachs Harbour, Ulukhaktok (Holman), Cape Parry, and Norway Island, Northwest Territories. Observations of seals killed by polar bears were collected over 16 springs between early-April and late-May (range April 3 – May 28) in 1985-1987, 1992-1994, 2000, and 2003-2011. The study area is composed mainly of annual fast ice along the coast and pack ice farther offshore, separated by the Cape Bathurst polynya and related flaw lead system.

Observations of seals killed by polar bears were made opportunistically during ongoing polar bear ecology research. Seal kills were identified from a helicopter by either the presence of blood and/or carcass remains on the sea ice while tracking individual bears. Due to logistical constraints, it was not possible to land and investigate all kill sites, so some were noted only from the air. Kills sighted with only Arctic fox (*Vulpes lagopus*) tracks were excluded. Seals hauled out on the sea ice were enumerated when sighted, regardless of their distance from the helicopter. Polar bears were enumerated, regardless of whether capture occurred.

The likelihood of a predation event was modelled by relating counts of seals killed by polar bears to environmental variables at two temporal scales: intra- and inter-seasonal. Additionally, a detection model was built to account for variation in kill detectability. Stepwise model construction was employed, where top models for detection, intra-seasonal and inter-seasonal were built separately before combining. Covariates were screened with a Pearson's correlation coefficient, removing correlations $|r_s| > 0.6$ by retaining the covariate with the higher log-likelihood. In all models, continuous covariates were examined for nonlinearity using natural log and quadratic transformations. Potentially biologically significant interaction terms were examined for inclusion before model selection. Model selection for observation and process stages followed a backward-elimination procedure, starting with the full model, and removing covariates with the lowest Wald chi-square value, until all remaining covariates had a P-value ≤ 0.10. Top models for each stage were combined and evaluated using Akaike's Information Criterion for small samples (AIC_c; Burnham and Anderson 2002) to infer the relative influence of intra- versus inter-seasonal processes on kill likelihood, while accounting for variation in dectability with the detection model. All models were constructed using the gamlss package in R 3.1 (Rigby and Stasinopoulos 2005).

I considered four data models: poisson, negative binomial, zero-inflated poisson, and zero-inflated negative binomial. I selected the data model that maximized the log-likelihood value when applied to a global model containing a priori covariates for all stages of model building (detection, intra-seasonal, inter-seasonal).

Detection has become an increasingly relevant and tractable issue in probability modelling with count data. Common methods for incorporating detectability require repeated samples at the same point in space (Royle *et al.* 2005). However, the data in this study was collected opportunistically, and repeated spatial samples were unavailable. Advances in probability modelling suggest detectability can be incorporated without replicate samples using a conditional likelihood approach, random effects or hierarchical Bayesian models. However, each of these approaches increases model complexity. In contrast, model offsets for negative binomial and Poisson designs can incorporate a single covariate reflecting the time or area over which the count response was generated (Hilbe 2011). Following the principle of parsimony, I evaluated the need for a full detectability model versus a single covariate offset using information criterion.

I hypothesized detectability of kills could be influenced by the following four covariates: search effort, observer, flight region, and snowfall. Search effort was measured as the number of helicopter hours flown per flight day, and was natural-log transformed for fit. Observer was the primary surveyor during the flight, dummy coded, using I. Stirling as reference. Flight region was based on daily starting location and subdivided by polar bear subpopulation into either the Northern Beaufort (Norway Island, Sachs Harbour, Ulukhaktok) or Southern Beaufort (Cape Parry, Tuktoyaktuk). Snowfall was a binary variable indicating whether snow had fallen at some point over the previous day(s), as recorded in Environment Canada hourly weather station logs at Tuktoyaktuk and Sachs Harbour airports (www.climate.weather.gc.ca). Three temporal lags (1, 3, or 5 days) were tested for snowfall, with a 1-day temporal lag selected based on univariate fit. Fresh snow can enhance the visibility of polar bear tracks, as well as cover and hide fresh kills, potentially influencing the detection of predation events.

The intra-seasonal model was built with nine a priori covariates: number of seals hauled out, number of polar bears sighted, regional sea ice concentration (%), air temperature (°C), wind speed (km/h), seasonal day, and weather categorized as sunny, partly cloudy, cloudy or snowing. The number of polar bears sighted during the flight day was employed to control for changes in seal kill frequency due to local abundances of polar bears. Regional sea ice concentration was determined daily using the mean pixel value from Special Sensor Microwave Imager (SSM/I) satellite imagery (Cavalieri *et al.* 1996), calculated over the area inclusive to all helicopter flight paths. Weather conditions including air temperature and wind speed are influential in seal haul out patterns (Finley 1979; Smith and Hammill 1981; Carlens *et al.* 2006), which may increase seal vulnerability to predation. Weather conditions, air temperature, and wind speed were taken from Environment Canada hourly weather station logs at Tuktoyaktuk and Sachs Harbour airports. Weather was dummy coded and referenced against sunny conditions. To reflect the uncertainty between when a kill occurred and when it was observed, temporal lags were applied to wind and temperature covariates for the mean of the observation day, the previous 3 and 5 days. The best fit was the previous 5-day mean for wind and the observation day for temperature. Temperature was correlated with seasonal day ($r_s = 0.66$, $P < 0.01$), and removed from the analysis. To increase model fit, the number of seals hauled out was natural-log transformed and date was transformed to a quadratic.

The inter-seasonal model was built with four a priori covariates: the phase of the winter Arctic Oscillation (AO; Thompson and Wallace 1998), the phase of the Arctic Ocean Oscillation (AOO; Proshutinsky and Johnson 1997), ringed seal reproductive output, and year. Ringed seal reproductive output was a binary variable with years grouped into low or high natality based on ringed seal ovulation rates and pup production in the eastern Beaufort Sea (Kingsley and Byers 1998; Harwood *et al.* 2012). The AO is an index of sea level pressure anomalies north of 20°N (Thompson and Wallace 1998), with winter (Jan-Mar) having the largest effect on spring sea-ice conditions (Rigor *et al.* 2002). AO phase was a binary variable reflecting a mean negative index value over the winter referenced against years with a mean positive index. The AOO is also an index of Arctic climatic conditions, but focuses on wind-driven circulation regimes (Proshutinsky and Johnson 1997). The AOO phase was employed as a binary variable reflecting the Anti-Cyclonic Circulation Regime (ACCR) referenced against a Cyclonic Circulation Regime (CCR). During the ACCR phase, fresh water input is conserved within the Beaufort Gyre, the Arctic is colder, and combined with convergent forces and ridging, sea ice increases in volume across the polar basin (Proshutinsky 2002). Conversely, during the CCR phase, the Arctic is warmer, the Beaufort Gyre releases fresh water, and coupled with divergent forces, sea ice shrinks in volume (Proshutinsky 2002).

Data was rarified for intraspecific models to include kills that were identified by species and age-class to be ringed seal adults (≥7 years), juveniles (1-6 years) or pups (0 years). Ringed seal kills were identified by field observation corroborated with DNA evidence, and aged using tooth histology and claw samples (McLaren 1958; Stewart *et al.* 1996). Models were built for each age-class using the same procedure and covariates as the predation event model.

I re-examined the likelihood of polar bears being in a fasting state in the springs 1985, 1986, 2005 and 2006 using a binomial logistic regression and the data from Cherry *et al.* (2009). A ratio of urea to creatinine (U/C) of ≤ 10 in the serum is indicative of a fasting condition in polar bears (Nelson *et al.* 1984). Cherry *et al.* 2009 reported that the age-class of the individual and the year in which the sample was obtained were significant predictors of polar bear fasting. Because adult polar bears captured with mates were more likely to be fasting, I simplified age-class into a binary variable (Mating). Adults that were accompanied by an adult of the opposite sex when captured were referenced against the rest of the population (subadults, adult females with cubs, and solitary adults). In addition to year and mating, I considered two other parameters in the candidate model set: the expected rate of seal kills and the mean seal kill biomass. Biomass and year were correlated (r_s = -0.81, $P < 0.01$), and biomass was retained over year in the candidate models to increase fit (ΔAIC_C = 1.34). The expected rate of seal kills was calculated at a daily scale by applying the observed conditions for 1985, 1986, 2005 and 2006 into the top seal kill model. Because experimental trials suggest a U/C > 10.0 for at least seven days after a polar bear has fed (Derocher *et al.* 1990), I used the mean expected seal kill rate of the seven days before the day blood samples were taken. The temporal lag provided a better univariate fit than the expected seal kill rate of the sample day (ΔAIC_C = 9.25). Mean seal kill biomass was determined from the observed ringed seal age-class composition for each year (Chapter 2). I excluded bearded seals (*Erignathus barbatus*) from the seal biomass estimations due to a small sample size.

I also compared the mean kill rate across the spring season between 1985-86 and 2005-06 to explore the potential cause of the increase in fasting rates. Mean ringed seal kill biomass was multiplied with the number of expected kills from the model to assess both quantity and quality of seal kills for each period. Expected rates of kills/day and kill biomass/day were compared between 1985-86 and 2005-06 using a Mann-Whitney U-test, and reported with a standardized Z-test statistic. For all significance tests, alpha was set to 0.05.

5.3 Results

Between 1985-2011, 370 flight days resulted in 650 seal kill observations. Zero seal kills were observed on 37.6% of the days (Fig. 5.2). Model selection suggested that the log-link negative binomial distribution was the most suitable out of the candidate data models (Appendix B). The negative binomial distribution showed no signs of overdispersion on the global model ($\hat{c}$ = 0.67).

With the exception of the ringed seal pup model, the most parsimonious detection model was a single covariate: survey effort (Appendix B). Therefore, detection was incorporated in all models using survey effort as an offset in the negative binomial regression. For the ringed seal pup model, Observer was also influential in the likelihood of observing a pup kill (Appendix B). To account for the potential bias, I used a mixed effects model for pup kills, with Observer set as a random intercept.

The top intra-seasonal model included five covariates: mean wind speed over the previous 5-days (WIND), number of seals hauled out (SEALS), number of polar bears sighted (BEARS), regional sea ice concentration (ICE), and seasonal day ($DAY + DAY^2$). The top inter-seasonal model included four covariates: ringed seal reproductive output (RS_Natality), AOO phase (ACCR), AO phase (Neg_AO), and year (YEAR). When the two top models were combined, the fit was significantly better than either temporal scale individually (LL ratio test; $\chi^2 = 24.48$, $df = 5$, $P < 0.001$; Table 1).

Predation event probability increased with concurrent observations of ringed seals hauled out (Fig. 5.3a), greater regional sea ice concentration (Fig. 5.3b), during years with high ringed seal reproductive output, after negative AO winters, and in years with an ACCR phase (Table 5.2). Predation event probability decreased with increasing mean wind speed (Fig. 5.3c), and peaked in early-May (Fig. 5.3d).

The probability of an adult ringed seal kill was significantly improved with both temporal scales in the model (LL ratio test; $\chi^2 = 22.67$, $df = 2$, $P < 0.001$), as well as for the juvenile ringed seal model (LL ratio test; $\chi^2 = 16.11$, $df = 3$, $P = 0.001$; Table 5.1). The inter-seasonal model provided the best fit for the probability of a ringed seal pup kill.

The probability of an adult ringed seal kill increased after negative AO winters, and in years with an ACCR phase (Table 5.2). The probability of an adult kill decreased with increasing mean wind speed, and peaked in early-May. The probability of a juvenile kill decreased with year and increased with the number seals hauled out (Table 5.2). The probability of pup kill increased with year (Table 5.2).

The top model for the probability of fasting in polar bears included the expected seal kill rate (KILL), the estimated mean biomass of the kills (BIOMASS) and whether the individual sampled was with a mate at capture (Mating). The top model was a significantly better fit than the next candidate model (LL ratio test; $\chi^2 = 5.48$, $df = 1$, $P = 0.02$; Appendix B). The probability that a polar bear was fasting decreased with increasing expected seal kill rate and kill biomass (Table 5.3). Mating polar bears were more likely to be fasting.

The mean of the expected seasonal kill rate for 1985-86 was 0.53 ± 0.07 kills/flight hour, which was not significantly different from the mean of 0.48 ± 0.04 kills/flight hour in 2005-06 ($Z = -1.63$, $P = 0.10$, Fig. 5.4a). The mean kill biomass estimated from aged ringed seals in 1985-86 was 55.5 ± 1.8 kg, significantly larger than the 36.9 ± 5.3 kg observed in 2005-06 ($Z = -6.31$, $P < 0.01$). The mean expected seasonal kill biomass rate for 1985-86 was 29.7 ± 4.0 kg/flight hour, significantly larger than the mean expected rate of 17.7 ± 1.4 kg/flight hour in 2005-06 ($Z = -3.51$, $P < 0.01$, Fig. 5.4b).

5.4 Discussion

Ringed seal reproduction was a significant predictor of predation events at both daily and yearly temporal scales. Predation events were much more likely in years with high ringed seal reproductive output. Polar bears are effective hunters of ringed seal pups (Hammill and Smith 1991), and an increase in the density of pups in high natality years likely increases prey encounter rates because pups have low mobility and are naïve to predators. The probability of a seal kill also peaked in early-May, approximately three weeks after the peak of ringed seal whelping. Ringed seal pups are born into subnivean lairs on the sea ice, and in the early stages of development remain mostly in the thermal protection of the lair (Smith *et al.* 1991). As nursing pups gain mass, diving bouts occur more often and for longer duration (Lydersen and Hammill 1993b). Because the water column is the main refuge from predation for ringed seals, increasing diving ability may reduce predation vulnerability (Lydersen *et al.* 1993), which could partially explain the decline in the probability of predation events after early-May.

Although the polar bear predatory response to ringed seal whelping in spring is well documented (*e.g.* Stirling and McEwan 1975; Smith 1980; Hammill and Smith 1991), in Chapter 2 I hypothesized that the haul-out behaviour of seals may also increase their vulnerability. I found support for this hypothesis, as the probability of a predation event increased when more seals were recorded hauled-out on the sea ice on the day of observation. Ringed seal adults haul-out on the sea ice surface more in April-June than at any other time of the year (Kelly *et al.* 2010), and in early spring restrict themselves to a breeding territory, reusing a self-maintained set of breathing holes (Smith and Hammill 1981; Kelly and Quakenbush 1990). Frequent surfacing at limited breathing holes and cracks may increase the likelihood of capture by a polar bear; a predominately sit-and-wait predator (Stirling 1974). Additionally, I found that a lower mean wind speed over the previous 5 days increased the probability of observing a predation event. Ringed seals haul-out more frequently during calm conditions (Finley 1979; Smith and Hammill 1981; Carlens *et al.* 2006) because lower wind speed increases skin temperature, promoting spring molting and epidermal growth (Feltz and Fay 1966). Mean wind speed over the previous 5 days may be considered a proxy for haul-out, covering the temporal uncertainty between when the predation event occurred and when it was observed.

Wind speed was not a significant predictor in the pup kill model, but was a significant predictor in the adult kill model. This supports the suggestion that wind is modifying the vulnerability of adults rather than pups, which is the expectation given pups' environmental conditions are regulated by the subnivean lair. Additionally, seasonal day was also a major predictor of adult kills, peaking in May. Adults shift from primarily using subnivean lairs to haul-out in April, to basking in the open in May (Kelly *et al.* 2010). In Chapter 2, I found no relationship between the frequency of polar bear hunting attempts at subnivean lairs and the frequency of adult ringed seal kills, suggesting that adults may be less vulnerable at subnivean lairs. However, as adults shift to hauling out at breathing holes and cracks, the lack of subnivean protection may increase their vulnerability (Stirling *et al.* 1975). Of adult kill sites recorded with an associated habitat description (n = 68), 70% were observed killed at breathing holes or near cracks in the sea ice.

Two large-scale climatic oscillation indices were included in the top predation model: the AO and the AOO. In comparison with the weather conditions measured on a local scale, only wind was retained as a significant effect in the top model. Regional climatic indices outperformed locally measured weather conditions, which may partially reflect the difficulty in accurately measuring weather conditions across a large, remote study area. Climate indices can package weather information and generalize patterns over hemispheric areas, representing conditions over months, which can have significant impacts on the formation of sea ice habitat. Negative winter AO and ACCR phases tend to enhance sea ice divergence for the eastern Beaufort Sea, resulting in the early formation of leads in spring (Rigor *et al.* 2002; Barber and Hanesiak 2004). However, across the Arctic basin overall sea ice increases in volume and surface air temperatures are colder, delaying the spring melt (Belchansky *et al.* 2004).

The dynamic between active ice formation and a slowed spring melt may prolong habitat conditions conducive to hunting for polar bears. Earlier lead formation likely increases predation opportunities because polar bears seek out new sea ice and active leads when hunting (Stirling *et al.* 1993;

Chapter 3). However, results from this study also suggest that predation events are more likely when sea ice concentration is high. Although divergent sea ice is important, too much open water reduces hunting opportunities because seals are generally too agile to catch in the water column. As a result, the faster the spring melts occurs, the more likely polar bears are to abandon the sea ice in favour of summer refugia (Cherry *et al.* 2013). However, the effect that climatic oscillations have on sea ice may be shifting with climate change. Due to a thinning sea ice cover, a strong 2009 negative winter AO phase promoted the export of sea ice through the Chukchi Sea (Stroeve *et al.* 2011). Warming global temperatures may also be creating more extreme and lengthy phases in climatic oscillations (Goodkin *et al.* 2008). As such, future climatic oscillation patterns may result in unexpected consequences for polar bear foraging ecology that do not reflect past responses.

Polar bears of the Beaufort Sea are being negatively affected by climate change, resulting in declines body size, reproduction and survival (Regehr *et al.* 2010; Rode *et al.* 2010). While these changes were associated with an increase in the number of ice-free days in the year, Cherry *et al.* (2009) reported that spring fasting rates in polar bears increased between 1985-86 and 2005-06, suggesting that spring feeding conditions may also be changing. I determined that the probability a polar bear was fasting during each of these years was related to the daily-expected kill rate from my model, the seasonal mean kill biomass estimate, in addition to whether the polar bear was engaged in mating activity. Applying the top predation model to the conditions observed in 1985-86 and 2005-06 suggested no significant difference in the mean rate of predation events between periods, despite more than double the frequency of fasting polar bears in 2005-06. Both periods had similar abiotic conditions as well as reduced ringed seal natality. Population sizes of the Northern Beaufort and Southern Beaufort polar bear subpopulations were also similar between periods (Regehr *et al.* 2006; Stirling *et al.* 2011). The local abundance of polar bears sighted each day was factored into the predation event model, suggesting polar bear density did not significantly alter the expected kill rate between periods.

The age-distribution of ringed seal kills differed across periods, resulting in a 50% increase in the biomass killed in 1985-86. The major difference appears to be the availability of juvenile ringed seals, which made up 40% of the ringed seal kills in 1985-86 but only 7% in 2005-06 (Chapter 2). In 2005-06 polar bears killed more pups proportionally (44%), despite a decline in ringed seal natality, which reached its lowest point in 20-years (Harwood *et al.* 2012). To prey on pups, some polar bears dug through thick rafted ice sheets to access birth lairs (Stirling *et al.* 2008), an energy inefficient hunting strategy. These observations suggest a degree of food stress, potentially associated with a reduction in the availability of both pups and larger bodied prey such as juvenile ringed seals.

Ringed seal gene flow suggests a pan-Arctic dispersal pattern (Martinez-Bakker *et al.* 2013) resulting in a lack of population structure (Davis *et al.* 2008). Juveniles do not restrict themselves to a territory, preferring to search out high quality foraging areas in spring (Crawford *et al.* 2011). Year was a major predictor in the juvenile kill model, suggesting that their abundance may be related to spatiotemporal distribution or underlying population dynamics, for which little is known. Alternatively, juveniles may have been present in the system, but less accessible. Ice in the Beaufort Sea in the mid-2000s had extensive rubble zones, which may have made hunting more difficult (Stirling *et al.* 2008). Further study on differentiating between the abundance and the accessibility of seals as it relates to climate and predation is warranted.

Because polar bears may acquire as much as two-thirds of their energetic intake in spring (Stirling and Øritsland 1995), a significant reduction in kill biomass could have population level consequences. Spring is mating season for polar bears, and successfully mated females can avoid implantation or abort fetuses prior to denning if sufficient fat has not been gained (Derocher *et al.* 1992). Additionally, Bromaghin *et al.* (2014) reported lower survival rates between 2004-2006 for the Southern Beaufort subpopulation and suggested measures of ice-availability were insufficient in explaining the decline. I suggest that poor hunting conditions in spring 2005-2006 could be a potential factor influencing lower survivorship.

While multi-scale approaches have become recognized for their importance in spatial ecological processes, the results here suggest multi-temporal scales should also be considered for long-term ecological data. Studies on the ecological effects of climate change have often focused on single explanatory variables measured at a single scale. In polar bear studies, the focus has been on comparing changes in survival, reproduction and body size to yearly reductions in the extent of the sea ice. However, climate change may also be contributing to modifications in the on-ice hunting conditions for polar bears. I determined that the probability of a predation event was influenced by abiotic and biotic factors on multi-temporal scales. While the applied model output could explain some the variation in polar bear fasting rates, I found significant model improvement was made by also including the size of the prey killed. Results suggest documented changes in polar bear fasting rates in the Beaufort Sea, Canada are likely due to a complex set of abiotic and biotic factors including potential underlying prey population dynamics. Future studies that integrate the population ecology of ringed seals in relation to patterns and success of polar bear predation rates will likely be needed to provide further insight into how climate change impacts polar bears beyond basic environmental correlations.

Table 5.1 Comparison of model fit for different temporal scales to the likelihood of seal predation events in the Beaufort Sea, Canada, 1985-2011. All models include an offset for survey effort, and ringed seal pup models include an additional random intercept for observer (see text).

Rank	Model	*k*	LL	AIC_C	ΔAIC_C
Predation Event Model (*n* = 650)					
1	INT + INTRA + INTER*	11	-583.20	1189.15	0.00
2	INT + INTRA	7	-595.44	1204.89	15.74
3	INT + INTER	5	-619.63	1249.43	60.28
4	INT	1	-639.13	1280.27	91.12
Adult Ringed Seal Kill Model (*n* = 150)					
1	INT + INTRA + INTER*	8	-270.35	555.01	0.00
2	INT + INTRA	5	-279.73	569.63	14.61
3	INT + INTER	4	-282.80	573.71	18.69
4	INT	1	-394.49	790.99	235.98
Juvenile Kill Ringed Seal Model (*n* = 62)					
1	INT + INTRA + INTER*	6	-149.01	310.25	0.00
2	INT + INTER	3	-157.07	320.20	9.95
3	INT + INTRA	3	-157.34	322.80	12.55
4	INT	1	-172.62	347.25	37.00
Pup Kill Ringed Seal Model (*n* = 132)					
1	INT + INTER	3	-233.57	473.13	0.00
2	INT + INTRA + INTER†	4	-233.56	475.23	2.09
3	INT + INTRA	2	-245.61	495.26	22.13
4	INT	1	-247.78	497.57	24.44

*Combined scales fit is a significant improvement: LL ratio test ($P < 0.001$)

†Combined scales fit is <u>not</u> a significant improvement: LL ratio test ($P > 0.05$)

Table 5.2 Mean beta values of covariates of the top models for all predation events and rarified by kills known to be ringed seal adult, juvenile and pups. 95% confidence intervals are in parentheses. Beta values in bold represent values significantly different than 0 ($P \leq 0.05$).

Model	Predation Event	Adult Kill	Juvenile Kill	Pup Kill
Inter-Seasonal Covariates				
RS_Natality	**0.959 (0.437, 1.480)**	-	-	0.490 (-0.059, 1.039)
Neg_AO	**0.509 (0.059, 0.958)**	0.482 (-0.110, 1.074)	-	-
ACCR	**0.669 (0.181, 1.158)**	**1.142 (0.260, 2.025)**	0.857 (-0.369, 2.083)	-
YEAR	-0.003 (-0.021, 0.015)	-	**-0.066 (-0.100, -0.032)**	**0.084 (0.044, 0.123)**
Intra-Seasonal Covariates				
WIND	**-0.051 (-0.079, -0.023)**	**-0.044 (-0.086, -0.001)**	-	-
SEALS	**0.105 (0.014, 0.195)**	-	**0.095 (0.007, 0.183)**	-
BEARS	**0.153 (0.067, 0.239)**	0.093 (-0.037, 0.222)	**0.502 (0.037, 0.966)**	-
ICE	**0.030 (0.001, 0.059)**	-	0.053 (-0.043, 0.149)	-
DAY	**0.124 (0.065, 0.184)**	**0.276 (0.157, 0.395)**	-	-
DAY^2	**-0.002 (-0.003, -0.001)**	**-0.004 (-0.006, -0.002)**	-	-

Table 5.3 Mean parameter estimates from the top polar bear fasting model for the spring in Beaufort Sea, Canada, using a binary logistic regression. Fasting determined as a blood serum urea/creatinine ≤ 10.0.

		95% Confidence Interval		Hypothesis Test		
Parameter	Beta	Lower	Upper	Wald χ^2	*df*	*P*-value
KILL	-2.05	-3.62	-0.47	6.47	1	0.01
BIOMASS	-0.03	-0.05	-0.01	6.21	1	0.01
Mating	0.75	0.13	1.36	5.70	1	0.02

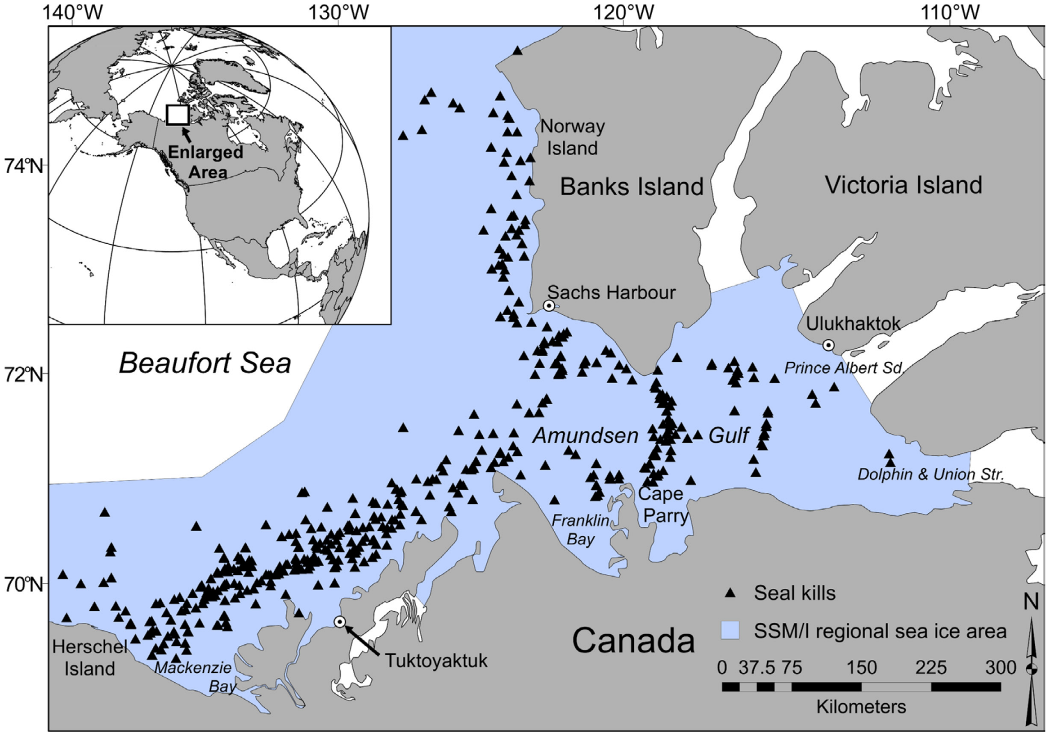

Figure 5.1 Study area in the Beaufort Sea, Canada, with locations of seals killed by polar bears (1985-2011; *n* = 650). Shaded area used for calculation of regional sea ice concentration with SSM/I satellite data.

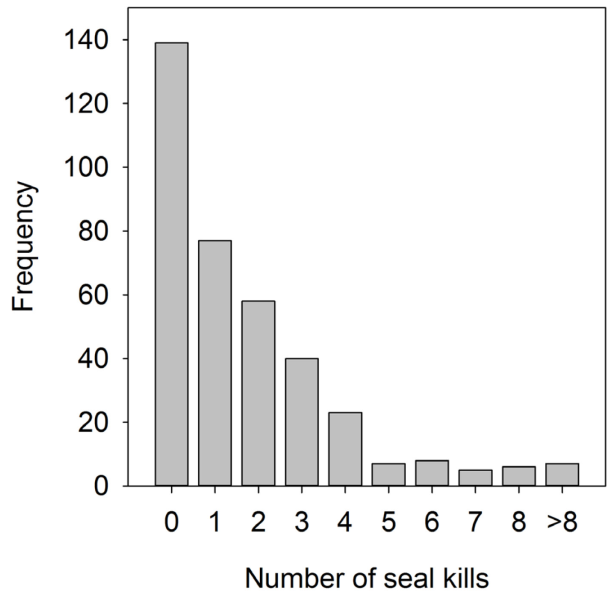

Figure 5.2 Frequency distribution of the number of kills observed per flight day in the spring in the Beaufort Sea, Canada, 1985-2011.

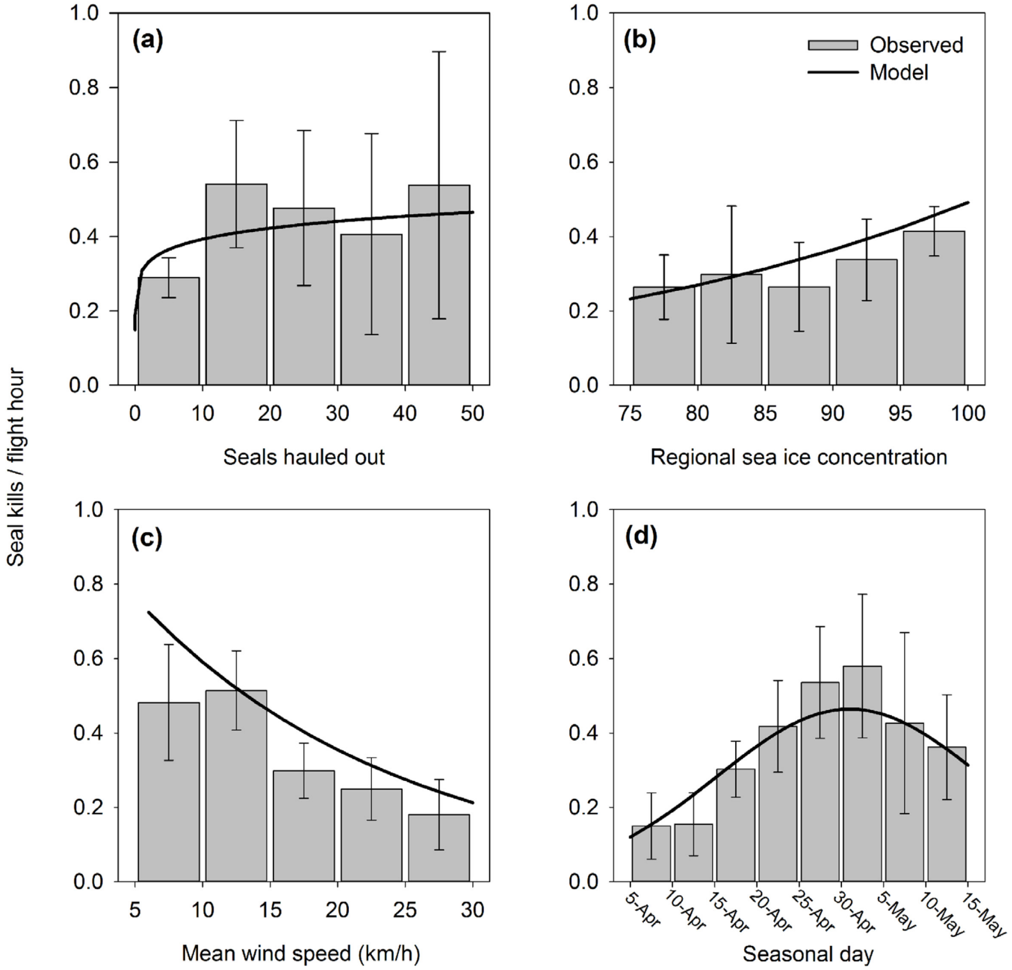

Figure 5.3 Response curves for continuous intra-seasonal covariates in the top predation event model, with binned observed values and 95% confidence intervals. All other covariates were held to their median values while computing the curve.

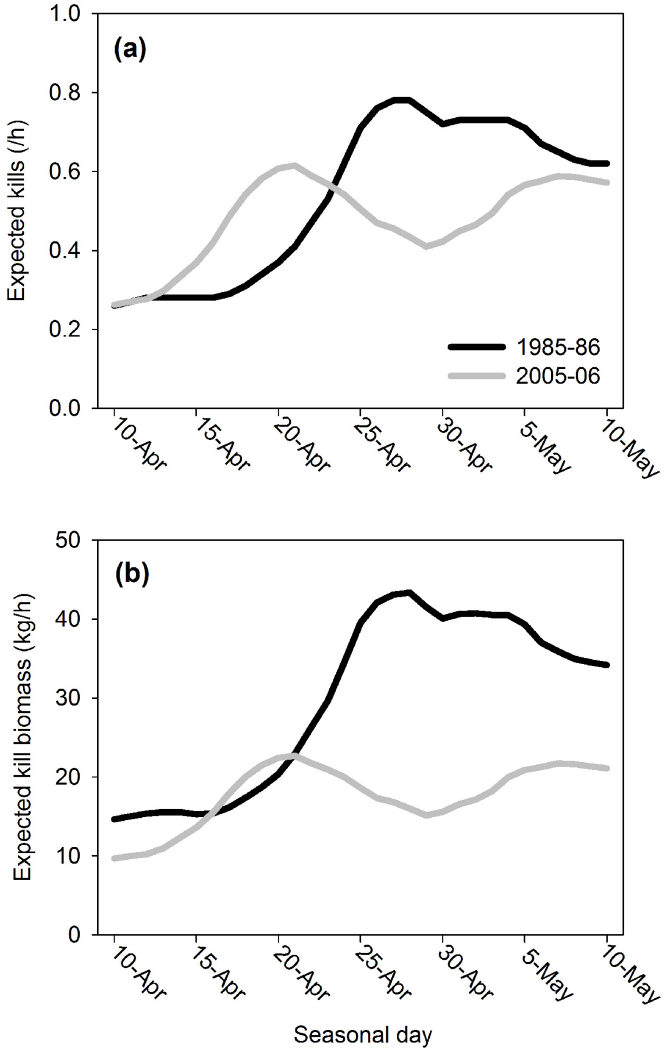

Figure 5.4. Expected (a) seal kills / flight hour and (b) seal kill biomass / flight hour for 1985-86 and 2005-06 spring in the Beaufort Sea, Canada using observed conditions applied to the top predation event model. Results suggest increased fasting rates in 2005-06 were likely influenced by lower kill biomass rather than kill rate alone.

Chapter 6

6 Discussion

6.1 A new ecological hypothesis for polar bear hyperphagia

In this thesis I analysed the demographic structure of seals killed by polar bears (*Ursus maritimus*), the habitat in which polar bears hunt and ringed seals (*Pusa hispida*) whelp, as well as the abiotic and biotic predictors of seal kills. In synthesizing these analyses, I propose a new hypothesis on the ecology of polar bear hyperphagia. It has been suggested that polar bears primarily focus on younger age classes of seal when hunting in spring, especially pups (Stirling *et al.* 1975; Stirling and Archibald 1977; Smith 1980; Hammill and Smith 1991; Stirling and Øritsland 1995). Adult seals were proposed to be less vulnerable due to experience (Stirling and Archibald 1977; Stirling *et al.* 1993), and adult males were hypothesized to have an additional anti-predator odour defense (Smith 1980; Hammill and Smith 1991; Furgal *et al.* 1996). In contrast, in Chapter 2 I established that ringed seal adults were a significant source of kills in the spring, males and females were killed in equal proportion, and 50% of the adults killed were at least 21 years of age. These results suggest that more life experience does not necessarily equate to lower vulnerability to predation, and adult male breeding odour has no apparent anti-predator benefit.

The hyperphagic increase in kill frequency was associated with the onset of ringed seal whelping, but correlated to the frequency of ringed seal adult kills, not pups. However, most of the seal kills were observed during periods of low ringed seal natality, reducing the frequency of pup kills and likely underestimating their role in hyperphagia. In periods of high ringed seal natality, pups composed >50% of the seal kills, a finding that supports previous estimates (Stirling and Archibald 1977; Hammill and Smith 1991; Stirling and Øritsland 1995). In Chapter 5, I determined that the likelihood of predation events in spring was positively correlated to ringed seal natality; suggesting kill frequency is higher when pups are more abundant. The increase in kill frequency may indicate a switch from hunting more mobile adult seals during periods of low ringed seal natality, to focusing on susceptible pups when natality is high. However, the likelihood of an adult kill was not correlated with ringed seal natality, suggesting that higher densities of pups may not necessarily alleviate predation pressure on adults.

I propose that the vulnerability of ringed seal adults to predation is dependent mostly on local abiotic and biotic modifiers of surfacing behaviour. Polar bear predation depends on the accessibility of seals from the sea ice. Seals are most vulnerable when in proximity to or on the surface of the sea ice, which occurs for respiration, reproduction, rest, and moulting. In Chapter 2, I suggested that adult ringed seals hauling out in subnivean lairs have low vulnerability to predation, which is in agreement with other predation studies (Smith 1980; Gjertz and Lydersen 1986; Hammill and Smith 1991; Furgal *et al.* 1996). In Chapter 3, I established that polar bears prefer active sea ice to hunt, particularly areas of new ice, composed mostly of refrozen leads. As the sea ice begins to break-up, new leads provide ringed seals surfacing options that avoid the intense competition over limited, self-maintained breathing holes (Smith and Hammill 1981; Moulton *et al.* 2002). Use of new ice areas with little subnivean protection has been suggested to increase predation vulnerability (Stirling *et al.* 1975), and in Chapter 5, I established a correlation between seasonal date and the likelihood of an adult kill, which coincides with adult ringed seals shifting from using subnivean lairs in April to hauling out in the open in May (Kelly *et al.* 2010). Wind was also a significant predictor of adult kills, a recognized modifier of seal haul-out (Finley 1979; Smith and Hammill 1981; Carlens *et al.* 2006). Evidence presented within this dissertation suggests that ringed seal adults become more vulnerable as the spring season progresses due to their increased propensity to surface in areas with less protection.

It has been suggested that polar bears prefer to hunt seals in areas of active ice near the floe edge in spring (Stirling and Archibald 1977; Smith 1980; Ramsay and Stirling 1986; Stirling *et al.* 1993; Ferguson *et al.* 2000), and in Chapter 3, I found support for this hypothesis. The paradox was if ringed seal pups are the dominant prey in spring, why do polar bears hunt in areas considered poor quality pupping habitat? In Chapter 4, I determined that the habitats in which ringed seals whelp is broader than previously appreciated, and includes offshore moving pack ice. The spatial distribution of pup kills was also linked with ringed seal natality. While shorefast ice may be preferred for whelping (McLaren 1958; Lydersen and Gjertz 1986; Smith *et al.* 1991), in years of high natality, ringed seals pups were killed as frequently in pack ice as in shorefast ice. I hypothesize that the age-class distribution of seal kills in spring is linked to the spatial overlap between the habitats in which ringed seals whelp and polar bears hunt (Fig. 6.1). When ringed seal natality is high in the Beaufort Sea, pups are more frequently born into or near the active ice habitats polar bears prefer when hunting. Polar bears can take advantage of the availability of an additional prey source, without leaving the habitat that provides access to larger prey.

A quick test of this hypothesis is to compare the distribution of polar bears between periods of low and high ringed seal natality. In Chapter 4, I established that in the Tuktoyaktuk Peninsula region, pup kills were found farther from shore in periods of high natality. Each spring, the floe edge in the Tuktoyaktuk Peninsula region occurs in a predictable location, formed by stamukhi and the current patterns of the Beaufort Sea (Barnes *et al.* 1987; Mahoney *et al.* 2007a). If polar bears prefer hunting in the floe edge environment, their distribution should remain constant, unaffected by high or low ringed seal natality. Using capture locations (see Chapter 3), I compared the distribution of polar bears as measured by their distance from land between 2003-06 and 2007-11 using a Mann-Whitney U-test. Despite pup kills being located closer to land in years of low natality (median$_{\text{low}}$ = 36 km, median$_{\text{high}}$ =

46 km, $Z = -2.17$, $P = 0.03$), polar bears did not change their distribution ($\text{median}_{\text{low}} = 43$ km, $\text{median}_{\text{high}} = 45$ km, $Z = 0.80$, $P = 0.42$). The result supports the hypothesis that when the distribution of whelping ringed seals shifts as a function of natality, it changes the spatial availability of pups to polar bears during spring hyperphagia (Fig 6.2). I hypothesize that polar bears of the Beaufort Sea do not necessarily follow the distribution of pups[1], but rather hunt in the environment that provides access to the largest prey, and opportunistically kill pups when they are born in nearby areas.

Finally, Kingsley (1979) reported that the body mass and growth rates of subadult polar bears had decreased significantly between periods of high and low ringed seal natality, but the body masses of adults remained similar. Subadult polar bears are smaller, less experienced hunters (Stirling and Latour 1978), and a reduction in the availability of vulnerable pups may reduce hunting success. Further, subadults may be dependent on scavenging to meet their energy requirements, and a reduction in the frequency of kills may lower the availability of carrion. The impact of scavenging is generally underestimated in predator-prey interactions (Wilson and Wolkovich 2011), and may be an important dietary contributor for subordinate or inexperienced individuals (Bennetts and McClelland 1997; Bustamante *et al.* 1997). Polar bears kill older, larger seals during periods of low ringed seal natality (Stirling and Archibald 1977; Chapter 2), and the results of Kingsley (1979) suggest that this shift in hunting strategy is more difficult for subadults than adults.

6.2 Predator-prey dynamics of polar bear hyperphagia

A cornerstone of predator-prey ecology is the study of whether predation has an additive or compensatory effect on mortality in a prey

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[1] With the exception of females with cubs-of-the-year (Stirling *et al.* 1993, Frietas *et al.* 2012)

population (Errington 1945; Bartmann *et al.* 1992; Boyce *et al.* 1999; Robinson *et al.* 2014). Studies have suggested that the maximum sustainable harvest from a ringed seal population includes mostly pups (Law 1979; Stirling and Øritsland 1995). In Chapter 2, I established that polar bears kill a significant number of adult seals in spring, especially during periods when pups are less available. Despite killing a large number of reproductive-aged animals, there are two possible explanations for how polar bear predation of adults could have compensatory aspects.

First, of the adult ringed seals killed, half were >20 years of age. Although ringed seals are reproductively active their entre lives (Smith 1987), survivorship is lower after 20 years of age (Smith 1973). Second, during periods of low natality, adult and juvenile ringed seals are in significantly poorer body condition as a result of a shortened open water foraging season (Smith 1987; Harwood *et al.* 2000; Harwood *et al.* 2012). The nutrition stress hypothesis suggests that the lowered availability of forage leading to reduced body condition can cause increases in mortality (Trites and Donnelly 2003). This effect is pronounced amongst seal age-classes with more limited diving capabilities (Trites and Donnelly 2003), such as older seals hindered by muscular senescence (Hindle *et al.* 2009). Therefore, during periods of lowered natality and body condition, polar bears may be killing the 'doomed surplus' (*sensu* Errington 1945), rather than contributing significant additive mortality to the ringed seal population. However, predation rarely operates in an absolute additive or compensatory manner (Sinclair and Pech 1996). Seasonality is also a critical component of how compensatory mortality occurs (Boyce *et al.* 1999). A reduction in the number of ringed seals prior to the open water foraging season may reduce competition for food resources and increase survival of the remaining population. However, assessment of the additive/compensatory nature of polar bear predation on ringed seals is still largely speculative, and further study is needed to resolve the impact of hyperphagia on ringed seal population dynamics.

6.3 Biologically relevant metrics in ecological models

A recurrent theme in my thesis was how the size of the prey killed provided a substantial improvement to the ecological models I employed. In Chapter 3, I used resource selection functions (RSFs) to quantify habitat quality as it related to foraging. Weighting each kill location by its estimated biomass provided a better fit to polar bear distribution than using only the density of kills. In Chapter 5, I developed a model of the probability of a predation event, and applied it to polar bear fasting rates in 1985-86 and 2005-06. Although the expected kill rate from the model was a significant predictor of polar bear fasting rates, substantial improvement was made by also including the mean estimated biomass of ringed seal kills across the season. One possible conclusion is that the size of seal kills is as important as the frequency to the predatory ecology of polar bears. However, I argue that these results are also vital to how analytical methods are employed in ecology.

Correlative models have become a standard approach in ecology, and their prominence can be associated with the development of remotely sensed animal location data (Guisan and Zimmermann 2000; Cagnacci *et al.* 2010). However, the growth in analytical modelling has come at the cost of having a mutual platform for which to comprehend results. For example, within the field of ecological niche models (ENMs) and species distribution models (SDMs), there are numerous techniques for identifying habitat suitability: Bioclimatic Envelope Models, Circuit Models, Ecological Niche Factor Analysis, Maximum Entropy Modelling, Occupancy, RSFs, Resource Selection Probability Functions, Resource Utilization Functions, and others. Despite the variety of modelling approaches, all depend on the strong assumption that the relative frequency of locations provides a suitable metric of quality (Sagarin *et al.* 2006; Cassini 2011). The biological accuracy of ENMs and SDMs is debated (Guisan and Thuiller 2005; Araujo and Luoto 2007; Lozier *et al.* 2009), with several empirical examples of model improvement by including measures of survival, reproduction or fitness (McLoughlin *et al.* 2006; Mosser *et al.* 2009; Decesare *et al.* 2013). However, most attention has been on the statistical theory (Austin 2007; Peterson *et al.* 2008; Aarts *et al.* 2013), rather than addressing the biological assumptions underpinning the models, or ways of collecting biological data that can act as proxies for species fitness.

For carnivores, the size and density of prey killed may provide a direct reflection of habitat suitability. Carnivore fitness depends largely on the quantity and quality of prey consumed relative to the cost of procurement, which can be regulated by ecological constraints, including habitat (Sunquist and Sunquist 1989). Habitat provides a diversity of predatory functions for carnivores including concealment for ambush predators, or open expanses for cursorial predators. For example, African lions (*Panthera leo*) in the Serengeti prefer to kill in habitats near river confluences (Hopcraft *et al.* 2005), and pride territories with greater access to riparian habitat have higher fitness (Mosser *et al.* 2009). Access to habitats that provide meat is recognized as an important determinant of the litter size and population density of brown bears (*Ursus arctos*) (Hilderbrand *et al.* 1999b; Mowat and Heard 2006). It has been well-documented that carnivore population dynamics are linked to prey (Elton and Nicholson 1942; Stenseth *et al.* 1997; Stirling 2002; Packer *et al.* 2005), suggesting that quantifying predatory behaviour is a practical approach to determining habitat suitability.

Current methods of tracking carnivores can be incorporated into identifying kill sites. GPS clusters from telemetry collars can identify kill locations (Merrill *et al.* 2010). Path tortuosity from movement data is also a burgeoning field in the identification of predatory landscapes (Benhamou 2004). Biases still exist though. Larger kills may be easier to detect, while smaller prey items may be consumed too quickly to detect with remote sensing or survey methodologies (Cristescu *et al.* 2014). Such bias is particularly relevant for small carnivore species, which predominantly kill prey weighing less than half their own mass (Carbone *et al.* 1999). Conversely, large bodied carnivores generally seek out larger prey (Carbone *et al.* 1999), while smaller prey are likely more abundant on the landscape (Damuth 1981) and may be killed opportunistically. Given the potential for bias, the proportions of species in the observed kills should be compared against an independent dietary analysis (*e.g.* scat, fatty acid, stable isotope) to validate data.

When kill sites are difficult to identify, camera trapping can provide a non-invasive index of body condition (*e.g.* Bertram 1975), which could be used in place of, or supplement, kill data. Body condition could be used to weight each location of use, reducing the influence of locations with individuals showing emaciation. A key assumption is that body condition is a function of habitat quality. One can imagine circumstances in which this may not hold (*e.g.* body condition could be related to age or disease). However, it is unlikely that a territorial carnivore in poor body condition would retain control of high quality habitat. Subordinate animals are often found in sub-optimal habitat waiting to gain access of high quality areas (Ferreras *et al.* 1997). Dominance through contest competition generally correlates positively with body condition (Parker 1974), although prior rights to a habitat may also play a role in maintaining control (Maynard Smith and Parker 1976).

Within this dissertation I have used a metric for the size of seal kills made by polar bears to identify the fragility of SDM assumptions, and improve the biological understanding of an apex carnivore living in a habitat undergoing rapid alteration. Ecological models may not only be improved through statistical means, but by collecting relevant contextual information to understand the biology of the study species. Climate change, human habitat alteration and unregulated harvest all pose threats to the continued existence of populations of large carnivores (Ripple *et al.* 2014) and biodiversity in general (Wake and Vredenburg 2008; Estes *et al.* 2011). Ecological models therefore must provide information that can be applied across rapidly changing landscapes and populations. Model results that are not portable suffer in their ability to sufficiently increase understanding of the core factors that regulate and maintain populations. The challenge to ecologists is to improve the portability of ecological models not only through statistical advances, but also with the data collected in the field.

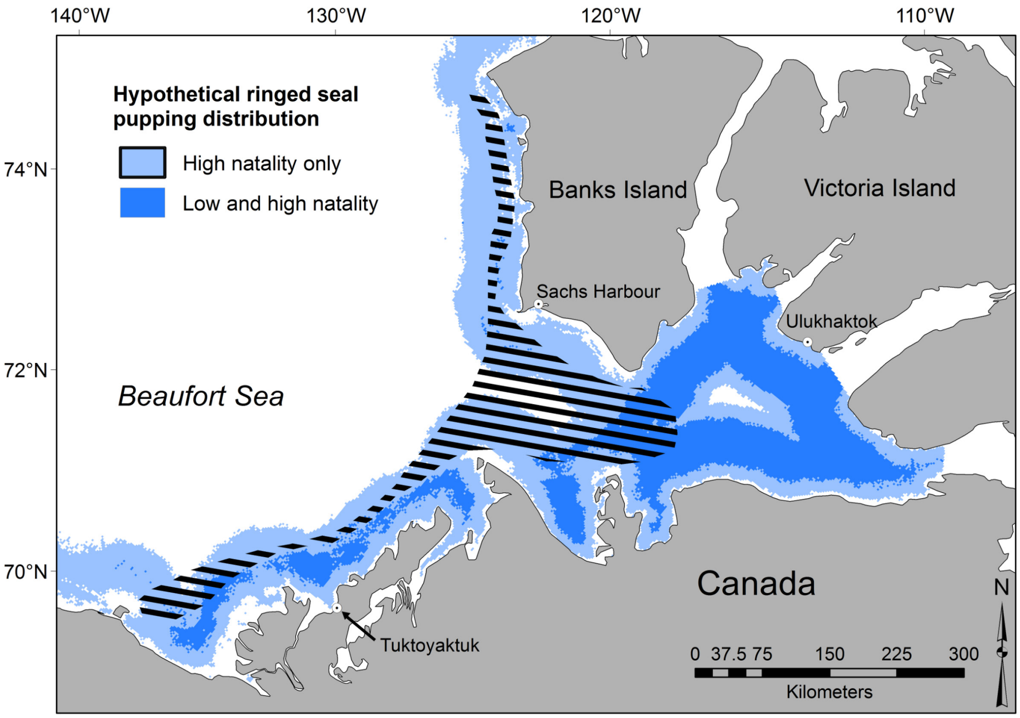

Figure 6.1 A proposed distribution of ringed seal pups between periods of low and high natality. As the natality of the population increases, the habitats in which breeding seals occupy expand. This expansion overlaps with the floe edge and moving ice habitat polar bears prefer (hatched area), resulting in an increase in the frequency of pup kills.

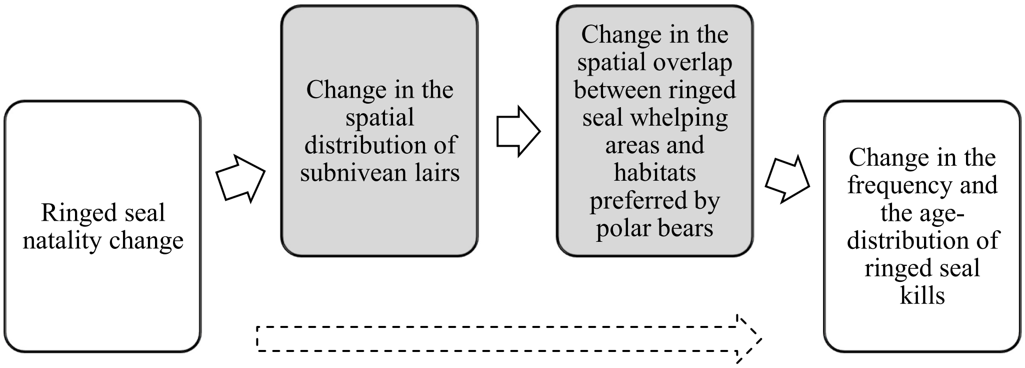

Figure 6.2 A process diagram for the steps that result in the change in the age-class distribution of ringed seal kills as a function of ringed seal natality, for the Beaufort Sea, Canada. The spatial aspects of the ecological explanation (shaded) are the additions provided by this thesis.

Glossary of Terms

Active ice: Sea ice that is dynamic, regularly changing in shape. Usually consists of highly fractured, unconsolidated ice that can melt in unpredictable patterns.

Annual ice: Sea ice that forms and melts within the span of a single year.

Consolidated ice: High concentration pack ice with floes either very close or frozen together.

Flaw lead: Open water existing between pack ice and shorefast ice.

Floe: Any piece of pack ice larger than 20 m across.

Floe edge: Boundary between sea ice and open water.

Lead: Any fracture in the sea ice with open water.

Multiyear ice: Sea ice that has survived at least one melt season.

New ice: Recently formed sea ice, generally $\leq$30 cm thick.

Pack ice: Sea ice that is not shorefast.

Polynya: A recurring, non-linear area of open water surrounded by sea ice.

Pressure ridge: A line or wall of sea ice forced upward by pressure.

Rubble: An area with extensive pressure ridges of similar characteristic, and little to no flat ice.

Shorefast (landfast / fast) ice: Sea ice that forms along the coast and is affixed to shore.

Shorefast ice edge: Seaward edge of the shorefast ice.

Stable ice: Sea ice that forms and melts in a predicable pattern. Usually consists of consolidated or shorefast sea ice.

Stamukhi: Coastal area where ridges of shorefast ice are grounded and adhere to the sea floor.

Unconsolidated ice: Lower concentration pack ice with areas of open water between floes.

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Appendix A

Table A1 The *a priori* set of resource selection function models describing habitat quality using an unweighted binomial logistic regression design, ranked according to AIC_c for polar bears of the Beaufort Sea, Canada, 2003-2011.

Model	k	AIC_c	Δ_i	w_i
Fast_Ice + New_Ice + L_DIST + I_DIST	5	1303.58	0.00	0.12
Fast_Ice + New_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	7	1303.73	0.15	0.11
Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH	6	1303.81	0.24	0.10
Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	8	1304.09	0.51	0.09
New_Ice + L_DIST + I_DIST	4	1304.73	1.16	0.07
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST	6	1305.26	1.69	0.05
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH	7	1305.46	1.89	0.05
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	8	1305.48	1.91	0.05
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	9	1305.72	2.15	0.04
New_Ice + L_DIST + I_DIST + DEPTH	5	1305.78	2.20	0.04
New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	7	1306.33	2.75	0.03
F_Edge + New_Ice + L_DIST + I_DIST	5	1306.62	3.04	0.03

Table A1 Continued The *a priori* set of resource selection function models describing habitat quality using an unweighted binomial logistic regression design, ranked according to AIC$_c$ for polar bears of the Beaufort Sea, Canada, 2003-2011.

L_DIST + I_DIST	3	1306.83	3.25	0.02
L_DIST + I_DIST + REG_ICE + REG_ICE^2	5	1307.09	3.51	0.02
F_Edge + New_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	7	1307.11	3.54	0.02
Fast_Ice + L_DIST + I_DIST	4	1307.34	3.77	0.02
Fast_Ice + L_DIST + I_DIST + DEPTH	5	1307.36	3.78	0.02
Fast_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	7	1307.47	3.90	0.02
L_DIST + I_DIST + DEPTH	4	1307.52	3.95	0.02
F_Edge + New_Ice + L_DIST + I_DIST + DEPTH	6	1307.67	4.09	0.02
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH + LOC_ICE + REG_ICE + REG_ICE^2	10	1307.74	4.17	0.01
L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	6	1307.90	4.33	0.01
F_Edge + New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	8	1308.14	4.57	0.01
F_Edge + L_DIST + I_DIST	4	1308.58	5.01	0.01
F_Edge + Fast_Ice + L_DIST + I_DIST + DEPTH	6	1308.87	5.30	0.01
F_Edge + Fast_Ice + L_DIST + I_DIST	5	1308.90	5.33	0.01
F_Edge + Fast_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	7	1308.99	5.41	0.01

Table A1 Continued The *a priori* set of resource selection function models describing habitat quality using an unweighted binomial logistic regression design, ranked according to AIC$_c$ for polar bears of the Beaufort Sea, Canada, 2003-2011.

F_Edge + Fast_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	8	1309.03	5.46	0.01
F_Edge + L_DIST + I_DIST + DEPTH	5	1309.29	5.72	0.01
F_Edge + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	7	1309.64	6.06	0.01

Table A2 The *a priori* set of resource selection function models describing habitat quality using a weighted binomial logistic regression design, ranked according to AIC$_c$ for polar bears of the Beaufort Sea, Canada, 2003-2011. Each used point is weighted by the estimated biomass of the kill.

Model	k	AIC$_c$	Δ_i	w_i
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	9	3279.48	0.00	0.50
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH + LOC_ICE + REG_ICE + REG_ICE^2	10	3281.49	2.01	0.18
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	8	3282.16	2.68	0.13
F_Edge + Fast_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	8	3282.50	3.03	0.11
F_Edge + New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	8	3284.26	4.78	0.05
Fast_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	7	3286.87	7.40	0.01
New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	7	3286.94	7.46	0.01
F_Edge + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	7	3287.80	8.32	0.01
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH	7	3291.54	12.07	0.00
Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	8	3291.55	12.07	0.00
L_DIST + I_DIST + DEPTH + REG_ICE + REG_ICE^2	6	3292.06	12.59	0.00
F_Edge + Fast_Ice + L_DIST + I_DIST + DEPTH	6	3294.61	15.13	0.00
F_Edge + Fast_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	7	3295.23	15.76	0.00

Table A2 Continued The *a priori* set of resource selection function models describing habitat quality using a weighted binomial logistic regression design, ranked according to AIC$_c$ for polar bears of the Beaufort Sea, Canada, 2003-2011. Each used point is weighted by the estimated biomass of the kill.

F_Edge + New_Ice + L_DIST + I_DIST + DEPTH	6	3295.95	16.47	0.00
Fast_Ice + New_Ice + L_DIST + I_DIST + DEPTH	6	3295.96	16.48	0.00
Fast_Ice + New_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	7	3296.70	17.22	0.00
F_Edge + New_Ice + L_DIST + I_DIST + REG_ICE + REG_ICE^2	7	3296.79	17.31	0.00
Fast_Ice + L_DIST + I_DIST + DEPTH	5	3298.88	19.40	0.00
New_Ice + L_DIST + I_DIST + DEPTH	5	3299.33	19.85	0.00
F_Edge + L_DIST + I_DIST + DEPTH	5	3302.16	22.68	0.00
L_DIST + I_DIST + DEPTH	4	3305.11	25.63	0.00
F_Edge + Fast_Ice + New_Ice + L_DIST + I_DIST	6	3305.40	25.92	0.00
L_DIST + I_DIST + REG_ICE + REG_ICE^2	5	3308.62	29.15	0.00
Fast_Ice + New_Ice + L_DIST + I_DIST	5	3308.77	29.29	0.00
F_Edge + Fast_Ice + L_DIST + I_DIST	5	3309.59	30.11	0.00
F_Edge + New_Ice + L_DIST + I_DIST	5	3312.77	33.30	0.00
Fast_Ice + L_DIST + I_DIST	4	3312.77	33.30	0.00
New_Ice + L_DIST + I_DIST	4	3314.91	35.43	0.00

Table A2 Continued The *a priori* set of resource selection function models describing habitat quality using a weighted binomial logistic regression design, ranked according to AIC_c for polar bears of the Beaufort Sea, Canada, 2003-2011. Each used point is weighted by the estimated biomass of the kill.

F_Edge + L_DIST + I_DIST	4	3321.44	41.96	0.00
L_DIST + I_DIST	3	3323.07	43.60	0.00

Table A3 Model averaging for the unweighted regression. Average (β) used to construct daily habitat quality maps. Selection ratio for each covariate is indicated by exp (β), where values that are greater than 1 indicate selection and values less than 1 indicate avoidance.

Covariate	L_DIST	I_DIST	DEPTH	LOC_ICE	REG_ICE	REG_ICE^2	F_Edge	Fast_Ice	New_Ice
β (Model 1)	0.749	-0.213						0.294	0.942
β (Model 2)	0.748	-0.217			0.287	-0.002		0.312	0.926
β (Model 3)	0.711	-0.225	0.085					0.333	0.919
β (Model 4)	0.710	-0.228	0.082		0.291	-0.002		0.346	0.908
β (Model 5)	0.675	-0.229							0.755
β (Model 6)	0.755	-0.222					-0.135	0.305	0.932
β (Model 7)	0.717	-0.234	0.086				-0.143	0.346	0.909
β (Model 8)	0.752	-0.224			0.303	-0.002	-0.144	0.318	0.922
β (Model 9)	0.714	-0.236			0.312	-0.002	-0.177	0.354	0.902
β (Model 10)	0.643	-0.239	0.062						0.721
β (Model 11)	0.639	-0.240	0.061		0.293	-0.002			0.708
β (Model 12)	0.677	-0.235					-0.083		0.745
β (Model 13)	0.669	-0.240							
β (Model 14)	0.664	-0.245			0.289	-0.002			

Table A3 Continued Model averaging for the unweighted regression. Average (β) used to construct daily habitat quality maps. Selection ratio for each covariate is indicated by exp (β), where values that are greater than 1 indicate selection and values less than 1 indicate avoidance.

β (Model 15)	0.672	-0.237			0.299	-0.002	-0.106		0.730
β (Model 16)	0.716	-0.231						0.194	
β (Model 17)	0.676	-0.243	0.090					0.237	
β (Model 18)	0.678	-0.246	0.086		0.292	-0.002		0.253	
β (Model 19)	0.631	-0.251	0.072						
β (Model 20)	0.645	-0.245	0.062				-0.082		0.711
Average (β)	**0.710**	**-0.228**	**0.079**		**0.294**	**-0.002**	**-0.134**	**0.315**	**0.876**
Upper CI (β)	0.957	-0.140	0.204		0.639	0.000	0.373	0.646	1.607
Lower CI (β)	0.463	-0.316	-0.046		-0.051	-0.004	-0.641	-0.016	0.145
exp (β)			1.082		1.342	0.998	0.875	1.307	2.402^{*}

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Table A4 Model averaging for the weighted regression. Average (β) used to construct daily habitat quality maps. Selection ratio for each covariate is indicated by exp (β), where values that are greater than 1 indicate selection and values less than 1 indicate avoidance.

Covariate	L_DIST	I_DIST	DEPTH	LOC_ICE	REG_ICE	REG_ICE^2	F_Edge	Fast_Ice	New_Ice
β (Model 1)	0.378	-0.255	0.134		0.337	-0.002	0.411	-0.207	0.498
β (Model 2)	0.378	-0.254	0.134	0.000	0.335	-0.002	0.409	-0.207	0.498
β (Model 3)	0.364	-0.267	0.138		0.341	-0.002	0.409	-0.249	
β (Model 4)	0.413	-0.250	0.143		0.341	-0.002	0.401		0.607
Average (β)	**0.380**	**-0.256**	**0.136**	**0.000**	**0.338**	**-0.002**	**0.409**	**-0.214**	**0.513**
Upper CI (β)	0.502	-0.199	0.206	0.005	0.552	-0.001	0.717	-0.032	0.969
Lower CI (β)	0.258	-0.312	0.066	-0.005	0.123	-0.003	0.101	-0.396	0.057
exp (β)				1.000	1.402**	0.998**		0.808*	1.671*

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Appendix B

Table B1. Candidate data models ranked by log-likelihood score using all a priori variables.

Model	LL
Negative Binomial	-561.6
Zero-Inflated Negative	-562.6
Zero-Inflated Poisson	-579.6
Poisson	-583.7

Table B2. Observation models examining potential factors influencing kill detection. In all models survey effort (EFFORT) was a primary factor, and used as an offset in the regression. Only the pup kill model had another significant factor, Observer, which was used as a random intercept for the pup ringed seal kill model.

Model	k	AIC_C	ΔAIC_C	w_i
Predation Event Model (n = 650)				
INT + EFFORT	2	1278.58	0.00	0.51
INT + EFFORT + Region	3	1279.58	1.00	0.31
INT + EFFORT + Region + Snow	4	1281.13	2.55	0.14
INT + EFFORT + Observer + Region +	6	1283.89	5.31	0.04
Adult Ringed Seal Kill Model (n = 150)				
INT + EFFORT + Snow*	3	615.32	0.00	0.39
INT + EFFORT	2	615.71	0.40	0.32
INT + EFFORT + Region + Snow	4	616.38	1.06	0.23
INT + EFFORT + Observer + Region +	6	619.32	4.00	0.05
Juvenile Ringed Seal Kill Model (n = 62)				
INT + EFFORT	2	349.15	0.00	0.49
INT + EFFORT + Observer	3	350.12	0.97	0.30
INT + EFFORT + Observer + Region	4	351.44	2.29	0.16
INT + EFFORT + Observer + Region +	6	353.55	4.41	0.05
Pup Ringed Seal Kill Model (n = 132)†				
INT + EFFORT + Observer	3	500.29	0.00	0.71
INT + EFFORT + Observer + Snow	4	502.14	1.85	0.28
INT + EFFORT	2	511.04	10.75	0.00

† Observer and Region were correlated (r_s = 0.61), Region dropped from Pup models

*Not a significantly better fit than EFFORT alone (LL ratio test, χ^2 = 2.43, df =1, P = 0.12)

Table B3. Candidate models ranked by AIC_C for the probability of polar bear fasting in the Beaufort Sea, Canada. Fasting determined as a serum Urea/Creatinine ≤ 10.0.

Rank	Model	*k*	LL	AIC_C	ΔAIC_C
1	INT + KILL + BIOMASS + Mating	4	-108.31	224.72	0.00
2	INT + KILL + BIOMASS	3	-111.03	228.11	3.39
3	INT + BIOMASS + Mating	3	-111.41	228.87	4.16
4	INT + KILL + Mating	3	-111.71	229.48	4.76
5	INT + KILL	2	-113.32	230.67	5.95
6	INT + BIOMASS	2	-115.48	234.99	10.27
7	INT + Mating	2	-118.98	241.98	17.26