

**THE MEETING OF TWO DYNAMICS:  
POLAR BEARS AND SEA ICE**

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By  
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## ABSTRACT

Controversy exists concerning the role of geography in speciation. The freezing of the Arctic sea was a significant event in the evolution of a number of species including the polar bear. This geological event created a new habitat that eventually resulted in the separation of two ancient bear populations. The subsequent developments of biological differences between the brown and polar bears are based on differences in geography (land versus ice). Therefore, for polar bears, a geological event (i.e., freezing of the Arctic ocean) resulted in speciation while the ice landscape now maintains this diversity. The dynamics of sea ice and polar bears are inextricably intertwined.

First, I investigated patterns of space use for polar bears during the ice-free period using satellite telemetry and capture locations. Although ice is essential to polar bears, in some regions, such as Baffin Bay, the sea ice melts for a few months each year. Usually at the end of August, polar bears were forced to live on land due to reduced availability of ice. The pattern of removal of sea ice influenced when and where bears moved onto land. Females with cubs-of-the-year were first to leave the ice for land and they rarely used snow shelters. In contrast, pregnant females were the last to leave the ice for land, and after about 1 week on land, they entered a maternal den



for the winter. Most females with 1-year-olds entered a shelter after about 3 weeks on land and remained there for about 2 months. While awaiting the return of sea ice, bears conserved energy by reducing movement and decreasing activity. Bears left the land shortly after ice formed, usually in mid-November. During the ice-free period, females with cubs-of-the-year were farther inland, closer to fjords, and less likely to use islands than males.

In the last two chapters, I focused on the relationships between two dynamics; polar bears and sea ice. The process of adaptation is linked to the interaction between organism and its physical and biological environment. Organisms and environment are dynamical systems. Hence, defining polar bears requires an understanding of the sea ice environment that they live in.

Spatially, polar bears grouped into clusters that matched the fractal pattern of seasonal sea ice interspersed among arctic islands. I argue that the winter and spring seasons, before and during mating, respectively, best described groupings of polar bears and their relationship to sea ice. A relationship between polar bear fractal movement patterns and the fractal dimension of sea ice indicated a possible mechanism linking population structure and geography. The sea ice dominates as a structuring agent as evidenced by the spatial structuring of groupings of polar bears.

Evolution is historic and I found a temporal scale that connected the spatial grouping of polar bears in an explanation of how polar bears may have evolved. Here, speciation occurred at an evolutionary scale (brief geological time and isolated space), whereas natural selection continued at ecological scales (long time and large space).

Next, I looked at polar bears on a temporal scale to understand how the cycles of sea ice affected the seasonal rhythms of polar bears. Seasonal cycles of ice determine the location of major phytoplankton blooms and thereby the distribution of zooplankton for cod, cod for seals, and seals for polar bears. As the location and accessibility of seals to bears depends on characteristics of ice, I used radio telemetry and satellite images to describe seasonal patterns of ice selection by female polar bears for two Canadian Arctic regions. Whereas the Arctic Archipelago remained mostly ice covered throughout the year, Baffin Bay cycled seasonally from 100% ice in winter to <25% in early autumn. Changes in sea ice characteristics and resource selection by female polar bears were tested using sine wave functions. Polar bears responded to physical cycles by shaping their own rhythmic life processes. Sometimes they followed sea ice cycles, sometimes they amplified seasonal cycles, and at other times they dampened their response or

shifted their phase. This process of accommodating environmental cycles was not passive.

I conclude that considering the interface between the two dynamics, polar bears and sea ice, helps to describe the evolution of polar bears. I suggest continuing this effort in the future by investigating further how polar bears have responded to the dynamics of sea ice. For example, future research can test for (1) a relationship between inter-annual predictability of sea ice and size of area used by polar bears and (2) a pattern in use of shelters and dens according to a gradient in environmental predictability.

## ACKNOWLEDGEMENTS

"If organisms are seen as mechanisms, they will be treated as such, and as such we will treat each other." (Goodwin 1994). The study of complexity (e.g., chaos, fractals, self-organization) has helped me to understand biology and provided an antithesis to reductionism. I am glad for a scientific view that encourages a process concept of health, of wholeness, and of organisms.

Very special thanks to my colleagues, Terry Armstrong, Stephen Atkinson, Kim Brown, Damien Joly, Serge Larivière, Phil McLoughlin, Maria Pasitschniak-Arts, Susan Polischuk, Jim Rettie, Jim Schaefer, John Virgl, Lyle Walton, and Bonita Wong. And my peers, François Messier, for giving me the chance and in believing I could achieve; Mitchell Taylor for accepting me despite my lack of guts and glory; Malcolm Ramsay for sharing his enthusiasm for science; and Alex Aitken and John Sheard for their help and input into my research.

To the Arctic, the most fascinating place on earth, and the people who live there, I share your empathy. And thanks to all the people who helped during the field work. Like Jacobi who had eyes of an eagle and the kindness to share his last cigarette.

Polar bear research is an example of circumpolar management coordinated by local, provincial, national, and international levels of government. This cooperative

project includes participants from Greenland, Parks Canada, Canadian Wildlife Service, University of Saskatchewan, and Hunter Trapper Associations of the eastern Canadian Arctic.

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The failings are all my own.

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## 1. GENERAL INTRODUCTION

The freezing of the Arctic sea allowed for the evolution of a number of species. This geological event created a new habitat that eventually resulted in the separation of two ancient bear populations. The subsequent developments of biological differences between the brown and polar bears are based on differences in geography (land versus ice). The following describes the studies of space-use of polar bears (*Ursus maritimus*) in the Canadian Arctic, spring 1991 to spring 1996.

Limited information is available on the space-use patterns such as home range size, habitat use and movement of polar bears in relation to ice conditions. Research into the arctic ecosystem is relatively new and as with any research on new phenomena descriptive studies are followed by models based on postulated mechanisms. Descriptive studies ask whether patterns exist that need to be explained in biological terms, or whether this variation can be explained by chance or random processes. With mechanistic modelling, we test whether the derived variables and model structure, predict, or improve our understanding of ecological phenomena.

In the following, I introduce the general ecology of polar bears. Following this introduction I provide a description of sea-ice dynamics of the Canadian Arctic environment relevant to the ecological studies of polar

bears. The next three chapters are specific studies of land use by polar bears (Chapter 2), how sea ice structures polar bear populations (Chapter 3), and how seasonal cycles of sea ice affect polar bear rhythms of habitat selection (Chapter 4). In the discussion, I weave among the ideas of evolution, origin of species, philosophy of science, cycles, dynamics, future research, and management.

### **1.1 Polar Bear Dynamics**

Although polar bears recently evolved from brown bear ancestors (Kurtén 1964, Wozencraft and Hoffmann 1993), they differ considerably from other bear species (Stirling and Derocher 1990). Polar bears are functionally members of the carnivore trophic level and live as a marine mammal preying primarily on ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and McEwan 1975, Stirling and Archibald 1977, Smith and Stirling 1978, Smith 1980, Demaster and Stirling 1981). Marine bears living off seals is an unusual combination but perhaps unusual only in the sense that the speciation event is recent (<2 mya). For example, seals evolved from terrestrial carnivores >40 mya (Reidman 1990). The arctic ecosystem is a relatively new system (Dunbar 1968) and, as such, the polar biota is considered immature, with a relatively short and disturbed evolutionary history (Crame 1997). The formation of the arctic ecosystem resulted in

one of the most recent large-scale speciations on earth and thereby provide us with a good opportunity to learn about how species evolve.

The arctic marine ecosystem is characterized by extreme amplitude in seasonal oscillations of both climate (Jacobs and Newell 1979, Mysak et al. 1990) and food availability (Vibe 1967, Cushing 1982, Stirling et al. 1982, Wooster 1983, Kingsley et al. 1985). Also, between year variability and unpredictability likely increases in the high arctic as a general latitudinal pattern (Ferguson and Messier 1996). Although highly variable temporally and spatially, sea-ice conditions do follow a general seasonal pattern (Barry 1989).

High latitude mammals are physiologically, behaviourally, and morphologically adapted to a seasonal cycle of high and low food availability (Dunbrack and Ramsay 1993). For polar bears, the spring offers the greatest concentration of food resources while periods of low energy availability occur throughout the remainder of the year. Female polar bears exploit the vulnerable young seals available during the April to July period (Stirling and McEwan 1975, Ramsay and Stirling 1988, Hammill and Smith 1991). During summer, adult female ringed seals may be caught (Smith 1987) but otherwise polar bears have lower success hunting adult ringed seals (Stirling and Archibald 1977, Smith 1980, Hammill and Smith 1991). In



autumn, pregnant female polar bears cease feeding and enter dens in which they spend the winter without food and water (Watts and Hansen 1987, Ramsay and Stirling 1988).

In Hudson Bay and Baffin Bay, most of the pack ice melts or breaks-up by mid- to late-summer, and the bears are forced on shore waiting for the ice to freeze again. The polar bears of Baffin Bay use land during a period from mid-August to late October each year. The length of time spent on land depends on the timing of ice break-up and formation, which shows considerable interannual variation. During this period, they live mainly on their fat stores and reduce activity to conserve energy and avoid overheating (Ramsay and Stirling 1988, Derocher et al. 1990, Ramsay et al. 1991, Derocher et al. 1993). The choice of habitat by polar bears during the ice-free season depends on avoidance of conspecifics, energy conservation, philopatry, and available denning habitat (Derocher and Stirling 1990). To avoid possible intra-specific predation, family groups and pregnant females move away from the adult males that generally occupy the coastal areas where most potential food can be found.

Polar bears range throughout most of the arctic sea ice (DeMaster and Stirling 1981) and availability and accessibility of seals as food for polar bears depends on sea-ice conditions (Calvert and Stirling 1985, Kingsley et al. 1985, Hammill and Smith 1989). This sea ice shows

considerable changes spatially and temporally, in form and extent, providing polar bears with an unusually dynamic habitat. The arctic sea surface ranges from flat, unbroken snow-covered ice, to fractured ice, to polynyas characterized by open water. Also, spatial ice characteristics change rapidly over the short periods of ice formation and ablation.

The characteristics of sea ice influence the distribution and abundance of seals and also the availability of seals as prey. Areas of stable pressure ridges and drifted with snow in spring are considered suitable ice-snow conditions for ringed seal haul-out and birth lairs, since drifting along pressure ridges protects birth lairs and breathing holes from predation (Smith and Stirling 1975, 1978, Smith and Hammill 1981, Hammill and Smith 1989). Kingsley et al. (1985) found significantly fewer ringed seals on multi-year versus annual ice. They attributed this pattern to the difficulty, for seals, of maintaining breathing holes in thick ice and finding food under multi-year ice.

Because of the dynamic nature of ice, conditions vary between years, in the number and location of leads, amount of open water, distribution of floe-edge, and abundance of different ice types. Hammill and Smith (1989) found that, in Barrow Strait, ringed seals preferred the combination of late consolidating but stable ice and deep snow

conditions. Late consolidating ice offers increased food resources (Bradstreet and Cross 1982) and greater mobility for seals (Hammill and Smith 1991). Deep snow is important, especially to pregnant ringed seals, for construction of subnivean lairs. Kingsley and Stirling (1991) found that ringed seals hauled out at the edge of self-maintained breathing holes or narrow cracks, either in fast ice or in the centre of large floes in pack ice. This is likely an antipredator behaviour.

The structure and extent of sea ice directly influences polar bears' ability to acquire food, as it depends on the terrestrial-like platform from which to kill ringed and bearded seals. Sea ice affects the spatial distribution of seals. For example, seal hunting is less successful in stable fast ice with drifts than where the snow cover is reduced or absent (Hammill and Smith 1991). Seals tend to concentrate near active ice areas such as floe edge, tidal cracks and at the edge of landfast ice (Burns 1970, Stirling and Archibald 1977, Smith 1980). Also, ice ridges on stable landfast ice are important ringed seal pupping areas. Therefore, polar bears will hunt seals in ice conditions that not only concentrate seals but also promote accessibility.

Although little research on the characteristics of ice used by polar bears for Baffin Bay has been conducted, results from other studies indicate the importance of

leads and moving ice habitat (Stirling et al. 1993). In a study along southeast Baffin Island, Stirling et al. (1980) found most polar bears along coastal pressure ridges compared with the lower polar bear densities found in the more shallow coastline of the eastern Beaufort Sea. In contrast to the Beaufort Sea, Finley et al. (1983) documented a large population of ringed seals, some with pups, inhabiting the moving pack ice of Baffin Bay. Upwelling along floe edges provides local enrichment and increased productivity and, subsequently more seals and polar bears (Buckley et al. 1979, Bradstreet and Cross 1982). Stirling et al. (1993) expected a similar pattern along smaller leads, floe-edges and within moving ice habitat.

Polar bears travel long distances throughout a large area (Garner and Knick 1991) mainly as a response to the dynamic and locally unpredictable nature of their ice habitat. While on the arctic sea ice, polar bears move at a slow 5-6 km/h gait using their keen sense of smell to locate seal breathing holes and lairs (Harrington and Stirling 1992). Daily movements of 6-26 km/day (Schweinsburg and Lee 1982, Messier et al. 1992) and annual movements of 6000 km (Garner et al. 1990) are common as bears follow the cycle of ice formation and break-up.

Other bears (Pearson 1975, Craighead 1976, Amstrup and Beecham 1976, Lindzey and Meslow 1977) and most mammals (Sanderson 1966, Sandell 1989) show an affinity for particular areas. Unlike terrestrial bears, polar bears do not defend territories or a home range but rather range wherever seals are available (Ramsay and Stirling 1988). Results from marked polar bears in Northwest Territories (Stirling et al. 1975, 1977, 1978, Schweinsburg et al. 1982) and satellite tracking (Schweinsburg and Lee 1982, Amstrup and Gardner 1991) suggest that polar bears nevertheless display regional fidelity. Garner et al. (1990) speculated that polar bear range sizes vary between regions due to different ice patterns, as indicated by different range sizes recorded for Lancaster Sound (2,300-22,900 km<sup>2</sup>; Schweinsburg and Lee 1982), Beaufort Sea (9,700-270,000 km<sup>2</sup>; Amstrup 1986) and the Bering and Chukchi seas (145,000-351,000 km<sup>2</sup>; Garner et al. 1990). Occasional long distance travels have been observed for some marked polar bears (Schweinsburg et al. 1982, Garner and Knick 1991, Durner and Amstrup 1995). Polar bears move greater distances in the Greenland Sea (Larsen 1986), north coast of Alaska (Amstrup and Gardner 1991), and Bering Strait (Garner and Knick 1991), relative to polar bears of the Canadian Archipelago (Schweinsburg et al. 1982, Messier et al. 1992).

Understanding the behaviour, space-use patterns and social structure of polar bears is of particular interest because of the potential for bear-human conflicts (Gjertz and Persen 1987, Fleck and Herrero 1988).

## 1.2 SEA ICE DYNAMICS:

The study area includes the Canadian Arctic associated with the coastal waters of the Arctic Ocean, the eastern Beaufort Sea, Baffin Bay, and the channels and passages of the Canadian Arctic Archipelago (Fig. 1.1). The study area extends south into Davis Strait during maximum ice growth ( $60^{\circ}\text{N}$ ), north into Kane Basin ( $80^{\circ}\text{N}$ ), east to the west coast of Greenland ( $65^{\circ}\text{W}$ ) and west to the eastern Beaufort Sea ( $130^{\circ}\text{W}$ ). This area supports a more or less continuous mantle of sea ice for at least six months of the year. More open water occurs in the eastern Beaufort Sea and the Baffin Bay-Davis Strait areas than other regions.

Marine currents influence movements of sea ice southward. The pattern of surface water circulation in Baffin Bay is generally in an anti-clockwise direction (Dunbar 1951). The West Greenland Current, comprised of warmer Atlantic waters, flows north along the coast of West Greenland at  $14\text{-}16\text{ cm}\cdot\text{s}^{-1}$  (Collin and Dunbar 1964) before turning westward about latitude  $63^{\circ}\text{N}$  and northward to the north end of Baffin Bay. The North Water polynya, located at the north end of Baffin Bay, is created by

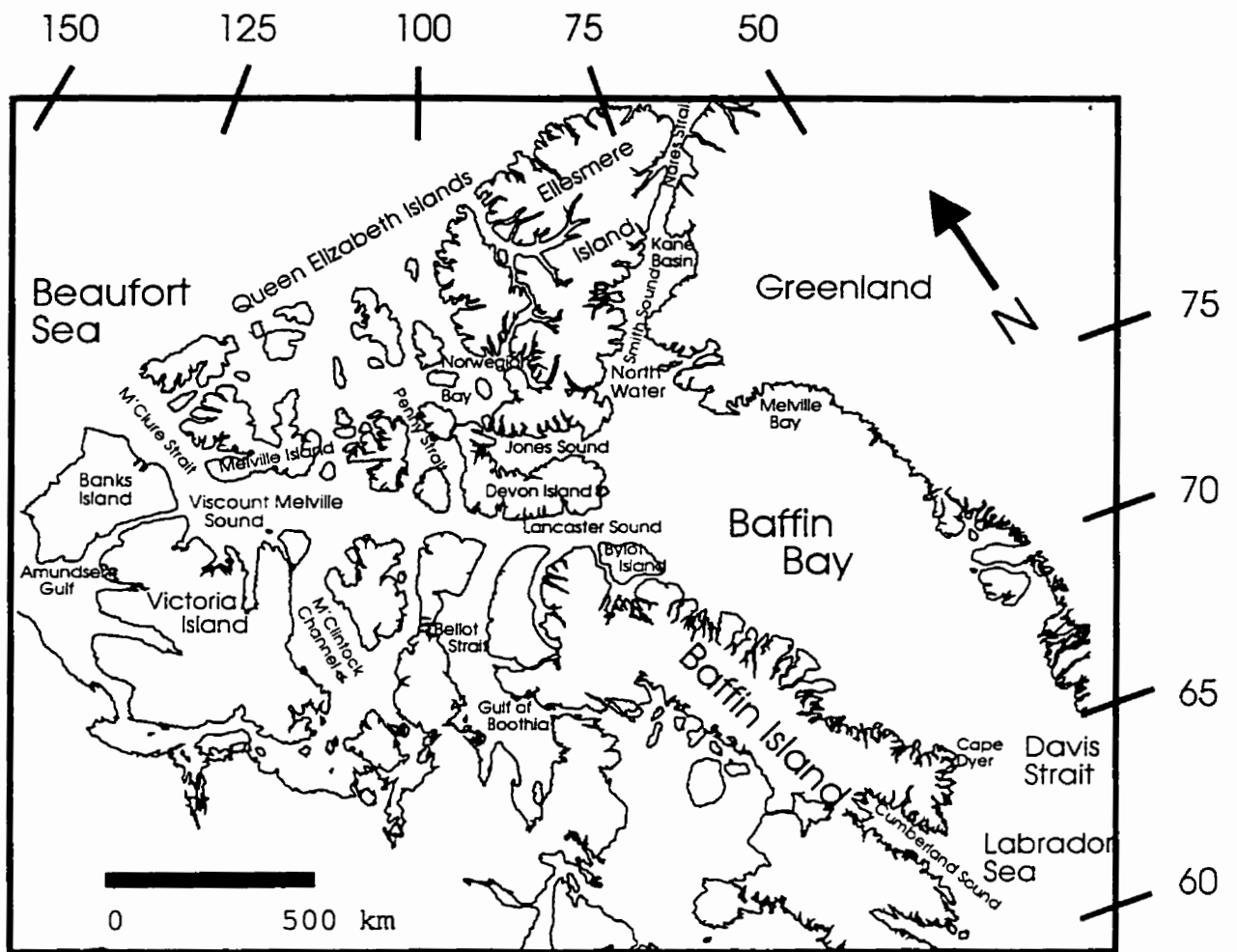


Figure 1.1 Canadian Arctic study area and place names

prevailing north winds, water current and an ice bridge in the northern part of Smith Sound (Stirling and Cleater 1981). While annual ice covers most of Baffin Bay throughout the winter months, only new or young ice develops briefly over the North Water polynya during calm periods. The Baffin Island Current is formed of polar water from Lancaster Sound, Jones Sound and Smith Sound and some west Greenland water carrying colder, and less saline water at  $16-24 \text{ cm}\cdot\text{s}^{-1}$  southward into Davis Strait. Ocean currents in the Lancaster Sound region are dominated by southward and eastward flows out of the Arctic Ocean into Baffin Bay. A westward-flowing current exists along the north side of Lancaster Sound with an eastward out-flowing current along the south side ( $11-21 \text{ cm}\cdot\text{s}^{-1}$ ).

Water currents in the Arctic Archipelago are primarily the result of the outflow of water from the Arctic Ocean. Some of this water flows into Baffin Bay and some travels through Foxe Basin and Hudson Strait directly into the Labrador Sea. The outflow through Jones Sound is small ( $11 \text{ cm}\cdot\text{s}^{-1}$ ) while the outflow through Smith Sound is stronger on the western side ( $21-30 \text{ cm}\cdot\text{s}^{-1}$ ). Southward water currents through M'Clure Strait and Penny Strait move ice along the south coast of Melville Island. In Prince Regent Inlet and the Gulf of Boothia area, a southward movement of water occurs along the west side, and northward movement along the east side. Arctic Ocean



currents are clockwise bringing multi-year pack ice along the north coast of the Queen Elizabeth Islands and west through the Beaufort Sea.

Spatial and temporal patterns of ice distribution, including leads and polynyas, are influenced by meteorological (temperature and wind) and oceanographic factors (currents, bathymetry and salinity), as well as long-term climatic patterns. A cycle of almost total ice cover in late winter and minimum ice extent in autumn dominates the climate of the Arctic region. The sea ice effectively insulates the atmosphere from the water of the Arctic Ocean (Barry 1989). Sea ice is a mixture of young and old floes of highly variable thickness as a result of a complex annual cycle of growth and decay of ice. Winter snow accumulates on arctic ice to about 40 cm and drifts to over 1 m around hummocks and ridges (Hammil et al. 1989). Ice movement causes ridging through ice pile-up and break-up through shearing of adjacent ice fields.

Interannual variation in ice extent is primarily regional in occurrence and related to interannual changes in atmospheric circulation characteristics (Johnson 1980, Walsh and Johnson 1979). Short-period fluctuations in temperature and climate are most pronounced near areas of sea ice growth and decay (Kelly et al. 1982). Bathymetry or sea bottom contour can affect currents and in unique conditions cause upwelling which also affects ice

formation. Ice generally forms and decays in shallow water first. Land masses will restrict the movement of sea ice and therefore the numerous islands within the Archipelago result in a lessening of ice movement. Salinity has considerable influence over the process of ice formation and melt. Ice generally forms first in waters of low salinity and again this generally occurs in shallow coastal waters.

Maximum ice occurs for Baffin Bay in March-April although the West Greenland Current keeps the western coast of Greenland relatively ice free. During the winter months, fast ice becomes established along the Baffin Island and Greenland coasts while the offshore pack ice is kept in motion by storms and tidal current. The width of the shore fast ice varies from about 8 to 32 km, with a maximum width recorded for Melville Bay (Ice Climatology Notes 1987). Summer disintegration of sea ice begins in certain areas of weak ice concentration and expands outward from these centres. Almost all ice in Baffin Bay and Davis Strait is first-year ice with a small percentage of multi-year ice along the western sides. This first-year ice comes predominately from Smith Sound and a small portion comes out of Lancaster Sound and Jones Sound. In sheltered harbours and bays, the ice grows to 150 to 180 cm while multi-year ice floes are 240 to 320 cm thick (Ice

Climatology Notes 1987). Greater thickness are possible with ridging, rafting and hummocking of aggregate ice.

For the Arctic Archipelago, a line can be drawn from King William Island to Prince of Wales Island to Bathurst Island to Penny Strait to Hell Gate and to Smith Sound. East and south of this line the ice regime consists primarily of first-year ice with only a small amount of multi-year ice as floes. The main exception to this pattern is Committee Bay where multi-year ice predominates. West and north of this line most of the ice is multi-year with the amount of first-year ice depends on the extent of break-up during the previous summer. In sheltered harbours and bays, first-year ice grows during winter to 190 to 240 cm in thickness (Ice Climatology Notes 1987). Multi-year ice ranges in thickness between 300 to 450 cm with thicker ice in the western and northern areas (Ice Climatology Notes 1987). In areas with sufficient current or wind pressure, ridging, rafting, and hummocking causes a significant increase in total ice thickness. During the winter months, most waterways of the Arctic Archipelago consist of a consolidated ice sheet. The main exceptions are Lancaster Sound and central Prince Regent Inlet where restricted ice motion occurs. The Hell Gate polynya creates significant open water. Also, small tidal openings occur in Penny Strait and Bellot Strait.

## 2.0 SPACE-USE OF POLAR BEARS IN AND AROUND AUYUITTUQ NATIONAL PARK, NORTHWEST TERRITORIES, DURING THE ICE-FREE PERIOD

### 2.1 Introduction

Unlike terrestrial bears and most carnivorous mammals (Burt 1943, Sanderson 1966, Pearson 1975, Craighead 1976, Sandell 1989), polar bears (*Ursus maritimus*) do not defend their home ranges against conspecifics (Ramsay and Stirling 1988). Lack of defence likely reflects the low density of polar bears and the labile nature of their sea-ice landscape. Still, polar bears display some form of seasonal fidelity to specific areas of sea ice (Stirling et al. 1975, 1977, Schweinsburg et al. 1982, Schweinsburg and Lee 1982, Garner et al. 1990), and defence behaviour may occur toward localized resources (food, den sites, mates). Space use of polar bears on land may be different than when they are on ice due to the differing social and ecological conditions encountered. These differences include a relatively high density of bears, constant landscape features, and reduced access to prey.

Land use by polar bears in the Hudson Bay area has been examined by Stirling et al. (1977), Knudsen (1978), Latour (1981), Derocher and Stirling (1990b), Ramsay and Hobson (1991), and Derocher et al. (1993). However, only limited research has been conducted in more northern latitudes during the ice-free period (Harrington 1968, Schweinsburg 1979, Stirling et al. 1980). Baffin Bay has a

counter-clockwise marine current of seasonal ice formation and break-up that brings most bears to the southwest portion of the bay. The northeastern coast of Baffin Island is characterized by many glaciers, mountainous terrain rising to >2000 m, and many long fjords. During the ice-free period, bears segregate according to age, sex and reproductive status (Derocher and Stirling 1990b) perhaps to minimize predation on family groups by adult males (Taylor et al. 1985), and to allow pregnant females to excavate maternity dens.

The ice-free season generally lasts for 2-3 months for the northeast coast of Baffin Island. I describe segregation of polar bears by sex-reproductive class during the ice-free period in and around Auyuittuq National Park in relation to regional philopatry, pattern of sea ice ablation and formation, habitat selection, avoidance of conspecifics, and selection of den and shelter sites. These patterns are of particular interest for the Auyuittuq National Park because of the potential for bear-human conflicts (Gjertz and Persen 1987, Fleck and Herrero 1988).

## **2.2 Study Area**

The study area is centred on Auyuittuq National Park, 64-69°N and 61-72°W and includes Cumberland Peninsula on Baffin Island (Fig. 2.1). Baffin Island is devoid of trees and continuous vegetation covers 15% of the park area primarily in valley bottoms and on lower slopes (Gray

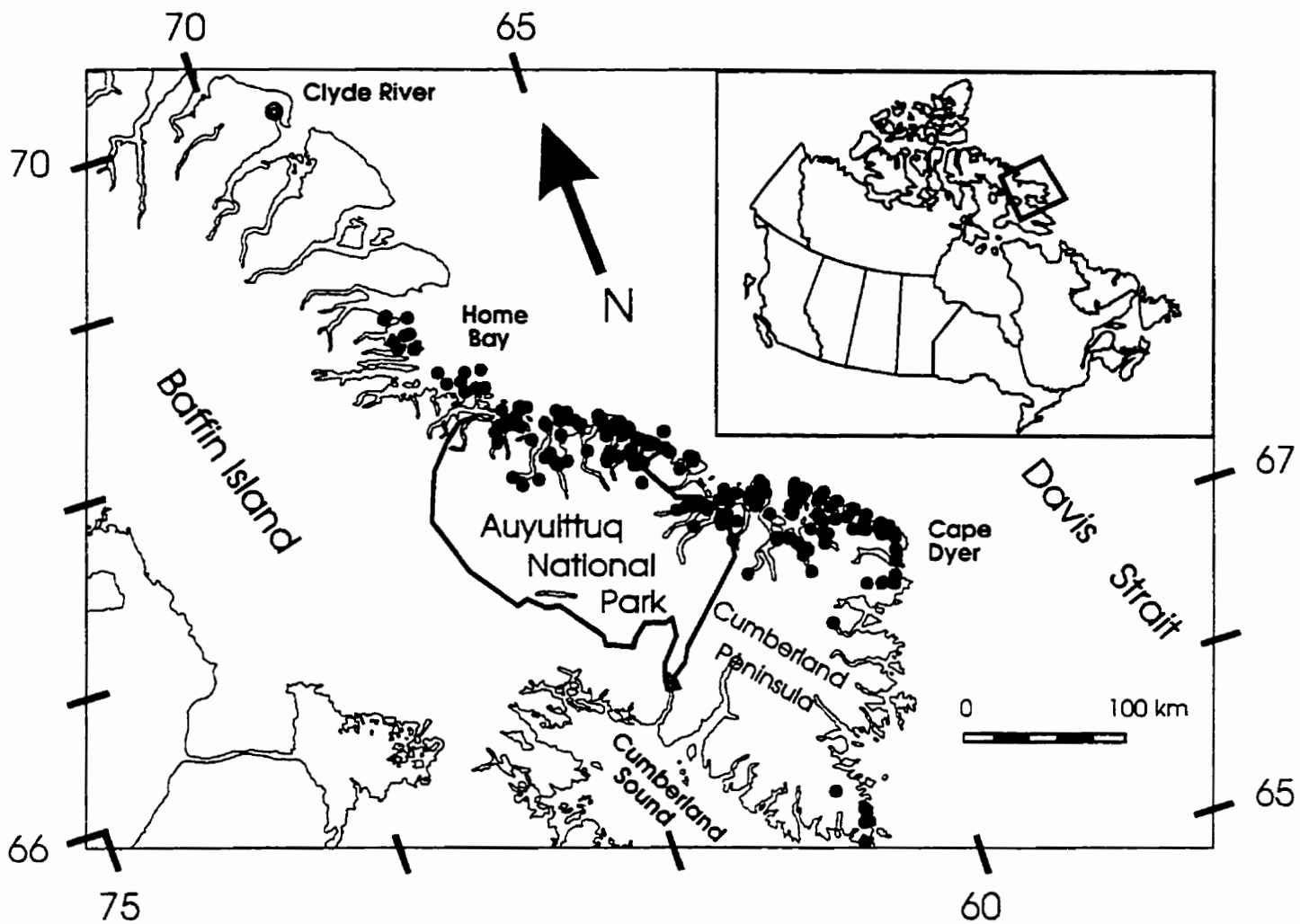


Figure 2.1. Location of polar bears captured in the Auyuittuq National Park study area, 1991-95. Inset shows location of study area (extents: latitude 64-69° N, longitude 61-72° W) on Baffin Island, Northwest Territories, Canada.

1989). Upland and mountainous areas that are not glaciated have little soil and are poorly vegetated (Polunin 1948).

The Canadian arctic climate is characterized by long, cold winters and short, cool summers. High topography results in increased precipitation, particularly along the seaward tip of Cumberland Peninsula (Dunbar and Greenaway 1956). Mean annual precipitation ranges from 245 mm (Dewar Lakes) to 663 mm (Cape Dyer: Seidel 1987). High latitude, steep-walled fjords, and rugged glaciated mountains create complex and unpredictable weather patterns (Seidel 1987).

The pattern and timing of break-up and freeze-up of sea ice in the Auyuittuq region varies considerably among years (e.g. Jacobs and Newell 1979). In June, the ice begins to melt rapidly. Because of the prevailing winds and cyclonic current, the remaining pack ice at the beginning of August extends from Cape Dyer to Clyde and northward to near latitude 74°N (Fig. 2.2). This remaining pack ice typically clears completely by the second week of September (Clyde River, range: 2 July-2 Oct., 1953-1986; Cote 1992). The remaining ice on Baffin Bay congregated and remained in the Auyuittuq vicinity for about a month longer than other areas and varied in extent from a small area in 1991 to an extensive coverage in 1993 (Fig. 2.2). Home Bay and Cumberland Sound were consistently the first areas to clear of ice and Cape Dyer generally was the last area to become ice free. New ice forms first in fjords, bays and inlets,

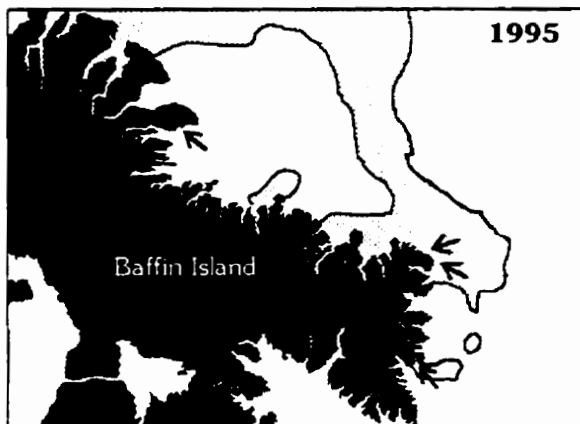
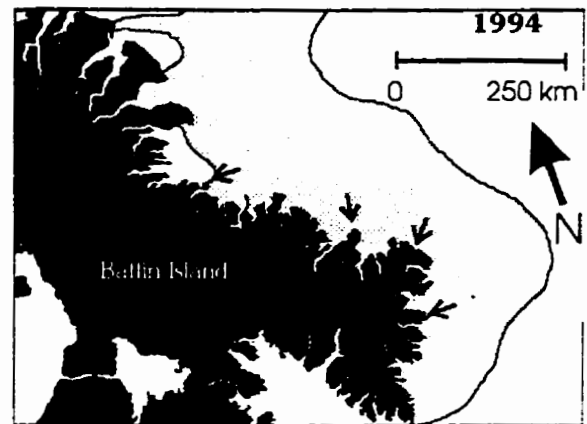
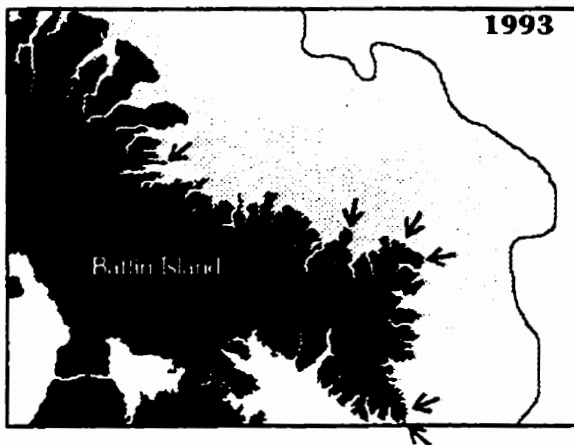
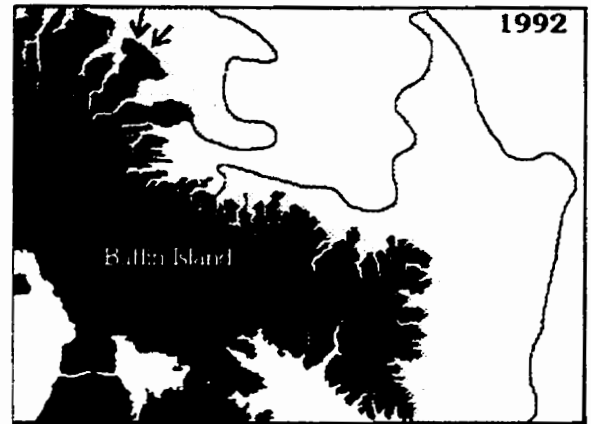
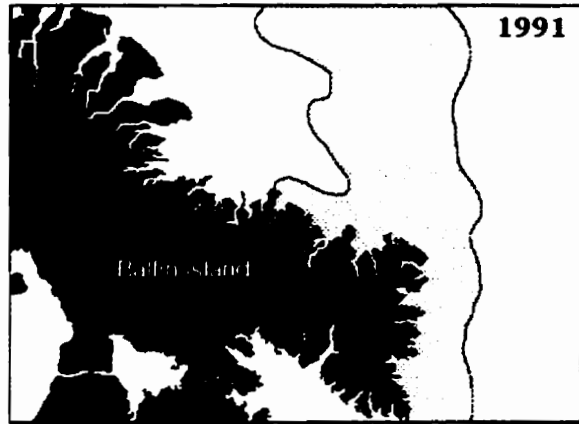


Figure 2.2 Inter-annual variability of extent of pack ice (shaded) off northeast coast of Baffin Island in mid August, 1991-95. Locations of points of entry of polar bears onto land from sea ice (arrows) were determined by satellite telemetry.



and by the second half of November it spreads southward along the coast of Baffin Island. By the end of November, most of Baffin Bay is ice covered (median ice cover, 1960 to 1990 mean data; Ice Climatology Notes, Envir. Can. 1987).

### **2.3 Methods**

I documented polar bear movements and habitat use from captures during autumn and locations from female bears equipped with satellite radiocollars (hereafter referred to as telemetry), 16 August to 31 November, 1991-95. Captures were made in September-October using a Bell 206L helicopter and darting equipment (Stirling et al. 1989). I did not systematically survey the entire study area each year due to weather and logistic problems and flight paths generally covered coastal areas more than inland areas. Another potential bias is that capture data underrepresented sheltering and denning bears due to the difficulty in locating snow shelters. I recorded age, sex, morphometric measures, location, date, and accompanying animals. I measured axillary girth behind the forelegs to the nearest cm. I used male- and female-specific equations to calculate weight estimates from axillary girth measurements (Kolenosky et al. 1989). I measured straight-line body length from tip of nose to base of tail and not following the curvature of the spine. Ageing was done using a vestigial premolar (Grue and Jensen 1979), and sex-

reproductive classes were recorded as females with cubs-of-the-year, females with 1-year-olds, solitary adult females (5+ years), subadult males and females (2-4 years old), and adult males (5+ years). Female polar bears in this region tended to follow a regular 3-year reproductive cycle. Mature females gave birth to cubs in mid-December and nursed their young for about 2 years before mating again during the following spring.

Mature females weighing >100 kg were equipped with satellite collars (Telonics, Inc., Mesa, Arizona, USA) that weighed 1.5-1.7 kg and had an expected life of 20-24 months. Information was transmitted to a satellite for 8 hours every 2, 4, or 6 days depending on the duty cycle of the transmitter. The decimal latitude-longitude coordinates received via satellite were transformed to Universal Transverse Mercator coordinates using SPANS<sup>TM</sup> GIS (Intera Tydac Technologies, Inc. 1991). Two sensors located in the collar also transmitted information on internal temperature of the collar circuitry, and activity level for the previous 24 hours (Messier et al. 1994). To minimize the degree of dependence among data, only one set of sensor data and one relocation per transmission period (i.e., 8 hours every 2, 4, or 6 days; see Messier et al. 1994) were kept for each bear. Activity data was converted to percent day active and then arcsine-square root transformed. For similar topography, Keating et al. (1991) estimated the 68

percentile errors at 1.2 km for good quality locations (factor 1-3).

The minimum distance travelled by each polar bear between two successive locations was calculated as the straight-line distance between the points. The mean seasonal rate of movement for each polar bear was calculated by summing the lengths of line segments and dividing by the corresponding time interval for bears with >10 locations from mid-August to 31 October, excluding periods in dens or shelters. Date of entry and exit from land was determined as the mid-point date between locations specific to such movements.

I recognized two kinds of snow denning: "sheltering" referred to a short period (>7 days and <3 months) of confinement in a snow den or a snow pit by a bear for purposes other than reproduction (Messier et al. 1994), and "denning" referred to the use of a maternity den for about 6 months when pregnancy, birth, and early lactation occurred. Denning and sheltering activity of bears captured after 15 September was analyzed only for subsequent years. Denning and sheltering by a bear was determined by a series of stationary locations, reduced levels of activity, and higher than seasonal temperatures of collars (see Messier et al. 1994). I estimated date of entry into a den or shelter as the mid-point date between the last location associated with movement and the first location at a den or

shelter. I estimated date of emergence from a shelter as the mid-point date between the last location at a shelter and the first movement.

To test for segregation of polar bears while on land I used telemetry locations and capture sites. Availability and use of habitat characteristics were determined using a geographic database developed with SPANS™ by Heritage Canada Parks Service for the area in and around Auyuittuq National Park. Distances to coastline and fjords, elevation, and use of islands and glaciers were calculated using GIS.

I used nearest neighbour analysis to investigate conspecific avoidance or attraction of different sex-reproductive classes. For each of 1993 ( $n = 53$ ), 1994 ( $n = 66$ ), and 1995 ( $n = 73$ ) captures, I used the geographic location of marked polar bears to calculate the shortest distance from a polar bear to its nearest marked neighbour, as well as recording the sex-reproductive class of that neighbour. The statistical results from each capture survey, 1993-95, were pooled for analyses.

Data were analyzed using SAS (SAS Institute Inc., Cary, NC) statistical software. I pooled data on habitat selection, movement, and activity among years to assess general patterns. I used mean activity for each bear for each period and included only animals with greater than 14 readings per season. If significant differences were found

with analysis of variance (ANOVA:  $F_{df}$ ), then Tukey multiple comparison tests were performed. Kruskal-Wallis (KW using chi-square approximation:  $\chi^2_{df}$ ), and Mann-Whitney (MW:  $Z_{n_1, n_2}$ ) tests were used for most comparisons, as data distributions were highly skewed. Chi-square was used to test for independence of sex-reproductive class between nearest neighbours. I also calculated Spearman's rank-correlation coefficients (SR:  $r_s$ ) between date of capture, latitude, longitude, size of islands, elevation, and distance to coast and fjords. Values are reported as mean  $\pm$  SE unless stated otherwise.

#### 2.4 Results

I captured 327 bears (Fig. 2.1; Table 2.1). Adult body weight was lowest for females with cubs-of-the-year ( $244 \pm 8$  kg,  $n = 34$ ), followed by females with 1-year-olds ( $270 \pm 13$  kg,  $n = 14$ ), and then solitary adult females ( $377 \pm 51$  kg,  $n = 3$ ; KW:  $\chi^2_2 = 9.17$ ,  $P = 0.01$ ). In contrast, total length (KW:  $\chi^2_2 = 3.50$ ,  $P = 0.17$ ) and age (KW:  $\chi^2_2 = 1.73$ ,  $P > 0.40$ ) did not differ among the three reproductive classes for adult females.

I equipped 26 female polar bears with satellite collars: 4 in 1991, 8 in 1992, 6 in 1993, 2 in 1994, and 6 in 1995, for a total of 48 bear-seasons. For female polar bears, telemetry locations and capture sites did not differ in latitude (MW:  $Z_{46, 473} = 1.57$ ,  $P = 0.12$ ), longitude (MW:  $Z_{46, 473} = 1.78$ ,  $P = 0.08$ ), distance to the coast (MW:  $Z_{46, 473} =$

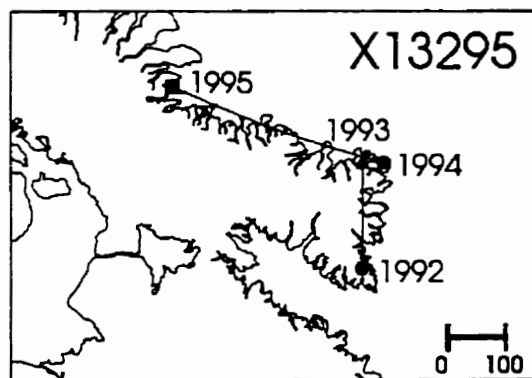
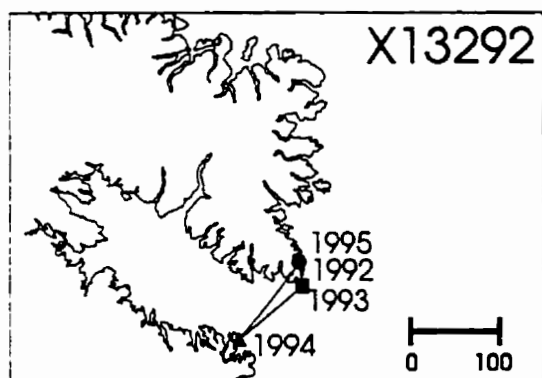
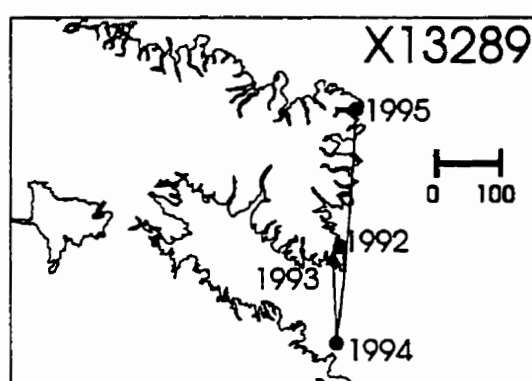
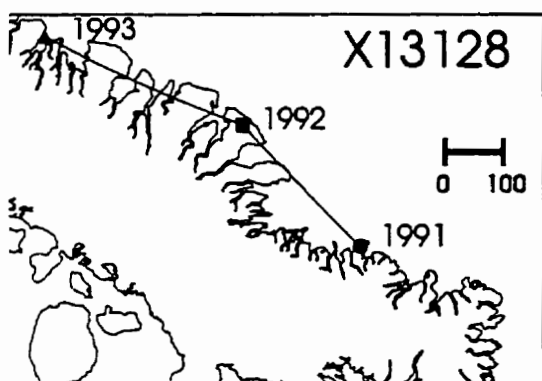
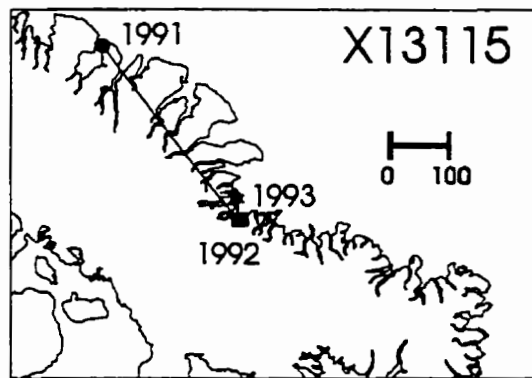
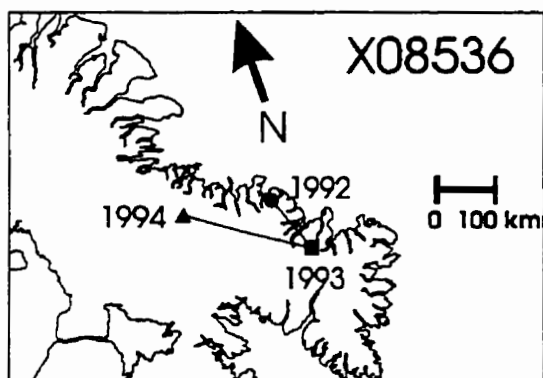


Figure 2.3 Fidelity of radio-collared female polar bears assessed during successive ice-free periods. The arithmetic center point of locations for active bears (circle), shelters (square), and den sites (triangle) are depicted for 6 bears.

Table 2.1. Classification of polar bears captured in and around Auyuittuq National Park, 1991-95.

	COY+1YR	SUB	F-COY	F-1YR	F-SOL	MALE	Total
1991	2	1	2	0	0	1	6
1992	16	4	10	1	0	4	35
1993	26	12	9	7	2	20	76
1994	33	16	14	6	1	31	101
1995	38	26	13	8	4	20	109
Total	115	59	48	22	7	76	327

Note: COY+1YR = Cubs-of-the-year and 1-year-olds, SUB = Sub-adults (2 to 4 years of age), F-COY = Females with Cubs-of-the-year, F-1YR = Females with 1-year-olds, F-SOL = Females Solitary, MALE = Males (females and males were  $\geq 5$  years of age).

0.07,  $P = 0.94$ ), and distance to fjords (MW:  $Z_{14,134} = 1.58$ ,  $P = 0.11$ ), but differed in elevation (mean = 298 m for telemetry locations versus 200 m for capture locations; MW:  $Z_{46,473} = 2.67$ ,  $P < 0.01$ ).

#### **2.4.1 Site Fidelity**

Female polar bears equipped with satellite collars did not show strong site fidelity in autumn while on land (Fig. 2.3). Distance between successive median centre points of all autumn locations or den or shelter location was 148 km ( $SE = 26$ ,  $n = 22$ ). Seven bears had successive annual denning or sheltering bouts in autumn and the mean distance between sites was 199 km ( $SE = 51$ ).

#### **2.4.2 Timing of Leaving Ice and Leaving Land**

On average polar bears were on land in the Auyuittuq region for 84 days, from 23 Aug. (range = 25 July - 18 Oct.) to 15 Nov. (range = 29 Oct. - 1 Dec.). Fifteen of the 16 points of entry (1992-95) on land for radio-tracked bears were associated with the remaining pack ice in mid-August (Fig. 2.2). Timing of entry onto land was related to reproductive status of females (KW:  $\chi^2_2 = 6.78$ ,  $P = 0.03$ ). Females with cubs-of-the-year left the ice first (8 Aug, range = 26 Jul - 15 Aug,  $n = 4$ ) followed by females with 1-year-olds (22 Aug, range = 8 Aug - 5 Sep,  $n = 7$ ) and solitary adult females (28 Aug, range = 14 Aug - 16 Oct,  $n = 9$ ). Solitary adult females ( $n=7$ ) that were to den left the ice later (1 Sep, range = 14 Aug - 16 Oct). Latitude



also had an effect, with polar bears located farther south arriving on land earlier than bears located farther north (SR:  $r_s = 0.64$ ,  $n = 20$ ,  $P = 0.002$ ). Females about to den were on land a mean of 9 days ( $n = 7$ ) before entering a den compared to 24 days ( $n = 11$ ) for females that used a shelter, although this difference is not significant (MW:  $Z_{7,11} = -1.27$ ,  $P = 0.20$ ).

Timing of leaving the land and returning to the ice generally coincided with freeze-up. Polar bears left the land at about the same time (*SE* ranged from 1 day in 1995 to 8 days in 1991) regardless of reproductive class (KW:  $\chi^2_2 = 0.11$ ,  $P = 0.94$ ) or latitude (SR:  $r_s = -0.04$ ,  $n = 32$ ,  $P = 0.82$ ). Freeze-over occurred in early November (mean = 6 Nov.; range 15 Oct. to 26 Nov.; Clyde River 1954-1991; Cote 1992). While on land, polar bears moved closer to the coast and to fjords as the time of freeze-up approached. This pattern was indicated by the negative correlation between the distances to the coast of capture sites and Julian date (SR:  $r_s = -0.12$ ,  $n = 327$ ,  $P = 0.03$ ) and the distances to fjords and Julian date (SR:  $r_s = -0.17$ ,  $n = 268$ ,  $P < 0.01$ ).

#### **2.4.3 Segregation**

Environmental differences likely affect the sex-reproductive class distribution of polar bears. Larger islands occurred farther south (size of island versus latitude; SR:  $r_s = -0.631$ ,  $P > 0.001$ ,  $n = 102$ ) and east (longitude; SR:  $r_s = -0.613$ ,  $P > 0.001$ ,  $n = 102$ ). Not only

did more large islands occur towards the end of Cumberland Peninsula but this area also includes some of the most rugged terrain. For all sex and reproductive classes, elevation at capture was negatively correlated with latitude (SR:  $r_s = -0.631$ ,  $P > 0.001$ ,  $n = 102$ ) and longitude (SR:  $r_s = -0.613$ ,  $P > 0.001$ ,  $n = 102$ ). Distance to the coast for captured bears was similarly negatively correlated with latitude (SR:  $r_s = -0.122$ ,  $P = 0.03$ ,  $n = 327$ ) and longitude (SR:  $r_s = -0.193$ ,  $P = 0.004$ ,  $n = 327$ ). Therefore, bears captured along the northeastern tip of Cumberland Peninsula were found farther from the coast and at higher elevations relative to the more western and northern region of the study area.

For capture sites, I found no significant difference in elevation for the different sex and reproductive classes (KW:  $\chi^2_5 = 2.34$ ,  $P = 0.80$ ). However, telemetry results found that solitary adult females, most of which were about to den, were at higher elevations than other females (KW: mean elevation = 434 m,  $n = 72$  for solitary adult females versus 280 m,  $n = 415$ , for females with cubs-of-the-year or 1-year-olds; KW:  $\chi^2_2 = 7.72$ ,  $P = 0.02$ ).

Captured females with young (cubs-of-the-year and 1-year-olds) were farther from the coast (2.0 km,  $n = 70$  bears) than solitary adult females or males (0.9 km,  $n = 91$ ; MW:  $Z_{70,91} = 1.89$ ,  $P = 0.006$ ). For telemetry locations, solitary adult females were farther from the coast than

other females (3.5 km,  $n = 72$  locations for solitary females compared to 2.5 km,  $n = 202$ , for females with cubs-of-the-year, and 1.3 km,  $n = 213$ , for females with 1-year-olds; KW:  $\chi^2_2 = 14.7$ ,  $P < 0.001$ ). However, this finding may be due to solitary adult females looking for a den site. Captured females with cubs-of-the-year or 1-year-olds were closer to fjords (2.7 km,  $n = 37$ ) than solitary adult females and adult males (3.7 km,  $n = 74$ ; MW:  $Z_{17,74} = -2.23$ ,  $P = 0.03$ ).

Captured females with cubs-of-the-year used islands less than other females (21%,  $n = 48$ , for females with cubs-of-the-year compared to 42.5%,  $n = 167$ , for other bears; KW:  $\chi^2_1 = 4.15$ ,  $P = 0.04$ ). For telemetry locations, females with cubs-of-the-year used larger islands (135 km<sup>2</sup>,  $n = 78$ ) relative to females with 1-year-olds and solitary adult females (87 km<sup>2</sup>,  $n = 32$ ; KW:  $\chi^2_2 = 15.4$ ,  $P < 0.001$ ). Most radio-collared solitary adult females and females with 1-year-olds denned or sheltered (20 of 29) and they rarely used islands (8% of locations).

Only 2 captured polar bears were observed on glaciers and both were males. For telemetry, solitary adult females (7% of total locations,  $n = 72$ ) were observed on glaciers more than females with young (1% of total locations,  $n = 411$ ; KW:  $\chi^2_1 = 12.1$ ,  $P = 0.001$ ) possibly related to the greater likelihood of solitary adult females to den at high elevations.

For nearest neighbour analysis, my null hypothesis was that the probability of an animal being a nearest neighbour will equal the proportion of animals in that class in the study population. The null hypothesis was not rejected for females with cubs-of-the-year, females with 1-year-olds, and solitary adult females (Chi-square:  $P > 0.40$ ). However, males (Chi-square:  $\chi^2_4 = 27.4$ ,  $P < 0.001$ ) and subadults ( $\chi^2_4 = 29.6$ ,  $P < 0.001$ ) were disproportionately associated with other sex-reproductive classes of polar bears (Fig. 2.4). Males were less likely to be close to either females with cubs-of-the-year ( $\chi^2_1 = 3.3$ ,  $P = 0.07$ ) or females with 1-year-olds, and more likely to have other males as their nearest neighbours (Fig. 2.4). Subadults were less likely than expected to have adult females with cubs as their nearest neighbours (Fig. 2.4). This suggests that females with cubs-of-the-year tended to isolate themselves from other bears, particularly adult males and subadults. Males were occasionally found in groups of 2 or 3 animals ( $1.2 \pm 0.5$  (SD),  $n = 111$ ) while females were never found closer than 800 m from each other.

If females with cubs-of-the-year generally avoided males then those few that were in close proximity may provide some information on male characteristics. Adult males with females with cubs-of-the-year as their nearest

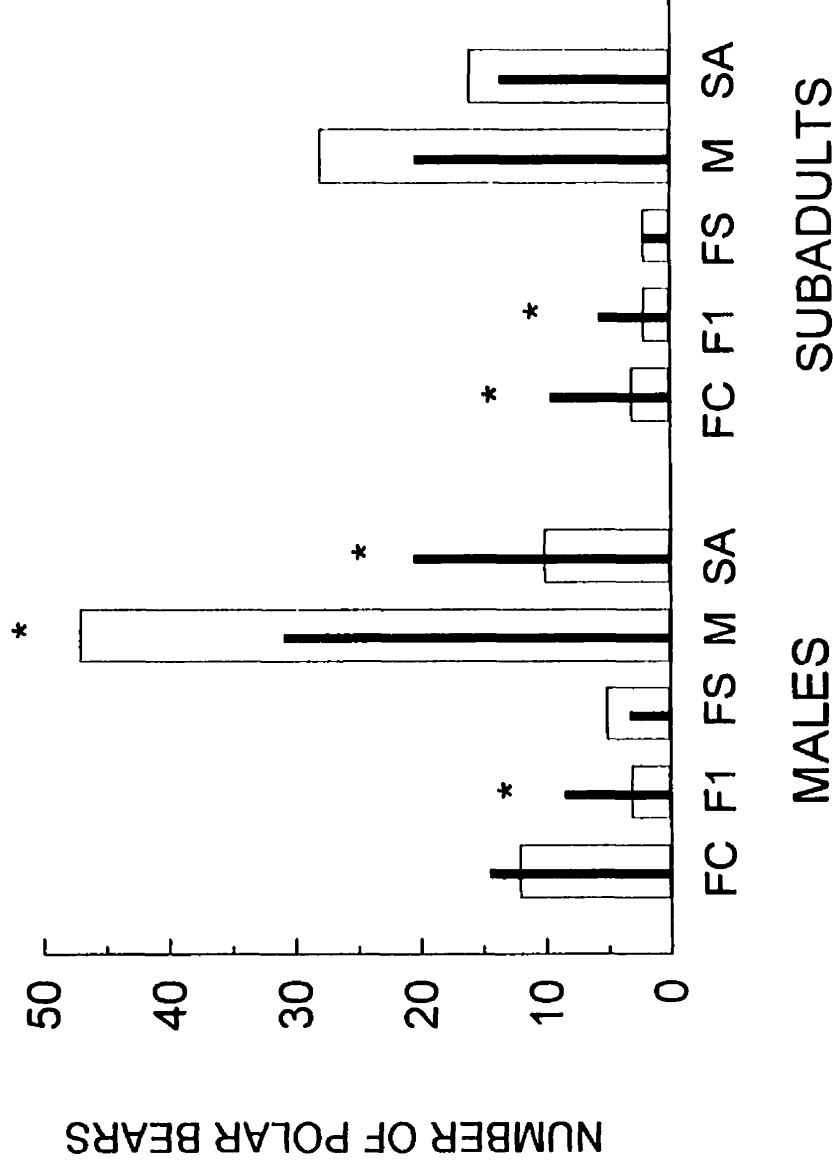


Figure 2.4. Observed (bar) and expected (line) frequencies of polar bears of different sex-reproductive class as nearest neighbours for males (+5 years) and subadults (2-4 years) in Auyuittuq National Park area, 1993-95. Sex-reproductive classes: FC = female with cubs-of-the-year, F1 = female with 1-year-olds, FS = solitary female, M = male, SA = subadult. Significant differences (Chi-square  $P < 0.05$ ) denoted by \*.

neighbour ( $5.6 \pm 1.0$  km) weighed 28% less than other male bears ( $n = 12$ ; MW: 303 versus 421 kg;  $Z_{10,101} = -2.13$ ,  $P = 0.037$ ). However, these same 12 bears did not significantly differ from the other captured males in age (MW:  $Z_{10,101} = 0.45$ ,  $P = 0.66$ ) or size (total length; MW:  $Z_{10,101} = 0.86$ ,  $P = 0.39$ ). Subadults and females with cubs-of-the-year were seldom in close proximity ( $<5.0$  km,  $n = 3$ ).

#### 2.4.4 Denning and Sheltering

No radio-collared females with cubs-of-the-year denned or sheltered ( $n = 7$ ). All radio-collared females with 1-year-olds sheltered ( $n = 9$ ). Duration of sheltering averaged 61 days (50-76 days,  $n = 7$ ). Seven of nine solitary adult females that were radio-collared denned, whereas the other two sheltered. Only 1 of 47 captured females with cubs-of-the-year were found in a shelter compared to 5 of 17 females with 1-year-olds (Test of 2 independent proportions:  $Z = 3.30$ ,  $n_1 = 47$ ,  $n_2 = 17$ ,  $P < 0.001$ ). Two of seven captured solitary adult females were found in a den. None of the 29 captured subadult females were found in dens or shelters.

Ten male and 8 female polar bears captured in dens or shelters provided information on habitat selection. Two sites were likely maternity dens as the inhabitants were solitary adult females. Capture sites of males and females in dens and shelters differed in distribution from the sites of active polar bears. Locations of polar bears found

in dens or shelters, relative to capture sites of active bears, were more to the east (longitude, MW:  $Z_{18,197} = -3.02$ ,  $P = 0.003$ ). Dens and shelters were more likely to be found on the northeastern tip of Cumberland Peninsula with 12 of 18 located east of  $64^{\circ}\text{W}$  longitude. For adult females, dens or shelters were found at higher elevations ( $460 \pm 66$  m versus  $219 \pm 18$ ; MW:  $Z_{8,99} = 3.36$ ,  $P < 0.001$ ), and farther from the coast ( $1.9 \pm 0.6$  km versus  $1.6 \pm 0.4$ ; MW:  $Z_{8,99} = 2.15$ ,  $P = 0.03$ ) than capture sites of active females. Adult female bears that were found in a den or shelter compared to active adult females were not older (MW:  $Z_{7,97} = -0.34$ ,  $P = 0.74$ ) but they were heavier (estimated weight  $254 \pm 14$  kg versus  $227 \pm 6$ ; MW:  $Z_{7,98} = 1.75$ ,  $P = 0.08$ ). In contrast, den and shelter sites for adult males were not significantly different from capture sites of active males ( $P > 0.10$ ). Male bears that were found in a den or shelter were older ( $13.7 \pm 1.9$  years old versus  $8.8 \pm 0.6$ ; MW:  $Z_{10,101} = 2.36$ ,  $P = 0.02$ ) and heavier (estimated weight  $578 \pm 59$  kg versus  $388 \pm 16$ ; MW:  $Z_{10,102} = 3.01$ ,  $P = 0.003$ ) than active male bears.

For bears that did not den or shelter, decreased activity and movement was observed over the autumn period when bears were on land. Female polar bears were the less active during August, September and October than at other times of the year (11% in autumn versus 21% of the day active for the remaining 9 months, ANOVA:  $F_{11,225} = 10.1$ ,  $P <$

0.001; Table 2.2). While on land, females with cubs-of-the-year ( $6.7 \pm 0.3\%$ ,  $n = 26$ ) were less active than either females with 1-year-olds ( $8.2 \pm 0.5\%$ ,  $n = 8$ ) or solitary adult females ( $10.7 \pm 1.0\%$ ,  $n = 12$ ; ANOVA:  $F_{2,225} = 8.47$ ,  $P < 0.01$ ).

Female polar bears had the slowest movement rate when on land ( $8.8 \text{ km}\cdot\text{day}^{-1}$ ,  $n = 22$  bears) compared to a mean of  $12.8 \text{ km}\cdot\text{day}^{-1}$  ( $n = 149$ ) during winter, spring, and summer (ANOVA:  $F_{3,167} = 3.70$ ,  $P = 0.013$ ; Table 2.3). Females with cubs-of-the-year had the smallest movement rate in autumn ( $5.9 \text{ km}\cdot\text{day}^{-1}$ ,  $n = 10$ ), followed by females with 1-year-olds ( $9.5 \text{ km}\cdot\text{day}^{-1}$ ,  $n = 4$ ) and solitary adult females ( $15.8 \text{ km}\cdot\text{day}^{-1}$ ,  $n = 8$ ; ANOVA:  $F_{2,19} = 3.73$ ,  $P = 0.043$ ).

## 2.5 Discussion

Our investigation demonstrates the plasticity of polar bear movements in response to social and ecological factors. In general, four factors influenced polar bear locations during the ice-free season: (1) regional philopatry; (2) pattern of sea ice ablation and formation; (3) the avoidance of males by females with cubs-of-the-year; and (4) denning behaviour.

### 2.5.1 Regional Philopatry

Site fidelity in polar bears has been inferred by their ability to return to specific regions each year, particularly for using over-winter dens (Schweinsburg et al. 1982, Lentfer 1983, Ramsay and Andriashek 1986). In



Table 2.2. Differences in activity level by month, for non-denning female polar bears in the Baffin Bay region, 1991-1995. Means with the same letter are not significantly different according to Tukey's test ( $\alpha = 0.05$ ).

Month	Percent of day active		
	$\bar{x}$	SE	n
January	ab 20.2	0.91	20
February	ab 20.1	0.81	15
March	ab 19.6	0.76	15
April	a 24.9	0.71	21
May	a 25.9	0.65	23
June	a 21.5	0.48	22
July	ab 18.6	0.51	23
August	bc 12.7	0.47	15
September	c 8.9	0.48	13
October	c 8.9	0.73	18
November	ab 20.3	0.80	18
December	ab 20.6	0.85	23
Mean	19.1	0.22	226

Table 2.3. Speed of movement ( $\text{km}\cdot\text{day}^{-1}$ ) for female polar bears, by season in the Baffin Bay region, 1991-1995. Means with the same letter are not significantly different according to Tukey's test ( $\alpha = 0.05$ ).

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Season <sup>a</sup>	Rate of movement ( $\text{km}\cdot\text{day}^{-1}$ )				
	$\bar{x}$	SE	Minimum	Maximum	n
Spring	a 13.1	0.72	5.1	30.5	55
Summer	a 12.7	0.81	3.8	24.2	43
Autumn	b 8.8	1.14	0.8	19.9	22
Winter	a 12.8	0.75	3.5	30.7	51

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<sup>a</sup> Winter = 1 Nov. - 15 March, Spring = 16 Mar. - 31 May,  
 Summer = 1 June - 15 Aug., Autumn = 16 Aug. - 31 Oct.

contrast, over most of the Arctic including the Auyuittuq region, maternity dens are found at low densities and within a few km of the coast of the mainland or offshore islands (Harington 1968, Messier et al. 1994) or occasionally on drifting sea ice (Lentfer 1975, Amstrup and Gardner 1994). Possibly, site fidelity in autumn is more strongly expressed in areas with a concentration of over-winter dens. For the Churchill area, mean distance between successive captures or den sites was 34 km (range 3-57 km) and pregnant females showed little fidelity to specific den sites but returned to the same region and general area each year (Ramsay and Stirling 1990). For the Auyuittuq region, mean distance between autumn median locations in consecutive years was  $148 \pm 26$  km, with female bears showing fidelity to the region but little fidelity to specific geographic areas and no site-specific fidelity.

#### **2.5.2 Sea Ice Ablation and Formation**

Although the dispersion of resources is considered fundamental to the spacing of carnivores (MacDonald 1983, McNab 1989), polar bears during the ice-free period do not compete for mates or food. Polar bears in the Churchill area, when on land were found resting 70-90% of the time (Knudsen 1978, Latour 1981, Lunn and Stirling 1985). Auyuittuq bears exhibited this pattern, with a 50% decrease in activity level and a 30% reduction in movement rate by females during autumn compared to the rest of the year.

Increased energy costs of lactation and efforts to segregate from adult males probably cause females with cubs-of-the-year to be 21% less active and move 63% less than solitary adult females. Distribution on land may be related to the location of the remaining sea ice in mid-August when bears left the sea ice for land.

Water circulation, salinity, and latitudinal pattern of insolation interact to create the temporal and spatial pattern of sea ice ablation and formation. Females with cubs-of-the-year were the first bears to leave this concentrated ice pack about the first week of August, perhaps to avoid the concentration of bears on the pack ice. About 2 to 3 weeks later, females with 1-year-olds and solitary adult females left the ice pack for the land. Females that were about to den left the ice pack last, possibly trying to use the remaining sea ice in efforts to obtain food. Females without cubs-of-the-year were likely not at a great risk from male aggression. Females about to den spent only a short time on land, about 9 days, before entering a den. Mean dates of arrival on land depended on where the last pack ice was grounded onto Baffin Island as well as when the last of the ice broke up and drifted south. Timing of leaving the land depended only on the date of ice formation. Polar bears congregated close to the coastline and along fjords in anticipation of ice forming.

All sex and reproductive classes of polar bears left the land onto the newly formed ice at about the same time.

### **2.5.3 Segregation**

Cannibalism has been proposed as a form of population regulation in bear populations and victims are predominately cubs-of-the-year, and sick and starved individuals (Taylor et al. 1985a, Craighead et al. 1995 and references cited therein). Adult male polar bears are 2 to 3 times heavier than adult females (DeMaster and Stirling 1981). Avoidance of males by females with cubs-of-the-year has been inferred through this study as well as other studies of differential habitat use (Derocher and Stirling 1990b, Stirling et al. 1993).

If infanticide in polar bears could act as a regulatory mechanism (Larsen and Kjos-Hanssen 1983, Larsen 1985, Taylor et al. 1985, Derocher and Taylor 1994), then autumn is a likely season for regulatory mortality to occur. In areas where the melting sea ice results in polar bears being forced onto land, the autumn season is characterized by greater aggregation of bears, limited movement, and low food availability. As a consequence bears lose weight while on land (Atkinson and Ramsay 1995). In this study, I found that males in close proximity to females with cubs-of-the-year weighed 28% less than the average male (303 versus 421 kg) despite the fact that they were comparable in age. Some males may actively seek out

females with cubs-of-the-year as a food resource. The alternative hypothesis is that segregation of males and females with cubs-of-the-year is due to different food or habitat preferences. Future research should combine finer temporal and spatial scales to adequately test the alternate hypotheses.

Possible explanations for the lack of sheltering behaviour by females with cubs-of-the-year include (1) greater activity by cubs, including nursing, (2) the continued need for food, and (3) avoiding cannibalistic attacks by adult males while in snow dens. I found that females with cubs-of-the-year are less active and have the lowest movement rates relative to other classes of females. Therefore, females with cubs-of-the-year are using relatively small areas and likely are not actively searching for food. I hypothesize that females avoid sheltering because of the risk of attack by males.

#### **2.5.4 Denning and Sheltering**

Pregnant females are able to amass considerable adipose tissue before denning (Ramsay and Stirling 1988, Atkinson and Ramsay 1995). For the Churchill area in autumn, females with cubs weighed 34% less than solitary adult females (152 versus 230 kg; Ramsay and Stirling 1988). Although overall, Auyuittuq females were larger, females with cubs-of-the-year weighed 35% less than

solitary adult females that were likely to den (244 versus 377 kg).

Other age and reproductive classes generally remain active throughout the year. The exception to this pattern is sheltering in snow shelters which are used during the ice-free period as well as during periods of inclement weather or when food is relatively unavailable (Messier et al. 1994). Polar bears are able to switch facultatively to a physiological state of fasting in response to the absence of suitable food (Ramsay et al. 1991). Adult bears that sheltered in the Auyuittuq region were older, larger and in better condition than other bears captured in autumn. I found 61% of non-denning females in shelters on land for the Auyuittuq region in autumn, whereas only 24% of non-denning females were in shelters during autumn in the Churchill area (Ramsay and Stirling 1990). Although 60% of female bears sheltered in the western Canadian Arctic Archipelago (Messier et al. 1994), all of these occurred during winter on sea ice.

Stirling et al. (1980) identified the seaward tips of Cumberland, Hall and Meta Incognita Peninsulas as important maternity denning areas. I located most (67%,  $n = 18$ ) dens and shelters near the end of Cumberland Peninsula where high altitude, rugged terrain, and larger islands occur more frequently. Higher elevations receive greater snow:rain precipitation and therefore drifted snow was

likely more available for denning sites in high elevation areas. I seldom located active bears on glaciers and I never recorded a den or shelter on a glacier. From this I infer that bears generally avoided glaciers and therefore the distribution of glaciers in some areas may restrict the available habitat for polar bears along the coast.



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### 3.0 FRACTALS, GEOGRAPHY, AND EVOLUTION OF POLAR BEARS

#### 3.1 Introduction

Evolutionary patterns result from a hierarchy of time and space (Eldredge 1985, DiMichele 1994, Grantham 1995, Riddle 1996). For example, biogeographical patterns reflect the spatial and temporal interactions between the biology of an organism and the physical history of its environment (Graham and Grimm 1990, Haydon et al. 1994). Species' biology has a phylogenetic component representing historical contingency, as well as emergent adaptations to their environment. Of the processes of species dynamics, much more is known about extinction than about colonization and speciation (Brown 1995). How a species evolves is still controversial (Mayr 1988, Gibbons 1996, Morell 1996), as is defining what is a species (Cracraft 1987, Williams 1992, Mallet 1993). One process of species evolution, called allopatric speciation, can start with geological changes in the physical structure of the earth (Connell 1978, Morrone and Crisci 1995, Wright 1978, Vrba 1985).

Habitat changes over the recent hundreds of thousands of years (shallow time; Riddle 1996), which includes glacial-interglacial cycles beginning about 2.5 mya, have been implicated as a mechanism driving population differentiation (Bartlein and Prentice 1989, Bennett 1990) or speciation via geographic isolation of populations (Findley 1969, Vrba 1992, Hewitt 1993, Bush 1994). As well,

episodic landscape transformations have occurred throughout the past tens of millions of years (deep time) coincident with changes in species diversity (Potts and Behrensmeyer 1992, Vrba 1992, Van Valkenburgh and Janis 1993, Hedges et al. 1996, Borero 1996). Organisms adapt to changes in their physical environment, sometimes resulting in the emergence of new species and the development of new trophic interactions. The formation of two species from a single ancestral one must be the result of an interaction between the ecological and biogeographic setting and the evolutionary processes that cause genetic differentiation (Brown 1995). Describing this evolutionary process can help us to define a species as a collection of biologically similar populations that occupy a particular environment. Implicit in this definition is the history of geological transformations for that environment and the evolutionary response of the species to that history. In particular, characteristics of a specific environment often limit and structure the distribution and abundance of populations within a species.

The polar bear (*Ursus maritimus*) is a good species to study this process of speciation, and to assess how their phylogenetic history (i.e., contingent and preadaptive biological attributes) and the physical nature of their habitat interact. The timing of Arctic Ocean freezing, although controversial (Barry 1989), has been estimated to

have occurred 2.4 mya (Flohn 1982, Burton et al. 1997). At this time, the scale of glacial cycles in the northern hemisphere began to increase (Uchida 1996). Permanent arctic sea ice likely formed as a result of the final closure of the Panama Isthmus about 3 mya (Maier-Reimer et al. 1990; Burton et al. 1997) and a renewed link between the Mediterranean Sea and the North Atlantic (Shackleton et al. 1988, Barry 1989, Vrba et al. 1989). The extent of sea ice during the glacial-interglacial period alternated between intervals of extended and closed sea ice, and intervals of open and thin-ice conditions (Ruddiman and Raymo 1988, Dyke et al. 1996). Therefore, like most species (Lawton 1993, Gaston 1996), the range distribution of polar bears has likely undergone marked fluctuations through time.

Polar bears evolved from brown bears (*Ursus arctos*) during the Pleistocene (<2 mya), after the formation of the arctic ice (Kurtén 1964, Wozencraft and Hoffmann 1993, Talbot and Shields 1996a). Numerous climatic changes (20-100 ky; Bennett 1990, Webb and Bartlein 1992) have occurred since polar bears evolved but the climate during the last 6-10 ky has been relatively stable (Wolfe 1980, Bartlein and Prentice 1989). The paleoecological record of the past 20 ky demonstrates that orbitally-induced climatic changes produce changes in the distribution of organisms. These changes have led to a quasi-cyclical alternation between

sympatry and allopatry, and between continuous distribution and fragmentation (Webb 1987, Huntley and Webb 1989, Bartlein and Prentice 1989, Riddle 1996, Roy et al. 1996). Polar bears evolved and adapted to a marine habitat considerably different from the terrestrial habitat of their phylogenetic history. Here, I ask how has this new habitat influenced the spatial structure of groups of polar bears?

A species can be defined according to the physical characteristics of their environment, which in the case of polar bears is primarily defined by sea ice. Also, polar bears bring with them, the biological attributes of their phylogenetic history which include large size, homeothermy, carnivorous habits, terrestrial locomotion, and physiological adaptations to seasonal shortages in food. The expansion of the sea ice in the Arctic provided a new ecological niche for the radiation of pinnipeds and the trophic opportunity for the evolution of polar bears as the primary predator of ringed seals (*Phoca hispida*; Smith and Stirling 1975, Stirling and Archibald 1977, Smith 1980, Kingsley 1990). The ringed seal is the smallest and most abundant of the northern phocids and its distribution is limited to the closed sea ice conditions that exist during most of the arctic year (Finley et al. 1983, King 1983, Smith et al. 1991, Furgal et al. 1996). This otherwise "terrestrial brown bear" evolved as a marine predator of

seals living on the terrestrial-like platform of sea ice (Kurtén 1988). The sea ice defines the spatial distribution of the species. Therefore, I hypothesized that a hierarchical organization of groups of polar bears within a circumpolar distribution is primarily determined by the spatial and seasonal patterns of sea ice interspersed among large arctic islands. My primary goal in this research was to develop and describe a hierarchical connection between spatial effects in geography, and spatial effects in the evolution of a metapopulation structure for a large mammal (see Cantrell and Cosner 1994).

## **3.2 Methods**

### **3.2.1 Study Area**

The Canadian Arctic waters that I investigated included the coastal waters of the Eastern Beaufort, Arctic Ocean, Baffin Bay, and the channels and passages of the Canadian Arctic Archipelago (Fig. 3.1). All of this area supports a more or less continuous mantle of sea ice for at least 6 mo. of the year. More open water occurs in the Baffin Bay-Davis Strait area than other regions. Summer disintegration of sea ice in the Archipelago shows a predictable pattern (Collin and Dunbar 1964). The Arctic region is dominated by a cycle of almost total ice cover in late winter and minimum ice extent in September. The sea

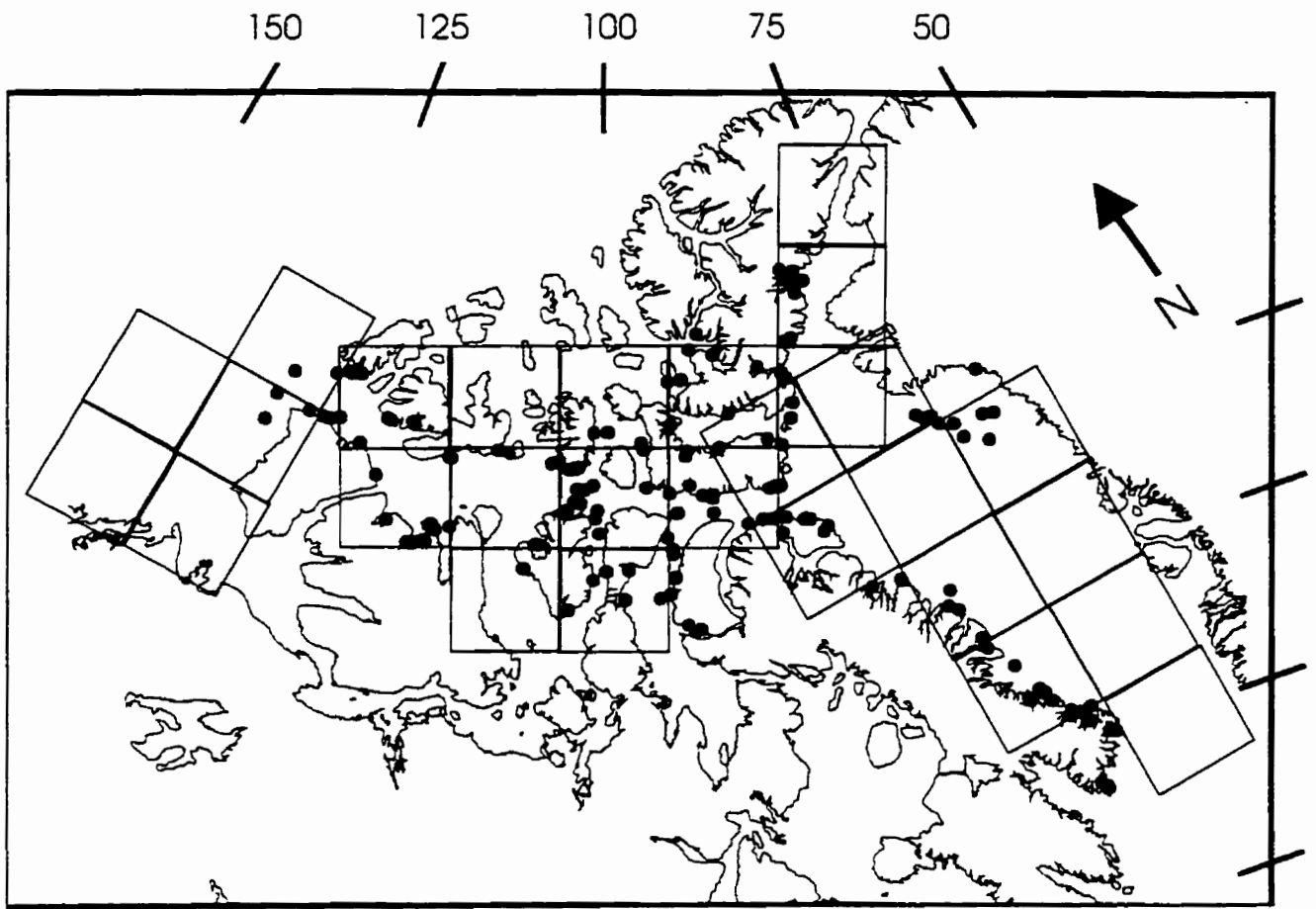


Figure 3.1 Map of the study area in the Canadian Arctic with original capture locations (solid dots) of radio-tracked polar bears and the layout of 90,000 km<sup>2</sup> blocks used to study sea ice characteristics (see methods).

ice effectively insulates the atmosphere from the water of the Arctic Ocean (Barry 1989). Sea ice is a mixture of young and old floes of highly variable thickness as a result of a complex annual cycle of growth and decay of ice. Winter snow accumulates on arctic ice, and drifts around hummocks and ridges. Interannual variation in ice extent are primarily regional in occurrence and related to interannual changes in atmospheric conditions (Jacobs and Newell 1979, Johnson 1980, Kelly et al. 1982, Walsh and Johnson 1979). In particular, the distribution of sea ice, leads, polynyas, and the chronology of freeze-up and break-up are determined by marine currents, wind, temperature, and short- and long-term climatic changes.

### 3.2.2 Data Analyses

Delineation of polar bear populations have been based on evidence for spatial separation of individual bears (Bethke et al. 1996). For species with a large geographical range, we can expect a hierarchy of clumping of individuals. For polar bears, the species' range can be considered a metapopulation as this range is continuous and circumpolar. Within this metapopulation, 'populations' exist (Bethke et al. 1996) and within each population 'subpopulations' may be present (see Wells and Richmond 1995). I am interested in the hierarchical pattern of polar bear groups within the Canadian Arctic, and the factors responsible for this pattern. I am not describing a method

of population delineation as Bethke et al. (1996) have already formulated an appropriate technique.

Two sets of attributes were used in cluster analysis, one based on information from satellite-collared polar bears, and the other from the spatial pattern of sea ice. Four biological seasons were delineated according to seasonal changes in activity level and mobility (Messier, Taylor and Ramsay 1992) and ecological considerations: winter (1 Nov. - 15 March), spring (16 March - 31 May), summer (1 June - 15 August), and autumn (16 August - 31 October).

Cluster analysis was used to group objects (polar bears or sea ice) according to resemblance (Romesburg 1984). The standardized data matrix of objects (e.g., polar bears) and attributes (e.g., seasonal range) were used to compute the values of the Euclidean distance or resemblance coefficient. Average linkage clustering method (UPGMA) processed the values of the resemblance coefficient to create a dendrogram that shows the hierarchy of similarities among all pairs of objects. The dendrogram was divided into clusters for each of four seasons. The interpretation of clusters was based on a hierarchical separation into a small number of well defined groups ( $n = 5$  to  $8$ ).



### 3.2.3 Polar Bears

I used the radio locations of polar bears captured in the eastern Beaufort and western Arctic Archipelago (45 bears successfully tracked, 5003 locations, 1989-1993; Messier et al. 1992) and those captured in the eastern Arctic Archipelago and Baffin Bay (111 polar bears, 8632 locations, 1991-1995; see Ferguson et al. In press) for a total of 608 bear-seasons. The radio-collars had a 4-6 day duty cycle and provided 10-20 locations per season. I did not use location data from females while in dens or shelters.

Three variables were calculated for individual polar bears for each season. First, I determined the median easting and northing for all locations of each polar bear within each season. I transformed the decimal latitude-longitude coordinate system to Universal Transverse Mercator coordinates using SPANS™ GIS (Intera Tydac Technologies, Inc. 1991). Second, the seasonal range (>9 locations) was calculated as the 100% minimum convex polygon using a SAS™ program written by White and Garrott (1990). Third, the fractal dimension of seasonal movements was calculated using the line segment method (Hastings and Sugihara 1993, Ferguson et al. In press). The fractal dimension,  $D$ , of a movement pathway is a quantifiable measure of roughness or irregularity and varies between 1 and 2 (Fig. 3.2). I spatially and temporally restrict

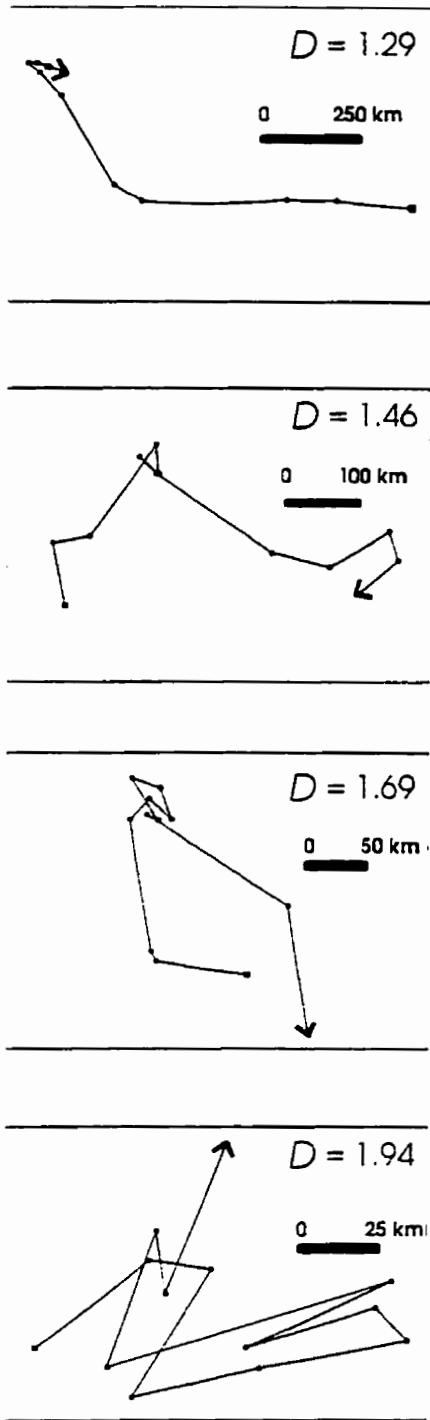


Figure 3.2 Example showing how fractal dimension (D) changes with the degree of tortuosity of polar bear movement pathways.

calculations of fractal dimension to polar bears within the study area and for each season to avoid the problem of scale dependence of movement pathways (Turchin 1996).

I performed two cluster analyses for polar bear classifications. First, I used all four variables: the fractal dimension of polar bear movement pathways, seasonal range, and x- y-median location. Because of the reduced sample size of fractal dimension of movement pathways (28-57 versus 98-178; four seasons) I chose to only show the results of the second cluster analysis which used three variables (excluding fractal dimension). The groupings (76-93% match) of the two classifications were similar.

#### **3.2.4 Sea Ice**

To assess the spatial pattern of sea ice, I selected 28 300X300 km blocks (90,000 km<sup>2</sup>) across the study area (Fig. 3.1). The size of these blocks approximated the mean annual home range of an adult female polar bear (99,000 km<sup>2</sup>, n = 96; data on file). Five blocks were located in the Eastern Beaufort, 13 in the Arctic Archipelago and 10 in Baffin Bay. Firstly, I considered the spatial nature of sea ice within each block. I divided blocks into 100X100 km cells and used the centre of each cell for point sampling (total n = 252). Only points that were on ice or within 5 km of sea-ice were used in the analysis (n = 186). I took the 10-year ice normals from the Ice Centre (Ice

Climatology Notes 1990) to select sampling points for each season.

Secondly, for each block, the percent of the area covered by sea ice (i.e., available habitat) was assessed using composite sea ice maps prepared by Environment Canada, Ice Centre and digitized using SPANS™ GIS. Only areas >20% ice cover were included in this analysis as polar bears seldom used thinly distributed pack ice (data on file). For those areas and seasons (usually autumn) with <20% ice cover, the coastline was used as a measure of available habitat. Here, I summed the available land within 5 km of the shoreline as 99% of polar bear capture locations were within 5 km of the coast (Ferguson et al., In press).

Thirdly, I calculated the fractal dimension of ice cover for each block using the following procedure. I recorded the presence of sea ice for each season to create a black (ice) and white (land and open water) picture (Fig. 3.3). For the autumn season, the shoreline was included as a black line as polar bears in some areas were forced onto land during the periods when sea ice melts. I used the box counting method (Morse et al. 1985; FDC program for Macintosh computers, Paul D. Bourke, University of Auckland, New Zealand) to calculate the fractal dimension of available sea ice (and land for some blocks in autumn) for these pictures (28 blocks·4 seasons·4.25 years = 476

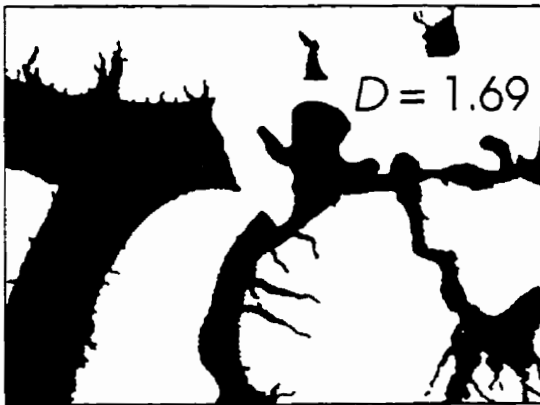
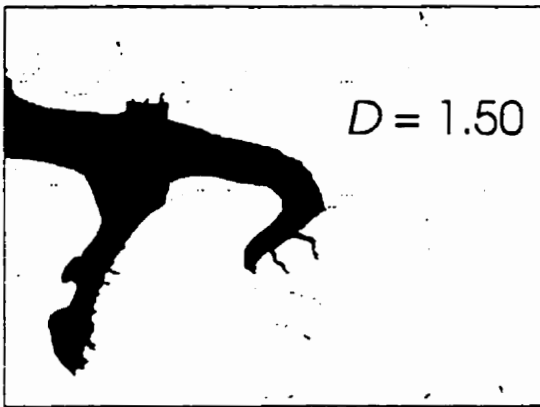
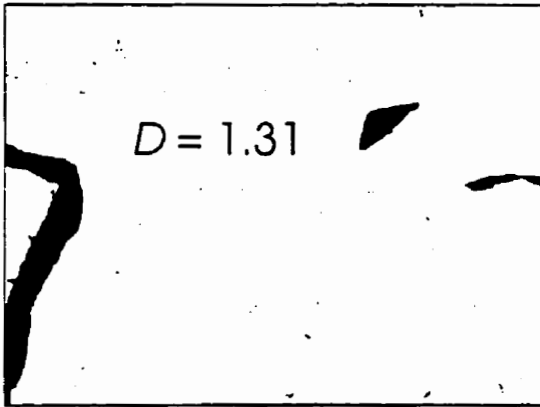


Figure 3.3 Example illustrating how fractal dimension ( $D$ ) increases with increasing irregularity in the distribution of sea ice and increasing ice cover.

pictures). I averaged each season over years (1991-1995) to obtain a mean measure of percent ice cover and its fractal dimension for each block. Then, these values were assigned to the sampling points (above) specific to each block.

### **3.2.5 Statistical Analyses**

ANOVAs, correlation and regression analyses (Sokal and Rohlf 1969) and cluster analyses were performed using SAS statistical packages (SAS 1990). To investigate the relationship among variables and perform the cluster analysis for sea ice characteristics, I took the average of 4-5 years of data for each season (above). I also averaged bear movement data within each block and season for regression analysis to derive partial regression coefficients ( $r_p$ ). For all multiple regressions, I used the forward step-wise selection method for entry of independent variables.

## **3.3 Results**

### **3.3.1 Relationships Between Sea Ice and Polar Bear Variables**

Seasonal ranges of polar bears were related to the amount of sea ice available ( $r_p = 0.20$ ,  $P < 0.01$ ,  $n = 79$  blocks) and the spatial pattern (fractal dimension) of sea ice ( $r_p = -0.30$ ,  $P < 0.01$ ,  $n = 79$ ). Polar bears that ranged within regions with a high proportion of sea ice, for example Baffin Bay during winter (77%) and spring (75%), had large seasonal ranges (66,200 km<sup>2</sup>). In contrast, polar bears living in the Arctic Archipelago, a region

characterized by an interspersed pattern of numerous land masses, had smaller seasonal ranges (13,200 km<sup>2</sup>), despite the reduced overall coverage of sea ice in the region (56%). Regions with a high proportion of sea ice also had a high fractal dimension of sea ice habitat as shown by a positive correlation between these two variables ( $r = 0.86$ ,  $P < 0.01$ ,  $n = 112$ ). Partial correlation described a negative relationship (30% of variation explained) between the fractal dimension of sea ice and the seasonal range of polar bears. For example, the Arctic Archipelago is characterized by an interspersed pattern of land resulting in a fractured pattern of sea ice available to polar bears. This pattern of sea ice may explain the relatively small ranges observed. Although, the relative proportion of sea ice is lower in the Arctic Archipelago region, the fractal dimension of this sea ice is correspondingly high.

The fractal dimension of polar bear movement varied with both the spatial pattern of sea ice ( $r_p = 0.18$ ,  $P < 0.001$ ,  $n = 60$ ) and the percentage of ice coverage ( $r_p = -0.44$ ,  $P < 0.001$ ,  $n = 60$ ). Polar bears ranging within regions consisting of mostly sea ice, showed less irregular and less tortuous movement patterns as described by a smaller fractal dimension. Similarly, with greater irregularity in the spatial structure of their sea ice (higher  $D$ ), polar bears responded with greater irregularity in their movement patterns.

### 3.3.2 Clustering

3.3.2.1 Spring: Clustering polar bears based on their seasonal range generally matched clusters based on the amount of ice available and the fractal dimension of sea ice. Eighty-four percent of the median polar bear locations ( $n = 126$ ) grouped according to polar bear characteristics matched with the spatial classification of sea ice (8 regions; Fig. 3.4). For the classification based on sea ice (Fig. 3.5), the High Arctic and Eastern Beaufort separated as the most distinct regions and the two Baffin Bay regions grouped with the Davis Strait region. In contrast, for the classification based on polar bears (Fig. 3.6), Davis Strait separated out as the most distinct region and the Southern Arctic Archipelago grouped with the two Baffin Bay regions.

For the spring, the same eight regions were delineated based on polar bears as for sea ice (Fig. 3.4). The Eastern Beaufort (EB), Baffin Bay (NBB and CBB), and Davis Strait (DS) regions are characterized by the greatest percent ice cover (63 to 87%) compared to Arctic Archipelago regions (HA, NAA, CAA, and SAA; 27 to 63%; Table 3.1). The largest polar bear seasonal ranges (69,000 km<sup>2</sup>) and lowest fractal dimension of movement ( $D = 1.52$ ) were recorded for the Northern Baffin Bay and Davis Strait bears. These two regions also had the largest expanse of sea ice (83%) and a correspondingly high fractal dimension for the sea ice



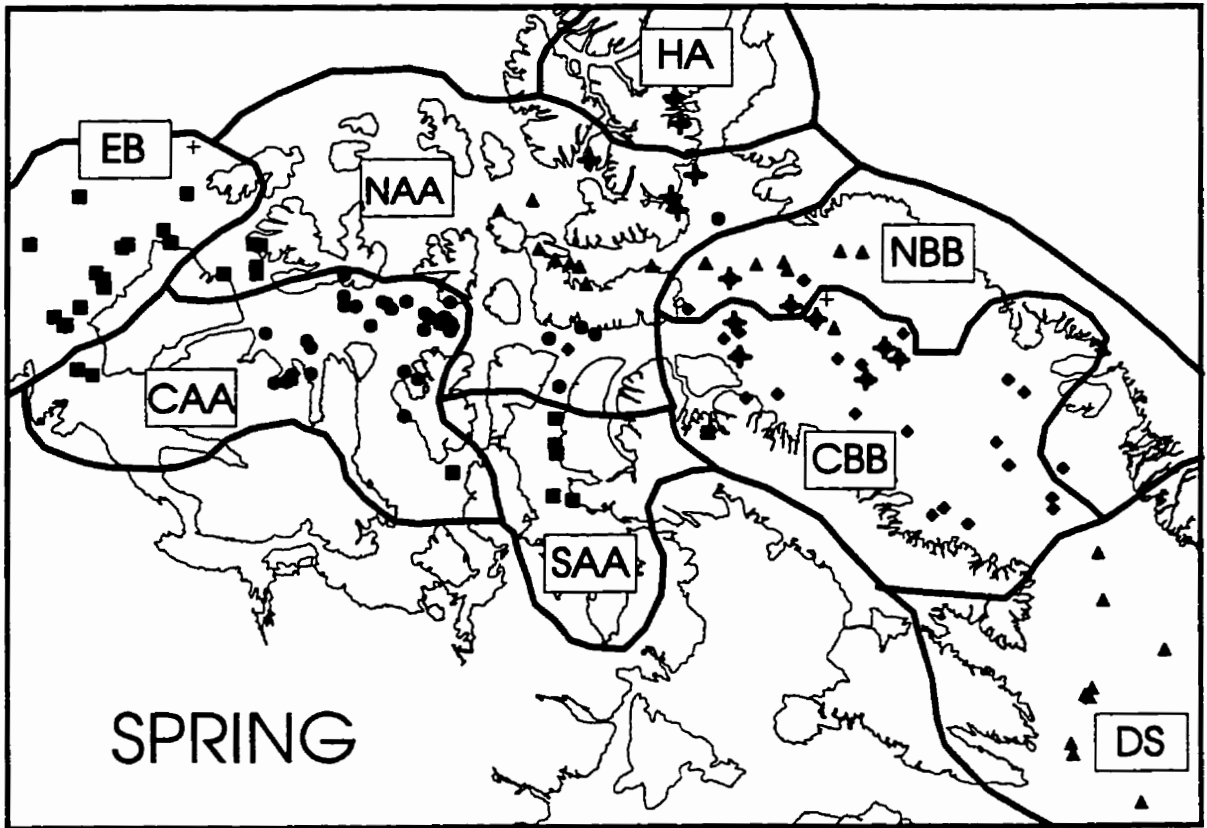


Figure 3.4. Map of sea-ice regions by season (see Table 3.1) as revealed by clustering of sea-ice characteristics (Fig. 3.5). Symbols denote separate clustering of polar bears based on range size and geographic location (Fig. 3.6).

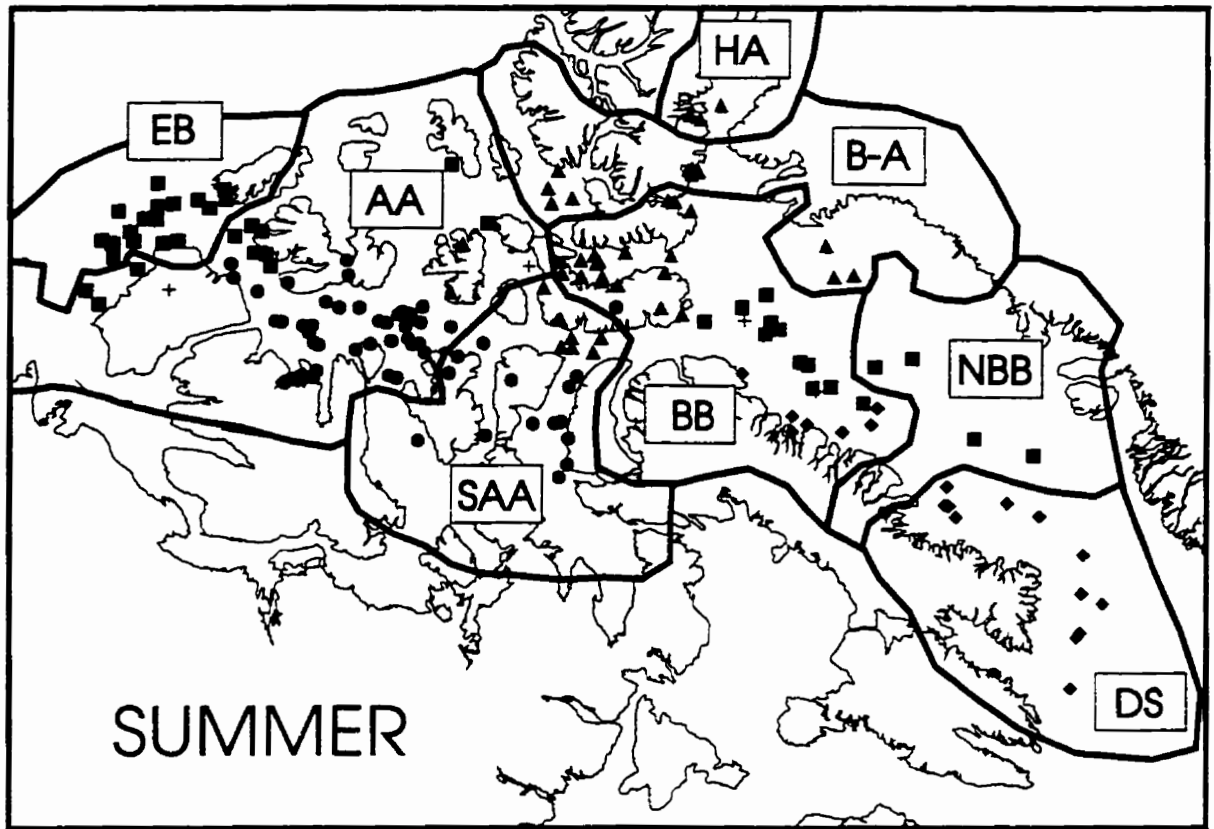


Figure 3.4 cont. Map of sea-ice regions by season (see table 3.1) as revealed by clustering of sea-ice characteristics (Fig. 3.5). Symbols denote separate clustering of polar bears based on range size and geographic location (Fig. 3.6).

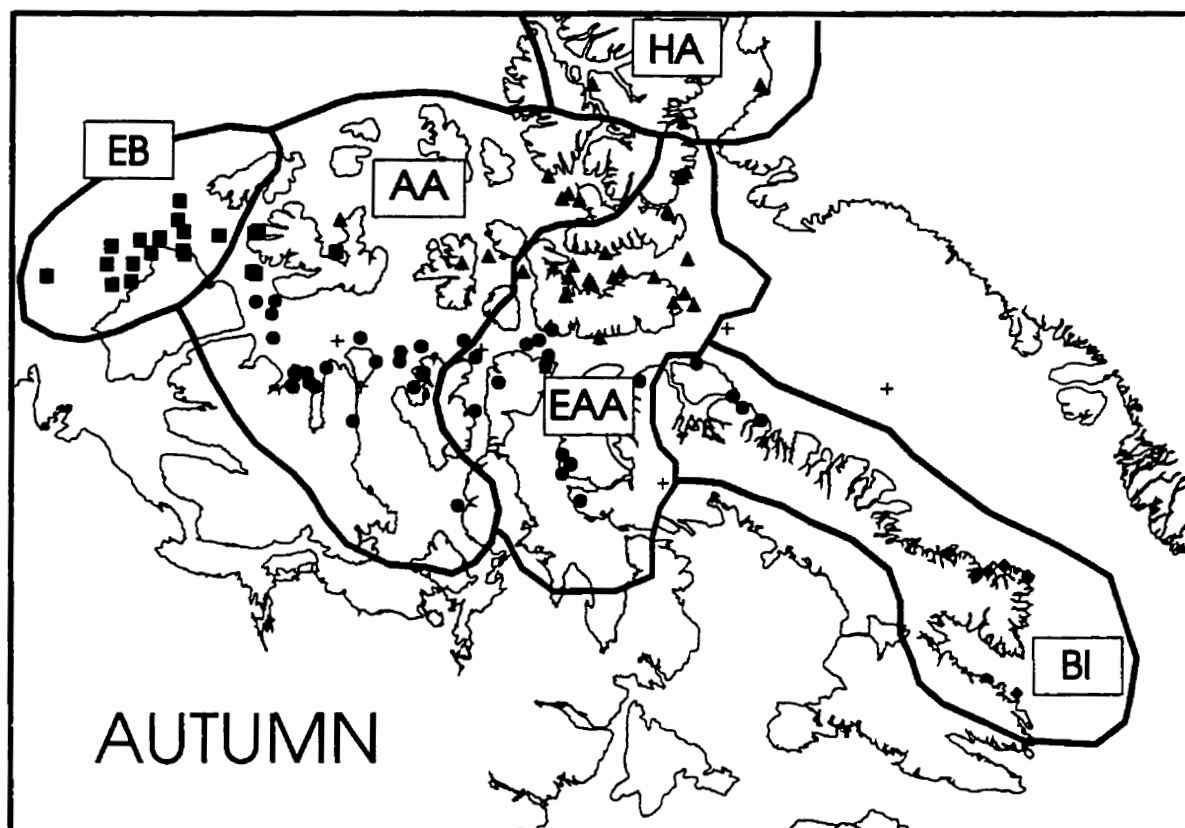


Figure 3.4 cont. Map of sea-ice regions by season (see table 3.1) as revealed by clustering of sea-ice characteristics (Fig. 3.5). Symbols denote separate clustering of polar bears based on range size and geographic location (Fig. 3.6).

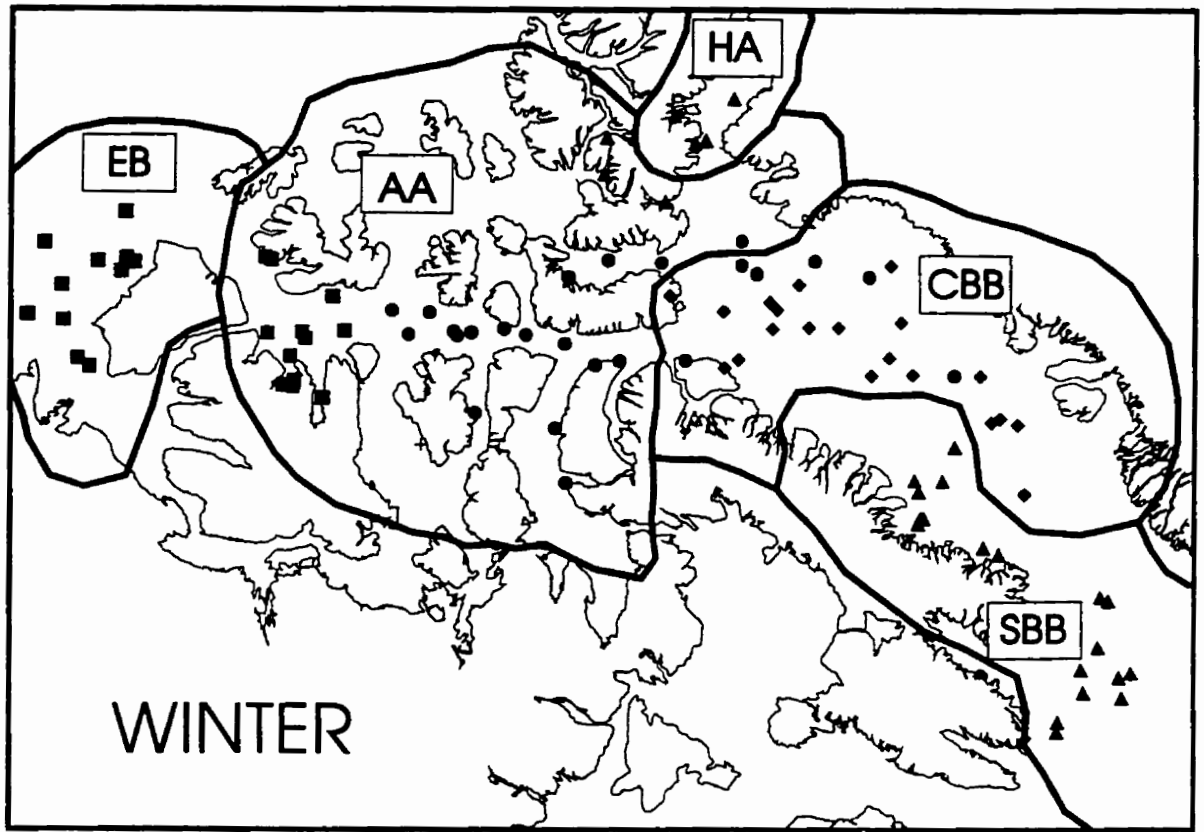


Figure 3.4 cont. Map of sea-ice regions by season (see table 3.1) as revealed by clustering of sea-ice characteristics (Fig. 3.5). Symbols denote separate clustering of polar bears based on range size and geographic location (Fig. 3.6).

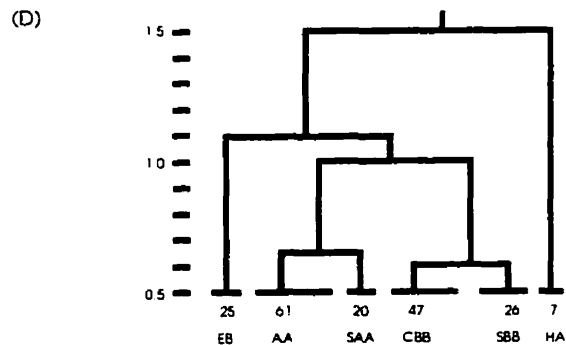
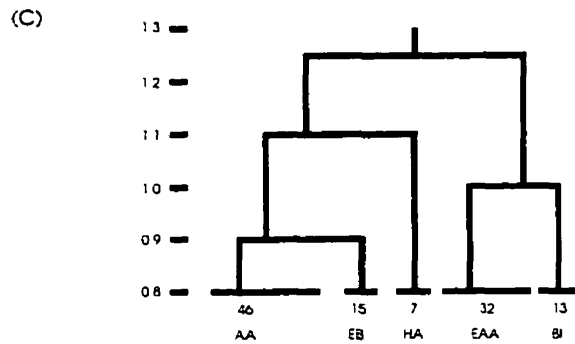
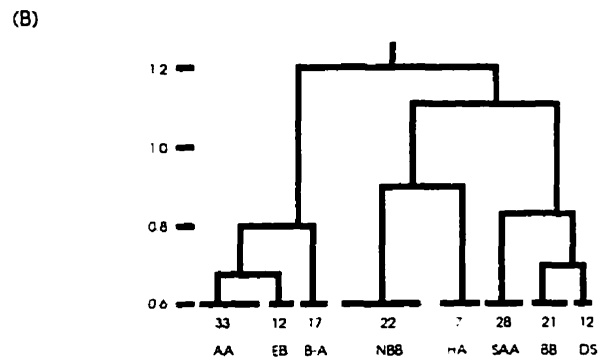
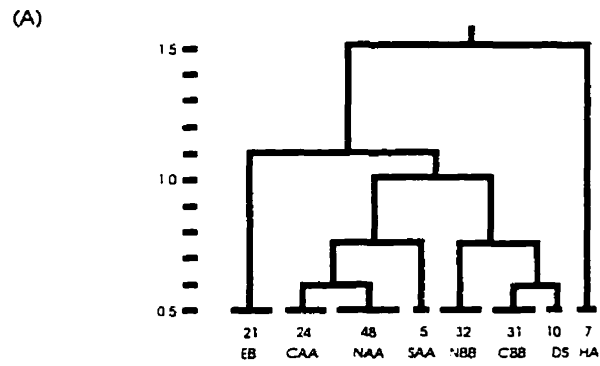


Figure 3.5. Cluster analysis of dendrograms based on sea ice characteristics from 186 sampling points (100 km apart) for the Canadian Arctic: (A) Spring season (16 March to 31 May), (B) Summer season (1 June to 15 August), (C) Autumn season (16 August to 31 October), and (D) Winter (1 Nov. to 15 March).

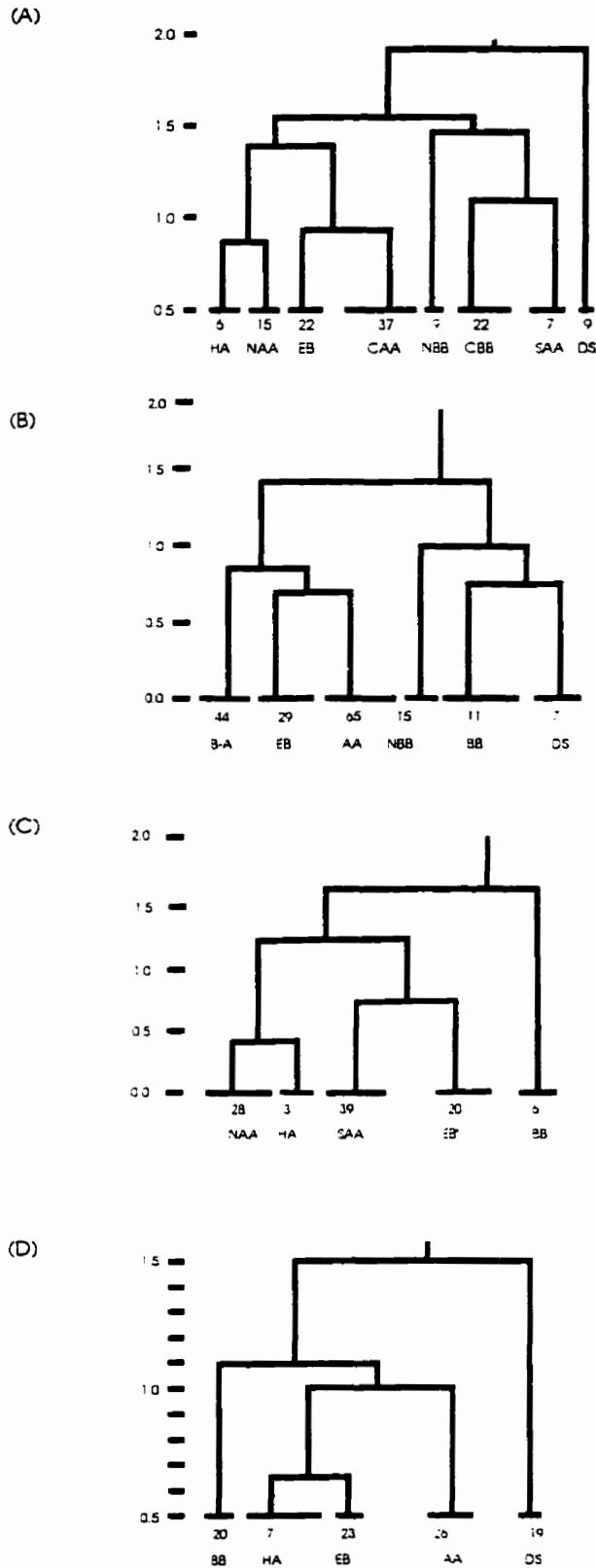


Figure 3.6. Cluster analysis of dendrograms based on movement data of polar bears (n = 156): median telemetry location, and seasonal range size. (A) Spring season (16 March to 31 May), (B) Summer season (1 June to 15 August), (C) Autumn season (16 August to 31 October), and (D) Winter (1 Nov. to 15 March).

Table 3.1. Statistics for season range, fractal dimension (*D*) of polar bear movements, percent sea-ice cover, and fractal dimension (*D*) of sea ice ( $\bar{X} \pm SE$  (*n*)) for various regions of the Canadian Arctic. Data are presented by biological season pooled across years, 1991-1995.

		<u>Polar Bear</u>			<u>Ice</u>		
Season'	Cluster'	Range (km <sup>2</sup> )	<i>D</i> of movement	Percent ice cover	<i>D</i> of sea ice		
Spring	CAA	7900 ± 1486 (37)	1.72 ± 0.035 (10)	58.7 ± 1.01 (24)	1.80 ± 0.0030 (24)		
	EB	11300 ± 1930 (22)	1.60 ± 0.068 (4)	86.6 ± 2.16 (21)	1.86 ± 0.0044 (24)		
	NAA	8791 ± 1618 (15)	1.60 ± 0.064 (2)	54.2 ± 1.20 (48)	1.76 ± 0.0030 (48)		
	CBB	26312 ± 2621 (22)	1.71 ± 0.066 (6)	62.9 ± 1.01 (31)	1.81 ± 0.0028 (31)		
	NBB	66826 ± 3992 (9)	1.48 ± 0.0059 (2)	87.0 ± 1.10 (32)	1.87 ± 0.0034 (32)		
	SAA	11877 ± 4309 (7)	1.56 (1)	45.6 ± 0.04 (13)	1.71 ± 0.0014 (13)		
	DS	71413 ± 17856 (9)	1.55 (1)	76.6 ± 0.00 (10)	1.85 ± 0.0000 (10)		
	HA	7963 ± 1325 (6)	1.67 (1)	27.3 ± 0.00 (7)	1.66 ± 0.0000 (7)		
	All	22469 ± 2620 (129)	1.64 ± 0.028 (28)	65.1 ± 1.28 (186)	1.80 ± 0.0043 (186)		

Table 3.1.; continued

Summer	AA	14608 ±	1700 (65)	1.72 ± 0.040 (21)	60.8 ± 0.75 (38)	1.80 ± 0.0019 (38)
	EB	18349 ±	2273 (29)	1.62 ± 0.049 (18)	84.4 ± 0.72 (12)	1.85 ± 0.0035 (12)
	B-A	8588 ±	1161 (44)	1.68 ± 0.032 (5)	54.1 ± 0.98 (17)	1.79 ± 0.0096 (17)
	NBB	49320 ±	3661 (15)	1.56 ± 0.064 (7)	23.0 ± 1.28 (22)	1.63 ± 0.0046 (22)
	BB	14233 ±	2277 (11)	1.77 ± 0.058 (4)	39.0 ± 0.93 (21)	1.77 ± 0.0092 (21)
	DS	38972 ±	6193 (8)	NA	43.8 ± 0.59 (12)	1.70 ± 0.0023 (12)
	SAA		NA	NA	46.5 ± 1.00 (28)	1.73 ± 0.0059 (28)
	HA		NA	NA	20.5 ± 0.00 (7)	1.60 ± 0.0000 (7)
	All	20945 ±	1790 (178)	1.65 ± 0.025 (57)	47.9 ± 1.38 (158)	1.74 ± 0.0060 (158)



Table 3.1; continued

Autumn	SAA	13387 ±	1672 (39)	1.53 ± 0.036 (17)	NA	NA
	NAA	11433 ±	2230 (28)	1.70 ± 0.040 (5)	NA	NA
	AA	NA	NA	NA	47.1 ± 1.07 (46)	1.74 ± 0.0062 (46)
	EAA	NA	NA	NA	19.3 ± 0.82 (32)	1.47 ± 0.0176 (32)
	EB	15661 ±	2692 (20)	1.54 ± 0.044 (12)	82.7 ± 2.38 (15)	1.85 ± 0.0016 (15)
	BI	843 ±	347 (6)	1.47 (1)	5.2 ± 0.36 (13)	1.19 ± 0.0000 (13)
	HA	8252 ±	3297 (3)	1.42 (1)	26.2 ± 0.00 (7)	1.66 ± 0.0000 (7)
	All	17237 ±	2111 (104)	1.54 ± 0.025 (37)	37.9 ± 2.25 (113)	1.61 ± 0.0199 (113)

Table 3.1; continued

Winter AA	18122 ±	2853 (26)	1.63 ± 0.036 (19)	57.7 ± 0.84 (61)	1.77 ± 0.0028 (61)
EB	9255 ±	1889 (23)	1.67 ± 0.110 (4)	83.8 ± 2.53 (25)	1.86 ± 0.0040 (25)
SBB	63271 ±	11052 (19)	1.52 ± 0.041 (13)	67.6 ± 2.25 (26)	1.83 ± 0.0041 (26)
CBB	108398 ±	12699 (20)	1.47 ± 0.031 (18)	86.1 ± 1.15 (47)	1.87 ± 0.0053 (47)
HA	6698 ±	2315 (7)	1.62 ± 0.137 (3)	28.1 ± 0.00 (7)	1.67 ± 0.0000 (7)
SAA	NA	NA	NA	49.0 ± 0.99 (20)	1.74 ± 0.0073 (20)
All	46791 ±	5789 (98)	1.55 ± 0.022 (59)	67.7 ± 1.31 (186)	1.81 ± 0.0045 (186)

Seasons: spring (16 March - 31 May), summer (1 June - 15 August), autumn (16 August - 31 October), and winter (1 Nov. - 15 March).

Clusters (see Fig. 3.5 & 3.6): CAA = Central Arctic Archipelago; EB = Eastern Beaufort; NAA = Northern Arctic Archipelago; CBB = Central Baffin Bay; NBB = Northern Baffin Bay; SAA = Southern Arctic Archipelago; DS = Davis Strait; HA = High Arctic; All = Combined regions; AA = Arctic Archipelago; B-A = Baffin-Archipelago; BB = Baffin Bay; EAA = Eastern Arctic Archipelago; BI = Baffin Island. Table 3.1

(1.86). The lowest polar bear seasonal ranges (9,100 km<sup>2</sup>) and highest fractal dimension of movement (1.64) came from the Arctic Archipelago bears (HA, NAA, CAA, and SAA). These regions also had similar proportions of sea ice (46%) and land (54%) intermixed. Although less sea ice generally results in reduced fractal dimension, the irregular distribution of land masses in the Archipelago resulted in a relatively high fractal dimension of sea ice (i.e., more edge effect).

The spring season was the time for mating in polar bears but not all females participated. To test whether those potentially breeding females grouped differently than all females together I ran a separate cluster analysis using only solitary adult females (i.e., likely breeders,  $n = 48$ ). The match of bears with groupings ( $n = 8$ ) was almost identical (97%) with the clustering based on all females.

**3.3.2.2 Summer:** For the summer period, I found less congruence between the polar bear and sea ice clustering. Sixty-three percent of the grouped median polar bear locations matched the cluster classification of sea ice (Fig. 3.4). Eight regions were identified using ice characteristics (Fig. 3.5) and six using polar bear characteristics (Fig. 3.6). High Arctic and Southern Arctic Archipelago bears did not form a cluster in summer likely because of the few bears radio-collared in these regions.

As in the spring, Northern Baffin Bay and Davis Strait regions supported polar bears with the largest seasonal range (44,100 km<sup>2</sup>) and the lowest fractal dimension of movement (1.56; Table 3.1). These two regions were characterized by proportionately less sea ice (33%) and a lower fractal dimension of sea ice (1.67), likely resulting from the melting sea ice and movement of ice floes south. The Eastern Beaufort region contained polar bears with the next largest summer range (18,300 km<sup>2</sup>) and a correspondingly low fractal dimension of movement (1.62). The remaining regions consisted of the Arctic Archipelago and western Baffin Bay and were characterized by bears with small summer range (12,400 km<sup>2</sup>) and highly irregular or tortuous pathways (high  $D > 1.68$ ). These remaining regions generally had greater amounts of sea ice available (51%) during the summer and a correspondingly higher fractal dimension of sea ice (1.79).

**3.3.2.3 Autumn:** The autumn period recorded the smallest seasonal ranges (17,200 km<sup>2</sup>) and lowest fractal dimension of polar bear movements (1.54), as well as the least amount of sea ice (38%) and the lowest measure of fractal dimension of the remaining sea ice (1.54; Table 3.1).

Ninety percent of the median polar bear locations grouped according to polar bear characteristics matched the spatial classification based on sea ice characteristics (Fig. 3.4). Whereas Baffin Island grouped as the most distinct region

for polar bears (Fig. 3.6), the sea-ice classification grouped the two regions with the least amount of sea ice together, Baffin Island (5%) with the Eastern Arctic Archipelago (19%; Fig. 3.5). The autumn period was also noteworthy in how the Arctic Archipelago subdivided. Based on information from polar bears, northern and southern regions grouped separately. In contrast, eastern and western regions grouped according to sea ice characteristics.

In autumn, polar bears in Baffin Bay are forced onto land with the disappearance of sea ice. One consequence of living on land is small home ranges (800 km<sup>2</sup>) and low fractal dimensions of movement (1.47; Table 3.1). This pattern likely resulted from the removal of any significant sea-ice cover (5%) for the autumn period. In contrast, the bears of the Arctic Archipelago showed fewer differences in seasonal range and fractal dimension of movement between summer and fall seasons. The Archipelago regions did show a reduction in the amount of sea ice available and the fractal dimension of this sea ice. In particular the Eastern Archipelago recorded considerable loss of sea ice in the autumn period that also corresponded with a decreased fractal dimension. Polar bears that lived within the High Arctic region displayed small seasonal range (8300 km<sup>2</sup>) and low fractal dimension of movements (1.42) which were likely related to the relatively smaller area of sea

ice available (26%) and the correspondingly low fractal dimension of this ice (1.66).

**3.3.2.4 Winter:** The winter period was characterized by the maximum extent of sea ice (68%) and highest fractal dimension of sea ice (1.81; Table 3.1). Polar bears recorded their largest seasonal ranges (46,800 km<sup>2</sup>) and one of their lowest fractal dimensions of movement pathways (1.55). The two classifications were very similar with 79% of grouped polar bear locations matching the spatial grouping of sea ice (Fig. 3.4).

The Baffin Bay regions recorded large ranges (85,800 km<sup>2</sup>) and low fractal dimension of movement (1.50; Table 3.1). Polar bears of the Eastern Beaufort region recorded small range (9,300 km<sup>2</sup>) even though this region as well as the two Baffin Bay regions were characterized by the most sea ice (79%) and the highest fractal dimension of sea ice (1.85).

Polar bears in the High Arctic region recorded the smallest seasonal range (6,700 km<sup>2</sup>) in winter. However, seasonal range did not vary among seasons for this region and remained small year round (6,700 - 8,300 km<sup>2</sup>). In fact, all parameters for this region remained relatively constant throughout the seasons (Table 3.1).

**3.3.3 Hierarchy of groupings:** Regions occurred within a hierarchical structure (Fig. 3.5 and 3.6). During the winter and spring periods, the High Arctic and Eastern

Beaufort were the most distinct regions based on sea-ice characteristics. The Arctic Archipelago and Baffin Bay-Davis Strait separated next as two large regions. In contrast, for the same winter and spring periods, groupings based on characteristics of the polar bears, showed the Davis Strait group as the most distinct whereas the Eastern Beaufort grouped with the Arctic Archipelago as one group, and the Southern Arctic Archipelago grouped with the Baffin Bay bears (Fig. 3.4). These patterns broke down during the summer and fall periods with the ablation of sea ice. Still, some general relationships among regions for both sea ice and polar bear groupings are evident (Fig. 3.5 & 3.6): Davis Strait clustered with Baffin Bay, Eastern Beaufort clustered with Arctic Archipelago, and the High Arctic generally remained distinct.

### **3.4 Discussion**

The spatial arrangement of resources, habitat, and barriers affects the location, movement patterns, foraging dynamics, and persistence of organisms (Kareiva 1990; Danielson 1991, Pulliam, Dunning and Liu 1992, Turner et al. 1995). I tested whether patterns in the sea ice related to the hierarchical organization of groups in polar bears within the Canadian Arctic. Polar bears are unique among bear species as they live in a marine world but are functionally adapted to use a terrestrial-like platform

from which to obtain their food (Ramsay and Stirling 1988, Stirling and Derocher 1992). This ice platform should define the world of polar bears. Sea ice in the arctic region is seasonally transformed and fractured with considerable interannual variation (Jacobs and Newell 1979, Mysak et al. 1990, Brown and Cote 1992). This transmutable nature of sea ice results in spatial and temporal variability in access to food for polar bears (Stirling and McEwan 1975, Smith 1980, Ramsay and Stirling 1986, Ramsay and Stirling 1988). The Arctic is predictably unpredictable (Ferguson and Messier 1996) and as a result changing ice conditions limit the distribution of polar bears and circumscribe their seasonal and annual movements (Derocher and Stirling 1990, Garner et al. 1990, Stirling et al. 1993, Messier et al. 1994). In consequence, polar bears do not maintain relatively discrete home ranges, and the distribution of female polar bears during breeding is less predictable among years (Ramsay and Stirling 1988). Taylor and Lee (1995; Fig. 2) reported a 4% exchange rate of marked polar bears among Arctic populations. Low rates of exchange can prevent genetic isolation while maintaining population discreteness. My results indicate that spatial characteristics of the sea-ice landscape influence the hierarchical pattern of polar bear groupings. I have not identified the mechanism of spatial patterning although



water currents and barriers to movement likely influence areas of den use, hence bear groups.

Classifications based on sea ice characteristics are difficult because spatial patterns of sea ice changes continually throughout seasons and among years. Still, relative to longer time scales geological activity has remained constant over the past inter-glacial period (10 ky to present; Bartlein and Prentice 1989, Dyke et al. 1996). Sea-ice history has been used to distinguish populations of bowhead whales (*Balaena mysticetus*; Dyke et al. 1996). I propose that groupings of polar bears within a circumpolar range could be accomplished by a clustering based primarily on the distribution and pattern of sea ice and islands. For the Canadian Arctic, this landscape pattern has resulted in four or five major groupings of polar bears: the Eastern Beaufort, Arctic Archipelago, High Arctic, Baffin Bay, and possibly Davis Strait. The winter and spring seasons provided the most parsimonious groupings of polar bears likely due to the occurrence of mating in spring (Ramsay and Stirling 1988) and relatively constant sea-ice landscape over winter (January through April). Similar groupings of polar bears have been determined from previous (Bethke et al. 1996) and current research (data on file).

Two approaches can be used to explain the existence of populations: characteristics intrinsic to the population may define differences among populations (sympatry), or

physical characteristics of the extrinsic environment can result in separation of groups of animals (allopatry). Both factors are likely involved as well as temporal- and spatial-scale. However, for an allopatric speciation event, I argue that evolutionary adaptations specific to that new environment should ensure that those physical characteristics will predominate as the major factor structuring populations. Populations structured spatially within a metapopulation, due to a landscape pattern, will subsequently evolve distinct adaptations including differing life-history traits.

#### **3.4.1 Geography and Evolution**

Evolutionary theory provides answers to two questions: how do organisms become adapted to their environment and how does biological diversity arise (Mayr 1963, Lewontin 1978, Brandon 1990). The first question deals with adaptive changes within a population of organisms over time due to selection of better adapted phenotypes (or genotypes). To study the process of adaptation, the emphasis is clearly on populations. The second question deals with issues of biological diversity and understanding how species diverge, i.e, the process of speciation. Wilson (1996) argued for an understanding of diversity based solely in terms of populations rather than in terms of species. Therefore, variation within a population is necessary for the process of adaptation, and variation among populations is the basis

of the diversity in nature. This is the approach I have taken with polar bears; to understand adaptation and speciation (diversity) I delineate the spatial hierarchy of polar bear populations relative to their major landscape-structuring agent, sea ice.

Variation exists among populations in the form of genetic, morphological, ecological, and behavioral differences. The most important interpopulation variation, from the standpoint of the synthetic theory (Mayr 1942), is reproductive isolation among populations. But reproductive isolation is a continuum, not a dichotomy. Partial reproductive isolation describes populations in the process of developing isolating mechanisms (i.e., speciating; see Mayr 1963). Natural selection may serve to isolate populations or natural selection may serve to maintain partial reproductive isolation among populations. A similar process occurs for populations of polar bears occupying the Arctic sea-ice landscape. Polar bears may be composed of local populations that are genetically, morphologically, or behaviorally distinct. Given appropriate combinations of selection, mutation, emigration, and immigration, these differences among populations may be maintained without leading to reproductive isolation among populations. Natural selection is the cause of evolutionary change during periods when rapid change occurs (due to intense directional selection), and serves as a stabilizing force

during periods of stasis (due to stabilizing or normalizing selection). By highlighting the role of evolutionary processes in producing diversity, I emphasize interpopulation variation and not just reproductive isolation.

Controversy exists concerning the role of geography in speciation, not whether allopatric speciation occurs (Ridley 1993, Coyne 1994, McPeck 1996). The evolution of polar bears appears to conform to Eldredge and Gould's (1972) theory of punctuated equilibrium which appeals to Mayr's (1963) theory of allopatric (or geographic) speciation to account for the origin of species. Allopatric speciation "implies that a lineage's history includes long periods of morphologic stability, punctuated here and there by rapid events of speciation in isolate subpopulations" (Eldredge and Gould 1972: pp. 109-110). For polar bears, Kurtén (1964) postulated that a population of brown bears, possibly from Siberia, became geographically isolated from other brown bears as a result of the advance of glaciers. Natural selection for features adaptive to hunting seals on sea ice led to the gradual divergence of the original species (brown bears) and the emerging population (polar bears; see Zhang and Ryder 1994, Talbot and Shields 1996a). The freezing of the Arctic sea ice was a significant event that resulted in the evolution of a number of new species (Riddle 1996). A geological event which creates a new

habitat and causes the separation of two isolated populations changes only the spatial relations between the two populations, and does not create, by itself, any intrinsic biological differences between the two populations. The founder population (polar bears) still represents a reproductive and genetic continuity with respect to the original species (brown bear; Kurtén 1988). It is the subsequent developments of biological differences (genetical, morphological, behavioral, etc.) between the two populations that serves to distinguish them as distinct species (Talbot and Shields 1996b, Slattery and O'Brien 1995).

#### **3.4.2 Fractal Movements and Fractal Sea Ice**

Movement pathways are strongly influenced by environmental structure (Burrough 1981, Burrough 1983, Palmer 1988, Milne 1992, DeCola 1989) and therefore measuring fractal dimension may help to understand how conspecific groupings relate to landscape patterns. Wiens and co-workers (Wiens and Milne 1989, Crist and MacMahon 1991, Crist et al. 1992, Crist and Wiens 1994, With 1994, Wiens et al. 1995, With and Crist 1995) recorded the movements of beetles, grasshoppers, and ants in the same microlandscapes and compared the fractal measures of pathways among taxa. In general, the scale-dependent pathway measures varied significantly among species and with variations in the spatial heterogeneity of the

landscape (Wiens et al. 1995). My results for polar bears (Table 3.1) also indicate a link between fractal movements and fractal landscape, suggesting that consequences of environmental heterogeneity probably result from similar processes for insects (Wiens et al. 1995) as for large mammals (Swihart, Slade and Bergstrom 1988). For example, polar bears living in the Arctic Archipelago are characterised by relatively small seasonal ranges and higher fractal dimension of movement pathways. This movement pattern is likely related to the higher fractal dimension of the ice landscape (controlling for amount of ice cover) which is interspersed by numerous large islands.

The study of the temporal dynamics of a species' geographic range and the spatial distribution of populations can help to determine how the size and geometry of habitats affect both population dynamics and community structure (Cantrell and Cosner 1994, Gaston 1995, Uchida 1996). Identifying and naming groups of polar bear population lineages can provide a reference point for the purposes of studying the effects of natural selection over time. The species range for polar bears persists as a metapopulation - an assemblage of local populations inhabiting a sea-ice landscape fragmented by islands. Future multidisciplinary studies that examine morphological, behavioral, and genetic variation among populations (e.g., Paetkau et al. 1995) will provide

critical information for addressing questions concerning the evolutionary biology of polar bears. Molecular phylogeography offers biogeographers and paleoecologists one approach to examining patterns of range shift, population differentiation, speciation, and illuminating patterns of hierarchical structure of organisms in response to geological events (Riddle 1996). Equally important, the quantitative understanding of metapopulation dynamics is critical for the successful management and conservation of a species like polar bears (Edwards, May and Webb 1994, Hanski and Gilpin 1996).

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## DO SEASONAL RHYTHMS OF FEMALE POLAR BEARS FOLLOW SEA-ICE CYCLES?

### 4.1 Introduction

Time cycles include those aspects of nature that follow simple repeating oscillations (Gould 1987). Environmental rhythms, such as major physical cycles, synchronize animal rhythms, such as activity, metabolism, feeding, growth, and reproduction (Palmer 1976, Boyce 1979). Reproductive rhythms are also ubiquitous in nature and animals living in temperate and high latitude areas follow annual cycles of reproduction (Kiltie 1984, May and Rubenstein 1985). Environmental seasonality also has a profound effect on habitat selection patterns in temperate, boreal, and arctic ecosystems (Turchin and Hanski 1997).

Seasonal rhythms can be portrayed graphically as sine curves in which a response variable is plotted against the seasons of a year (Fig. 4.1). A *cycle*, is defined as a sequence of events that repeat themselves through time in the same order and at the same interval (Palmer 1976). The *period* is the time interval of one complete cycle (e.g., the time elapsed between consecutive peaks or troughs). For these analyses, the *amplitude* measures seasonality and is calculated as the height of a peak in a cycle (e.g., Myneni et al. 1997). The *phase* is used to describe the positional relationship between two or more cycles. As used here, the phase describes the time of year when the greatest height

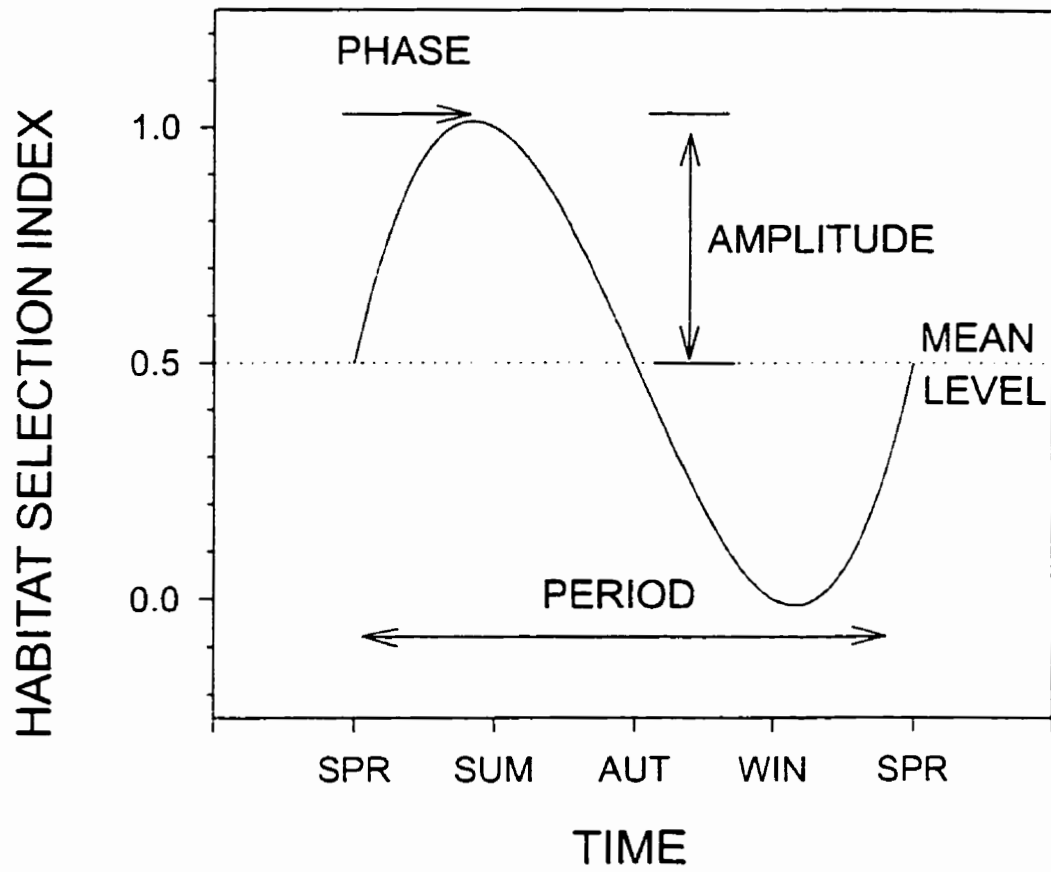


Figure 4.1 Graphic depiction of sine wave terminology used in this study. Period was fixed at 12 months of 4 seasons to depict year-long seasonal changes.



of a peak occurs. An additional parameter, *level*, measured the mean value of the sine wave (e.g., Gibson et al. 1996). Seasonal variations are periodic patterns in a time series that complete themselves within a calendar year (Bowermann and O'Connell 1987). These variations are best described mathematically using sine curves (Rinaldi et al. 1993, Turchin and Ostfeld 1997).

Polar bears (*Ursus maritimus*) live at high latitudes and are therefore exposed to large seasonal environmental cycles (Lindstedt and Boyce 1985, Ferguson and Messier 1996). If cyclic variations in polar bear movements are environmentally imposed, then we would expect a good correspondence between the two systems. Here, I test how well the rhythms of polar bear movements reflect the physical cycles of sea ice in the Canadian Arctic. Concurrent season-to-season correlations are almost invariable between any two cycles sharing a common period. To account for season-to-season variation, I correlated only single parameters that represented features of an annual cycle, such as amplitude.

Female polar bears follow a multi-annual reproductive cycle. Mating occurs in spring, implantation of the blastocysts occurs the following autumn and cubs are born during early winter while pregnant females are denning (Ramsay and Stirling 1988, Messier et al. 1994). The following spring, cubs exit the den with their mother and

follow her on a seasonal cycle of feeding on seals. In some areas, sea ice melts completely and bears are forced onto land in late summer (e.g., Baffin Bay, Ferguson et al. in press a). Sheltering is common at this time as well as during extremes in weather during the winter. During their second year, yearlings remain with their mother and typically disperse in their third spring, when their mother is ready to mate again. Ramsay and Stirling (1988) suggested that female's resource requirements vary depending on whether she is alone, or with cubs-of-the-year, or with yearlings.

For polar bears, the location and accessibility of their prey varies with the structural and spatial characteristics of sea ice (Stirling and Archibald 1977, Smith 1980, Messier et al. 1992) as they use this terrestrial-like platform to hunt ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*). Not surprisingly, polar bear movements and habitat preferences seem to follow a seasonal cycle of ice distribution and characteristics (Garner et al. 1990, Stirling et al. 1993, Born et al. 1997). Recent research on polar bear movements in relation to ice conditions has used satellite-based remote sensing data (Arthur et al. 1996). Previous studies of polar bear habitat selection have relied on direct observation (Martin and Jonkel 1983), aerial surveys of bears and tracks (Stirling et al. 1993), and mark/recapture surveys

(Schweinsburg et al. 1982, Lentfer 1983). In contrast, I tested, using sine wave analyses, whether sea ice availability and selection by female polar bears differed in amplitude, phase, or level relative to regions or reproductive class. For example, I predicted that the movement of polar bears is in phase with the seasonal changes of sea ice.

I estimated habitat selection from satellite-telemetry data, and ice characteristics from remotely-sensed data. Because of the unusually dynamic nature of ice, monthly ice maps were required to follow spatial and temporal changes in form and extent of ice cover. Differences in ice conditions included the locations of major ice edges and the differences in cover, size and thickness of ice floes.

In the Arctic, although significant ice flora occurs on the under-side of ice, the highest productivity occurs near ice edges (Sakshaug et al. 1994). Here, phytoplankton feeds zooplankton; polar cod (*Boreogadus saida*) in turn prey on amphipods; cod represent an important prey for ringed seals; and seals are the main staple food for polar bears (Welch et al. 1992, Ryg and Øritsland 1991). Therefore, I predicted that polar bears will follow the seasonal cycle of ice openings and show a greater selection of ice edges.

## 4.2 Study Area

The limits of the arctic environment that I investigated extend south into Davis Strait during maximum ice growth (60°N), north into Kane Basin (80°N), east to the west coast of Greenland (65°W), and west through the channels and passageways of the Arctic Archipelago and the Viscount-Melville Sound (110°W; Fig. 4.2). Of the total study area, 45% is land (1,024,500 km<sup>2</sup>). Delineation of boundaries for the two eco-regions (Arctic Archipelago, 56% land, and Baffin Bay, 31% land) was based on discrete polar bear population analysis (Bethke et al. 1996), biological differences (Dunton 1992), and ice-climate differences (Lewis 1981, Walsh and Johnson 1979).

The distribution of ice, leads, and polynyas, and the chronology of freeze-up and break-up are determined by marine currents, wind, temperature, and short- and long-term climatic changes. The study area is covered by 1,265,000 km<sup>2</sup> mantle of sea ice for at least 6 mo. of the year. More open water occurs in the Baffin Bay-Davis Strait area than other regions. Summer disintegration of ice in the Archipelago follows a predictable pattern (Collin and Dunbar 1964). The Arctic region is dominated by a cycle of almost total ice cover in late winter and minimum ice extent in September. Over a large scale, sea ice is a mixture of young and old floes of highly variable thickness as a result of a complex annual cycle of growth and decay.

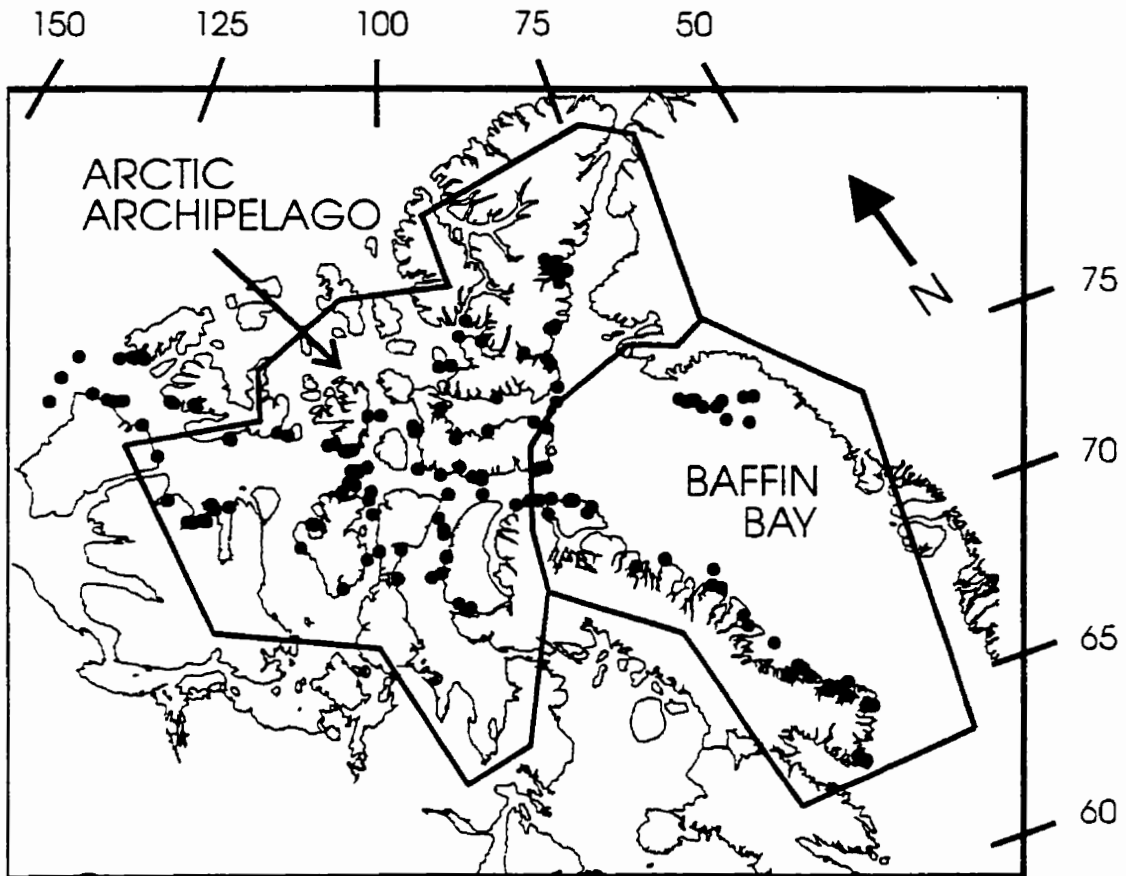


Figure 4.2 Location of polar bears captured in the Canadian Arctic, 1991-95. Line shows the extent of study area and boundaries of the two eco-regions.

Interannual variations in ice extent are primarily regional and relate to changes in atmospheric conditions (Crane 1978, Johnson, C. M. 1980, Mysak and Manak 1989).

#### **4.3 Methods**

##### **4.3.1 Polar Bear Locations**

I documented polar bear movements from radio locations of polar bears equipped with satellite radio-collars. I used information from 45 bears captured in the western Arctic Archipelago (Messier et al. 1992) and 111 bears captured in the eastern Arctic Archipelago and Baffin Bay (Ferguson et al. in press a). I conducted captures each spring (April-May) and autumn (September to late October) of 1991-95 using a helicopter and darting equipment (Stirling et al. 1989).

Mature females weighing >100 kg were equipped with satellite radio-collars (Telonics, Inc., Mesa, Arizona, USA) that weighed 1.5-1.7 kg and had an expected life of 20-24 months. Radio-collared bears were tracked by satellites using the Argos Data Collection and Location System (Fancy et al. 1988). Transmitter duty cycles were set for an 8-hour transmission period every 4 or 6 days (Messier et al. 1994). The latitude-longitude coordinates received via satellite were transformed to Universal Transverse Mercator coordinates using SPANS™ GIS (Intera Tydac Technologies, Inc. 1994) for the spatial analyses.

Each radio-collar provided 10-20 daily locations per season (defined below). Mapping of polar bear locations was done using QUIKMap™ (Axys Software Ltd. 1992) and SPANS™ GIS. Few satellite telemetry locations of questionable accuracy (Telonics class 0) were used (4.5%), and only if 'confirmed' by a second location within 0.2 degrees latitude and longitude within the same 8-hour transmission period. Keating et al. (1991) estimated that class 0 locations had an average error of 12 km (1 SD) while the remaining locations would have an associated error of <1.2 km. Of the total 11,282 locations available, 9,443 were within the study period (1991-1995) and geographic limits (Fig. 4.2). Locations associated with land (e.g., dens and shelters) were not used in the analyses, leaving 6,943 locations.

Reproductive classes were recorded as females with cubs-of-the-year, females with 1-year-olds, and solitary females (5+ years). I assigned reproductive classes post-capture according to the following 3-year reproductive cycle discussed above, or updated when additional information was available (e.g., subsequent captures or satellite collar denning information; 63% of reproductive classes were substantiated from such direct information).

#### **4.3.2 Habitat Delineation**

I measured the characteristics of sea ice that likely relate to polar bear survival and reproduction. The units

of scale (i.e., 1-km resolution) and space-use patterns under consideration matched the perception of polar bears as described by previous research (Garner et al. 1990, Stirling et al. 1993, Arthur et al. 1996). Specific characteristics of sea ice included ice cover, ice thickness (age of development) and ice floe size (i.e., grain). I also measured distance to ice edge (km) for each polar bear location using GIS algorithms. I defined ice edges as the perimeter of ice polygons as demarcated on monthly ice maps, including the ice-land interface and major lead systems.

Digitizing and measures of ice polygons were done using GIS (SPANS™). Satellite telemetry data were processed within the GIS by overlaying polar bear locations with ice information. For the habitat selection analyses, available ice types were restricted to bears that provided more or less continuous locations ( $\leq 8$  days between locations and  $\geq 10$  locations per season). These restrictions resulted in a mean of 4.9 days between average locations (SD = 1.06) and a sample of 3,294 locations in 280 bear-seasons for the habitat selection analyses. I assumed that all bears monitored during this study were capable of travelling to any part of one of the two eco-regions.

Ice characteristics were derived from composite ice maps (1:4 million) interpreted by the Ice Centre



Environment Canada (MANICE 1994). The preparation of ice maps involved the use of two major data sources: first, remotely-sensed information as obtained from NOAA satellites, SSM/I microwave sensors on U.S. Navy satellites, and visible and near infrared sensors on LANDSAT satellites; second, all-weather remote sensors (i.e., synthetic aperture radar or SAR) on board aircraft during seasonal surveys. The NOAA satellites usually made two passes per day and each pass covered a swath over 1000 km wide with a resolution in the order of 1 km (MANIS 1992). No one data source provided the area of coverage, or the detailed information, to interpret the entire Arctic. The primary image data sources used were the airborne radar (SAR) and NOAA images. Synthetic Aperture Radar images were used to identify ice polygons, floe sizes, and surface roughness. NOAA satellite images were used to identify ice edges, thinner ice, total ice cover, and leads. The format and ice symbols used to denote sea ice information for each polygon were determined according to MANICE (1994) and World Meteorological Organization standards.

The ratio of location measurement error ( $\approx 1$  km) to average ice polygon size was low, indicating little potential for classification error (White and Garrot 1986). Median size of ice polygons was 8,253 km<sup>2</sup> (range 5-788,825 km<sup>2</sup>; 25% quartile = 2,827 and 75% quartile = 24,590). The summer season had the smallest patch size (5,389 km<sup>2</sup>; 25%

quartile = 1,885 and 75% quartile = 13,732) and winter and spring the largest (13,885 km<sup>2</sup>, 4,204-33,155; 13,299 km<sup>2</sup>, 4,154-33,155, respectively). Patch size of available ice types did not vary among years ( $F_{5,2352} = 0.70$ ,  $P = 0.62$ ) but differed among seasons ( $F_{3,2352} = 7.58$ ,  $P < 0.001$ ).

Generally more than one ice type was identified within a particular ice polygon (65% of ice polygons had 2 ice types and 10% had 3 ice types). When more than one ice type was identified I used the dominant (>50%) ice type to represent the ice polygon. For each ice polygon, three variables were recorded according to various categories: percent cover (15 categories), ice thickness (16 categories), and floe size (12 categories). As described below, I reduced the number of ice types to facilitate statistical testing by combining similar classes into broader types ( $n = 4$  or  $5$ ) on the basis of ice cover, ice thickness, and floe size.

Total ice cover was reported in tenths with cover of <1/10 (i.e., traces) not being reported except to describe open water. For the analyses I grouped ice cover into five categories: <70% (6.7% of available ice and 10.7% of bear locations), 70-90% (6.4% and 7.5%, respectively), 95% (38.2% and 39.0%, respectively), 100% (33.5% and 38.6%, respectively), and bergy ice (15.2% and 4.2%, respectively). Bergy ice occurs with <1/10 ice present and

generally consists of icebergs and small pans of multi-year ice.

Stages of development of sea ice followed a pattern from new ice (<10 cm thick), young ice (10-30 cm), first-year ice (>30 cm) to old ice. I grouped new and young ice as a single category called new ice (0-30 cm thick). This latter category of ice development totalled 9.0% of the ice coverage and 6.8% of bear locations. First-year ice is ice of not more than one winter and develops from young ice. I divided this stage of development into first-year ice (30-120 cm thick; 9.2% available and 8.4% of bear locations) and thick first-year ice (>120 cm; 15.5% and 28.5%, respectively). Old ice included sea ice that had survived at least one summer's melt and amounted to 66.0% of the ice coverage and 56.3% of bear locations.

Ice floes were defined as any relatively flat piece of ice  $\geq 20$  m across (Ice Centre Environment Canada; MANICE 1994). I grouped floe sizes into small floes (<500 m in width). This group accounted for 26.3% of the ice in the study area and 17.7% of polar bear locations. Medium floes (500-2000 m) made up 26.8% of the area and 24.7% of locations. Large ice floes (>2 km in width) amounted to 31.5% of the area and 37.2% of observations. Landfast ice forms and remains fast along the land masses. This category represented 7.9% of available floe sizes and 14.1% of bear locations.

To assess the characteristics of available ice, I systematically sampled the intersection points of a 100X100 km grid ( $n = 186$  points) across the study area that included only points on ice or within 5 km of ice cover. I used the sea-ice maps for each month to estimate availability of ice characteristics for each season (defined below).

#### **4.3.3 Habitat Selection Analysis**

Habitat use-availability analysis was done using standardized selection ratios (Manly 1974; i.e., the ratio of use and availability for each habitat category was standardized so that they add to 1; Manly et al. 1993, p. 40). Using multiple observations for each individual I estimated the resource selection probability function as recommended by Arthur et al. (1996) which takes into consideration temporal changes in ice cover. Other techniques of evaluating habitat selection assume availability of habitat is constant (Neu et al. 1974, Johnson, D.H. 1980, Chesson 1983, Alldredge and Ratti 1992). The resource selection probability function was estimated using the technique of maximum likelihood (Manly 1974). I used likelihood-ratio tests to compare models by testing if selection of habitats was selective or random. In the results, I refer to "selection" as a quantitative measure of the relative use of habitats (i.e., ranking) and avoid the terms "preference" and "avoidance" (Johnson

1980). Specifically, the selection index for each habitat type refers to the standardized selection ratios following assignment of ranks (Arthur et al. 1996).

Two conditions are necessary to consider sequential observations of an animal's position to be independent measurements of the animal's use of an area. First, the observations must be separated by sufficient time to allow an animal to select from available habitats and to avoid autocorrelations. Second, since radio-tracking studies obtain many observations per animal, observations from a given animal usually cannot be considered independent with respect to the population of animals (White and Garrot 1990). Within an animal, I assumed independence of data with respect to habitat choice because movements between successive satellite locations averaged 46.4 km (25% quartile = 16.4 km, 75% quartile = 61.8 km; see also Messier et al. 1992), compared to a median ice polygon width of 102 km (25% quartile = 60 km, 75% quartile = 176 km). However, a habitat selection analysis was performed for each bear individual to respect dependency of data within an animal.

I estimated available habitat using a circle centred on the bear's previous location (Arthur et al. 1996). I chose a 200-km radius for the circle corresponding to 99% quartile for bear distances between successive locations. For a short time scale, polar bears appear to move in a

near random fashion as shown by a fractal dimension of movement pathways approaching 2.0 (Ferguson et al. in press b).

#### 4.3.4 Time Series Analysis

I delineated four biological seasons according to ice phenology, shifts in food habits by polar bears, and seasonal changes in activity level and mobility of polar bears (Messier et al. 1992, Ferguson et al. in press a): winter (1 Nov. - 15 March), spring (16 March - 31 May), summer (1 June - 15 August), and autumn (16 August - 31 October). Mathematicians typically test monthly (1/12) or quarterly (¼) time series data for seasonal variations using smooth trigonometric functions (Bowerman and O'Connell 1993, Rinaldi et al. 1993, Turchin and Ostfeld 1997). The length of one complete cycle is  $2\pi$  radians. I transformed measures of time to radians ( $2\pi$ ) and used sine and cosine terms to represent trigonometric functions. Turchin and Ostfeld (1997) provide some empirical evidence that, although simplistic, a smooth sine wave adequately models seasonal variation of ecological variables. Therefore, I modelled cyclic variation of ice characteristics using the following equation:

$$y = b_1 + b_2 \sin \frac{2\pi t}{12} + b_3 \cos \frac{2\pi t}{12} + \epsilon_t \quad (1.0)$$

which describes a cycle repeating every 12 months. The  $b_i$  are regression coefficients that represent the expected value of the variable as a function of time,  $t$ , measured in months. I used least-squares regression models to estimate the regression coefficients.

To respect dependency of movement data, I fit separate curves for each animal and calculated the mean values and standard deviations of these values to estimate the response at the population level (degrees of freedom = number of bear\*years - 1). Amplitude and phase were calculated according to the following formulas:

$$amplitude = \sqrt{(b_2)^2 + (b_3)^2} \quad (1.1)$$

$$phase_{radians} = \arctan (b_2/b_3) \quad (1.2)$$

Phase was converted from radians to time units as follows:

$$\text{if } b_3 > 0 \text{ then } phase = phase_{radians}/2\pi$$

$$\text{if } b_3 < 0 \text{ and } b^2 < 0 \text{ then } phase = (phase_{radians} - \pi)/2\pi$$

$$\text{if } b_3 < 0 \text{ and } b^2 > 0 \text{ then } phase = (phase_{radians} + \pi)/2\pi.$$

#### 4.3.5 Statistical Analysis

To evaluate polar bear habitat selection, I considered the following effects: space (2 eco-regions), time (seasons: spring, summer, autumn, winter), and reproductive class. I used the following testing format: (1) a sine wave was fitted to each bear-year of data (12 mo for distance measures and 4 seasons for habitat use); (2) for each bear-year I calculated amplitude, phase, and level of the sine wave; and (3) these 3 parameters were tested using an ANOVA

for differences among region and reproductive class. I used a nonlinear curve-fitting function (SigmaPlot™, Jandel Scientific 1992) to graphically show the seasonal relationships. Other statistical methods of testing for seasonal differences (e.g., MANOVA) were impractical due to a mixture of repeated and independent measures among seasons (cf. Arthur et al. 1996). Year was not included in the model as the method of calculating habitat selection allowed for habitat availability to change over time (Arthur et al. 1996).

Analysis of variance (ANOVA) and regression analyses (Sokal and Rohlf 1969) were done using SAS™ statistical packages (SAS 1990). I used one- and two-way unbalanced fixed model ANOVAs (region and reproductive class fixed). Parsimonious criteria was used with the full model to eliminate the interaction term (region\*reprod) if insignificant (i.e.,  $P > 0.05$ ). I used independent ANOVAs for each ice variable. To avoid dependency, I did not include land (44.7% of study area) and open water (3.1 ± 0.65%) as categories for each variable (i.e.,  $n - 1$  comparisons), although both habitat categories were used by polar bears primarily during non-hunting activities (3 of 6943 bear observations were in habitat classed as open water while 1430 of 9443 observations were on land). All distance values were log-transformed to meet the assumptions of normality (Shapiro-Wilk Statistic:  $P >$



0.23). Results for distance to ice edges (km) were anti-logged for graphic presentation. Values are reported as mean  $\pm$  SE unless stated otherwise.

#### 4.4 Results

I measured habitat availability and selection based on 5,084 polar bear locations partitioned in 280 bear-seasons. Likelihood-ratio tests for all seasons found selection when data from all bears were pooled ( $P < 0.01$ ). Although the effect of season was statistically significant ( $P < 0.01$ ), this factor alone explained only 7.2-14.9% of variation in selection of ice characteristics ( $n = 14$  separate ANOVA tests). Including region and reproductive class improved the models ( $P < 0.001$ ) and explained more of the variation (33.1-47.4%).

##### 4.4.1 Physical Cycles

Changes in ice characteristics followed regular seasonal cycles that differed markedly between the two regions (Fig. 4.3). The ice of the Arctic Archipelago changed less dramatically (i.e., smaller amplitude) compared to Baffin Bay, which flushed almost completely of ice every year (Archipelago annual average ice cover was  $93.6 \pm 0.02\%$  versus  $74.4 \pm 0.05\%$  for Baffin;  $t = 3.80$ ,  $df = 98$ ,  $P < 0.001$ ).

Most areas in the Archipelago had 100% ice cover from December to June and >70% ice cover from August to November (Fig. 4.4a). Throughout the year, most ice (c. 60%) in the

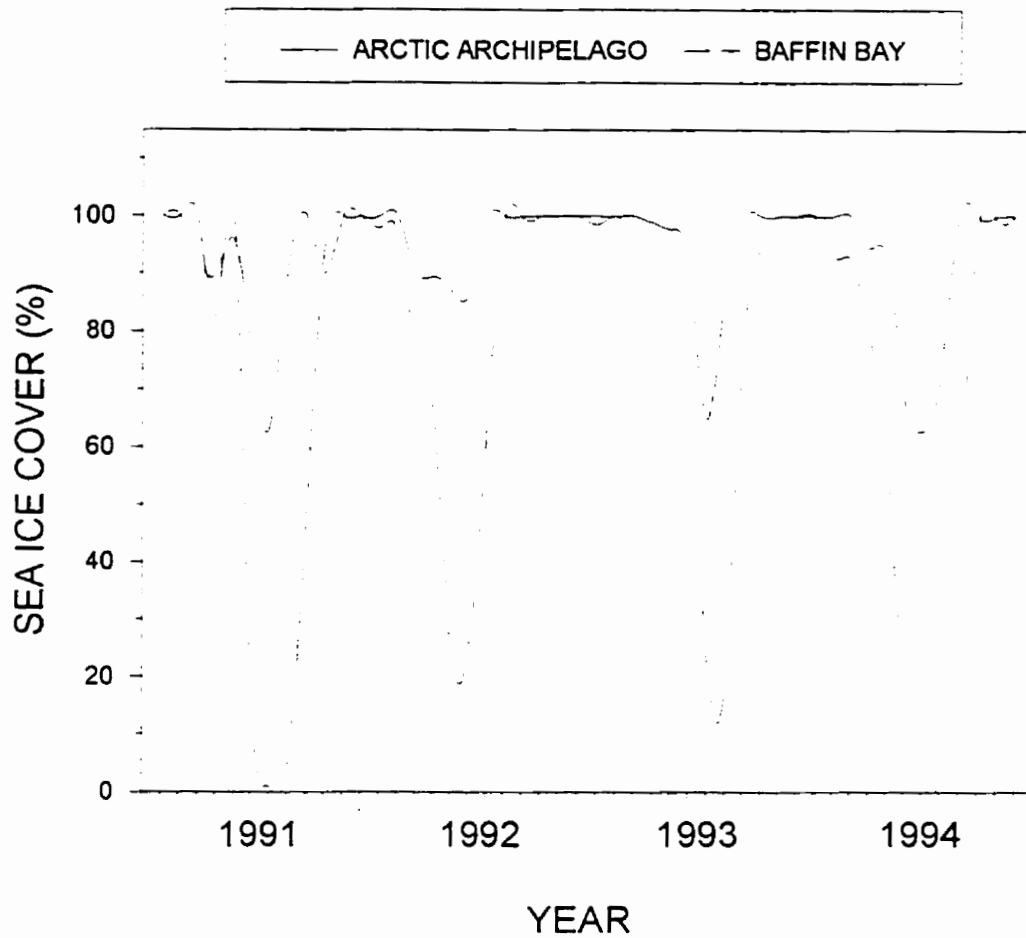


Figure 4.3 Seasonal changes in sea-ice coverage compared between the Arctic Archipelago and Baffin Bay, 1991-94.

Archipelago was multi-year ice (Fig. 4.5a). From February to July, the second most common ice type was first-year ice (20-30%) while from September to December new ice and thin first-year ice were common (10-15%). Landfast ice predominated in the Archipelago from January to April (40-50%) whereas large floes dominated from June to November (c. 40%; Fig. 4.6a).

In contrast, ice cover in the Baffin Bay region changed from 100% in winter to <25% in October (3% in 1991, 24% in 1992, 17% in 1993, and 2% in 1994; Fig. 4.3). From November to May, the Baffin Bay region was dominated by 95% ice coverage while bergy ice dominated from July to October during the melting season (Fig. 4.4b). Ice break-up and formation followed an annual cycle: new ice formed mainly in October and November, first-year ice dominated from November to January, thick first-year ice from February to July, and in August multi-year ice passed from the Archipelago out through Davis Strait (Fig. 4.5b). From February to June, large floes and landfast ice predominated, while small floes formed the major cover from August to December (Fig. 4.6b).

In contrast with the Archipelago, ice cover in Baffin Bay was characterized by greater distances to ice edges ( $49.6 \pm 0.1$  km versus  $15.4 \pm 0.3$  km,  $t = 16.2$ ,  $P < 0.001$ ), greater amplitude of seasonal changes in distances to ice edges ( $18.3 \pm 1.3$  km versus  $4.3 \pm 0.6$  km,  $t = 7.4$ ,  $P <$

BERGY 100% 95% 70-90% <70%

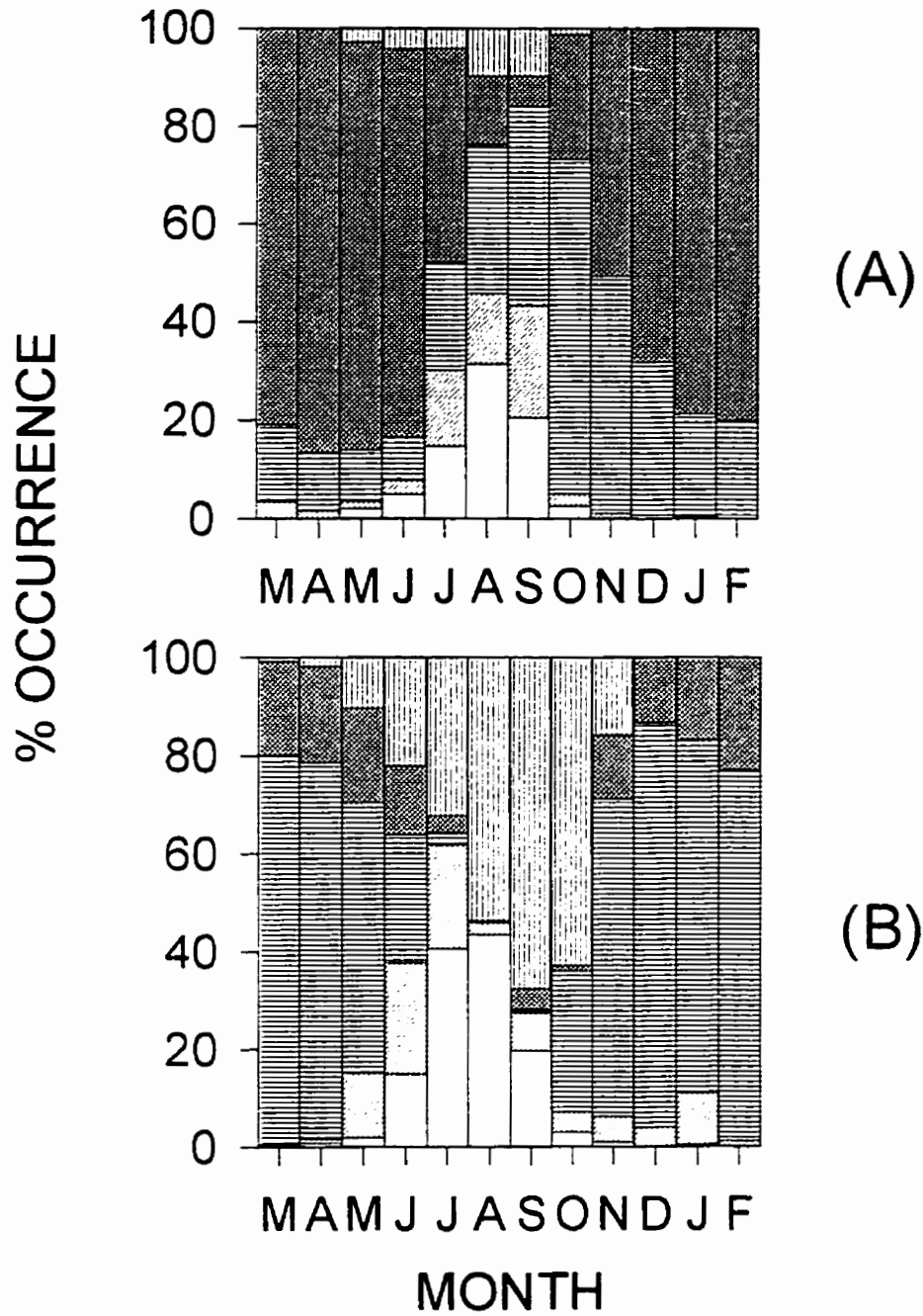


Figure 4.4 Seasonal changes in sea-ice cover for (A) the Arctic Archipelago and (B) Baffin Bay regions, 1991-94.

NEWICE
  FIRST YEAR
  THICK FIRST YEAR
  MULTI-YEAR

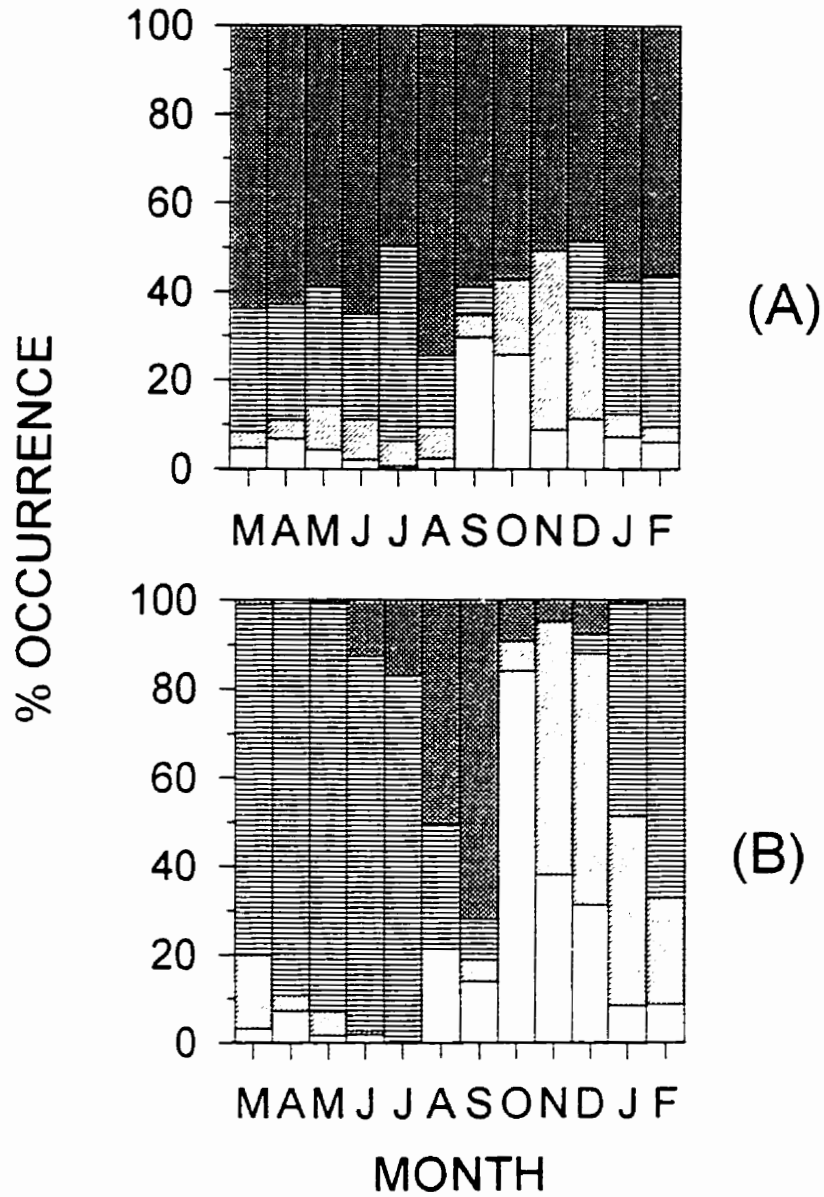


Figure 4.5 Seasonal changes in sea-ice thickness for (A) the Arctic Archipelago and (B) Baffin Bay regions, 1991-94.

LANDFAST
  LARGE
  MEDIUM
  SMALL

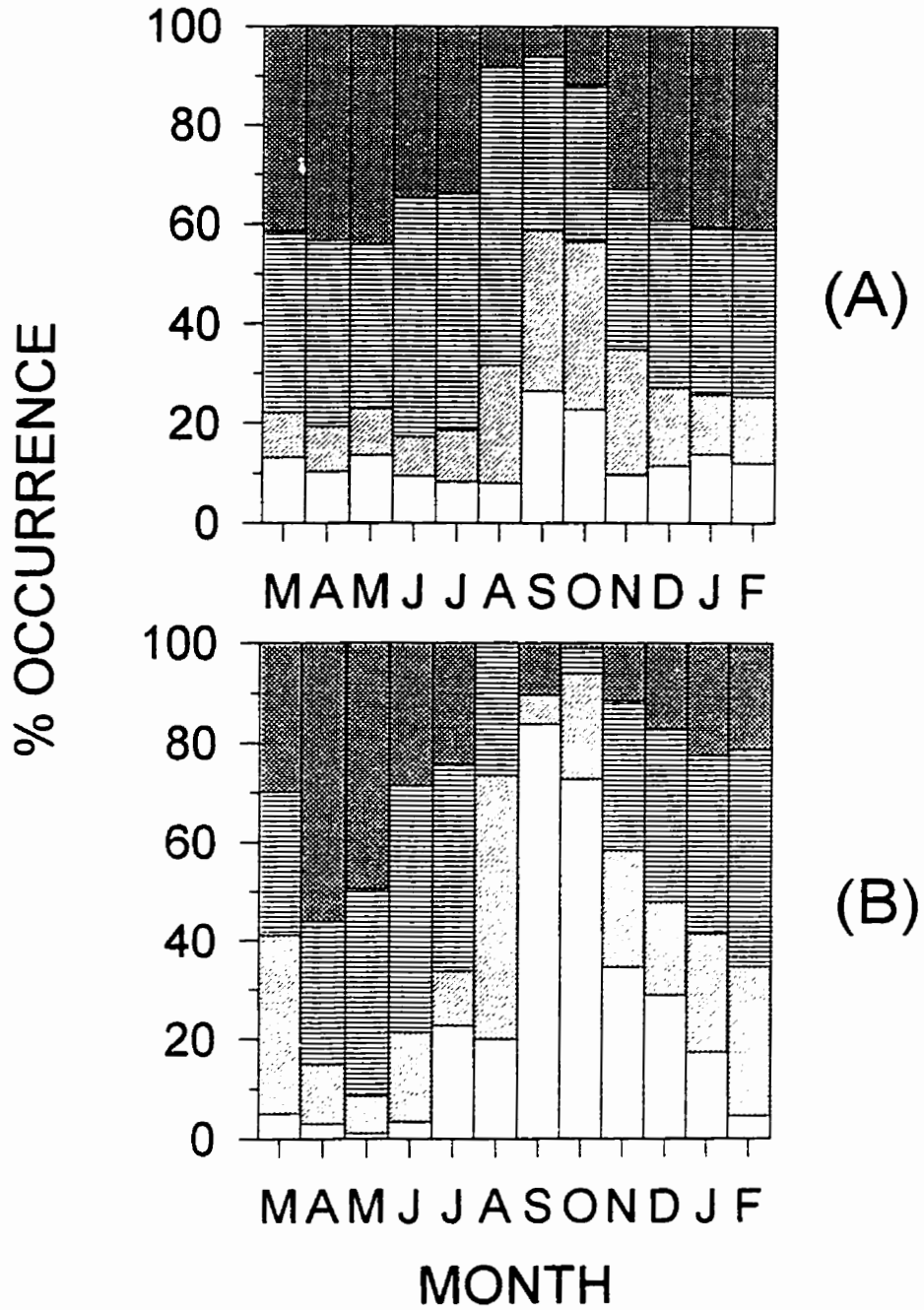


Figure 4.6 Seasonal changes in size of sea-ice floes for (A) the Arctic Archipelago and (B) the Baffin Bay regions, 1991-94.

0.001), as well as earlier peak distances to ice edges (i.e., phase; Sept.  $\pm$  0.4 months versus Dec.  $\pm$  0.8 months,  $t = 5.0$ ,  $P = 0.002$ ; Table 4.1).

The Arctic Archipelago had more closed ice (i.e., 100% ice cover) relative to the Baffin Bay region (58% versus 12%) whereas Baffin Bay had more partially open ice (i.e., 95% cover: 47% versus 27%, Table 4.2). The Baffin Bay region was also characterized by more bergy ice (22% versus 3%). The amplitudes of change in partially open ice and bergy ice were greater in Baffin Bay, whereas seasonal changes in complete ice cover (i.e., 100%) was greater in the Arctic Archipelago (Table 4.2). Differences in phase between the two regions were restricted to partially open ice, with Baffin Bay recording an earlier peak (March versus October in Archipelago;  $F_{1,95} = 113$ ,  $P < 0.01$ ).

The Arctic Archipelago had more multi-year ice (59 versus 15%) but less thick first-year ice (21% versus 49%; Table 4.3) than Baffin Bay. The amplitude in seasonal changes was greater for Baffin Bay for all ice thicknesses although not significantly so for first-year and multi-year ice. Multi-year ice recorded the only regional difference in phase with the peak occurring in August for Baffin Bay and May for the Arctic Archipelago ( $F_{1,79} = 4.2$ ,  $P = 0.04$ ).

The Arctic Archipelago had more fast ice (31% versus 23%;  $P = 0.06$ ) and less ice with small floes (13% versus

Table 4.1. ANOVA tests of availability and selection of ice edges by polar bears living in two regions of the Canadian Arctic (Arctic Archipelago and Baffin Bay). Available ice was assessed from systematic point sampling across the study area ( $n = 132$ ). Selection by polar bears was derived from satellite telemetry locations from 110 bear-years of tracking.

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Distance to ice edges (km):

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		<u>Available</u>			
	<i>df</i>	<i>F</i>	<i>P</i>	Arctic Archipelago	Baffin Bay
Mean level (km):					
Region	1,131	13.4	<0.001	15.4 (63)	49.6 (69)
Amplitude (km):					
Region	1,131	77.8	<0.001	4.3 (63)	18.3 (69)
Phase (month):					
Region	1,131	10.1	0.002	Dec (63)	Sept (69)
		<u>Selection</u>			
Mean level (km):					
Class <sup>1</sup>	2,109	0.2	0.80		
Region	1,109	37.6	<0.001	16.6 (74)	35.3 (36)
ClasXreg <sup>2</sup>	5,109	9.5	<0.001		
Amplitude (km):					
Class	2,109	0.7	0.49		
Region	1,109	34.8	<0.001	12.5 (74)	32.6 (36)
ClasXreg	5,109	0.6	0.55		
Phase (month):					
Model	5,109	0.6	0.67		

<sup>1</sup> reproductive class: females with cubs-of-the-year, females with yearlings, females without cubs

<sup>2</sup> interaction term



Table 4.2. ANOVA tests of availability and selection of different percent cover of sea ice by polar bears living two regions of the Canadian Arctic (Arctic Archipelago and Baffin Bay). Available ice was assessed from systematic point sampling across the study area ( $n = 96$ ). Selection by polar bears was derived from satellite telemetry locations ( $n = 39$  bear-years of tracking) and classified satellite images of sea-ice characteristics.

Ice cover:	Open <70%	Medium 70-90%	Partial 95%	Closed 100%	Bergy <10%
<u>Available</u>					
Mean level (%):					
Region (1,95) <sup>1</sup>	n.s. <sup>2</sup>	n.s.	*** <sup>3</sup>	***	***
Archipelago (48)			27.3	58.1	2.7
Baffin Bay (48)			47.2	12.2	22.2
Amplitude (%):					
Region (1,95)	n.s.	n.s.	**	***	**
Archipelago (48)			21.9	38.0	4.7
Baffin Bay (48)			43.4	10.8	33.3
<u>Selection</u>					
Mean level (habitat selection index) <sup>4</sup> :					
Class <sup>5</sup> (2,38)	n.s.	n.s.	n.s.	n.s.	n.s.
Region (1,38)	n.s.	*	***	***	**
RegionXclass	n.s.	n.s.	n.s.	n.s.	n.s.
Arctic Archipelago (21)		0.050	0.311	0.551	0.018
Baffin Bay (18)		0.113	0.521	0.177	0.071
Amplitude (habitat selection index):					
Class (2,38)	n.s.	n.s.	n.s.	n.s.	n.s.
Region (1,38)	n.s.	n.s.	n.s.	**	n.s.
RegionXclass	n.s.	n.s.	n.s.	n.s.	n.s.
Arctic Archipelago (21)				0.342	
Baffin Bay (18)				0.113	

<sup>1</sup> degrees of freedom

<sup>2</sup> not significant ANOVA results ( $\alpha < 0.05$ )

<sup>3</sup> probability ( $P$ ): \*  $0.05 < P < 0.01$ ; \*\*  $0.01 < P < 0.001$ ; \*\*\*  $P < 0.001$

<sup>4</sup> habitat selection index calculated according to Arthur et al. (1996): 0 not selected and 1 highly selected.

<sup>5</sup> reproductive class: females with cubs-of-the-year, females with yearlings, females without cubs

Table 4.3. ANOVA tests of availability and selection of different sea-ice thickness by polar bears living in two regions of the Canadian Arctic (Arctic Archipelago and Baffin Bay). Available ice was assessed from systematic point sampling across the study area ( $n = 96$ ). Selection by polar bears was derived from satellite telemetry ( $n = 30$  bear-years of tracking) and classified satellite images of sea-ice characteristics.

Ice thickness:	New <30 cm	First Year 30-120 cm	Thick >120 cm	Multi-Year >1 yr
<u>Available</u>				
Mean level (%):				
Region (1,95) <sup>1</sup>	n.s. <sup>2</sup>	n.s.	*** <sup>3</sup>	***
Archipelago (48)			20.9	58.6
Baffin Bay (48)			48.6	14.7
Amplitude (%):				
Region (1,95)	*	n.s.	***	n.s.
Archipelago (48)	8.9		16.3	
Baffin Bay (48)	26.1		51.0	
<u>Selection</u>				
Mean level (habitat selection index) <sup>4</sup> :				
Class <sup>5</sup> (2,29)	n.s.	n.s.	n.s.	n.s.
Region (1,29)	**	n.s.	**	***
RegionXclass	n.s.	n.s.	n.s.	n.s.
Archipelago (17)	0.075		0.451	0.370
Baffin Bay (13)	0.156		0.601	0.097
Amplitude (habitat selection index):				
Class (2,29)	n.s.	n.s.	n.s.	n.s.
Region (1,29)	n.s.	n.s.	n.s.	n.s.
RegionXclass	n.s.	n.s.	n.s.	n.s.

<sup>1</sup> degrees of freedom

<sup>2</sup> not significant ANOVA results ( $\alpha < 0.05$ )

<sup>3</sup> probability (P): \*  $0.05 < P < 0.01$ ; \*\*  $0.01 < P < 0.001$ ; \*\*\*  $P < 0.001$

<sup>4</sup> habitat selection index calculated according to Arthur et al.

(1996): 0 not selected and 1 highly selected.

<sup>5</sup> reproductive class: females with cubs-of-the-year, females with yearlings, females without cubs

Table 4.4. ANOVA tests of availability and selection of different sea-ice floe size by polar bears living in two regions of the Canadian Arctic (Arctic Archipelago and Baffin Bay). Available ice was assessed from systematic point sampling across the study area ( $n = 95$ ). Selection by polar bears was derived from satellite telemetry ( $n = 29$  bear-years of tracking) and classified satellite images of sea-ice characteristics.

Ice floe size:	Small <500 m	Medium 500-2000 m	Large >2000 m	Landfast Ice
	<u>Available</u>			
Mean level (%):				
Region (1,95) <sup>1</sup>	* <sup>2</sup>	n.s. <sup>3</sup>	n.s.	n.s.
Archipelago (48)	13.2			
Baffin Bay (48)	24.8			
Amplitude (%):				
Region (1,95)	•	n.s.	n.s.	n.s.
Archipelago (48)	8.9			
Baffin Bay (48)	26.1			
	<u>Selection</u>			
Mean level (habitat selection index) <sup>4</sup> :				
Class <sup>5</sup> (2,28)	n.s.	n.s.	n.s.	n.s.
Region (1,28)	*	*	n.s.	***
RegionXclass	n.s.	n.s.	n.s.	n.s.
Archipelago (17)	0.100	0.145		0.404
Baffin Bay (12)	0.171	0.234		0.160
Amplitude (habitat selection index):				
Class (2,28)	n.s.	n.s.	n.s.	n.s.
Region (1,28)	n.s.	n.s.	n.s.	n.s.
RegionXclass	n.s.	n.s.	n.s.	n.s.

<sup>1</sup> degrees of freedom

<sup>2</sup> probability (P): \*  $0.05 < P < 0.01$ ; \*\*  $0.01 < P < 0.001$ ; \*\*\*  $P < 0.001$

<sup>3</sup> not significant ANOVA results ( $\alpha < 0.05$ )

<sup>4</sup> habitat selection index calculated according to Arthur et al. (1996): 0 not selected and 1 highly selected.

<sup>5</sup> reproductive class: females with cubs-of-the-year, females with yearlings, females without cubs

25%) than Baffin Bay (Table 4.4). Also, the amplitude in small floes was greater in Baffin Bay (0.32 versus 0.13). No differences in phase occurred between the two regions with respect to floe size.

#### 4.4.2 Polar Bear Cycles

With differing seasonal ice conditions, polar bear selection of ice habitat differed between the two regions. During the spring and summer, Archipelago bears selected 100% ice cover of thick first-year ice found largely as landfast ice. In contrast, Baffin bears selected 95% ice cover of thick first-year ice found in large ice floes during spring and summer. Similarities in selection of ice occurred with bears selecting first-year ice in winter in both regions. However even at this time, bears in the Archipelago selected landfast ice whereas Baffin bears selected large floes. During autumn, female polar bears from both regions selected 95% ice cover of multi-year ice.

Female polar bears were found closer to ice edges than a random distribution ( $24.9 \pm 4.2$  km,  $n = 109$ , versus  $33.3 \pm 0.52$  km,  $n = 131$ ,  $t = 12.5$ ,  $P < 0.001$ ). Seasonal changes (i.e., amplitude of sine wave) in selection of ice edge was greater for polar bears ( $19.1 \pm 1.8$  km,  $n = 110$ ) than available ( $13.3 \pm 0.9$  km,  $n = 131$ ;  $t = 2.4$ ,  $P = 0.02$ ). Whereas Baffin bears were closer to ice edges than expected from April to July, no significant differences were found for Archipelago bears (Fig. 4.7). Also, female polar bears

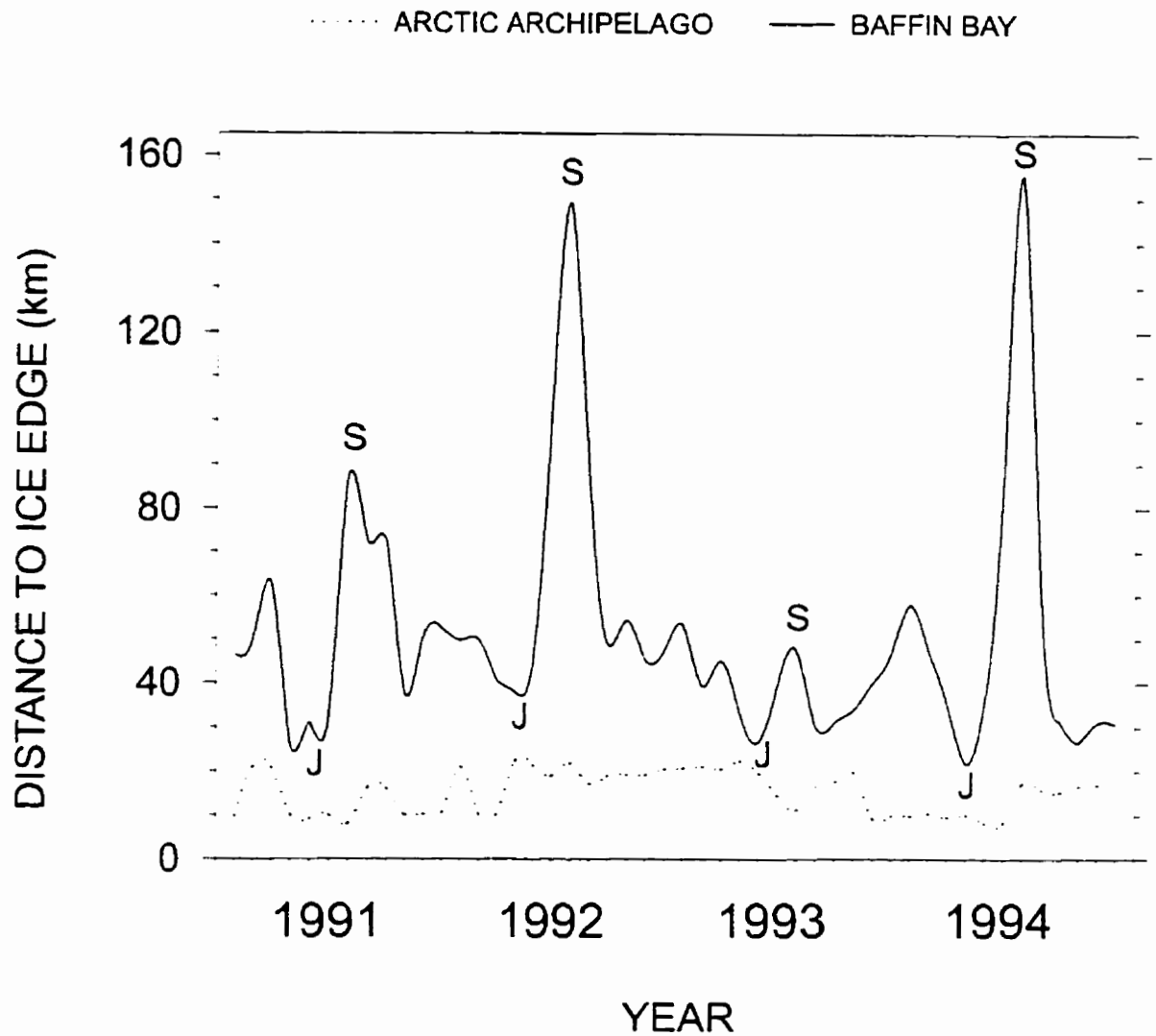


Figure 4.7 Seasonal cycle of distance to sea-ice edges used by female polar bears in the Arctic Archipelago and Baffin Bay regions, 1991-94 (J = June, S = September).

in the Baffin Bay region were closest to ice edges in late spring and early summer and farthest in September while on land (Fig. 4.7). Seasonal changes in selection of distance to ice edge was greater for Baffin bears than Archipelago bears ( $32.6 \pm 2.1$  km versus  $12.5 \pm 1.3$  km,  $t = 14.1$ ,  $P < 0.001$ ).

Differences among reproductive classes occurred in the Arctic Archipelago region during the spring to summer period (Fig. 4.8). From April through July, solitary adult females were closer to ice edges ( $13.3 \pm 0.6$  km,  $n = 716$ ) than either females with cubs-of-the-year ( $18.7 \pm 0.8$  km,  $n = 589$ ) or females with yearlings ( $16.6 \pm 1.0$  km,  $n = 260$ ,  $F_{2,1564} = 6.0$ ,  $P = 0.003$ ). Females with cubs-of-the-year showed the greatest amplitude compared to other females ( $14.4$  km versus  $3.8$  km). Also, females with cubs-of-the-year were found closest to ice edges in November (i.e., phase) compared to July for other females ( $F_{2,1564} = 3.4$ ,  $P = 0.014$ ).

Female bears selected partially open (i.e., 95%) and closed (i.e., 100%) ice relative to other ice cover categories (Fig. 4.9). In a comparison of selection among bears from the two regions, Arctic Archipelago bears selected closed ice more than Baffin Bay bears (0.55 versus 0.18 mean habitat selection) whereas bears in Baffin Bay selected medium ice cover (70-90%; 0.11 versus 0.05), partially closed ice (0.52 versus 0.31), and bergy ice

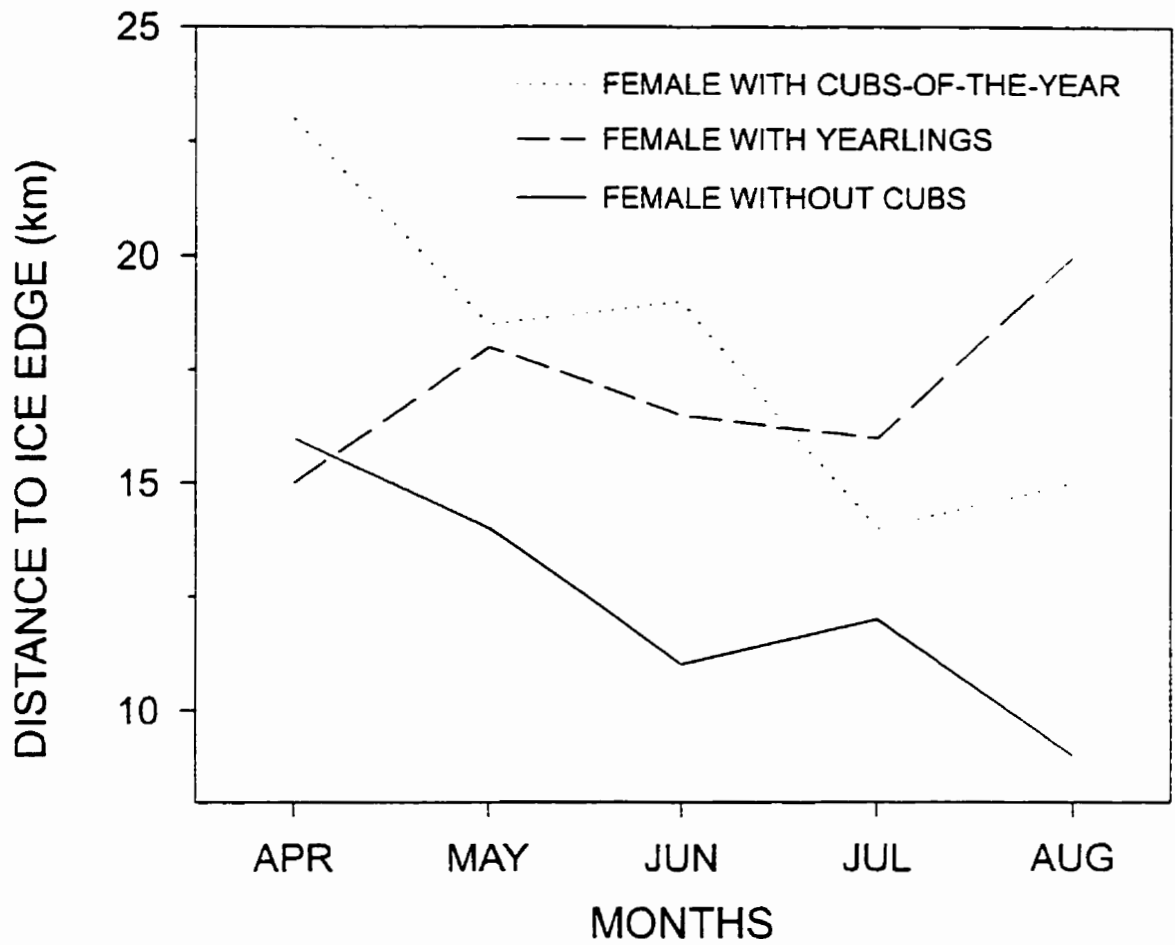


Figure 4.8 Seasonal cycle of distance to sea-ice edges used by three reproductive classes of female polar bears in the Arctic Archipelago.

BERGY —○— <70% —□— 70-90% —◇— 95% —△— 100%

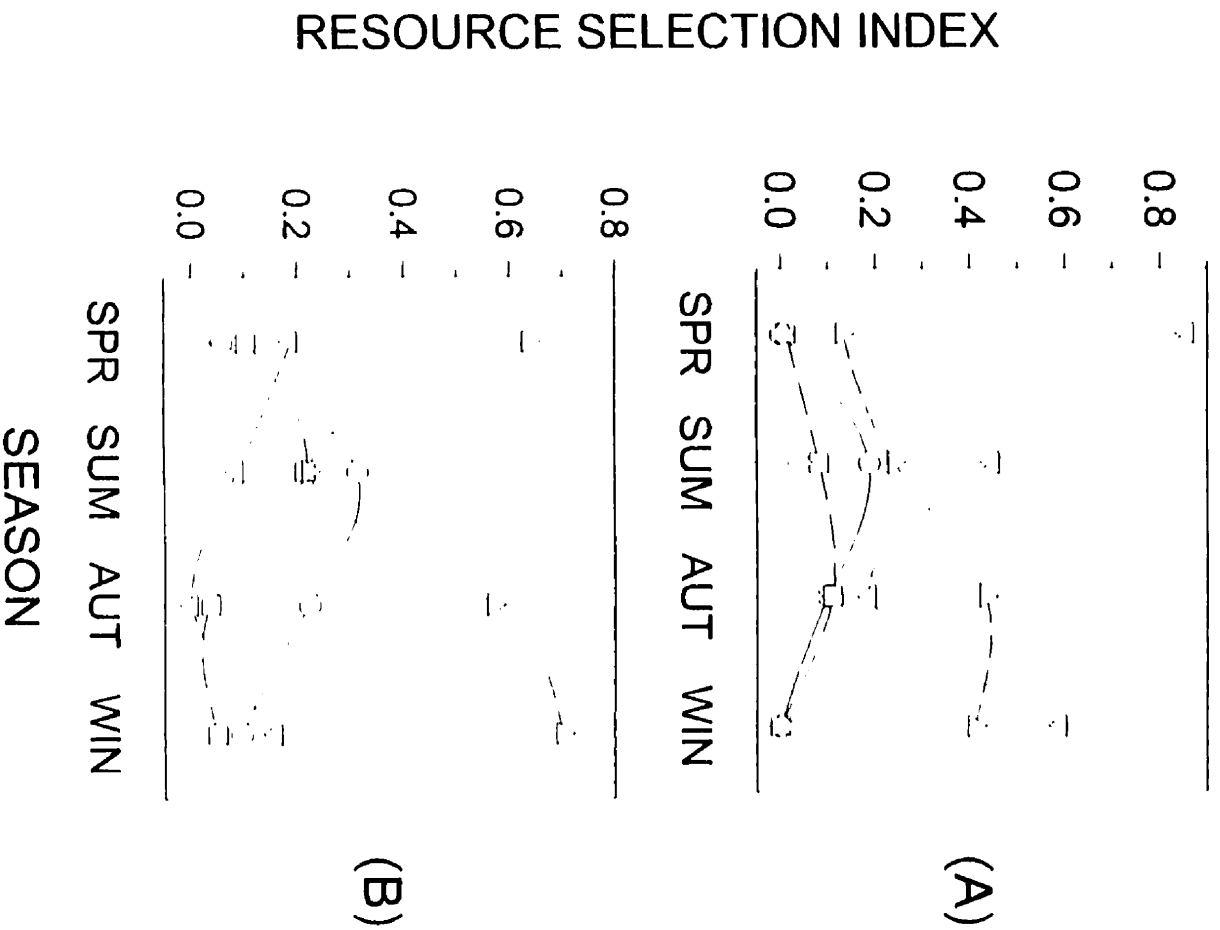


Figure 4.9 Seasonal cycle in selection by female polar bears of five sea-ice cover types found in (A) the Arctic Archipelago and (B) Baffin Bay regions, 1991-94. Resource selection index calculated according to Arthur et al. (1996) where 1 indicates highly selected.



(0.07 versus 0.02; Table 4.2). Amplitude differed significantly between the two regions for closed ice cover, where Archipelago bears showed greater amplitude than Baffin bears (Table 4.2). Time of peak preference (i.e., phase) for partially closed ice cover occurred in autumn for Archipelago bears compared to winter for Baffin Bay bears ( $F_{1,79} = 83.7, P < 0.01$ ).

Polar bears selected thick first-year ice in spring and summer while multi-year ice was selected in autumn relative to other ice thickness categories (Fig. 4.10). Bears in the Arctic Archipelago selected multi-year ice more than Baffin bears (0.37 versus 0.10; Table 4.3). In contrast, Baffin bears selected new ice (0.16 versus 0.08) and thick first-year ice (0.60 versus 0.45) more than Arctic Archipelago bears. No differences in amplitude or phase were found for selection of ice thickness.

Female polar bears selection for floe sizes varied considerably between the two regions (Fig. 4.11). The Arctic Archipelago not only had considerably more landfast ice than Baffin Bay but Archipelago bears showed greater selection for landfast ice, particularly in winter and spring (0.40 versus 0.16 in Baffin Bay). Large floes were selected by Archipelago bears in summer and autumn. Baffin bears showed less selection for landfast ice relative to Archipelago bears and Baffin bears selected large floes in

—○— NEW    -□- FIRST YEAR    -△- THICK    -◇- MULTI-YEAR

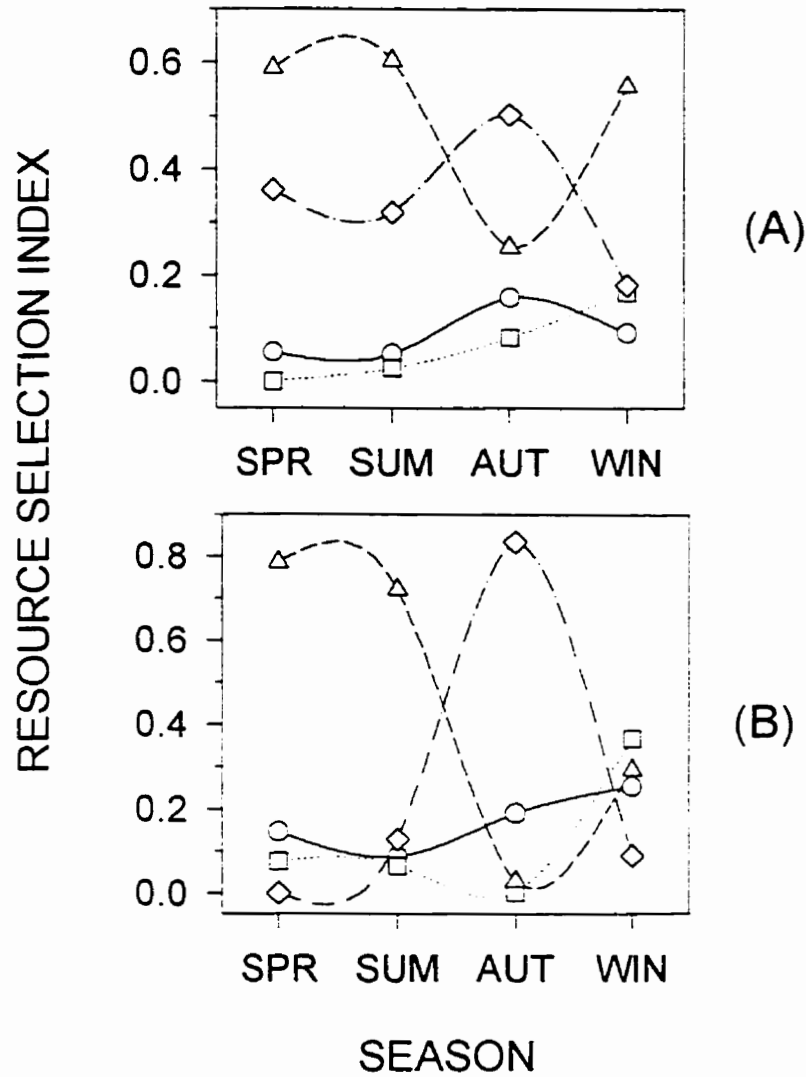


Figure 4.10 Seasonal cycle in selection by female polar bears of four ice age (thickness) found in (A) the Arctic Archipelago and (B) Baffin Bay regions, 1991-94. Resource selection index calculated according to Arthur et al. (1996) where 1 indicates highly selected.

—○— SMALL ···□··· MEDIUM —△— LARGE —◇— LANDFAST

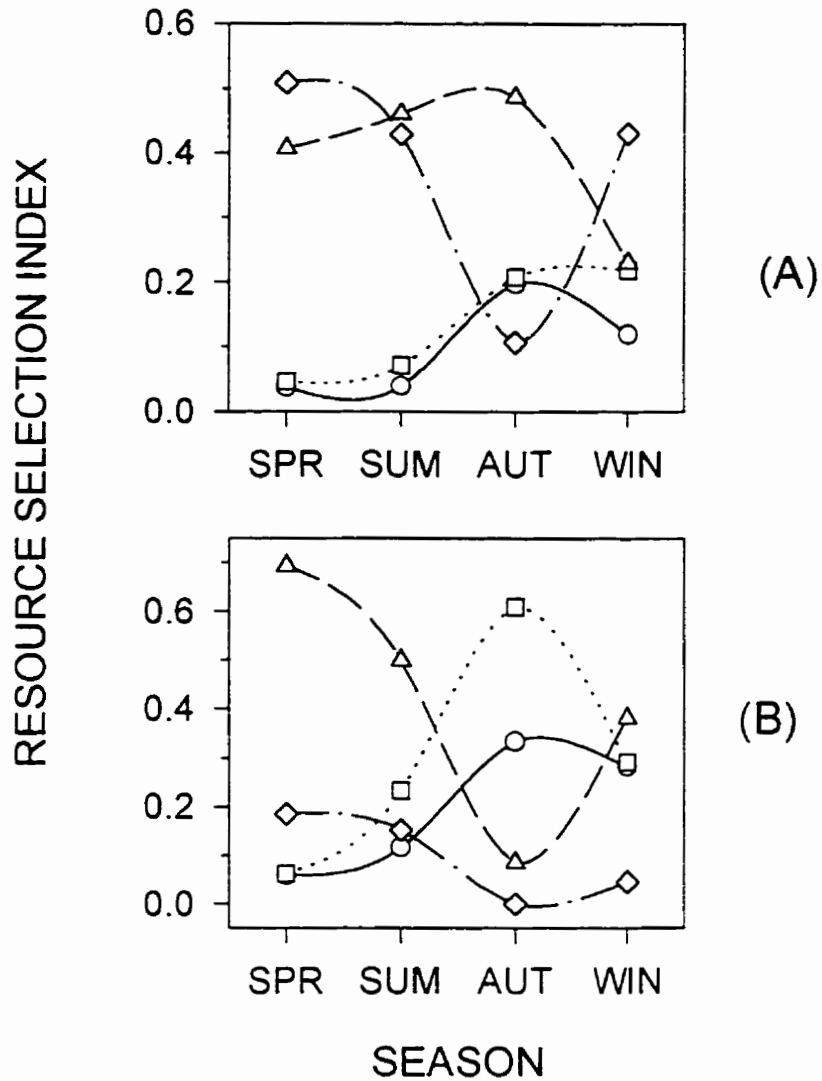


Figure 4.11 Seasonal cycle in selection by female polar bears of four sizes of sea-ice floes found in (A) the Arctic Archipelago and (B) Baffin Bay regions, 1991-94. Resource selection index calculated according to Arthur et al. (1996) where 1 indicates highly selected.

spring and summer relative to other ice types ( $P = 0.07$ ; Table 4.4).

Differences in timing of selection (i.e., phase) of floe size by female polar bears differed between the two regions. Indications of an earlier peak in selection of medium ( $P = 0.05$ ), large ( $P = 0.11$ ), and landfast ( $P = 0.20$ ) floes occurred for Archipelago bears compared to Baffin bears. Although amplitudes did not differ significantly between regions, the overall mean amplitude of the seasonal sine wave for selection of floe sizes by polar bears ( $0.297 \pm 0.021$ ,  $n = 4$ ) was greater than available ( $0.173 \pm 0.016$ ,  $n = 4$ ;  $t = 4.72$ ,  $P = 0.003$ ).

#### 4.5 Discussion

Our study demonstrated that polar bears respond to fluctuations in sea ice characteristics. Previous research has focused on the spatial response by polar bears to patterning in sea ice (Ferguson et al. submitted) and changes in body size to seasonal fluctuations in sea ice and associated prey (Stirling and Archibald 1977, Ramsay and Stirling 1988, Atkinson and Ramsay 1995). Here, I describe temporal variation by polar bears to seasonal cycles in arctic ice characteristics. Polar bears reacted to seasonal sea-ice cycles in a number of ways. First, the level of seasonal variation differed. For example, Arctic Archipelago bears selected closed ice cover (100%) more than Baffin Bay bears. Second, the amplitude of seasonal

variation differed. For example, selection for multi-year ice showed greater seasonal variation by female polar bears in the Baffin Bay region than in the Arctic Archipelago region. Third, the rate of response to changes in the ice conditions may differ from the fluctuations in the level of resources. For example, female polar bears with cubs-of-the-year were found at their closest to ice edges in autumn whereas solitary females were closest during spring when the amount of ice edge peaked. Therefore, a phase shift likely occurred in the response by females with cubs-of-the-year to the seasonal cycle of available ice edge.

I found similarities in seasonal variation between polar bears and their physical environment. Here, I make the simplifying assumption that seasonal changes in ice reflect changes in resources for polar bears when actual trophic level interactions occur from changes in ice cover to phytoplankton production up to seal distribution and abundance. Habitat selection by female polar bears in the Arctic Archipelago and Baffin Bay regions were strongly influenced by seasonal patterns of sea ice. Other researchers have noted that movements of polar bears follow the development of ice cover during autumn and winter and the receding of the ice pack in spring and summer (Larsen et al. 1983, Garner et al. 1990, Amstrup and Gardner 1991). A major difference between the Arctic Archipelago and Baffin Bay regions is the extent to which the ice pack

recedes. In Baffin Bay, sea ice almost completely disappears in autumn while in the Archipelago, sea ice is interrupted and constricted by land masses and shows less seasonal differences in cover.

The distribution and seasonal movements of ice affects the availability of ringed and bearded seals as prey for polar bears (Stirling and Archibald 1977, Smith 1980, Stirling et al. 1993). Seals tend to be abundant in areas with naturally occurring open water, such as in open leads, floe edges, or spaces between unstable ice floes. The ice classification of 95% cover areas of thick first-year ice found in large floes is equivalent to "moving ice" for the eastern Beaufort region (Stirling et al. 1993). Seals prefer these open water areas presumably because they offer breathing areas and also because of greater productivity (Bradstreet and Cross 1982). "Moving ice" areas are also where seals are vulnerable to polar bear predation (Stirling et al. 1993), particularly subadults (Stirling and Archibald 1977, Stirling and Øritsland 1995). Also, polar bear predation on ringed seals peaks during spring (Stirling and Archibald 1977, Smith 1980, Ramsay and Stirling 1986, Messier et al. 1992). I found that female polar bears selected "moving ice" habitat (i.e., 95% cover, thick-first year, large floes) in Baffin Bay during spring and summer and that female polar bears use of ice edge habitat also peaked in spring.

Whereas the availability of annual ice is a major influence on ice use by polar bears for the Baffin Bay region, the temporal and spatial distribution of landfast ice has major consequences for habitat selection for Arctic Archipelago bears. The Arctic Archipelago ice environment differs from the Baffin Bay region in having (1) mostly multi-year ice, (2) less variable seasonal ice changes, and (3) less open water. The Arctic Archipelago landfast ice areas (i.e., 100% ice cover, thick first-year ice, fast ice) selected by female polar bears in spring and summer were likely areas suitable for the birth lairs of ringed seals. The seals available in this habitat are predominately breeding adult ringed seals that reside there all winter (McLaren 1958, Smith and Stirling 1975). In spring, female ringed seals create subnivean lairs and give birth to pups that are weaned at six weeks of age (McLaren 1958, Smith and Stirling 1975, Stirling and McEwan 1975). Polar bears break through the snow cover over a lair and prey on pups (Stirling 1974, Stirling and Archibald 1977).

Leads in pack ice of the Canadian Arctic Archipelago can be as narrow as 1 m wide or up to several kilometres wide, depending on winds. Annual ice forms between multi-year floes during winter, providing important areas where seals are able to maintain breathing holes (Stirling 1997). Satellite tracking of polar bears indicated that when they are in multi-year ice, bears are often associated with

leads (Stirling 1997) which is similar to observations from bears in areas dominated by annual ice (Stirling et al. 1993). I found female polar bears closer to ice edges and coastline than expected, particularly from April to July. This is the season when polar bears experience the greatest seal hunting success (Ramsay and Stirling 1988).

Habitat selection by polar bears is likely influenced by the availability of their main prey - ringed seals. A general latitudinal cline occurs from low seal density in year-round ice areas to greater seal density in areas with greater seasonal changes in ice extent. Kingsley et al. (1985) and Stirling and Øritsland (1995) reported that the density of ringed seals in multi-year ice is significantly less than in annual ice. Likely, this trend is a result of the difficulty of maintaining breathing holes in multi-year ice and the greater productivity of annual ice (Stirling et al. 1993, Stirling 1997). Kingsley et al. (1985) reported the lowest densities of ringed seals ( $0.28 \text{ seals} \cdot \text{km}^{-2}$ ) in the most northerly areas receiving nutrient-poor water from the polar basin and largely covered by thick multi-year ice (little light for photosynthesis). The Barrow Strait area, which consists of mixed pack and fast ice, was preferred by ringed seals and had average densities of  $0.97 \text{ seals} \cdot \text{km}^{-2}$  (Kingsley et al. 1985, Stirling and Lunn 1996). Density of seals recorded in similar areas of offshore pack ice in northwestern Baffin Bay were  $1.4 \text{ seals} \cdot \text{km}^{-2}$  (Finley et al.



1983). In similar habitat, but with greater seasonal changes in annual ice cover, density of ringed seals along the coast of southeastern Baffin Island were 2.1 seals·km<sup>-2</sup> (Stirling and Øritsland 1995).

Research in the eastern Beaufort Sea (Stirling et al. 1993) and northeast Greenland (Born et al. 1997) found that in late winter and spring, females accompanied by cubs-of-the-year preferred fast ice, while males and females of other reproductive classes preferred floe-edges and offshore moving ice. They attributed this preference to an avoidance of males that might prey upon cubs as observed in related species (e.g., *Ursus arctos*, May-June in Sweden, Swenson et al. 1997). During spring in the Arctic Archipelago I found females with cubs-of-the-year farther from ice edges than solitary females and females with yearlings.

One goal in ecological studies of a particular species is to determine the relevant features of their environment. I used an approach that focused on the species-specific response to environmental fluctuations. This response can be through body size, spatial distribution and timing of life history events. Organisms can alter behaviour and reproduction to buffer fluctuations in the physical environment. Using the sine wave approach allows for a description of how organisms respond to cyclic variation. I conclude that the significant responses by polar bears to

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## 5.0 GENERAL DISCUSSION

As Schrödinger (1992) and Ho (1993) asked the question: what is life? I begin this discussion with the question: what is a species? We can start by defining organisms not as molecular machines but rather as functional and structural unities resulting from a self-organizing, self-generating dynamic (Goodwin 1994). Organisms are systems that can produce a whole from a part, thereby regenerating their own natures (Thompson 1942). We usually describe the nature of an organism in terms of the properties of the species to which it belongs. The speciation process operates at the level of populations and embodies the ontological development of individual organisms (Wright 1996). An organism involves the following dimensions: it is spatial, both by the pattern of parts that defines its morphology and by the physical location in space that it occupies; it is temporal, involving particular patterns of activity that define behaviour, and living in a particular geological time context; it has momentum, such as the maternal effects seen in life history; and it has energy, such as seen in optimal foraging. A member of a species is recognized by these features. These are qualities, the expression of an integrated whole; they are not quantities, the sum of separately existing parts. So we may say that organisms

express their natures through the particular qualities of their form in space, time, momentum, and energy (Ho 1993).

Hence, an organism of a particular species is an integrated whole with a particular set of characteristics that allows it to function in its environment, pursuing its life cycle. Conventionally, natural selection describes the dynamics of the interaction of these life cycles with their environments and an adaptation makes a species better able to survive in a particular habitat. The question arises as to whether the process of evolving organisms is best described as one in which there is progressive adaptation to changing environments? Many species possess striking adaptations to their habitats. But there are just as many characteristics that are not adapted (Gould and Lewontin 1979).

The relevant image of evolving systems is dynamic stability (Kauffman and Johnsen 1991, Ho 1993). A species' life cycle maintains dynamic stability within a particular environment. This stability refers to the dynamics of the whole cycle, involving the whole organism as an integrated system. The organismic system integrates itself into a greater system called community. Focusing on the changes that can occur in the parts of an organism provides information about the small-scale, or local, aspects of organismic plasticity. The extent to which a polar bear can swim better or dive for longer periods are examples of

small changes from their brown bear ancestors. Darwin believed that the sum of these small-scale changes explained the large-scale properties of evolution (see Ho and Saunders 1984). However, there is no evidence for the gradual emergence of any evolutionary novelty by the accumulation of small adaptive modifications (Mayr 1988). New species seem to arrive on the scene and remain pretty much unchanged during their long or brief lifetimes (Gould 1989). The problem is still the origin of species: adaptation does not explain the major, large-scale features of evolution.

The problem of origins requires, first, an understanding of how new levels of order emerge from complex patterns of interaction and, second, an understanding of the properties of these emergent structures relative to their robustness to perturbation and their capacity for self-maintenance (Kauffman 1993). New levels of order emerge from large-scale landscape transformations that can give rise to macroevolutionary changes such as speciation. The most recent major macroevolutionary change occurred 2.5 mya when an abrupt increase in the scale of glacial cycles in the northern hemisphere resulted in the formation of the arctic ecosystem (Vrba 1992, Bartlein and Prentice 1989, Bush 1994). Speciation by marine life forms such as cod and seals created new trophic interactions.

The peculiar features of sea ice presented the opportunity for a marine predator of seals. Such a predator required terrestrial adaptations to use the sea ice platform for long-distance travel and employ terrestrial ambush techniques. Indeed, all large marine mammals that cover large seasonal ranges in an annual cycle are forced out of ice-covered areas during winter. Using a terrestrial-like hunting strategy, polar bears can capture some arctic marine mammals that require breathing holes and above-water birth lairs. Brown bears were already preadapted for these predatory characteristics, as well as possessing life-history traits favourable to high latitude environments (Ferguson et al. 1996). Even today, brown bears that wander onto the sea ice are able to survive through predation of seals (Taylor 1995). Once such a precursor to polar bears began to live off the seals among the arctic sea ice then the speciation event occurred.

The emergent properties of the arctic ecosystem have shown robustness to perturbations (Dyke et al. 1996). The system's capacity for self-maintenance is shown by the stability of microevolutionary dynamics that have lead to population differentiation within a species. Following speciation, polar bear evolution appears to follow a pattern of population stability with the geographic range for the species restricted to the seasonally variable sea ice. Natural selection now serves as a stabilizing force

due to exchanges among populations at the time of breeding. This dynamic stability weaves the hierarchical spatial structure of polar bear populations within a circumpolar metapopulation that fits the fractal pattern of sea ice created by the interspersion of arctic islands.

The approach I have just outlined to understand evolution and how sea ice and polar bear systems interact required a study of processes over events, relationships over entities, and development over structure (e.g., Ingold 1990). This view highlights the importance of the choice of scientific methods. Scientific reductionism has successfully helped western industrial society understand quantitative aspects of internal details (Cohen and Stewart 1994). In contrast, current understanding of external large-scale effects is mostly descriptive and qualitative, geometric rather than numerical (Hengeveld 1992). For example, researchers can recognize pattern from satellite photos but they cannot predict what it's going to do. Science needs to combine the best aspects of these two approaches.

An example of the 'reductionist tree of everything' comes from my research on polar bears' use of land. The initial question I addressed was what determines spatial distribution of individual polar bears while on land. Four factors were considered important: regional philopatry, pattern of sea ice ablation and formation, avoidance of

conspecifics, and selection of den and shelter sites. Of particular interest was the avoidance of conspecifics. During the ice-free period, females with cubs-of-the-year were farther inland, closer to fjords, and less likely to use islands than were males. Two alternatives were considered: male cannibalism of cubs and sexual segregation due to different habitat requirements. In areas where the melting sea ice results in polar bears being forced onto land, the autumn season is characterized by greater aggregation of bears, limited movement, and low food availability. As a consequence bears loose weight while on land (Atkinson and Ramsay 1995). On Baffin Island, males found close to females with cubs-of-the-year were 28% thinner than the average male, suggesting that segregation may result from the threat of intraspecific predation. The alternative hypothesis is that segregation of males and females with cubs-of-the-year is due to different food or habitat preferences. It remains difficult to test between these alternative hypothesis while controlling for spatial and temporal changes.

I used a different approach with the following two chapters in investigating the relationship between polar bears and sea ice. Here, I treated polar bears and sea ice as two separate dynamics that have distinct space-time dimensions. The objective was to describe the qualitative behaviour of their interactions. I assumed that the key to

understanding the relationship between these two dynamics was not to develop an incredibly complex reductionist network, but, rather, to look at the qualitative forms and features of systems.

An example of using this approach is the third chapter where I investigated cycles. Organisms are dynamic on all scales as they respond to and counteract environmental fluctuations. Coupled cycles go on at all levels from the ecological down to the molecular. Major biological rhythms are closely attuned to the natural rhythms of the earth, which are in turn tied to periodic variations in solar and lunar activities (Ho 1993). Living systems, whether regions of sea ice or populations of polar bears, do very different things at different rates, generating flow patterns and cycles of different spatial extensions. Frequency coupling is well known in biological rhythms, which often show harmonic relationships with one another (Breithaupt 1989). This is the space-time structure I found with polar bear life cycle rhythms coupled to sea ice cycles. But, this meeting of two dynamics does not mean uniformity. I found examples of different rates and cycles of different phase and amplitude.

Polar bears living at high latitudes are exposed to large amplitude physical cycles. To determine the relevant physical nature of an organism's environment, I observed how their dynamic life processes respond in size, distance,



and time to environmental fluctuations. I represented changes in sea ice characteristics using sine wave functions and tested for differences in level, amplitude, and phase. I found evidence that polar bears could average and buffer out fluctuations in the physical environment, as well as react to rates of seasonal change. For example, arctic organisms experience huge fluctuations in food availability (Vibe 1967, Wooster 1983, Lindstedt and Boyce 1985, Meldgaard 1986, Stirling and Lunn 1996). Polar bears sustain hyperphagia during spring and summer, the period of greatest food availability, whereas during autumn and winter they can use stored fat while fasting (Pond and Ramsay 1992). Conversely, organisms have techniques of reacting to the rates of change of the external environment rather than actual fluctuations in the levels of resources. For example, seasonal rhythms in use of sea ice by polar bears were generally of a larger amplitude than cycles in sea ice. Also, for some features, such as proximity to ice edge, polar bears advanced their phase over the available pattern. Additionally, I found some indication that patterns of use of sea ice varied for females depending on the stage of their reproductive cycle. In the Arctic Archipelago, solitary females were found closer to ice edges from April through July than females with cubs-of-the-year and females with yearlings. I concluded that polar

bears transform seasonal fluctuations into their own dynamic rhythms.

I suggest continuing the effort to study the ice-polar bear interaction to better elucidate the spatial-temporal dynamics of this system. Climate is likely a chaotic system of low-dimension (Nicolis and Nicolis 1984, Tsonis and Elsner 1988, but see Procaccia 1988) and a latitudinal cline in climatic variability may explain why the Arctic is so unpredictable (Ferguson and Messier 1996). Inherent chaos of the arctic climatic system could act as a forcing function that drives biological patterns. One hypothesis predicts that polar bear populations on the southern edge of their range (i.e., Hudson Bay) show slow unidirectional changes in population demography, whereas higher latitude populations (e.g., eastern Beaufort Sea) show considerable annual fluctuations (Stirling and Øritsland 1995). I suggest that predictability feedbacks through space and time to influence the interaction between climate and ecosystem. Sea-ice dynamics and polar bear movements resulted in seasonal oscillations at broad spatial and annual scales while near-random and unpredictable patterns appeared at smaller scales.

I suggest continuing this effort in the future by investigating how polar bears have responded to the dynamics of sea ice. Future research can test for a relationship between inter-annual predictability of sea ice

and size of area used by female polar bears. Also, I suggest testing whether environmental predictability relates to the pattern of use of dens and shelters along a latitudinal or environmental gradient. Continuing this approach can add to our understanding of polar bear biology.

The final question I address is whether the development of a model of ice-bear dynamics could provide management insights. Polar bears react to large-scale spatial patterns of seasonal changes in sea ice by displaying a spatial patterning of polar bear populations within a metapopulation structure. The arctic environment is likely more susceptible to changes due to global warming (Stirling and Derocher 1993) and metapopulation dynamics can help predict the effect on polar bear populations. Increased variations in the amplitude and timing of seasonal cycles have likely resulted from global warming (Myneni et al. 1997) and understanding the spatio-temporal processes of polar bears would assist predictions of the species' reaction to these changes. Managers cannot view the world as 'linear' as habitat destruction can result in complex 'nonlinear' responses (e.g., Tilman et al. 1994). Species extinction is one such unexpected outcome (Stone 1995).

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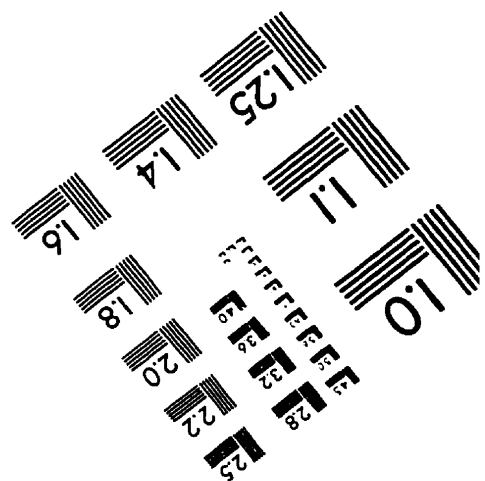
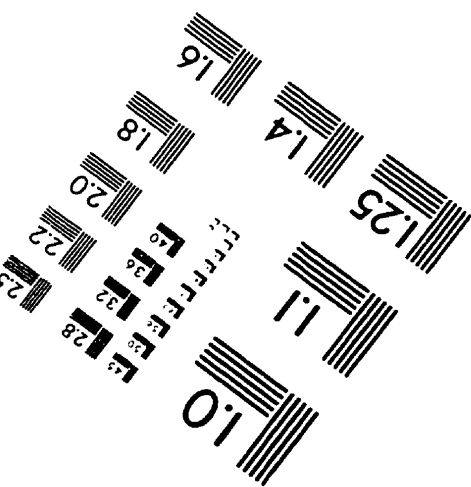
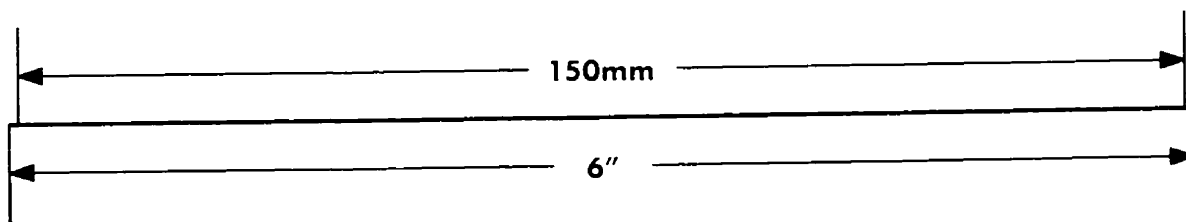
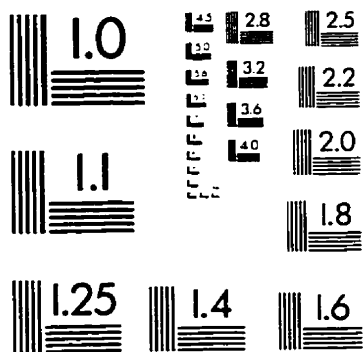
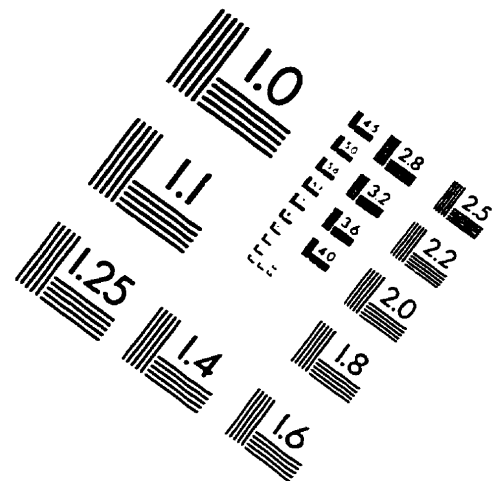
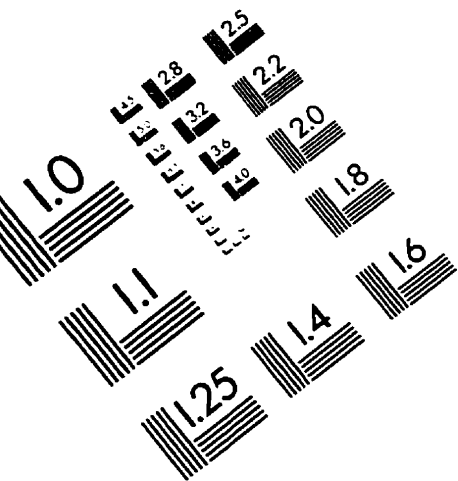
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