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UMI

MOVEMENTS, DISTRIBUTION, AND POPULATION DYNAMICS OF POLAR BEARS IN THE BEAUFORT SEA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

In Partial Fulfillment of the Requirements for the Degree of

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By

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UMI

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ABSTRACT

I used mark and recapture, and radio telemetry to describe movements and population dynamics of polar bears of the Beaufort Sea. Rates of movement were lowest for females with cubs in spring, highest for females with yearlings in winter, and varied from 0.30-0.96 km/h. Total distances moved each month and year were 186-492 km and 1,454-6,203 km respectively. Highest and lowest levels of activity were in June and September. Activity levels were highest from mid-day to late evening. Females with cubs were more active than other bears. Annual home ranges varied from 12,730 km^2 to 596,800 km^2. The Beaufort Sea population occupied a 939,153 km^2 area extending 300 km offshore from Cape Bathurst, Canada, to Pt. Hope, Alaska. Maternal denning in the Beaufort Sea region was common, but 52% of discovered dens were on the drifting pack ice. Bears denning on pack ice drifted as far as 997 km ($\bar{x}$ = 385 km). Bears followed to >1 den did not reuse sites. Consecutive dens were 20-1,304 km apart, but radio-collared bears were faithful to substrate and locale of previous dens. Of 44 polar bears that denned along the Beaufort Sea coast, 80% were located between 137°00'W and 146°59'W. Of those 44, 20 (45%) were on the Arctic National Wildlife Refuge, including 15 (34%) in the 1002 coastal plain area, which may contain >9 billion barrels of recoverable oil. Data indicated, however, that spatial and temporal restrictions on developments could prevent most disruptions of denned bears. Survival of adult female polar bears was higher than previously thought ($\hat{S}$ = 0.96). Survival of cubs ($\hat{S}$ = 0.65) and yearlings ($\hat{S}$ = 0.86) was lower than for adults, but increased rapidly with age.

Shooting accounted for 85% of the documented deaths of adult females. The population grew to ~1500 animals (≥2% per year) from 1967-1992. Condition of adult females, survival of young, and litter sizes declined, while age of maturity and reproductive interval appeared to increase. The population may have approached carrying capacity by the end of the study.

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CHAPTER I

INTRODUCTION AND JUSTIFICATION

S. C. Amstrup

Introduction

Bears (Ursidae) occur on all continents except Australia and Antarctica, and are prominent parts of many ecosystems (Nowak 1991). Bears are of current interest in many regions of the world because they comprise a portion of the endangered fauna. In other areas they are economically significant as game animals, as subsistence for indigenous people, or as depredators of crops and livestock. Ancient lore and recent legend are replete with accounts regarding bears (Rennicke 1987). Bears are relatively large compared with most other terrestrial mammals (Bourlière 1975; Bunnell and Tait 1981; Gittleman 1985). Their size and strength, ability to walk bipedally, and their secretive nature have spawned fear and respect among humans (Larsen 1978; Kaniut 1983; Rennicke 1987). Perhaps more than any other family of animals, bears have captured the human imagination, yet many aspects of their ecology and life history are poorly understood.

The polar bear (Ursus maritimus) is the largest of the extant bears (DeMaster and Stirling 1981; Stirling and Derocher 1990). Large adult males may weigh 800 kg (DeMaster and Stirling 1981), over twice the mass of a lion (Panthera leo) or tiger (Panthera tigris) (Nowak 1991). The polar bear is the apical predator of the Arctic marine ecosystem. Seals (Phoca hispida, Erignathus barbatus) are the primary prey of polar bears (Smith and Stirling 1975; Stirling and Archibald 1977; Smith 1980), but polar bears also have been known to kill much larger prey such as walruses (Odobenus rosmarus) and belugas (Delphinapterus leucas) (Killiaan and Stirling 1978; Fay 1982; Calvert and Stirling 1990; Stirling and Derocher 1990).

Polar bears occur in most ice-covered seas of the Northern Hemisphere, including the coastal waters of the Bering, Chukchi and Beaufort seas (Frame 1969). Periodically polar bears are as far south in the eastern Bering Sea as St. Matthew Island and the Pribilof Islands (Ray 1971) and as far north as 88°N latitude (Stefansson 1921; Papanin 1939). Sea ice disappears from most of the Bering and Chukchi Seas in summer, and polar bears occupying these areas apparently make extensive northerly migrations to stay with the southern edge of the pack ice. Pack ice is more persistent in coastal areas of the Beaufort Sea, and polar bears occur in those waters throughout most years (Frame 1969).

The global distribution of polar bears has long been known, but until recently, it was assumed that polar bears wandered across the polar basin as one fully mixed population (Pedersen 1945). Multi-year mark and recapture studies of polar bears conducted during the last 25 years have shown that bears often were recaptured near the sites at which they were first marked; and Stirling et al. (1980; 1984) concluded that polar bears are faithful to seasonal activity areas. At the start of this study, however, patterns in philopatry were not known. Short-term and long-term patterns of movement and activity, were only poorly understood, and bounds of the populations were uncertain.

Polar bears, like other ursids, have small litters and reach breeding age late in life. Most breeding appears to occur between March and June (Lønø 1970). Ovulation is thought to be induced by coitus (Wimsatt 1963). Implantation is delayed until autumn, and gestation is 195-265 days (Uspenski

1977). Precise estimates of breeding rates, litter sizes, or survival were not available at the start of this project, and the factors regulating these critical life-history parameters were uncertain. Reliable estimates of the abundance of polar bears in the Beaufort Sea or trends in population levels also were not available.

Despite their large adult sizes, the young of bears are among the most altricial of placental mammals (Ramsay and Dunbrack 1986). New-born polar bears have hair, but are blind and weigh only 0.6 kg (Blix and Lentfer 1979). The undeveloped young are nurtured within the protection of a maternal den until approximately 3 months old. Pregnant polar bears excavate the dens in snow and ice in early winter (Harington 1968; Lentfer and Hensel 1980; Ramsay and Stirling 1990), and give birth in those dens in December or early January (Kostyan 1954; Harington 1968; Ramsay and Dunbrack 1986). In most areas of the Arctic, family groups (mother bears accompanied by young) emerge from dens in late March or early April.

When this study began, the known world-wide distribution of birth dens consisted of a few widely scattered concentration areas on land (Harington 1968; Ramsay and Andriashek 1986). Among the best known denning concentrations were: the Svalbard Archipelago north of Norway (Larsen 1985); Franz Josef Land, Novaya Zemlya, and Wrangel Island, in Russia (Uspenski and Chernyavski 1965; Uspenski and Kistchinski 1972); and the west coast of Hudson Bay in Canada (Ramsay and Stirling 1990). Denning was either thought to be uncommon or was overlooked in gaps between these denning concentrations; and fidelity to denning areas, presumably an indication of

limited availability of necessary habitats, was assumed (Ramsay and Andriashek 1986). The Beaufort Sea of northern Alaska and Canada lies in the largest of gaps between denning areas that had been identified at the start of this project (Harington 1968). Hence the numbers of dens, the distribution of dens, and the chronology of denning in the Beaufort Sea were unknown when this study began.

Human interactions with polar bears have been largely one-sided since the white bears first were encountered. Early Eurasian explorers viewed polar bears as fearless marauders, and killed many in self-defense, or before they could become a threat (Larsen 1978). Seton (1937) wrote "For centuries, it has been the custom of Arctic travelers to kill all polar bears they could. It did not matter whether the bears were a menace, or whether the travelers needed the carcasses or not." Mowat (1985) suggested that explorers to the north killed polar bears at nearly every opportunity, and he attributed the present distribution to extirpation of polar bears from more southern climes rather than to a preference for existence in the polar regions. Prior to 1900, polar bears occupied St. Matthew Island in the Bering Sea west of Alaska. Unlike polar bears of the Beaufort Sea, many of these individuals spent the summer on land instead of remaining with the sea ice as it retreated to the north. Polar bears in Hudson Bay and some parts of the Canadian arctic archipelago still follow this lifestyle. Commercial hunters in search of seal skins and whale oil eliminated polar bears from St. Matthew Island by the early 1900's (Hanna 1920). In addition, over-wintering commercial whalers along with local residents may have reduced the number of bears that once denned along the

north coast of Alaska (Leffingwell 1919). From ca.1920 to ca.1950, polar

bears in Alaska were taken in smaller numbers primarily for subsistence

purposes and for the sale of hides by Native people hunting with dog teams.

Guided hunting by aircraft which occurred between the early 1950's and 1972

again resulted in excessive harvests. The average annual take between 1960

and 1972 was 260 animals (Amstrup et al. 1986).

In recognition of the polar bear's increasing vulnerability to human

activities, the five nations (the Soviet Union, Canada, Denmark, Norway, and

the United States) with jurisdiction over polar bear habitats negotiated the

International Agreement on Conservation of Polar Bears (Agreement). The

Agreement, negotiated in 1973 and ratified in 1976, prohibited the taking of

polar bears from aircraft or large motor vessels or in areas where they have

not been taken by traditional means in the past. This prohibition created a

defacto sanctuary in the central arctic basin. A resolution appended to the

Agreement requested governments to prohibit the taking of cubs or females

with cubs and hunting in denning areas, during periods when pregnant

females are moving into them or are denning. Another resolution requested

governments to establish an international system to identify and control the

trafficking of illegal hides (See Lentfer [1974] and Stirling [1986] for more

comprehensive reviews). Finally, the Agreement required each signatory

nation to conduct research, and to cooperate in management and research of

populations that overlap jurisdictional boundaries.

In Alaska, the Agreement was implemented by passage of the Marine

Mammal Protection Act (MMPA) of 1972. The MMPA vested management of

polar bears with the federal government. Under the MMPA, only Native people are allowed to take polar bears for subsistence. Nonetheless, hunting of polar bears will continue in the Beaufort Sea (Treseder and Carpenter 1989; Nageak et al. 1991), and there is now talk of resumed hunting in nearby areas of Russia where polar bears have not been harvested since 1955.

Current events in Arctic regions may cause new disruptions to the populations of polar bears. The discovery of the world's 10th-largest oil field at Prudhoe Bay, resulted in dramatic increases in human populations in Alaska's arctic. The influx of cash, as a result of oil and gas development, into previously cash-poor areas improved efficiency of harvest of polar bears. As humans increasingly invade the Arctic, harassment and other direct interactions between humans and bears will increase. In order to understand how perturbations related to hydrocarbon exploration and development, increased hunting, or other human activities may affect polar bear populations and how widespread effects may be, the status of populations must be known. With increasing human presence in the Arctic and a continuing or expanded harvest, informed management will be necessary if polar bears are not to go the way of some other large predators (Cain et al. 1972). Managers will need to be informed about natural history parameters such as survival and recruitment, population size, movements, and habitat use patterns, if they are to mitigate negative effects that may be caused by these changes.

Theoretical Background

Organisms are commonly described as "r- or K-selected." "r-selection" is usually associated with high and "K-selection" with low reproductive potential

(Pianka 1970). Species described as "r-selected" typically mature early, put large effort into reproductive output but little effort into parental care, and usually are not long-lived. Conversely, "K-selected" species show deferred reproduction, long life, and extended parental care. Populations of species described as "r- and K-selected" are regulated primarily by different factors. Fluctuations in the environment generally keep "r-selected" species below the levels at which density-dependent effects occur, whereas "K-selected" species are more resilient to environmental fluctuations and more likely to be controlled by factors related to density. Undoubtedly, all species are influenced by a combination of density-independent and density-dependent factors. Just as obvious is that carrying capacity of any environment for most organisms is dynamic rather than static. Further, the degree to which species fit one term of reference or the other depends, to some extent, upon geographic locality and climatic variation (Cody 1966).

Most large mammals fall on the "K-selected" end of the "r-K" scale. Intraspecific competition for resources is generally intense in large mammals. Increasing competition at higher densities is reflected in changes in various life history traits. Unlike smaller organisms that can respond numerically and dramatically to short-term changes in the environment; large mammals are more likely to respond functionally with changes in diet, shifts in movement patterns, and changes in behavior. Changes in age of maturity, numbers of young produced, survival (particularly of juveniles), and rates of body growth are expected results of sustained changes in relative population density (Bourlière 1975; Fowler 1987).

Their great longevity and low potential rate of increase suggest bears are among the most "K-selected" of all mammals (Cowan 1972). Nonetheless, researchers generally have not addressed the role of density or have concluded density plays little or no role in population regulation of ursids (Knight and Eberhardt 1985; Rogers 1987; Taylor et al. 1987). For example, after long-term studies of black bears (Ursus americanus), Rogers (1987:51) concluded that, "reproduction in black bears is controlled mainly in a density-independent manner by fruit and mast supplies." Bunnell and Tait (1981) also concluded that reproduction in bears was regulated largely by nutritional factors in a density-independent manner while survivorship was regulated by density-dependent factors such as forced emigration of young. Density-dependent responses have been documented for two populations of ursids (McCullough 1981; Young and Ruff 1982; Stringham 1983). Also, Rogers (1987) claimed that bears in his study area that made use of supplemental food at dumps raised cubs at rates comparable to bears in a Pennsylvania study area characterized by higher fecundity and recruitment. Bears that used dumps produced more cubs because they faced lower relative densities than those that competed only for natural foods. Hence, Rogers' (1987) argument against density-dependent responses in reproduction actually may be evidence for a density response.

Purpose

The polar bear is significant from the standpoint of subsistence, regional economics, circumpolar ecology, and world-wide vicarious appreciation. Perturbations of polar bears will increase as humans place increasing

pressures on the resources of the Arctic. Also, polar bears may be among the first large mammal species to show effects of broad scale environmental problems such as global warming (Stirling and Derocher 1993). Questions related to polar bear management and management of the polar ecosystem will increase in the future. Those questions can only be answered after a solid baseline of population information and knowledge of the effects of past perturbations is available. The purpose of this study was to continue development of that baseline by quantifying the movements and distribution of polar bears in the Beaufort Sea, and describing the dynamics of the population.

Strategy

I employed the following strategy during this study: First, I attempted to define the bounds of the population of polar bears under consideration. Estimates of size or life history parameters are most relevant when the population has been defined. Second, I determined survival and recruitment rates, and described the composition, status, and trend of the polar bear population in the Beaufort Sea. Next, I determined the distribution, timing, and numbers of maternal dens in the Beaufort Sea from 1981-1992. Finally, because I thought polar bears might be most vulnerable to human activities during the time of maternal denning, I examined available data regarding exposures of bears in dens to various kinds of human activities.

Polar bears live a long time. In order to be most successful at using their habitat in the long run, they must become familiar with their environment. Strong fidelity to particular geographic areas would be expected. In the case

of animals dependent upon seasonally-variable substrates, however, fidelity might be only seasonal in nature. Rates of movement, distances moved, and activity levels, after all, must be controlled by environmental conditions that vary by season and year. Fidelity in this situation may or may not lead to well-defined activity areas or population bounds. Changes in activity or mobility associated with maturation of dependent young must be superimposed over the pattern of variations due to changes in habitat. The costs of 2 years of lactation and other parental care to polar bear females must be great and must vary with age of young. These factors should result in cyclical variations in movements and activities. I formalized these predictions and tested hypotheses based upon them in Chapter II. That chapter, which is based upon thousands of satellite radio-telemetry locations, describes the movements, distribution, and population bounds for polar bears in the Beaufort Sea. Chapter II was prepared for submission to the <u>Canadian Journal of Zoology</u>.

In studies of polar bears and in studies of large mammals in general, survival rate is among the most difficult of parameters to estimate. In Chapter III, I describe how satellite radio-telemetry data from known individual bears were used to establish estimates of survival rates for adult female polar bears and dependent young. Those estimates were used where necessary, in subsequent chapters, to estimate other population dynamics variables. Chapter III appears here as it was accepted for publication in the <u>Canadian Journal of Zoology</u>.

In the Beaufort Sea, the intensity of hunting varied greatly after the turn of the century. The variation in harvest levels and the resultant changes in the

Beaufort Sea population of polar bears became one of the important tools I used to evaluate the status and trend in that population. For many years prior to the popularization of aerial hunting, polar bears in Alaska were harvested in limited numbers by subsistence hunters, but otherwise had been unperturbed since the early part of the century (Amstrup and DeMaster 1988). It is reasonable to conclude, therefore, the population prior to aerial hunting was high, possibly near "K-carrying capacity." After 1972, polar bear hunting by airplane ceased. This change in Alaska followed the 1968 introduction in Canada of harvest quotas in response to concerns over a possible over-harvest there (Stirling 1986). Harvests by local indigenous people continue to the present in both countries (Treseder and Carpenter 1989; Nageak et al. 1991). Those harvests, however, are thought to be below maximum sustainable yield. I reasoned, therefore, that the population must have grown after 1972.

As a population increases, the first negative effect of its own density is presumed to be increased mortality of young (Eberhardt 1977). At still-higher densities, age of maturity increases and then productivity of mature animals declines. Finally, at the highest densities, survival of adults may decline (Eberhardt 1977). If the population of polar bears in the Beaufort Sea continued to grow into the 1990's, density-related changes in population structure would be expected. In Chapter IV, I formally tested whether the population in the Beaufort Sea was showing density-related changes that should occur if the population was growing during my study. Chapter IV, which also was written for submission to the Canadian Journal of Zoology, was

based upon hundreds of capture and recapture records from 1981-1992. Comparisons were made between those records and capture and recapture records in archives of the Fish and Wildlife Service from 1967-1974, years in which the population should have shown evidence of over-harvest. Data from the Canadian portion of the Beaufort Sea (courtesy of I. Stirling) were combined with Alaskan data in order to assure that the study represented the whole population.

Historically, maternal denning of polar bears was known from many locales, but had been reported in the Beaufort Sea region only rarely (Lentfer and Hensel 1980). Yet, polar bears were thought to be year-round residents of the Beaufort Sea. I predicted polar bears did den in the Beaufort Sea region in large enough numbers to maintain the population, and that the distribution of dens would be uniform along the Beaufort Sea coast. I used radio telemetry to test these and other predictions about maternal denning in northern Alaska and adjacent Canada. Results of those studies are described in Chapter V which appears as it was published in the Journal of Wildlife Management (Amstrup and Gardner 1994). In Chapter VI, which was published in the journal Arctic (Amstrup 1993), I tested the sensitivity of polar bears in dens to human disturbances (Belikov 1976; Amstrup et al. 1986).

Chapter VII, the final chapter, encapsulates the findings of this study. Therein, I describe progress toward the objectives outlined here, and the outcomes of my tests of hypotheses. I also suggest a course for future polar bear research.

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CHAPTER II

ACTIVITIES, MOVEMENTS, AND DISTRIBUTION OF POLAR BEARS IN THE BEAUFORT SEA[1]

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Polar bears (Ursus maritimus) occur in most ice-covered seas of the northern hemisphere and are known to cross international boundaries. They are at the apex of the Arctic food chain, and may be indicators of the welfare of Arctic and global ecosystems. Humans are increasingly invading habitats of polar bears, and capabilities to deal with effects of those invasions vary among jurisdictions. Yet, little is known about how polar bears utilize their environment, and data resolving boundaries of sub-populations are unavailable. To improve information regarding movements and activities of individual polar bears and boundaries of the sub-populations they comprise, we fitted 153 satellite radio collars (PTT's) to 106 adult female polar bears in the Beaufort Sea and relocated them 37,277 times between 1985-1993. Polar bears were observed to move over 4 km/h for extended periods, but mean hourly rates of movement varied from 0.30-0.96 km/h. Females with cubs had lower hourly rates of movement than females with yearlings and those (single females) without young (P = 0.05). Movement rates varied significantly among months, and generally were lowest in spring and late summer and highest in early winter. Geographic displacements from the beginning to the end of each month were smaller for females with cubs of the year than for single females, and larger in November than in April (P = 0.05). In May, June, July, and August, radio-collared bears shifted locations to the north (all P's $\leq$ 0.01). Collared bears moved back to the south in October (P = 0.01). Mean total distances moved each month ranged from 186-492 km. Total movements in December were larger than those measured in April, May, July, August, and September (P = 0.05), and total monthly movements of females with cubs

were lower than those of single females (P = 0.05). Total annual movements ranged from 1,454-6,203 km. Bears that spent part of the year in dens moved less than others, but nondenning classes of bears did not differ in total annual movement (P = 0.7). Females with cubs were generally the most active group, and single females the least active. Highest and lowest levels of activity were recorded in June and September (P = 0.05), but there also was a strong activity peak in early winter. Activity levels were lowest in the early morning and higher from mid-day through late evening. Peaks in activity may be linked to haul-out patterns of ringed seals (Phoca hispida), the favored prey of polar bears. Indices of activity and mobility were not entirely concordant among months or reproductive categories of females. Annual activity areas, calculated with the harmonic mean method and defined as contours surrounding 95% of relocation sites, ranged from 12,730 km^2 to 596,800 km^2. Monthly activity areas ranged from a mean of 344 km^2 for females with cubs in April to 11,926 km^2 for females with yearlings in December. The Beaufort Sea population occupied an area extending up to 300 km offshore from Cape Bathurst in Canada to Pt. Hope, Alaska, and enclosed 939,153 km^2. Animals originally captured along the Beaufort Sea coast spent approximately 25% of their time in the northeastern Chukchi Sea, but animals captured in the Chukchi Sea ventured into the Beaufort Sea only 6% of the time. Bears captured in the Beaufort Sea were largely faithful to summer activity areas in the central portion of the Beaufort Sea.

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Introduction

The polar bear, apical predator of the Arctic marine ecosystem, occurs in most ice-covered seas of the Northern Hemisphere (DeMaster and Stirling 1981). Along the coast of Alaska and western Canada, the winter distribution of polar bears includes the Bering, Chukchi and Beaufort seas (Ray 1971; Amstrup and DeMaster 1988). Polar bears occur as far south in the eastern Bering Sea as St. Matthew Island and the Pribilof Islands (Ray 1971), and have been reported as far north as 88°N latitude (Stefansson 1921; Papanin 1939). In summer, ice in the Bering and Chukchi seas melts and polar bears retreat to the north. Much of the Beaufort Sea is ice-covered all year, however, and polar bears are permanent residents there (Frame 1969).

Polar bears are known to move across international boundaries, and although hunting occurs in most jurisdictions, management strategies vary. Humans are increasingly invading habitats of polar bears for purposes other than hunting (Amstrup et al. 1986). Effects of activities occurring in one jurisdiction could have ramifications in others (Lentfer 1983). Prevention and management of adverse effects only will be successful on an international level, and only after population boundaries are defined.

Polar bears are thought to occur in several largely discrete sub-groups, rather than one homogeneous pan-Arctic population (Harington 1968). Relatively little has been published about the movements of individual polar bears composing hypothesized sub-populations. Lentfer (1983) concluded that males and females did not move differently, but Messier et al. (1992)

concluded from radio-telemetry data, that females in different reproductive categories had different movement and activity patterns. Areas of seasonal and annual activity are poorly understood for all classes of polar bears, and daily and seasonal patterns of activity are unknown. Mark and recapture data suggest polar bears may be seasonally faithful to particular geographic areas (Stirling et al. 1980; 1984). Mark and recapture data however, cannot provide objective assessments of fidelity because recaptures are too infrequent to quantify patterns of distribution.

The role of polar bears in the ecosystem and their absolute dependence on sea ice as a foraging substrate, suggest that they may be important indicators of human perturbations of the environment. Effects of global warming on sea ice, for example, are likely to be reflected in alterations in movements, activity patterns, and changes in areas occupied by season or year; even before changes in population dynamics occur (Stirling and Derocher 1993). As human populations increase, we will more frequently compete for space used by polar bears. Therefore, managers need a more thorough understanding of movements and activities of polar bears. The objective of this study was to use satellite radio telemetry, which overcomes many logistical difficulties in polar bear studies, to describe activities of polar bears in the Beaufort Sea.

Females in high-latitude populations of polar bears have a reproductive cycle ≥3 years long (DeMaster and Stirling 1981; Ramsay and Stirling 1986; Amstrup and DeMaster 1988). This cycle results because young generally are

not weaned until early in their third year of life. Hence, we had the opportunity to examine activities of female bears in 4 different reproductive classes: 1) accompanied by cubs of the year, 2) accompanied by yearlings, 3) accompanied by 2-year-olds, and 4) not accompanied by young of any age (single). Reproduction is expensive (Oftedal 1985). Costs of reproduction in bears and other carnivores are not as well known as they are in some herbivores (Oftedal and Gittleman 1989). The costs of 2 years of lactation and other parental care to polar bear females, however, must be high. Costs of reproduction also must vary with time of the reproductive cycle. During their first year of life, cubs are entirely dependent on their mothers for nutrient uptake (Stirling and Latour 1978). Cubs (usually 2) are born in December or January weighing approximately 0.6 kg. They emerge from the den in March or April weighing 8-15 kg, and finish their first year of life weighing 60-150 kg (Amstrup unpubl. data). This rapid growth is achieved at great cost to the maternal female. Females with new cubs emerge from the den with fat reserves largely depleted (Derocher et al. 1992), and must begin foraging immediately. At this time, the cubs are growing rapidly, nourished solely by lactation, but are relatively immobile. Hence, the needs of the female to forage for resources necessary to nourish cubs must be balanced by the cub's immobility.

Through their second year, young continue to be a nutritional burden to their mothers—most continue to nurse, and they share in consumption of kills. They do, however, become more mobile, so that foraging needs of females are no longer compromised by immobility of young. Young polar bears apparently

do not effectively provision for themselves until near the time of weaning (Stirling and Latour 1978). For 2 years, therefore, energy demands placed on females provisioning for young remain high. We predicted that rates of movement and distances moved by adult females would be small when the cubs are very young and would increase as mobility of cubs improves through the age of 2 years. Females accompanied by 2-year-olds have few mobility limitations, and we predicted they should have movement patterns similar to those of single females. Although females with younger cubs should be less mobile than those with older cubs, the younger cubs require more attention in terms of frequency of nursing, grooming, and general supervision. Hence, we predicted that females with the youngest cubs would have high levels of activity. Superimposed over the pattern of increasing mobility with age of cubs, we also predicted that rates of movement and distances moved would be larger in spring when many bears hunt for seals in subnivian lairs, and smaller in summer and fall, when still-hunting is thought to predominate (Stirling and Latour 1978). Hence, we tested the following null hypotheses: rates of movement and levels of activity are independent of reproductive status and month of observation and time of day; geographic displacements, (shortest distance from first location for each month and the last location for each month) are independent of the month and the reproductive status of the female; total distances moved (sum of the distances between sequential relocations) by radio-collared polar bears do not differ among bears of differing reproductive status nor among months.

Because polar bears must hunt on the sea-ice throughout the year

(Amstrup and DeMaster 1988), we expected that net displacements in location would vary seasonally with the condition of the sea ice. Bears should move to the north, for example, as ice melts away from the coast in summer, and they should move to the south with freeze-up in fall and early winter. Therefore, we tested the null hypothesis that azimuths of geographic displacements are independent of month.

If distances moved by polar bears increased with increasing age of their accompanying young, it would also seem reasonable that areas occupied would increase. We predicted that areas occupied by female polar bears increase with increasing age of cubs, and the largest activity areas are occupied by single females that are unencumbered by cubs but which must build up their energy reserves to prepare for the birth of their next litter. We tested the null hypothesis that sizes of areas occupied by female polar bears are independent of reproductive status. Because polar bears catch seals mainly by still-hunting (Stirling and Latour 1978), we expected the volatile summer and fall ice would minimize predictability of seal hunting opportunity. That would necessitate wider ranging movements than during winter and spring. Hence, we predicted that monthly activity areas would be larger for all classes of bears in the summer and fall than during other times of the year. We tested the null hypothesis that sizes of areas occupied by polar bears are independent of the month of the year.

Polar bears live a long time and potentially can produce several litters during their lifetimes. Success in exploiting the environment should be

enhanced by knowledge gained from previous experiences. Fidelity to seasonal foraging areas, therefore, should be strong, and we predicted that polar bears would occupy the same seasonal and annual activity areas repeatedly. We tested the null hypothesis that polar bears lacked multi-annual fidelity to monthly activity areas. We also tested whether the portion of the population area used by individual polar bears is independent of the location at which they are captured.

Materials and Methods

Field Procedures

Polar bears were captured alive, marked, and released each spring (except for 1990) from 1985 to 1992. Polar bears also were captured and marked in autumn 1985, 1986, 1988, and 1989. Autumn captures occurred in October and November each year, and spring captures occurred between March and May. We captured bears throughout the Alaskan Beaufort Sea, which extends from Point Barrow, Alaska, (ca. 157°W) to the Canadian border (141°W). Our Canadian counterparts captured bears in the Canadian Beaufort Sea for us to radio-track. We captured polar bears by injecting immobilizing drugs [phencyclidine hydrochloride (Sernylan®, Park, Davis and Co.), etorphine hydrochloride (M-99®, Lemmon Co.), and tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Co.)] with projectile syringes fired from helicopters (Larsen 1971; Schweinsburg et al. 1982; Stirling et al. 1989). Capture protocols were approved by an independent animal care and welfare committee.

Each year we marked a limited number ($\bar{x}$ = 23) of adult females with radio-transmitter collars. To be certain of attaching collars to adults, we radio-collared only females with accompanying young, those that showed evidence of prior lactation, or those with zygomatic widths exceeding 18 cm—the smallest width observed for bears accompanied by young. Our collars were ultra high-frequency Platform Transmitter Terminals (PTT's) that were relocated by satellite. PTT's transmitted for short periods (e.g., 4-8 h) every 3-7 days. The high proportion of dormant time was designed to maximize battery life. Sensors on all PTT's recorded temperature of the collar and 2 indices of activity. Geographic locations of collared animals were determined by sensors on the satellite that interpreted frequency shift patterns caused by changes in relative positions of the satellites and animals. (Fancy et al. 1988). Data retrieved from PTT's were processed by the Argos Data Collection and Location System (ADCLS; Fancy et al. 1988). Collars carrying PTT's also carried VHF beacons that we located with aircraft (Chapter V).

Activity patterns of polar bears were recorded by closing or opening of a mercury tip switch inside each PTT. "Long-term" activity counters recorded the number of seconds during which the switch was actuated in the 72 h (or in some cases, the 24 h) prior to each transmission. Thus, for each 24 or 72 h period we received one measure of the percentage of time the bear was active. Short-term counters provided the number of seconds of activity for the minute prior to each transmission of data to the satelite. Short-term data were primarily useful as a near real-time indication that the bear was still alive and still wearing the collar. We compiled modal values of long-term activity

measures for each week of monitoring; and used those modal values to compare seasonal or monthly activity patterns and to examine differences among females of varying reproductive status. Long-term counters did not allow interpretation of diel activity patterns, and could not detect brief peaks or troughs in the percentage of time bears were active. Therefore, between 1988-1992, we attached PTT's with sensors that also recorded activity level on an hour-by-hour basis for 24-h periods. These "activity" PTT's could record up to 8 categories of activity for each hour of the day. Preliminary analyses of data on long-term activity suggested that average polar bear activity levels were low. To most accurately evaluate hourly activities, therefore, we programmed sensors so that more subdivisions were available for the lower levels of activity than for higher levels. Thus, "activity PTT's" tallied activity levels for each hour into one of the following 8 categories: 0: 0-179 seconds of activity; 1: 180-359 seconds of activity; 2: 360-539 seconds of activity; 3: 540-899 seconds of activity; 4: 900-1439 seconds of activity; 5: 1440-2159 seconds of activity; 6: 2160-2879 seconds of activity; 7: 2880 or more seconds of activity.

We located PTT-equipped polar bears using position fixes from satellites, radio-tracking from aircraft, and with visual sightings. We used Loran-C or very low frequency positioning devices to plot locations of bears located by aircraft on sea ice. All data were recorded in or converted to Alaska Standard Time. Instrumented females were single (not accompanied by young of any age), or accompanied by cubs (young aged < 1 year), yearlings (aged 1-2 years), or 2-year-olds (aged 2-2.5 years). Changes in reproductive status,

(e.g. losses of young) were verified by visual observations. Reproductive status of animals that were not reobserved frequently enough for confirmation were classified in a "suspected" reproductive category.

Analyses

All data generated by PTT's and transmitted to the ARGOS satellites were available for analyses. When examining movements, however, we deleted all observations for which the reported location may not have been within 1000 m of the true location of the animal (Harris et al. 1990). Also, although we usually recorded multiple observations during each transmission day, we deleted all but the one with the highest location quality.

We used Albers Conic Equal-Area projection (ESRI 1992) for plotting recorded locations of radio-collared polar bears. In areas like the Beaufort Sea, that extend more in east-west than north-south directions, Albers projected shapes have minimal distortion, and are proportional to the same areas on the earth (ESRI 1992). All locations of bears were recorded in north latitude and west longitude.

Females of all reproductive classes did not occur in all months. Hence analyses were temporally subdivided. In most analyses, females with yearlings and single females could be compared throughout the year. Females with 2-year-olds were available for monitoring only between January and April of each year, and were compared to females with yearlings and single females during that time. Movement patterns of females with cubs,

single females, and females with yearlings were compared for the period April-December. Comparisons of movements and activities within each of these periods were accomplished with analysis of variance (ANOVA).

Rates of hourly movement were determined by measuring the linear distance between consecutive radio locations and dividing by the number of hours separating those locations. Rates of movement recorded for females of known reproductive status were compared, over all time periods, with those for which reproductive status was only suspected with the Wilcoxon 2-Sample test (Conover 1980:215). The null hypothesis was that measured rates of movement are independent of whether status was confirmed. Differences among rates of hourly movement for bears of different confirmed status and during different months were evaluated with 3-factor ANOVA. Multiple comparisons among factor level means were made with the Tukey Studentized Range (HSD) test. The null hypothesis was that rates of movement are independent of reproductive status (e.g., female accompanied by cubs, female accompanied by yearlings, single female, female accompanied by 2-year-olds) and month of observation. Because we had numerous observations on each bear, we introduced an added factor, individual bear, in this and all other ANOVA's reported here. This allowed separation of the variability that was due to individual bears from that associated with the factors of interest. Hence, the partial sums of squares due to variation among individual bears did not influence our hypothesis tests.

Geographic displacement, or net shift in geographic position, of each

animal in each month was defined as the linear distance between the first and last radio locations recorded for that month. Total distance moved during each month was calculated by summing the distances (km) between consecutive satellite reobservations of each bear each month. Total distance moved and displacement for each month were measured only if ≥ 20 days lapsed between the first and last locations. Total distance moved per year was calculated by summing the distances (km) between consecutive relocations for the whole year. Independence of total distances moved and total displacements from month and status was compared with 3-factor ANOVA and Tukey's test. Direction moved from the first to the last location of each month (mean azimuth and angular deviation or "dispersion" from the mean) was determined by converting angles to the appropriate trigonometric functions (Zar 1984:422). We determined whether there were significant directional tendencies by comparing azimuths of displacements for each month with Rayleigh's test of uniformity of distribution (Zar 1984: 443). Total annual distances moved were calculated only for bears that were monitored for at least 292 days (80% of a 365 day year), and only if information gaps in their relocation records were shorter than 1 month. If a bear was monitored for >365 days, a 2nd tracking year was designated. Similarly, if monitoring time exceeded 730 days, a 3rd tracking year was designated. Tracking years did not coincide with any standardized calendar. Rather, they ran for 365 days beginning on the date of the first satellite observation for each bear. Gaps in relocation information ≥ 73 days (20% of a monitoring year) were not allowed, unless an animal occupied a maternal den during the gap in observations.

Because reproductive status of female polar bears changes during any year, we categorized animals, for analyses, according to the most common (modal) status for each year of monitoring. Annual movements of bears in each status were compared with 2-factor ANOVA.

Variations in activity levels among months were determined by comparisons of data recovered from long-term activity counters as well as hourly counters. The null hypothesis that the "long-term" percent of time bears are active was independent of month and reproductive status was tested with a 3-factor ANOVA and Tukey's test. Data on hourly activity were analyzed two ways. First, the frequency of each of the 8 activity categories was analyzed with contingency tables. Because there were different levels of reproductive status, month, and hour of the day, as well as the 8 categories of activity, a three-way contingency analysis was required. The necessary log-linear computations were performed with the "CATMOD" procedure of SAS V. 6.0 (SAS Institute Inc., Cary, NC). The large number of categories in this analysis resulted in many empty cells. Empty cells required collapsing of categories for the calculations to be completed; and this limited the number of comparisons that could be made. Categorical analysis was possible only when the number of activity categories was collapsed to 3 (0-359, 360-1439, and 1440 to 2880 seconds of activity per hour), when months of December to February were excluded from consideration, and when females with 2-year-old young were combined with single females.

Upon evaluation, these data reductions required by categorical

analyses appeared unduly restrictive. To gain insights into as many comparisons as possible, we did a second analysis in which the data were treated as if they were continuous rather than discrete. The number of seconds identified by the midpoint of each category was converted (to simulate continuous data) to an activity percentage for the hour [e.g., category 1 (180-359 s) was coded as 7.5% active). The mean activity level for each month, hour, and class of bear was derived by averaging the midpoints of each category . All observations for all bears during each hour of the day were then averaged to estimate the percentage of each hour polar bears were active. The hypothesis that diel activity patterns are independent of reproductive status, month, and hour of the day was tested with 4-factor ANOVA and Tukey's test.

Areas used by polar bears were analyzed on monthly and annual bases. We calculated areas of annual activity only for bears that were monitored for at least 292 days (80% of a 365 day year), and for which there were at least 25 high-quality relocations. We used the same criteria for the start and finish of each year of monitoring as described in calculation of annual movements. We calculated monthly activity areas for each month in which an individual bear generated at least 8 high quality relocations over a minimum period of 20 days within that month.

Activity areas were examined with the harmonic mean (Dixon and Chapman 1980), adaptive kernal (Worton 1989), and convex polygon (Hayne 1949) methods. We used program CALHOME V. 1.0 (Kie et al. 1994), for all

activity area calculations. Worton (1989) has shown that adaptive kernal estimators of activity area size are preferred, from both descriptive and probabilistic standpoints, over other models. In the Beta test version (1.0) of CALHOME, however, adjustment of the smoothing parameter to fit the distribution of data points was not possible. The multimodal nature of polar bear activity areas and the presence of long-distance movements away from core areas of use mandated a smaller smoothing parameter than used in this version of CALHOME (Worton 1989). The coarse smoothing parameter resulted in a poor fit of activity areas, derived by adaptive kernal methods, to observed data. The convex polygon method, as expected (Dixon and Chapman 1980), also provided a poor fit to our data, although we have reported some convex polygon estimates for comparisons to earlier studies. Conversely, harmonic mean contours closely-approximated the observed distribution of reobservations for most bears (Spencer and Barrett 1984; Lair 1987; Hayward et al. 1993). Therefore, we used the harmonic mean method to compare activity areas. We tested the null hypothesis that sizes of activity areas are independent of reproductive status and month with 3-factor ANOVA and Tukey's test.

Sizes of activity areas, theoretically, can be underestimated if observations are temporally-autocorrelated (Schoener 1981; Swihart and Slade 1985a,b; Solow 1989). Autocorrelation of sequential observations was evaluated with the distribution-free Multi-Response Permutation Procedure (Mielke et al. 1981; Biondini et al. 1988; Mielke 1991) in the sequence permutation (MRSP) subroutine of program BLOSSOM (Slauson et al. 1991).

We found significant autocorrelation, even when fewer than one location per month was considered. This apparent autocorrelation may have resulted from temporal and spatial clumping of data. Such clumping among relocations of radio-collared polar bears was neither seasonally nor annually predictable and varied among individuals of the same reproductive class. Hence, there was no way to minimize autocorrelation by partitioning the data. Because all animals were treated the same, however, any biases—whatever they may have been— were probably consistent and did not, we believe, affect comparisons among animals or time periods.

We examined fidelity of polar bears to monthly activity areas by comparing centers of activity (COA) calculated with the harmonic mean method for bears observed in the same month during different years. The hypothesis that fidelity to activity areas is independent of month was tested with 2-factor ANOVA and Tukey's test. When reproductive efforts are successful, the reproductive status of an individual female will only be repeated each 3 years. Hence, sample sizes were insufficient to evaluate monthly fidelity according to reproductive status. We evaluated fidelity of polar bears to locales where they were captured by comparing numbers of reobservations of bears in each of 6 longitudinal zones to the numbers of captures in each zone. Longitudinal zones were 10° wide, and extended from 127° to 167°. Because, in this analysis, we were interested in selection of geographic areas at the level of the population, we combined locations of all bears originally captured in each zone. We assumed that these noncorrelated samples from individuals on different days and under differing environmental

conditions, represented independent samples of spatial use patterns. This analysis incorporated data collected in the Chukchi Sea by G. W. Garner (unpubl.) that are not used elsewhere in this report.

To determine the bounds of the Beaufort Sea polar bear population we pooled all relocations of all bears originally captured in the Beaufort Sea (127° N to 160° N latitude) and calculated contours using the harmonic mean method (Dixon and Chapman 1980). Because program CALHOME could not handle sample sizes as large as ours, we plotted the distribution of 10 random subsamples of the total number of radio locations available. We defined the area occupied by the Beaufort Sea population as the mean 95% harmonic mean contour, excluding land, of those sampled points. The core use area was defined as the mean of the 50% contours.

Our criteria for different analyses were not identical (e.g., rates of hourly movement were not limited to months with at least 20 days of tracking). Therefore, sample sizes varied somewhat among different categories of analyses. The Tukey HSD family confidence level was held at $P = 0.05$ in all ANOVA's. We report actual probabilities of other statistical tests performed unless $P < 0.001$. In all Chi-squared analyses, cells with few occurrences were combined until expected values were at least 1, and fewer than 20% of the cells had expectations < 5 (Conover 1980:156). Statistical analyses were performed on a Data General AVIION 6200 computer (Data General Corp., Westboro, MA) running SAS version 6.07 software (SAS Institute, Inc., Cary, NC). Routine compilations of data were performed on a Power Macintosh

7100 computer running Excel (Microsoft Corp., Redmond, WA).

Results

We deployed 153 PTT's onto 106 adult female polar bears and obtained 37,277 location records between autumn 1985 and spring 1992. We excluded multiple daily locations and those with inadequate precision, leaving for analysis 10,678 location records from 106 individuals.

Movements

Rates of Movement

Polar bears were capable of making long movements over short periods of time, and sometimes maintained rapid movement rates for long periods. Five animals sustained movement rates of > 4 km/h for periods of > 20 h. One bear moved 4.3 km/h for a minimum of 45 h. Another moved 4.5 km/h for over 41 h, and a third bear moved 4.0 km/h for 46 h. Maximum movement rates must have exceeded these, because we suspect bears seldom moved along the straight lines we recorded.

We calculated 2,296 estimates of hourly movement rate for females confirmed to be with young of various ages and 2,576 estimates for females suspected of being with young. Movement rates of females known to be accompanied by cubs or yearlings were lower than movement rates of those suspected to have cubs or yearlings (Table 1). Therefore, we limited subsequent analyses to animals of confirmed status.

We measured 4,427 movements between consecutive relocations of instrumented bears with confirmed reproductive status. These relocations were separated by as little as 10 h and as much as 1 month. Hourly rates of movement declined as the interval between relocations increased. This decline was logarithmic and neared an asymptotic value when intervals 150-200 h or longer were used (Figure 1). Hourly movement rates measured at intervals of 100 h or less were significantly higher ($\bar{x}$ = 0.59 km, SE = 0.009) than those measured at longer intervals ($\bar{x}$ = 0.42 km, SE = 0.009; $\underline{t}$ = 13.58, df = 3,764, $\underline{P}$ < 0.001). Therefore, we used 3,071 observations separated by intervals of 100 h or less for comparisons of movement rates among animals of differing status and among months of the year.

Mean hourly rates of movement (km/h) varied from 0.96 for females accompanied by yearlings in December, to 0.30 for females with yearlings in March (Table 2). Rates of movement differed among months and reproductive categories. Comparisons of April-December movements indicated a significant difference in movement rates among females with cubs, females with yearlings, and single females ($\underline{F}$ = 5.13, df = 2, $\underline{P}$ = 0.006). Tukey pairwise comparisons revealed that females with cubs moved at lower rates overall than did single females or females with yearlings (HSD = 3.316, df = 2572, $\underline{P}$ = 0.05). Other differences in the main factor "reproductive status" were not observed. We recorded many differences in movement rates among months, however (Table 2). In all comparisons, spring and late summer months were characterized by the shortest hourly movements, whereas early winter (November-December) movements were the longest. We had correctly

predicted low rates of movement in summer; but the data did not support our prediction of high rates of movement in spring and low rates in autumn.

There were significant interactions among the main factors "month" and "status" in all 3 ANOVAs, suggesting caution in interpreting main effects of both factors. Although movement rates of females with cubs and single females increased from April to May, movement rates of females with yearlings declined in the same interval. Also, females with yearlings made longer hourly movements in February than in March, but females with 2-year-olds made shorter hourly movements in February than March. Likewise, single females made their longest hourly movements in November and moved much less in December whereas females with yearlings, which had very similar overall movement rates, increased movements from November-December (Table 2).

Monthly Displacement

There were few significant variations, among months or reproductive categories, in displacement (Table 3). Females with cubs corroborated our hypothesis that young cubs are relatively immobile, and moved significantly less distance from the beginning to the end of each month than single females (F = 2.54, df = 2, P = 0.08; HSD = 3.33, df = 384, P = 0.05). Contrary to our predictions, however, monthly displacements in November, averaged over all bears, were greater than they were in April (F = 1.62, df = 8, P = 0.12; HSD = 4.41, df = 384, P = 0.05). Other differences between status or month were not significant, and there were no significant interactions.

The azimuths of monthly movements recorded for instrumented polar bears were not independent of the month of measurement (Table 4). In February, March, April, September, and December, directions of polar bear movements were highly variable, and uniformly distributed around the compass rose. In January, however, the average polar bear movement was easterly, and the distribution of azimuths was significantly different from uniform. In May, June, July, and August, movements of polar bears deviated from uniformity, all in northerly directions as we predicted. In October, polar bears moved significantly south, as we predicted. Directions of polar bear movements in November did not differ from uniform. November displacements, however, appeared to be bimodal, with most animals moving either westerly or easterly.

Total Distances

Mean total distances moved per month varied from 186-492 km (Table 5). As with movement rates and displacements, distances moved did vary among months and reproductive categories of females. Total movements during April, May, July, August, and September were less than those in December (F = 1.88, df = 8, P = 0.06; HSD = 4.41, df = 384, P = 0.05). Movements each month of females with cubs also were lower than those of single females (F = 2.97, df = 2, P = 0.05; HSD = 3.33, df = 384, P = 0.05). Other differences among months and classes of female were not significant, and there were no interactions.

Annual movements of PTT-equipped polar bears ranged from 1,454-

6,203 km ($\bar{x}$ = 3,415, SE = 103). When total annual movements of bears in each confirmed reproductive status were compared, there were no significant differences ($\underline{F}$ = 0.32, df = 2, $\underline{P}$ = 0.73).

Activity Levels

Long-term Sensors

Activity estimates derived from long-term sensors indicated variation among bears of differing reproductive status and among months. The highest activity levels were consistently reported in May, June, and July, with the highest peak in June (Table 6). Winter activity levels were lower, and autumn and early spring levels were often the lowest. Single females were consistently recorded less active than females accompanied by young (Table 6). Month and status interacted only from April to December; hence, monthly trends among different classes of bears were largely concordant.

Hourly Sensors

We recorded 177,892 observations of hourly activity from 59 bears equipped with diel counting PTT's. We excluded from analysis animals in uncertain reproductive status and those that had entered maternity dens; leaving 69,563 records of hourly activity from 43 bears of varying reproductive status.

We were able to examine hourly activity levels during April through November for 19 single bears, 18 bears accompanied by cubs, and 16

accompanied by yearlings with multi-way contingency tables. This analysis, which included 54,780 individual activity records, suggested highly significant differences among categories of reproductive status (χ^2 = 201, $\underline{P} \leq 0.001$), months (χ^2 = 1349, $\underline{P} \leq 0.001$), and hours of the day (χ^2 = 426, $\underline{P} \leq 0.001$). Also there were significant interactions between status and month (χ^2 = 630, $\underline{P} \leq 0.001$). The interaction between status and hour (χ^2 = 116, $\underline{P}$ = 0.05) appeared to depend on females with cubs. When females with yearlings and single females were examined without females accompanied by cubs, the interaction between status and hour was not significant (54, $\underline{P}$ = 0.21) while all other tests remained highly significant.

When hourly activity levels were analyzed as continuous rather than discrete data, patterns in the conclusions were identical to those apparent from the categorical analyses. The continuous data approach, with ANOVA, however, provided more information on more categories of comparisons, and greater resolution of the variation in activity levels. During the months of April through December, 60,839 records of hourly activity were compared. During that period, 18 females with cubs were active a mean 20.2% (SE = 0.17) of each hour. They were more active than 16 females with yearlings ($\overline{\underline{x}}$ = 17.9%, SE = 0.17) which were more active than 19 single females ($\overline{\underline{x}}$ = 16.2%, SE = 0.14; $\underline{F}$ = 223.55, df = 2, $\underline{P}$ < 0.01; HSD = 3.32, df = 60,175, $\underline{P}$ = 0.05). There also were significant main effects of month ($\underline{F}$ = 199.49, df = 8, $\underline{P}$ < 0.001) and hour of the day ($\underline{F}$ = 24.35, df = 23, $\underline{P}$ < 0.001). Activity levels, averaged over all hours, were highest in June followed by December, May, and November. July and October activity levels were higher than in April, January, February,

August, and September (HSD = 4.39, df = 60,175, P = 0.05; Table 7). Hourly activity levels generally were lowest in the early morning and higher in late morning and afternoon [HSD = 5.14, df = 60,175, P = 0.05 (Table 8)]. There were no interactions between reproductive status and hour of the day (F = 1.17, df = 46, P = 0.21). There were, however, significant interactions between month and status (F = 32.35, df = 15, P < 0.001), and month and hour (F = 5.96, df = 184, P < 0.001).

Most females that were single when instrumented in spring or fall entered dens by December of each year. Relatively few bears, compared to the total number used in movements analyses, were instrumented with activity collars. Of single females fitted with activity collars, a small number may not have entered dens. Continuous darkness between late November and mid-February precluded visual confirmation that they were not in dens in that time period, however; and transmission patterns were not conclusive. Therefore, we did not report activity levels for females confirmed single between December and February. Between March and November, however, 40,281 records of hourly activity, including those from single bears, were compared. Activity levels of 19 single females ($\bar{x}$ = 16.2%, SE = 0.14) were lower than those for 19 females with yearlings ($\bar{x}$ = 16.9%, SE = 0.16; F = 37.17, df = 1, P <0.001). Main effects of month (F = 276.62, df = 8, P < 0.001) and hour (F = 11.30, df = 23, P < 0.001) also were significant. Activity levels were higher in May and June than in other months of this period, and lowest in March, August, and September (HSD = 4.39, df = 39,819, P = 0.05; Table 7). The highest levels of hourly activity, for all bears pooled, occurred between 1100

and 1500; and activities were generally higher after noon than before (Table 8). The lowest hourly activities occurred between 0000 and 0600. Differences in hourly activity were present throughout the day (HSD = 5.14, df = 39,819, $\underline{P}$ = 0.05), and there were significant interactions between months and hours ($\underline{F}$ = 5.02, df = 184, $\underline{P}$ < 0.001), indicating that diel activity patterns are not constant through the year. Reproductive status and month also interacted significantly ($\underline{F}$ = 17.01, df = 8, $\underline{P}$ < 0.001), but reproductive status and hour of the day did not ($\underline{F}$ = 1.24, df = 23, $\underline{P}$ = 0.195).

Between January and March, 8,576 records of hourly activity were compared. Six females with 2-year-olds spent more of each hour active ($\bar{x}$ = 14.1%, SE = 0.43) than 9 females with yearlings ($\bar{x}$ = 13.0%, SE = 0.26; $\underline{F}$ = 7.09, df = 1, $\underline{P}$ = 0.008). Radio-collared bears were more active in January and February than in March [$\underline{F}$ = 30.6, df = 2, $\underline{P}$ < 0.001; HSD = 3.32, df = 8419, $\underline{P}$ = 0.05 (Table 7)], but February activity did not differ from January activity. Also, hourly activity levels varied through the diel cycle. Minimal activity occurred in the early mornings, and the highest activity levels occurred in afternoon and early evening [$\underline{F}$ = 6.57, df = 23, $\underline{P}$ < 0.001; HSD = 5.15, df = 8419, $\underline{P}$ = 0.05 (Table 8)]. Females with 2-year-olds, which were most active in late morning, were an exception to this overall trend. There were significant interactions between reproductive status and month ($\underline{F}$ = 20.36, df = 2, $\underline{P}$ < 0.001) and hour and month ($\underline{F}$ = 1.62, df = 46, $\underline{P}$ = 0.005). Interactions between hours and status were apparent (Figures 2-6), but not significant ($\underline{F}$ = 1.14, df = 23, $\underline{P}$ > 0.29).

Although there were many differences among months, hours, and bears of differing status, activity levels in March, September, and August were usually the lowest recorded, whereas October—December and May and June consistently showed higher activity (Table 7, Figure 2). This pattern was confirmed by evaluation of month as a main factor with all classes of bears pooled (F = 223.32, df = 11, P < 0.001; HSD = 4.62, df = 69,234, P = 0.05). Activity levels generally were lowest in early morning and highest in the afternoon. When all months and all bears were pooled (Table 8), activity levels were highest between 1200 and 1300, and in general higher in the afternoon and evening than during earlier parts of the day (F = 28.02, df = 23, P < 0.001; HSD = 5.14, df = 69,234, P = 0.05). The lowest hourly activity levels were recorded between 0000 and 0600. There were exceptions to the overall trends, however. In March, April, July, October, and November, elevated levels of activity occurred between 0600 and 1000 (Figures 2-6). For single bears and females with 2-year-olds, March activity was highly elevated.

Diel activity curves for bears in most reproductive categories were similar (Figures 2-6). Similar patterns in hourly activity among bears of different classes were corroborated by the absence of interactions between the main factors of status and hour in all comparisons. Daily activity appeared to peak in late morning in January-March and October-December, but in afternoon and early evening in May-July. Daily activity peaks in March and April occurred in morning and early evening yielding a bimodal distribution of activity. March peaks for single bears and those with 2-year-olds were the highest recorded even though overall March activity was low. Activities in

August and September show the least variation among hours of any months, whereas the highest activities and the highest relative peaks in activity were in June.

<u>Activity Areas</u>

We calculated 96 annual activity areas for PTT-equipped polar bears (Table 9). Activity area estimates were derived from 29 to 166 ($\bar{x}$ =74) satellite relocations. Contours developed by the harmonic mean method provided the best fit to actual observations. Most contours estimated for individual bears included only sea ice habitats and small portions of land near den locations. Some unoccupied areas, however, were included in activity area estimates. A few estimated activity areas, based upon crescent-shaped distributions of relocations overlapped significant portions of land that were not occupied (Figure 7). Annual activity areas were large and varied among individual bears. They varied among individuals and with differences in reproductive status (Table 10), and ranged from 12,730 km^2 to 596,800 km^2. Single females and females accompanied by yearlings occupied the largest areas. The differences in sizes of areas were not significant for either 95% contours ($\underline{F}$ = 0.87, df = 2, $\underline{P}$ = 0.44) or for core activity areas within 50% harmonic mean contours ($\underline{F}$ = 0.69, df = 2, $\underline{P}$ = 0.52), apparently because the magnitude of variation among individual bears was so great. Hence, we failed to reject the null hypothesis that activity area size was independent of reproductive status. The annual variation in activity areas of individual bears verified that multiple years of monitoring are necessary to describe the

geographic distribution of polar bears in the Beaufort Sea. Over periods of at least 3 years, however, the activity areas of polar bears might reasonably be called home ranges (Figures 7 and 8).

We calculated 582 estimates of monthly activity areas for 95 individual polar bears. Of those, 289 were derived for 64 animals that were not in dens, and for which reproductive status was known. Variation in areas occupied was dependent upon month and reproductive class (Table 11). Our prediction that areas occupied would be largest in summer was not supported however. Two-factor ANOVA's, performed for time periods when each reproductive status was present, showed that only differences among months were significant, corroborating the analysis of annual activity areas. Therefore, all animals of known status were pooled to examine overall monthly differences with a 2-factor ANOVA. That analysis confirmed both that 95% contour areas occupied in December exceeded those of all other months except January, and that there were no differences among months January-November (F = 2.44, df = 11, P < 0.007; HSD = 4.67, df = 214, P = 0.05). Mean January activity areas were much smaller than those of December. The difference was not significant, apparently because of the large associated standard error (Table 11).

Geographic Patterns

Bounds of the Population

Ten random samples (405-500 points each) were taken from 9,568

relocations of polar bears equipped with PTT's in the Beaufort Sea. We excluded 1,110 relocations of polar bears originally captured outside of the Beaufort Sea from this boundary-definition process. The population boundary calculated as the mean of the 10 samples surrounded the region from Cape Bathurst in Canada to south of Pt. Hope on the Chukchi Sea coast of Alaska and extended approximately 300 km north of the coast (Figure 9). The perimeter of this region excluding land areas, was 8,655 km long, and the area was 939,153 km^2 (SE = 9,304). The core area (50% contour) of this population was the 122,089 km^2 (SE = 3,960) extending from the Beaufort Sea coastline to approximately 100 km offshore, and ranging from the Canada-US border in the east, to Barrow, Alaska in the west.

When the area occupied by the population was divided into 10° longitude zones, it was clear that PTT-equipped polar bears did not use the whole area equally (Figure 10). Bears captured along the Canadian and eastern Alaskan coast most commonly moved west when they left their area of capture. Only 8% of the relocations of bears marked near Tuktoyaktuk (127°-137°) were made east of Cape Bathurst. On the other hand, nearly 50% of the relocations of bears captured in the Tuktoyaktuk zone were in the zone west of their capture, and nearly 20% were 2 zones to the west. Bears captured between Barrow and 147° longitude were broadly distributed from Cape Lisburne to western Canada, and appeared as likely to move west or east from capture locations. Bears captured between Barrow and 147° longitude, however, seldom (<8%) were reobserved west of 167°. Overall, 25% of the relocations of bears originally captured in the zone from Barrow to

Cape Bathurst were west of Barrow. Conversely, only 6% of relocations of bears originally captured west of Barrow were in the zones east of Barrow (Figure 10). Bears captured in the Chukchi and Bering seas west or south of Cape Lisburne were rarely (<3%) reobserved east of Pt. Barrow. Likewise, polar bears instrumented in Canada east of Cape Bathurst were only observed in the Beaufort Sea 12% of the time, and only in the very eastern portions.

Seasonal Concentrations and Philopatry

There were significant differences in fidelity to monthly harmonic mean activity centers (F = 8.61, df = 11, P < 0.001). The greatest local fidelity occurred in July, when harmonic mean activity centers, for individual bears, among years averaged 202 km apart (Table 12). The least local fidelity occurred in December when activity centers were 450 km apart. Monthly differences in fidelity to geographic area were reflected in patterns of spatial use. Multi-year relocations of polar bears in July were concentrated in the Beaufort Sea between Barrow and the Canadian Border. Lines connecting centers of activity for bears monitored in more than one July were shorter than in other months, as reflected in Table 12, and they did not leave the Beaufort Sea (Figure 11). From July, the dispersion of multi-year locations increased each month through mid-winter, reached a peak in December, and declined through spring and early summer (Table 12). Polar bears captured along the Beaufort Sea coast frequently occupied different geographic regions during first and subsequent winters of location, but they returned to the central Beaufort Sea each summer. This is added evidence that areas occupied by

polar bears over multi-year periods can legitimately be called home ranges.

Discussion

Movements

Rates of Movement

Differences in movement rates between females of known and suspected status are unexplained. They may indicate losses of dependent young that were not verified, but which would have altered movement patterns of the females involved. Females with cubs, after all, did move less than females without young. Conversely, females with yearlings actually made longer hourly movements than single females. Also, few females lost young in their second year (Chapter IV), and 2-year-old young are mobile enough that they do not limit their mother's mobility. Actual movements of bears surely differed from those we recorded because bears did not walk in straight lines between relocation points. The fact that we examined only movement rates that were measured over periods of 100 h or less, however, provided us with more accurate representations of actual movements than would have measurements made over a longer duration.

Our recorded movements also differed from reality because the ice of the Beaufort Sea is constantly moving. Amstrup (unpubl. data) found that polar bears occupying dens built upon the pack ice drifted up to 0.7 km/h, and that the winter-long average drift was 0.15 km/h. The predominant drift direction was westerly. Hence, movement rates relative to the ice surface

could have been much lower than we recorded (Table 1) if bears were traveling to the west. Bears walking eastward may sometimes have been displaced to the west. Bears walking to the east would have had to walk 0.15 km/h, on average, in order to stay in the same place. Average movements of sea ice, like average polar bear movements, however, are of limited value. During this study, we observed pulses of ice movement, in both easterly and westerly directions, during which ice moved at rates of 2 km/h for periods of up to 3 or 4 days. Buoys placed on the ice and monitored by satellite, and satellite borne synthetic aperature radar may allow more meaningful corrections for movements of polar bears in the future.

As we predicted, rate of movement varied significantly among most months. Hence, rate of movement was not independent of the time of the year. Contrary to our predictions, however, movement rates generally were lowest in spring and greatest in winter (Table 2). Movement rates also were high in June and July but lower again in September. Movement rates might be tied to the pace of change in the pack ice environment. Bears had the highest rates of movement in November and December as the sea-ice was rapidly solidifying, and June and July when ablation began in earnest. Many other interpretations are possible, however, and these data confirm that interactions between polar bears, their prey, and the sea ice are not presently understood.

Messier et al. (1992) reported that peak movements of instrumented polar bears in Viscount-Melville Sound in the Canadian High Arctic occurred from May to July, and that movements were reduced from October-March.

Our observations deviated substantially from those. In the Beaufort Sea, movements rates were higher in November and December than in other months, and they were low in May. In the Beaufort Sea, movement rates were still high in January but began to decline thereafter. Contrasting measurements in the Canadian Arctic indicated an increasing trend in mobility from January through spring (Messier et al. 1992). Overall, the rates of movements reported for northern Canada were much lower than we observed. The peak movement of 0.46 km/h (Messier et al. 1992: Table IV), like ours, was for females with yearlings. However, theirs occurred in June, and was half the magnitude of ours which occurred in December. Likewise, the lowest movement rate (0.05 km/h for single females in January) recorded by Messier et al. (1992: Table IV) was far below our minimum of 0.30 km/h which occurred in March.

Low winter-time mobility among polar bears in the Viscount-Melville Sound area may result from the land-fast, multi-year ice that is most common there (Messier et al. 1992), and from the very low densities of ringed seals (Kingsley et al. 1985). By comparison, the mostly annual ice of the Beaufort Sea is more dynamic, supports a higher density of ringed seals (Stirling et al. 1982; Kingsley et al 1985) and may allow more foraging opportunities through winter. Polar bears in the Beaufort Sea may spend more time actively foraging, and those in the Viscount-Melville Sound area spend more time resting and conserving energy. Messier et al. (1992) reported that long periods of "sheltering" were common among bears wintering in Viscount-Melville Sound, and attributed this behavior to the poor foraging conditions

there. Another factor may be the greater predictability of the foraging conditions in the stable ice of Viscount-Melville Sound (Gloersen et al., 1992). With little change in the status of the sea-ice after freeze-up, polar bears may be able to determine the profitable hunting areas early on, and therefore minimize mid-winter searching for good hunting areas. The constantly changing sea ice of the Beaufort Sea, however, can require major modifications of strategy from month to month, or even day to day.

Contrary to our prediction that movement rates of females should increase steadily as their cubs aged, the only differences among reproductive classes we recorded were for females with cubs. Derocher and Stirling (1990) reported a maximum mean movement rate of 0.15 km/h for polar bears of all classes on land near Hudson Bay. Family groups, adult males, and subadult females moved less in September than during other months. Pregnant females, the only class of bears to vary from others in Hudson Bay, made shorter movements in November than in other months. This apparently indicates that females constrained their activities during the pre-denning period. In the Beaufort Sea, November movement rates were high for all bears. We did not detect reduced rates of movement of pregnant females, although those same bears were significantly less mobile upon emerging from their dens with cubs in the spring. We expected that movement patterns reported by Derocher and Stirling (1990) would differ from ours, because the bears observed near Hudson Bay were "trapped on land" throughout the period of monitoring, and they were not actively foraging for seals. Nonetheless, our bears, like theirs, showed relatively low movement rates in

September (Table 2).

Using mark and recovery data, Lentfer (1983) reported a mean movement rate for polar bears on the sea ice of 10.7 km/d ($\approx$ 0.45 km/h if 24 hour days are used) with no differences among different sex and age groups. Garner et al. (1990) reported mean movement rates of polar bears in the spring of 0.6 km/h, with peak movements of 1.7 km/h. During summer, mean movement rates we measured were 0.53 km/h with a maximum observed rate of 2.7 km/h. In autumn, movement rates increased to a mean 0.7 km/h and the maximum remained 2.7 km/h. Winter movements were 0.45 km/h with the maximum observed remaining at 2.7 km/h. By comparison to the monthly analyses we performed, much information is potentially lost when data are pooled over quarterly periods. Nonetheless, the patterns reported by Garner et al. (1990) were comparable to ours and may suggest that polar bears in the Chukchi Sea are responding to environmental patterns similar to those in the Beaufort Sea.

Monthly Displacements

Measured displacements of polar bears were not independent of the status of the bear or the time of year. As we predicted, females with cubs changed positions less noticeably than other bears. As with rates of movement, displacements in November were large. Still-hunting at breathing holes in the newly forming ice was the predominant form of hunting we observed in the fall. The volatile nature of the ice at that time may result in widely separated ephemeral patches of good hunting to which bears must

respond quickly. Hence, even though the method of hunting in those patches may require little movement, movements between hunting sites may be long. Our prediction that movements in the fall would be small because still-hunting was prevalent, did not account for volatility in acceptable still-hunting locales.

Variations in rates of movement and measured displacements among different classes of bears and different months were largely but not entirely concordant (Tables 2 and 3). Rates of movement, therefore, and travel are not necessarily the same thing. For example, monthly displacements of females with cubs were different than those of single females but not different from females with yearlings. Movement rates of females with cubs, on the other hand, differed from both of those groups. The greatest contrast appeared to be that females with yearlings had higher movement rates than single females but smaller geographic displacements. There also were inconsistencies among months. The lowest movement rates were in March, for single females and females with yearlings, but only single females had their smallest displacements in March. Also, mean displacements and movement rates for January-April were much different. Only one pair-wise comparison of monthly geographic displacements was significant, and there were no significant interactions.

At any one time, some radio-collared bears moved in one principal direction while others moved in the opposite direction. Examination of monthly displacements failed to discern any principal directionality of movement during 6 months of the year. The only significant deviations from uniformity were in

May-August when measured displacements were significantly to the north, in October when they moved south, and in January when they moved east. Those movements appeared to be correlated with general patterns of ice formation and ablation. Between May and August, the ice of the southern Beaufort Sea is degrading (Gloersen et al. 1992), and polar bears appear to displace themselves to the north accordingly. October is usually the month of freeze-up and may be the first time in months when near-shore ice is available. Polar bears appear to move into near-shore foraging habitat when it becomes available in October, and they disperse easterly and westerly as it solidifies in November. Stirling (1990) also reported seasonal north-south movements of polar bears in the Beaufort Sea.

Variation in monthly displacements did not explain all seasonal patterns of distribution. Plots of centers of monthly activity revealed an affinity of Beaufort Sea polar bears for the central Beaufort Sea in summer and a tendency for them to disperse to the east and west in winter. Hence, although analyses of monthly displacements suggested only north-south trends in movement, radio-collared polar bears that were in the eastern portions of the Beaufort Sea in late winter consistently moved to the west in late spring and summer. Likewise, bears that had moved into the Chukchi Sea in winter consistently moved back to the east as summer approached. Lentfer (1972; 1974; 1983) reported that polar bears moved significantly to the east in spring of the year. Our observations of monthly displacement as well as analyses of activity centers verify that some bears moved easterly in the spring, but that such movements did not constitute the pattern for all individuals in the

population. Rather, between February and April, there was no measurable net displacement of polar bears in any direction.

Total Distances

Lentfer (1983), Schweinsburg et al. (1981) and Stirling et al. (1980; 1984) reported from mark and recovery locations that distances moved by animals of different sex and age class were not different. Although sample sizes were small in those studies, and the main focus was on differences between males and females, the findings were consistent with our observation of few differences in total movements among bears of varying status. We recorded that total monthly travels of single females exceeded those of females with cubs, but other differences were not significant. Because we could not instrument young bears that were still growing, or male bears of any age, quantitative analysis of the movements of subadults of both sexes and comparisons of males and females is still needed.

Garner et al. (1990) reported a mean annual movement for polar bears in the Chukchi Sea of 5,542 km ±634 for a sample of 6 PTT-equipped polar bears. Our mean of 3,436 km/year was lower, indicating that polar bears in the Chukchi Sea may be more mobile than those in the Beaufort Sea. This difference may be due to the radical fluctuations of ice in the Chukchi Sea that require extensive north-south movements of bears (Garner et al 1990; Garner et al. 1994).

Movement rates, monthly displacements, and total distances moved

each month followed similar monthly patterns. Contrary to our null hypotheses, variations in all 3 were dependent upon reproductive status and month. They were not entirely concordant, however (Figure 12). Principal conclusions from all 3 evaluations were: females with cubs move less, and early winter movements by most classes of bears were large.

Activity Levels

Variations in activity levels of polar bears were strongly dependent upon hour of the day, month, and reproductive status. Early mornings were consistently characterized by the lowest activity levels. Activity levels increased in late morning, often reaching broad peaks in afternoon and early evenings (Figures 2 and 6). There were no interactions between reproductive class and hour, indicating that trends in hourly activity were similar among all reproductive classes even though absolute levels of activity did differ among reproductive classes. Activity levels also varied among months (Table 8). Bears were typically more active in October-December and May and June than in other months, and less active in January-March and September. Activity levels we recorded often were not concordant with our recorded movement patterns (Figure 12).

Messier et al. (1992) reported activity as well as mobility peaks in summer and lulls of both in winter. We observed high activity levels in May and June with declining activity through summer, but we also observed a peak of activity especially notable in females accompanied by young, during autumn and early winter. Messier et al. (1992) reported that single females were more

active than females with cubs in May, but that no other categories differed in activity levels. In contrast, we observed numerous differences in activities among reproductive categories; single females were often the least active class of bear, whereas females with cubs were often the most active (Table 6, Figures 3 and 6). Single females, on the other hand, made longer monthly movements than all other bears and occupied large areas; whereas females with cubs moved shorter distances than other bears and occupied small activity areas (Tables 3 and 10). As with human parents, high activity with little actual movement seems a reasonable observation for females with cubs.

Estimates of activity derived from 72-hour or long-term counters were similar to those derived from the hourly sensors (Tables 6 and 7). Long-term activity sensors, however, failed to detect the pulse in early winter activity recorded by hourly activity counters. Reasons for that failure are unknown, but it does reflect a limitation of sensors that record activity over long periods of time. This limitation also could account for the differences between our winter activity trends and those reported by Messier et al. (1992).

Messier et al. (1992) speculated that the similarity in activity levels of females with cubs and those with yearlings was an indication of comparable parental investment. Our data are not directly comparable to those of Messier et al. (1992) because they monitored fewer animals during a shorter duration of study and did not confirm reproductive status. Nevertheless, our data indicate significant differences between movements and activities of females with young of different ages. Differences were fewer when only long-term

sensors were evaluated, suggesting that measures of long-term activity or movement do not always accurately convey activity or mobility trends. Without substantial ground-truthing, neither long-term nor hourly activity measurements should simplisticly be related to parental investment. Mobility of females with cubs was low, but the investment in young cubs, in the form of milk, is high, and could overshadow other parental activities occurring at that time. Parental investment involves many behavioral, ecological, and even physiological phenomena (Verme 1969; Trivers and Willard 1973). Changes in movement patterns or activity patterns could reflect varying levels of investment. They could, however, reflect many other considerations faced by polar bears, and much more information regarding post-parturient care of young would be necessary in order to establish relationships.

Knudsen (1978) reported that polar bears were inactive 87% of the time in summer. Lunn and Stirling (1985) also reported that polar bears summering on land were largely inactive. Activity levels among bears feeding at the dump were much higher, however (Lunn and Stirling 1985). Knudsen (1978) speculated he underestimated the amount of time bears are really active because his samples were heavily biased toward mid-day, and because his bears were stranded on land and unable to hunt as they do on the sea ice. Activity level somehow must be related to opportunities to feed or engage in other essential activities. While trapped on land and unable to feed, the most essential activity is rest. It appears, however, that even polar bears actively hunting on the sea ice spend much time inactive. Our long-term activity sensors recorded that polar bears were active only 3-22% of the time (Table

6). Messier et al. (1992) recorded similar activity levels (5-24%) with long-term activity sensors on PTT-equipped polar bears in the Canadian High Arctic.

After over 600 h of visual observations, Stirling (1974) reported that polar bears spent 65.4% of their time in activities that sensors on PTT's would register as inactive. Stirling (1974) also reported that in summer, polar bears spent the most time sleeping during late afternoon and evening, with minimum time sleeping between 0100 and 0700. He attributed this pattern to: 1) the fact that greatest numbers of ringed seals hauled out on the surface of the ice in afternoon and fewest hauled out in the early morning, and 2) the relatively higher success rate polar bears had in catching seals by still-hunting at breathing holes as opposed to stalking seals that were hauled out. Overall, activity levels of female polar bears in the Beaufort Sea reached broad peaks from late morning to early evening. Further, activity levels we observed were universally low in the early morning (0000-0600). Polar bears in the Beaufort Sea did not maximize their rest activity in the afternoons and evenings, as those hours were the hours in which polar bears were most often active. However, because still-hunting at breathing holes and resting might transmit similar activity patterns to the satellite, we cannot overlook the possibility that Beaufort Sea bears still-hunt extensively in the mornings.

Kelly and Quakenbush (1990) observed that ringed seals (Phoca hispida) occupied their subnivian lairs most frequently in late evening and early morning (1800-0230) in March and April, but shifted to midday occupancy (1030-1630) in May and June. Kelly and Quakenbush (1990)

concluded the March and April haulout pattern served to minimize under-ice activities (e.g. foraging) during the darkest periods of the day. They further concluded that 24-hour daylight, available by May, removed any constraints on under-ice activities due to low visibility, and that the mid-day haul-out might be associated with the beginnings of the molting cycle—the warm temperatures of mid-day augmenting blood flow to the skin. Activities of radio-collared polar bears in the Beaufort Sea were elevated between 1800 and 0230 during March and especially April, or relatively constant (Figures 2-6). In May and June, on the other hand, activity levels of all classes of polar bears we observed were at local or absolute maxima shortly after midday. High mid-day activity levels in late spring and summer could correspond with basking behavior of seals in lairs and on the surface of the sea ice after snow melts. High activity levels in late spring fit our predictions more closely than any of the measurements of movement. In spring, polar bears actively search out ringed seal lairs (Smith and Stirling 1975; Smith 1980). Physical, physiological, and perhaps other unidentified constraints may determine when seals occupy lairs. Whatever the factors that determine temporal pattern of lair occupancy, it appears that polar bears may take advantage of the resultant pattern.

Activity Areas

Seasonal and Annual Activity Areas

Areas of annual activity for Beaufort Sea polar bears were large and variable (Table 10), reflecting, as did other measurements, the great mobility of this species. Areas of monthly activity also were large and provided more

evidence of the lack of concordance among various mobility and activity indices. Polar bears often are highly active and even highly mobile, while confining movements to previously established areas (Figure 12). Although significant differences among reproductive categories were not detected, females with yearlings did occupy larger areas in nearly all months than other classes. Yearling polar bears are large but not yet hunting effectively on their own (Stirling and Latour 1978). Therefore, females accompanied by yearlings have large energy demands. The large areas they occupy may reflect the exploration necessary to secure resources to meet those demands when availability of prey is fluctuating.

Annual activity areas of females monitored for multi-year periods showed that some new area was occupied in some new years, but also that core areas of activity were used each year. This observation suggests that activity areas of polar bears, when viewed over multi-year periods, can be called home ranges. It simply takes a long time for a polar bear to occupy all of its home range. The labile nature of the sea ice results in a variable distribution of food. Therefore, female polar bears cannot find adequate nutritional resources if they maintain the same defended territories each year. Likewise, males cannot defend territories if they are, each year, to maximize their potential for finding mates (Ramsay and Stirling 1986). This conclusion fits nicely with our observations of large activity areas of which only a portion may be used in any one season or year.

PTT-equipped polar bears in the Chukchi Sea occupied average activity

areas of 244,463 km^2 (Garner et al. 1990). Movements and activity areas in the Beaufort Sea appear to be intermediate in magnitude between those reported for the Chukchi Sea and those reported from parts of the Canadian Arctic Archipelago (Schweinsburg and Lee, 1982; Messier et al. 1992). Schweinsburg and Lee (1982) hypothesized that movements of polar bears should be inversely proportional to body stature and to habitat richness. Seasonal and annual variability in sea ice cover and character, and the resulting variation in availability of prey, may overshadow considerations of habitat richness, however (Garner et al. 1990). The sea ice of the Chukchi and Beaufort seas is more dynamic and unpredictable than the ice of the Canadian archipelago (Gloersen et al. 1992), and the mobility of polar bears appears to respond to that variability.

Best (1982) and Hurst et al. (1982a,b) concluded from treadmill tests that polar bears are inefficient walkers, using much more energy for locomotion than other similar sized animals. They attributed this to aspects of polar bear morphology, specifically the massive limbs evolved for capture of prey. Economy of transport, they suggested, was compromised by considerations of thermo-regulation and hunting strategy. Treadmill tests, however, do not appear to tell the whole story. Taylor et al. (1974) found that differing configurations and weights of limbs, even among diverse groups of mammals, had little effect on relative costs of locomotion. Also, costs of locomotion among very diverse groups of herbivores, including domesticated animals which are largely insulated from natural selection for mobility, are very similar (Fancy and White 1985). It seems unlikely, therefore, that polar bears

which as our studies suggest, have been under great selective pressure to be mobile, could be so relatively inefficient. Another inconsistency in these treadmill tests was the discovery that energy expenditures of the largest animal tested were very near the line for other mammals (Hurst et al. 1982b). Empirical observations (Taylor et al. 1985) suggest that rapid movement, at least, becomes more expensive as size of polar bears increases.

Our measurements, which were derived from many observations of numerous individuals, are unequivocal and indicate polar bears are among the most mobile of all quadrupeds. In some months, movements of polar bears may have been necessary to stay on the changing sea ice. For most months, however, all of our measurements suggested polar bears were highly mobile when stable sea ice would not have necessitated any movement at all. Large and rich food items might compensate somewhat for inefficiencies in travel. But, in the long run, a foraging strategy that includes extensive travel, would place strong selective pressure on developing efficient means of achieving that travel. High energy expenditures of polar bears walking on treadmills may have been due to levels of excitation resulting from the cramped and strange surroundings. Such excitation could result in posturing costs (Schmidt-Nielsen 1972; Fancy and White 1985) over and above the costs of the exercise being observed. We have shown that polar bears sometimes move long distances very rapidly. They typically move at relatively low rates of speed, however. Perhaps, treadmills used in energetics experiments were running at speeds that do not represent sustained movement rates for polar bears. We believe that enough questions about polar bear energetics remain that existing

conclusions regarding the efficiency of mobility in polar bears should be revisited.

Our mobility and activity measurements were largely but not entirely concordant (Figure 12). The most obvious deviations from concordance for single females were: peak monthly travel in February when activity was at the 12-month low, and May, June, and July, activity level peaks when activity area sizes were low. All indices were high for females with cubs in October-December. However, activity level also was near the peak in May, June and July, when activity area sizes were at their lowest levels. Also, in summer, the other movement indices were high relative to activity area. Clearly, neither activity nor linear movement were consistent predictors of activity area size. High rates of late winter movement combined with low levels of activity might reflect lots of travel while looking for relatively few places where hunting could be productive. High activity levels coupled with little movement in summer might reflect the opposite condition.

Geographic Patterns

Bounds of the Population

We confirmed Lentfer's (1983) conclusion that there is some movement of polar bears along the mainland coast of the Beaufort Sea between Canada and Alaska. We also demonstrated that the movement between Canadian and Alaskan Beaufort Sea areas is more extensive than previously suspected, and we quantified the amount of movement across the north coast.

Stirling et al. (1978; 1984) and Schweinsburg et al. (1981) concluded

that polar bear populations are comprised of many animals with overlapping

home-ranges. Separation of sub-populations, therefore, might not be

predictable from year to year. Schweinsburg et al. (1981) concluded that 5-

10% of bears in any one area commonly disperse to adjacent areas. Our

observations substantiate the hypothesis of small amounts of dispersal among

adjacent areas. Nonetheless, bears captured in the eastern Beaufort Sea

generally moved to the west as they dispersed from capture sites, and

returned seasonally to the eastern portions of the Beaufort Sea. Bears

captured in the Western Beaufort Sea generally moved to the east from their

capture locations and returned seasonally to the west. This seasonal

dispersal pattern, and the observation of summer fidelity of most bears to the

central Beaufort Sea, suggest that this population is discrete enough to be

managed as a unit. Stirling et al. (1978) also concluded movements of

animals adjacent to various Arctic settlements are seasonally local enough

that the concept of discrete subpopulations applies for management purposes.

After only 2 years of study, the cumulative activity area of 20

PTT-equipped polar bears in the Chukchi and Bering seas west of Alaska was

865,000 km^2 (Garner et al. 1990). With additional monitoring of more animals,

that area is sure to increase. Polar bears in the Chukchi Sea may be more

mobile than in other areas under consideration.

Seasonal Concentrations and Philopatry

Amstrup and Gardner (Chapter V) reported that maternal polar bears in the Beaufort Sea were faithful to denning substrate and to general geographic area, but not to specific den sites. Movements of nonpregnant bears appear to follow the same pattern. There was fidelity, in some seasons, to general areas but not to specific locales, and the degree of that fidelity varied according to time of the year. Maximum fidelity was in summer and minimal fidelity in mid-winter, with a pattern of decentralization from and concentralization back to summer areas in the Beaufort Sea. Thus, fidelity to late winter and spring activity areas was greater than that for mid-winter, but less than that demonstrated in summer (Figure 11). Even our summer season fidelity was relative, however, as consecutive centers of activity were separated by over 200 km (Table 12). Stirling et al. (1980; 1984) concluded polar bears in the Canadian High Arctic showed a high degree of fidelity to spring feeding and breeding areas. Schweinsburg et al. (1981) reported a high degree of geographic fidelity during March, April and May. Lentfer (1983) reported polar bears were most commonly recovered, in late winter and early spring, in the areas where they were marked in previous spring seasons. Schweinsburg et al. (1981) concluded polar bears disperse from late winter-spring activity areas as the ice breaks up, and return to those areas again in late winter. The pattern we observed in the Beaufort Sea has sharpened the image of seasonal distribution and movement patterns of polar bears and suggested that there may be broad geographical differences in those patterns.

Polar bears of Manitoba return each summer to the same stretch of the Hudson Bay coastline (Derocher and Stirling 1990). This pattern apparently is caused by similar annual patterns of ice ablation in Hudson Bay and by the fact that polar bears stay with the sea ice as long as possible. Similarly, the distribution of Beaufort Sea ice is most constrained in summer, the time when polar bears showed the greatest degree of fidelity. As summer progresses, Beaufort Sea ice deteriorates most quickly near Barrow, where the Beaufort Gyre meets the Chukchi Gyre, and in the east where the Cape Bathurst Polynya expands westerly and the flow of the MacKenzie River is constantly putting fresh water into the system. By mid-summer the most stable ice in the Beaufort Sea is in the central portion between Lonely and the Canadian border (Gloersen et al. 1992), and bears gravitate toward that area every year (Figure 11). Hence, although there are no geographic barriers to movement out of the Beaufort Sea, a relatively discrete subpopulation may be maintained by the general pattern of ice formation and ablation. Changes in that pattern, as reflected by changes in polar bear movement, may be among the first hard indications of the effects of global warming.

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Table 1. Movement rates of satellite radio-collared female polar bears in the Beaufort Sea, 1985-93, comparing known and suspected reproductive status. Reproductive status was confirmed if visual observations were obtained regularly enough to know that young survived through each stage of life.

Reproductive Status	Movement Rate (km/h)			Wilcoxon Z	$\underline{P}^b$
	$\underline{n}^a$	$\overline{x}$	S.E.		
Females With Cubs					
Confirmed	1012(34)	0.51	0.016	4.39	0.0001
Suspected	776(38)	0.59	0.020		
Females With Yearlings					
Confirmed	1100(39)	0.55	0.020	2.74	0.0060
Suspected	1301(39)	0.60	0.010		
Females With 2-Year-Olds					
Confirmed	184(13)	0.44	0.030	1.07	0.2850
Suspected	499(26)	0.49	0.020		

[a]Numbers of satellite relocations (numbers of individual PTT-equipped polar bears).

[b]Probability of difference this great between females of confirmed and suspected status occurring by chance.

Table 2. Movement rates (km/hr) of satellite radio-collared female polar bears in the Beaufort Sea, 1985-93. Rates were calculated only if reobservation interval was less than 100 hours. Significant differences among months (Tukey's HSD) are shown by non-overlapping lines.

MONTH [a]	FEMALES/CUBS Mean	S.E.	Obs.	Bears	SINGLE FEMALES Mean	S.E.	Obs.	Bears	FEMALES/YEARLINGS Mean	S.E.	Obs.	Bears	FEMALES/2-YR-OLDS Mean	S.E.	Obs.	Bears	MONTHLY TOTALS Mean	S.E.	Obs.	Bears	SIGNIFICANTLY DIFFERENT $P = 0.05$
Mar					0.48	0.06	45	8	0.30	0.05	55	7	0.49	0.11	29	6	0.40	0.04	129	21	
Feb					0.50	0.07	14	3	0.42	0.05	52	5	0.37	0.08	26	5	0.42	0.04	92	13	
Apr					0.47	0.03	109	15	0.63	0.05	102	18	0.49	0.08	32	4	0.54	0.03	243	37	
Jan					0.68	0.15	23	3	0.61	0.07	90	8	0.44	0.07	27	5	0.59	0.05	140	16	
SubTotal					0.50	0.03	191	29	0.53	0.03	299	38	0.45	0.04	114	20	0.50		604	87	
Apr	0.36	0.03	100	23	0.47	0.03	109	15	0.63	0.05	102	18					0.49	0.02	311	56	
Sep	0.43	0.04	33	8	0.53	0.02	166	29	0.45	0.07	26	8					0.50	0.02	225	45	
May	0.44	0.03	85	12	0.57	0.03	284	31	0.48	0.04	91	11					0.53	0.02	460	54	
Aug	0.50	0.04	36	8	0.60	0.03	170	29	0.48	0.06	35	7					0.57	0.02	241	44	
Oct	0.60	0.08	75	11	0.58	0.05	129	21	0.64	0.07	47	8					0.59	0.04	251	40	
Jul	0.58	0.06	44	8	0.62	0.03	192	31	0.59	0.06	49	8					0.61	0.02	285	47	
Jun	0.52	0.06	43	8	0.71	0.03	243	30	0.67	0.06	65	9					0.68	0.02	351	47	
Nov	0.62	0.04	142	13	0.93	0.11	49	6	0.75	0.06	114	15					0.72	0.04	305	34	
Dec	0.79	0.07	154	10	0.67	0.15	12	3	0.96	0.08	83	7					0.84	0.05	249	20	
SubTotal	0.57 [b]	0.02	712	101	0.61	0.01	1354	195	0.66	0.02	612	91					0.61		2678	387	
Mar					0.48	0.06	45	8	0.30	0.05	55	7					0.38	0.04	100	15	
Feb					0.50	0.07	14	3	0.42	0.05	52	5					0.43	0.04	66	8	
Sep					0.53	0.02	166	29	0.45	0.07	26	8					0.52	0.02	192	37	
Apr					0.47	0.03	109	15	0.63	0.05	102	18					0.55	0.03	211	33	
May					0.57	0.03	284	31	0.48	0.04	91	11					0.55	0.02	375	42	
Aug					0.60	0.03	170	29	0.48	0.06	35	7					0.58	0.03	205	36	
Oct					0.58	0.05	129	21	0.64	0.07	47	8					0.59	0.04	176	29	
Jul					0.62	0.03	192	31	0.59	0.06	49	8					0.62	0.03	241	39	
Jan					0.68	0.15	23	3	0.61	0.07	90	8					0.62	0.06	113	11	
Jun					0.71	0.03	243	30	0.67	0.06	65	9					0.70	0.03	308	39	
Nov					0.93	0.11	49	6	0.75	0.06	114	15					0.80	0.05	163	21	
Dec					0.67	0.15	12	3	0.96	0.08	83	7					0.93	0.07	95	10	
SubTotal					0.60	0.01	1436	209	0.61	0.02	809	111					0.61		2245	320	

[a] Interaction effects between month and status were noted in all time periods ($P < 0.05$).

[b] Females with cubs made shorter hourly movements than single females or those with yearlings ($F = 5.13$, $df = 2$, $P = 0.006$; $HSD = 3.32$, $df = 2572$, $P = 0.05$). Other differences among status categories were not significant.

Table 3. Linear displacement (km) from first to last location each month for satellite radio-collared female polar bears in the Beaufort Sea, 1985-93. n = # bears each status sampled each month. Significant differences are footnoted.

MONTH	FEMALES/CUBS			SINGLE FEMALES			FEMALES/ YEARLINGS			FEMALES/2 YROLDS			MONTHLY TOTALS		
	MEAN	S.E.	n	MEAN	S.E.	n	MEAN	S.E.	n	MEAN	S.E.	n	MEAN	S.E.	n
Jan				251	116	4	193	72	9	101	29	8	169	39	21
Feb				213	15	3	175	40	6	96	27	8	144	22	17
Mar				162	39	8	72	12	8	172	89	8	135	32	24
Apr				121	21	15	116	31	12	140	28	4	122	16	31
TOTALS				159	22	30	136	23	35	125	27	28			
Apr	79	14	10	121	21	15	116	31	12				108	14	37
May	129	18	15	162	17	56	125	19	15				150	12	86
Jun	105	25	12	201	20	53	136	29	12				176	16	77
Jul	130	24	10	144	12	50	177	38	12				148	11	72
Aug	125	27	12	170	16	40	166	30	11				161	12	63
Sep	155	28	11	171	18	37	178	73	6				169	16	54
Oct	171	39	10	195	36	20	131	38	7				176	23	37
Nov	194	39	15	196	44	6	215	50	13				202[b]	26	34
Dec	138	40	11	174	65	3	225	49	9				177	28	23
TOTALS	137[a]	10	106	170	7	280	161	13	97						
Jan				251	116	4	193	72	9				211	59	13
Feb				213	15	3	175	40	6				188	27	9
Mar				162	39	8	72	12	8				117	23	16
Apr				121	21	15	116	31	12				119	18	27
May				162	17	56	125	19	15				154	14	71
Jun				201	20	53	136	29	12				189	18	65
Jul				144	12	50	177	38	12				150	12	62
Aug				170	16	40	166	30	11				169	14	51
Sep				171	18	37	178	73	6				172	18	43
Oct				195	36	20	131	38	7				179	29	27
Nov				196	44	6	215	50	13				209	36	19
Dec				174	65	3	225	49	9				212	39	12
TOTALS				171	7	295	158	12	120						

[a] Females with cubs moved significantly less each month than single females (F = 2.54, df = 2, P = 0.08; HSD = 3.33, df = 384, P = 0.05).
[b] Mean monthly displacements were larger in November than in April (F = 1.62, df = 8, P = 0.12; HSD = 4.41, df = 384, P = 0.05).

Table 4. Azimuths (degrees true) of displacement from the beginning to the end of each month among satellite radio-collared female polar bears in the Beaufort Sea. All reproductive categories are combined.

Month	Mean Azimuth of Displacement	Angular Dispersion[a]	Rayleigh's Z-Test Value[a]	Probability Level P	Number of Animals n
January	81	65.3	6.03	0.005	49
February	36	79.7	0.04	0.5	39
March	58	77.9	0.27	0.5	48
April	296	76.9	0.78	0.5	80
May	26	71.3	6.11	0.005	122
June	4	71.6	5.32	0.005	111
July	328	67.0	10.44	0.001	105
August	44	71.9	4.15	0.02	92
September	88	74.8	1.53	0.2	70
October	167	68.6	5.14	0.01	64
November	250	72.7	1.98	0.1	52
December	83	76.2	0.58	0.5	51

[a]Zar (1984)

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Table 5. Total distances (km) moved per month by satellite radio-collared female polar bears of varying reproductive status in the Beaufort Sea, 1985-93. n = # bears each status sampled each month.

MONTH	FEMALES/CUBS			SINGLE FEMALES			FEMALES/ YEARLINGS			FEMALES/2 YROLDS			MONTHLY TOTALS		
	MEAN	S.E.	n	MEAN	S.E.	n	MEAN	S.E.	n	MEAN	S.E.	n	MEAN	S.E.	n
Jan				347	114	4	283	66	9	215	32	8	269	37	21
Feb				492	225	3	244	43	6	200	32	8	267	47	17
Mar				280	34	8	186	33	8	312	103	8	259	38	24
Apr				228	31	15	268	47	12	275	57	4	249	24	31
TOTALS				284	33	30	249	25	35	247	33	28			
Apr	192	44	10	228	31	15	268	47	12				231	23	37
May	251	21	15	305	19	56	238	24	15				284	14	86
Jun	192	25	12	345	19	53	296	28	12				313	16	77
Jul	252	47	10	291	17	50	305	36	12				288	15	72
Aug	227	23	12	316	22	40	267	35	11				290	16	63
Sep	249	24	11	296	23	37	268	62	6				283	18	54
Oct	294	43	10	338	39	20	218	56	7				303	27	37
Nov	317	41	15	347	29	6	337	62	13				330	30	34
Dec	418	74	11	333	65	3	420	92	9				408[b]	50	23
TOTALS	267[a]	14	106	310	8	280	291	17	97						
Jan				347	114	4	283	66	9				302	55	13
Feb				492	225	3	244	43	6				326	82	9
Mar				280	34	8	186	33	8				233	26	16
Apr				228	31	15	268	47	12				245	27	27
May				305	19	56	238	24	15				291	16	71
Jun				345	19	53	296	28	12				336	17	65
Jul				291	17	50	305	36	12				294	15	62
Aug				316	22	40	267	35	11				305	19	51
Sep				296	23	37	268	62	6				292	22	43
Oct				338	39	20	218	56	7				307	33	27
Nov				347	29	6	337	62	13				340	43	19
Dec				333	65	3	420	92	9				398	70	12
TOTALS[c]				311	8	295	281	15	120						

[a]Females with cubs moved less each month than single females (F = 2.97, df = 2, P = 0.05; HSD = 3.33, df = 384, P = 0.05).
[b]December movements exceeded movements in April, May and July-September (F = 1.88, df = 8, P = 0.06; HSD = 4.41, df = 384, P = 0.05).
[c]Other differences were not significant.

Table 6. Monthly activity levels (% of time active) of satellite radio-collared female polar bears in the Beaufort Sea, 1985-93, as determined by long term (24 or 72 hour) activity counters on satellite radio collars. Activity levels shown are means of the modal levels for each polar bear in each reproductive class for each week. Months that did not differ significantly are overlapped by lines in the final column of the table. Months and reproductive categories interacted significantly in all time periods. Significance of differences determined by ANOVA and Tukey's HSD procedure.

MONTH	FEMALES/CUBS MEAN	S.E.	N	SINGLE FEMALES MEAN	S.E.	N	FEMALES/YEARLINGS MEAN	S.E.	N	FEMALES/2 YROLDS MEAN	S.E.	N	MONTHLY TOTALS MEAN	S.E.	N	SIGNIFICANTLY DIFFERENT P = 0.05
Mar				11.7	1.8	45	12.0	1.4	43	19.5	1.30	37	14.1	0.9	125	
Jan				8.9	1.5	22	15.2	0.9	42	16.2	1.40	41	14.3	0.7	105	
Feb				6.4	1.5	19	15.5	1.5	34	18.7	1.80	40	15.0	1.1	93	
Apr				15.4	1.3	92	18.6	1.5	82	21.9	2.80	21	17.5	1.0	195	
SubTotal				a 12.7	0.8	178	15.9	0.8	201	18.6	0.80	139				
Sep	11.5	1.00	52	9.5	0.5	196	10.3	0.7	43				10.0	0.4	291	d
Aug	13.9	1.00	55	12.8	0.6	199	16.2	0.9	48				13.6	0.5	302	
Apr	10.6	0.90	93	15.4	1.3	92	18.6	1.5	82				14.7	0.8	267	
Oct	19.0	1.30	61	13.1	1.0	122	16.4	1.3	43				15.3	0.7	226	
Nov	19.0	1.10	66	15.4	1.7	44	15.7	1.2	66				16.8	0.7	176	
Dec	19.9	1.40	52	9.7	1.3	21	17.1	1.5	41				17.0	0.9	114	
Jul	20.0	1.20	53	18.6	0.7	241	22.3	1.4	57				19.4	0.6	351	
May	19.1	1.20	73	20.4	0.8	252	19.0	1.4	68				19.9	0.6	393	
Jun	21.0	1.20	51	22.0	0.8	242	21.4	1.6	51				21.7	0.7	344	
SubTotal	b 16.7	0.41	556	16.5	0.3	1408	17.7	0.5	499							
Sep				9.5	0.5	196	10.3	0.7	43				9.6	0.4	239	
Mar				11.7	1.8	45	12.0	1.4	43				11.8	1.1	88	
Feb				6.4	1.5	19	15.5	1.5	34				12.2	1.2	53	
Jan				8.9	1.5	22	15.2	0.9	42				13.1	0.8	64	
Aug				12.8	0.6	199	16.2	0.9	48				13.5	0.5	247	
Oct				13.1	1.0	122	16.4	1.3	43				13.9	0.8	165	
Dec				9.7	1.3	21	17.1	1.5	41				14.6	1.2	62	
Nov				15.4	1.7	44	15.7	1.2	66				15.6	1	110	
Apr				15.4	1.3	92	18.6	1.5	82				16.9	1	174	
Jul				18.6	0.7	241	22.3	1.4	57				19.3	0.6	298	
May				20.4	0.8	252	19.0	1.4	68				20.1	0.7	320	
Jun				22.0	0.8	242	21.4	1.6	51				21.9	0.8	293	
SubTotal				c 12.7	0.3	1494	16.9	0.4	616							

a Activity levels of all classes of females differed (F = 5.75, df = 2, P = 0.003, HSD = 3.33, df = 451, P = 0.05).

b Single females were less active (F = 4.45, df = 2, P < 0.001, HSD = 3.32, df = 2352, P = 0.05) than females with yearlings.

c Females with yearlings were significantly more active than single females (F = 6.41, df = 1, p = 0.01).

d Month and reproductive status interacted significantly only in this time period (F = 2.84, df = 16, P < 0.001).

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Table 7. Monthly activity patterns (% of hour active) of satellite radio-collared female polar bears of different reproductive status in the Beaufort Sea, 1988-93. All hours are included in each group. Months that did not differ significantly are overlapped by vertical lines. Significant differences (P < 0.05) determined by ANOVA and Tukey's HSD procedure.

Single Females and those with Cubs or Yearlings			Single Females and those with Yearlings			Single Females and those with 2-Yr-Olds or Yearlings			All Females of Known Status		
Month	Mean	Significance	Month	Mean	Significance	Month	Mean	Signficance	Month	Mean	Significance
Jan			Jan			Mar	12.0		Sep	10.3	
Feb			Feb			Feb	13.6		Aug	12.1	
Mar			Sep	9.6		Jan	14.2		Mar	12.6	
Sep	10.3		Mar	10.2		Apr			Feb	13.6	
Aug	12.1		Aug	11.3		May			Jan	14.2	
Apr	14.6		Oct	14.6		Jun			Apr	14.6	
Jul	18.0		Jul	17.2		Jul			Jul	18.0	
Oct	18.8		Apr	17.4		Aug			Oct	18.8	
Nov	21.0		Nov	17.8		Sep			Nov	21.0	
May	21.4		May	22.5		Oct			May	21.4	
Dec	21.7		Jun	23.3		Nov			Dec	21.7	
Jun	23.3		Dec			Dec			Jun	23.3	

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Table 8. Hourly activity patterns (% hour active at each hour) of satellite radio-collared female polar bears in the Beaufort Sea, 1988-93. Hours that did not differ significantly are overlapped by vertical lines. Significant differences (P < 0.05) determined by ANOVA and Tukey's HSD procedure.

Single Females and those with Cubs or Yearlings, April through December			Single Females and those with Yearlings, March through November			Single Females and those with 2-Yr-Olds or Yearlings, January through March			All Females of Known Status, All months		
Hour	Mean	Significance	Hour	Mean	Significance	Hour	Mean	Signficance	Hour	Mean	Significance
4	13.8		4	12.6		4	8.8		4	13.2	
5	14.2		2	12.9		5	9.3		5	13.6	
3	14.3		3	13.0		1	9.4		3	13.7	
2	14.5		5	13.1		2	9.6		2	13.9	
6	15.1		1	13.2		3	9.6		1	14.4	
1	15.3		0	13.9		0	10.4		6	14.7	
0	16.0		6	13.9		6	11.5		0	15.3	
7	16.8		23	15.5		23	11.5		7	16.2	
8	17.6		7	15.6		7	12.1		23	17.1	
23	17.9		22	15.8		22	12.3		8	17.4	
21	18.5		21	16.2		19	12.3		21	17.8	
20	18.6		8	16.5		21	12.7		22	17.9	
22	18.7		20	16.7		18	13.8		20	18.1	
9	18.9		19	17.2		16	14.2		19	18.4	
19	19.2		9	17.3		15	14.3		9	18.7	
18	19.5		18	17.8		20	14.5		18	18.9	
16	19.8		10	18.0		14	15.0		16	19.2	
10	19.9		11	18.2		17	15.1		17	19.4	
17	19.9		17	18.2		8	15.5		10	19.6	
11	20.2		16	19.2		13	15.9		14	19.8	
14	20.5		12	19.2		9	16.8		11	19.8	
12	20.5		13	20.0		12	16.8		15	19.9	
13	20.6		14	20.1		11	17.2		12	20.0	
15	20.7		15	20.4		10	17.6		13	20.1	

Table 9. Sizes (km^2) of annual activity areas for 96 satellite radio-collared female polar bears in the Beaufort Sea, 1985-93. Contours surrounding 95% and 50% of observed points are shown for both the adaptive kernal and harmonic mean methods. Convex polygon areas are shown for comparisons to other studies.

Method	Mean	Minimum	Maximum	Std. Error
Adaptive kernal				
95% contour	197,130	25,580	644,800	13,874
50% contour	34,851	2,979	112,700	2,619
Harmonic mean				
95% contour	162,124	12,730	596,800	13,194
50% contour	20,238	1,553	61,760	1,456
Convex polygon	178,033	14,440	616,800	13,762

Table 12. Fidelity of satellite radio-collared female polar bears to monthly activity areas in the Beaufort Sea, 1985-93. Distances are separations of activity centers, calculated by harmonic mean, among years. Fidelity to monthly activity areas was greatest in July and least in December. Months that did not differ significantly are overlapped by vertical lines. (F = 8.61, df = 11, P < 0.001; HSD = 4.64, df = 732, P = 0.05).

Month	N	Mean	Std. Error	Significance*
July	82	201.710	16.018	
May	110	240.479	20.210	
August	77	248.546	19.230	
June	101	258.350	24.281	
September	72	284.293	17.904	
April	108	292.757	23.499	
February	19	388.177	60.843	
October	66	352.051	23.166	
November	79	377.484	28.647	
March	38	392.392	35.505	
January	24	413.603	59.671	
December	37	450.116	49.981	

*Significance patterns for October and February do not follow relative values of their means due to higher variation among measures in those months.

Table 11. Monthly activity area sizes (km^2)for radio-collared female polar bears of different reproductive status in the Beaufort Sea, 1985-1992. Activity areas were calculated with 95% contour of the harmonic mean method (Dixon and Chapman 1980) using a minimum of 8 locations per month. Differences among status were not significant. December areas were larger than all others, except January (F = 2.44, df = 11, P < 0.007, HSD = 4.67, df = 214, P = 0.05). Other differences among months were not significant.

Month	Females/Cubs MEAN	S.E.	n	Single females MEAN	S.E.	n	Females/Yearlings MEAN	S.E.	n	Females/2-Year-Olds MEAN	S.E.	n	TOTALS MEAN	S.E.	n
Jan				9148	6693	2	3577	3053	6	744	228	2	4124	2222	10
Feb				1417	.	1	2620	841	4	856	350	3	1808	513	8
Mar				2792	1718	3	572	205	5	154	14	2	1155	580	10
Apr				2367	931	9	2505	1355	8	1548	601	3	1692	489	29
Totals				3293	1092	15	2384	908	23	901	246	10			
Apr	344	110	9	2367	931	9	2505	1355	8				1709	543	26
May	1411	319	11	2888	784	34	1968	631	9				2434	512	54
Jun	509	335	7	2370	460	25	5447	2650	5				2434	508	37
Jul	2124	925	5	1984	409	20	5278	4168	6				2644	838	31
Aug	427	117	6	2367	663	15	663	326	4				1629	437	25
Sep	1183	418	4	2600	901	15	740	273	2				2153	661	21
Oct	1634	529	8	2948	862	11	1802	1045	5				2271	483	24
Nov	4460	1637	10	2268	848	6	5397	3584	9				4271	1428	25
Dec	8701	3710	8	4996	4789	2	11926	6111	5				9282	2793	15
Totals	2461	580	68	2547	272	137	4113	1040	53						
Jan				9148	6693	2	3577	3053	6				4770	2725	8
Feb				1417	.	1	2620	841	4				2379	695	5
Mar				2792	1718	3	572	205	5				1404	704	8
Apr				2367	931	9	2505	1355	8				2431	779	17
May				2888	784	34	1968	631	9				2695	633	43
Jun				2370	460	25	5447	2650	5				2883	594	30
Jul				1984	409	20	5278	4168	6				2744	988	26
Aug				2367	663	15	663	326	4				2009	548	19
Sep				2600	901	15	740	273	2				2381	806	17
Oct				2948	862	11	1802	1045	5				2590	671	16
Nov				2268	848	6	5397	3584	9				4146	2162	15
Dec				4996	4789	2	11926	6111	5				9946	4528	7
Totals				2637	279	143	3718	856	68						

Table 12. Fidelity of satellite radio-collared female polar bears to monthly activity areas, in the Beaufort Sea, 1985-93. Distances are separations of activity centers, calculated by harmonic mean, among years. Fidelity to monthly activity areas was greatest in July and least in December. Months that did not differ significantly are overlapped by vertical lines. ($F = 8.61$, df = 11, $P < 0.001$, HSD = 4.64, df = 732, $P = 0.05$).

Month	N	Mean	STd. Error	Significance*
July	82	201.710	16.018	
May	110	240.479	20.210	
August	77	248.546	19.230	
June	101	258.350	24.281	
September	72	284.293	17.904	
April	108	292.757	23.499	
February	19	388.177	60.843	
October	66	352.051	23.166	
November	79	377.484	28.647	
March	38	392.392	35.505	
January	24	413.603	59.671	
December	37	450.116	49.981	

*Significance patterns for October and February do not follow relative values of their means due to higher variation among measures in those months.

Figure 1. Mean and 95% confidence intervals on the relationship between rate of movement of polar bears in the Beaufort Sea and time interval separating satellite telemetry relocations. Measurements from 106 females radio collared between 1985-1992. The steep slope of the left-hand end of the fitted curve suggested more realistic movement rates could be derived if relocation interval was kept shorter than 100 hours.
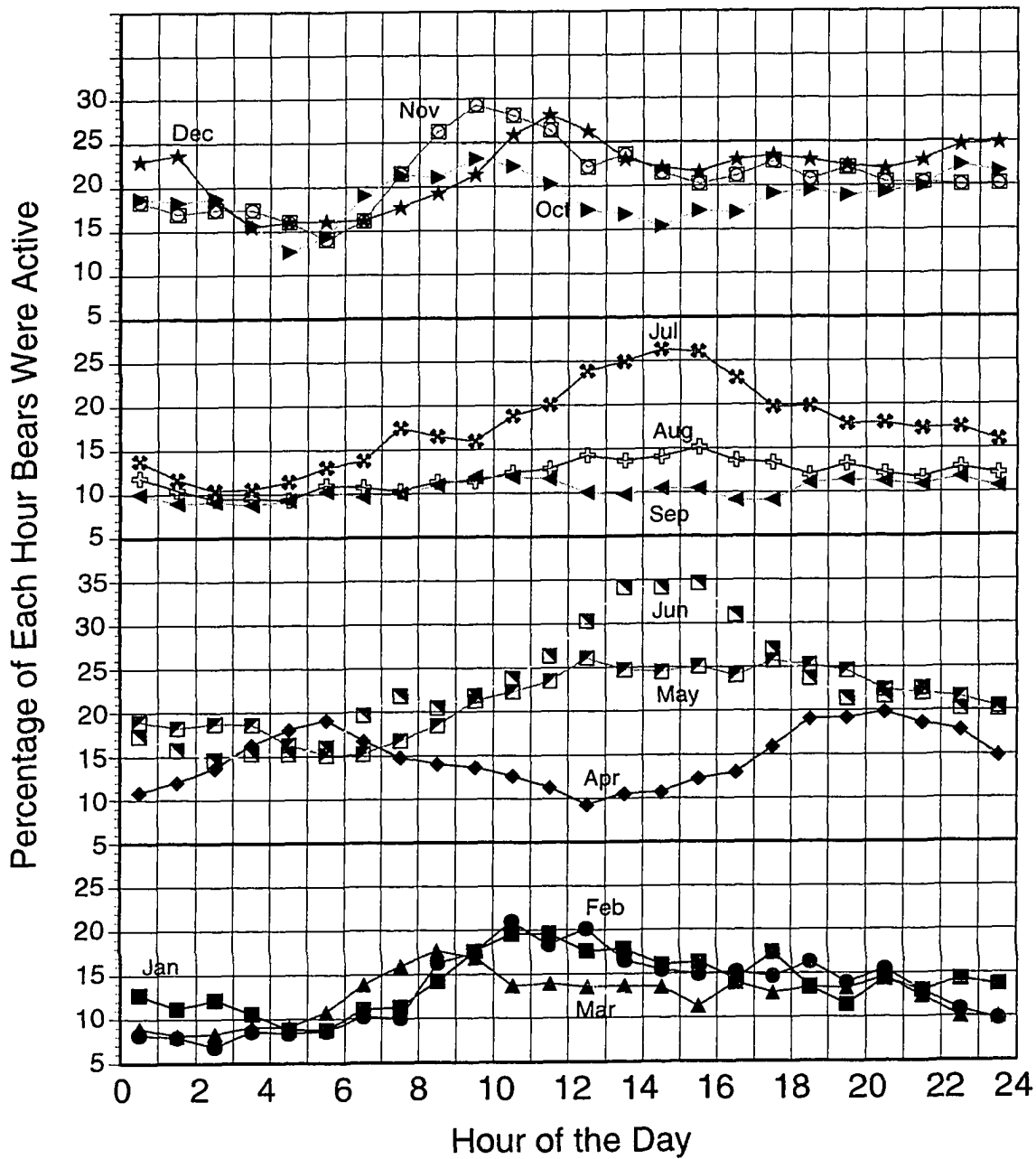
Figure 2. Diel activity patterns (% hour active at each hour) of satellite radio-collared female polar bears in the Beaufort Sea, 1988-93. Bears of all reproductive status categories are pooled in this figure to illustrate overall activity patterns.
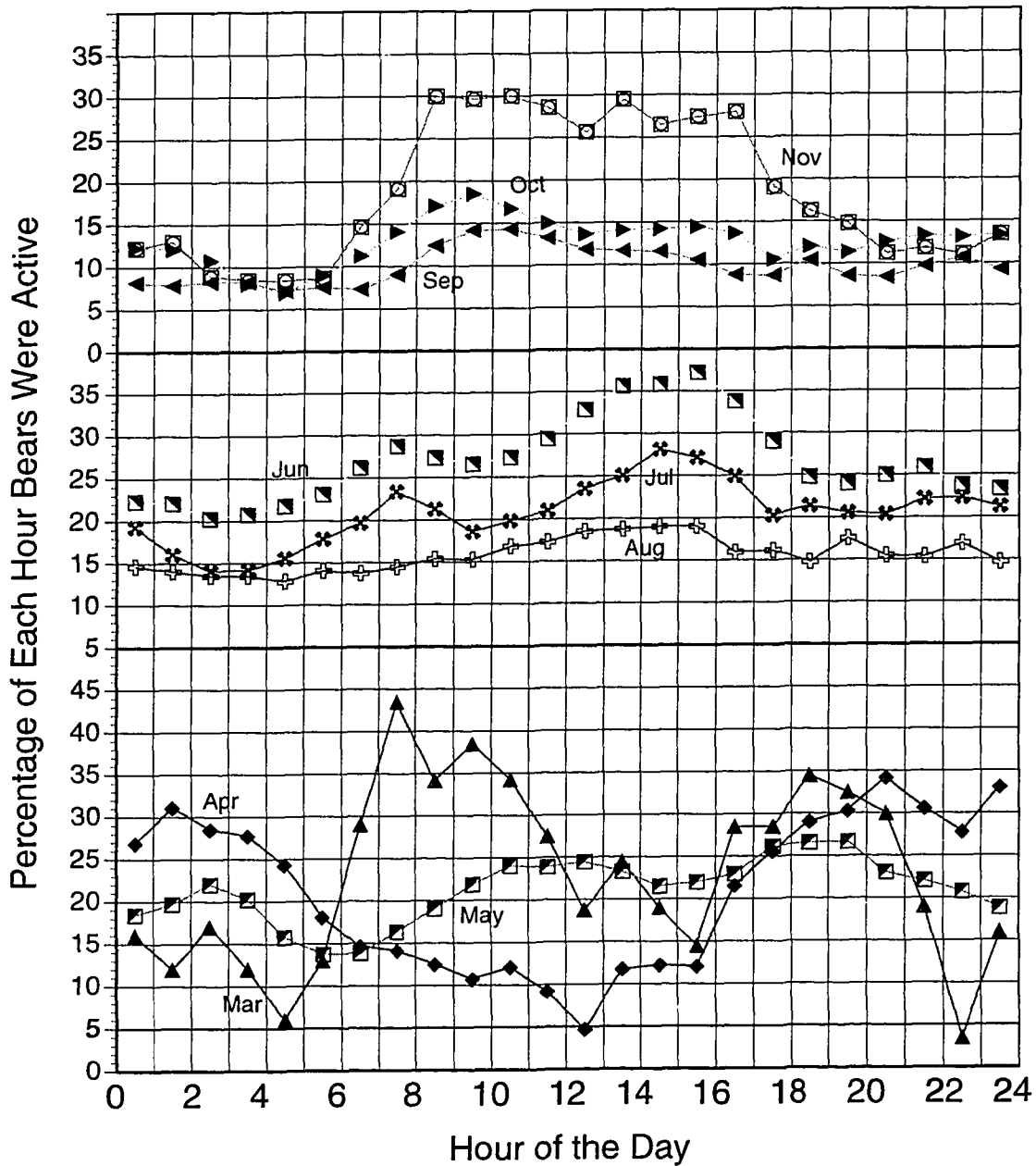
Figure 3. Diel activity (% hour active at each hour) of satellite radio-collared female polar bears not encumbered by young of any age in the Beaufort Sea, 1988-93.
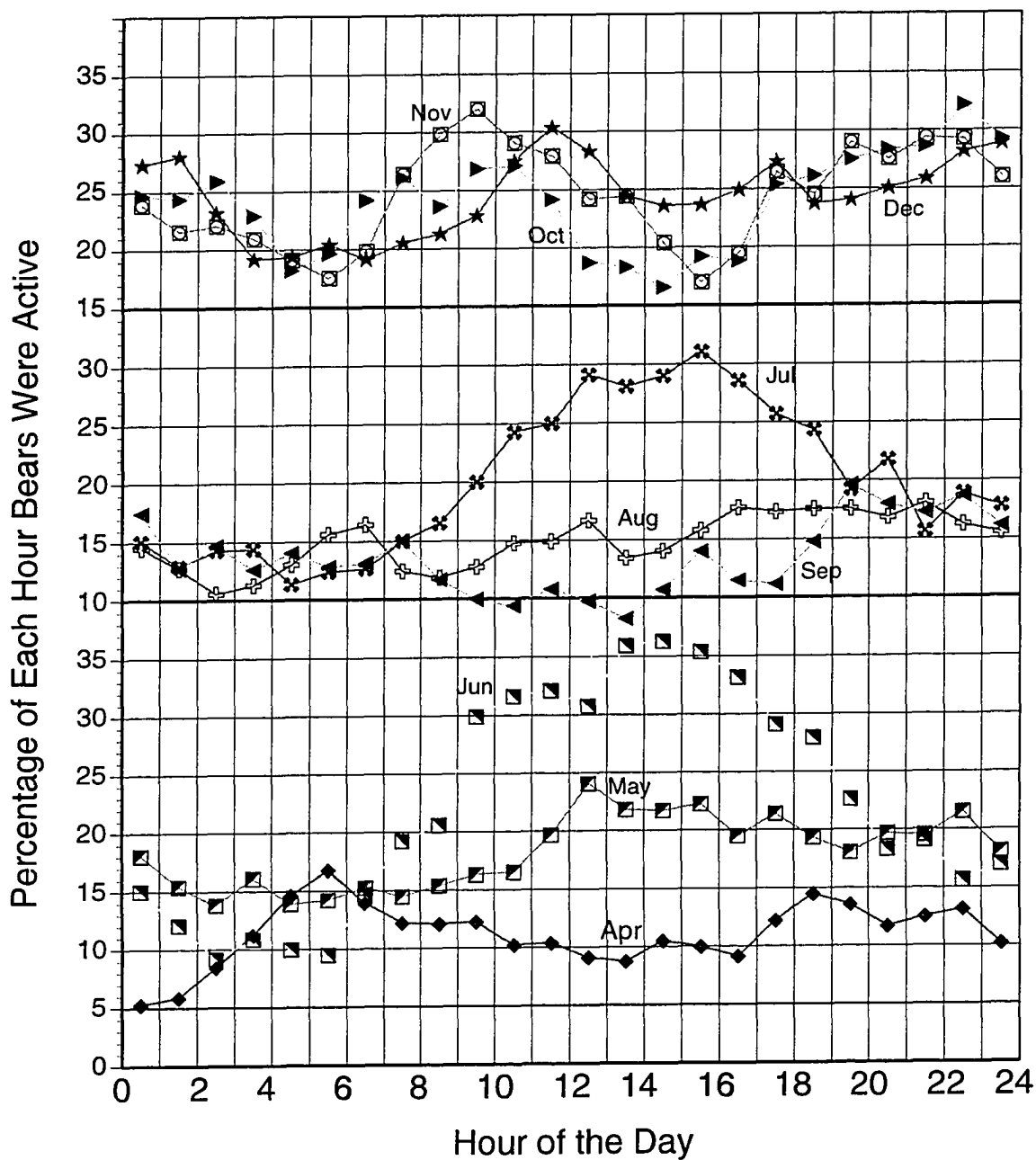
Figure 4. Diel activity patterns (% hour active at each hour) of satellite radio-collared female polar bears accompanied by cubs of the year, in the Beaufort Sea, 1988-93.
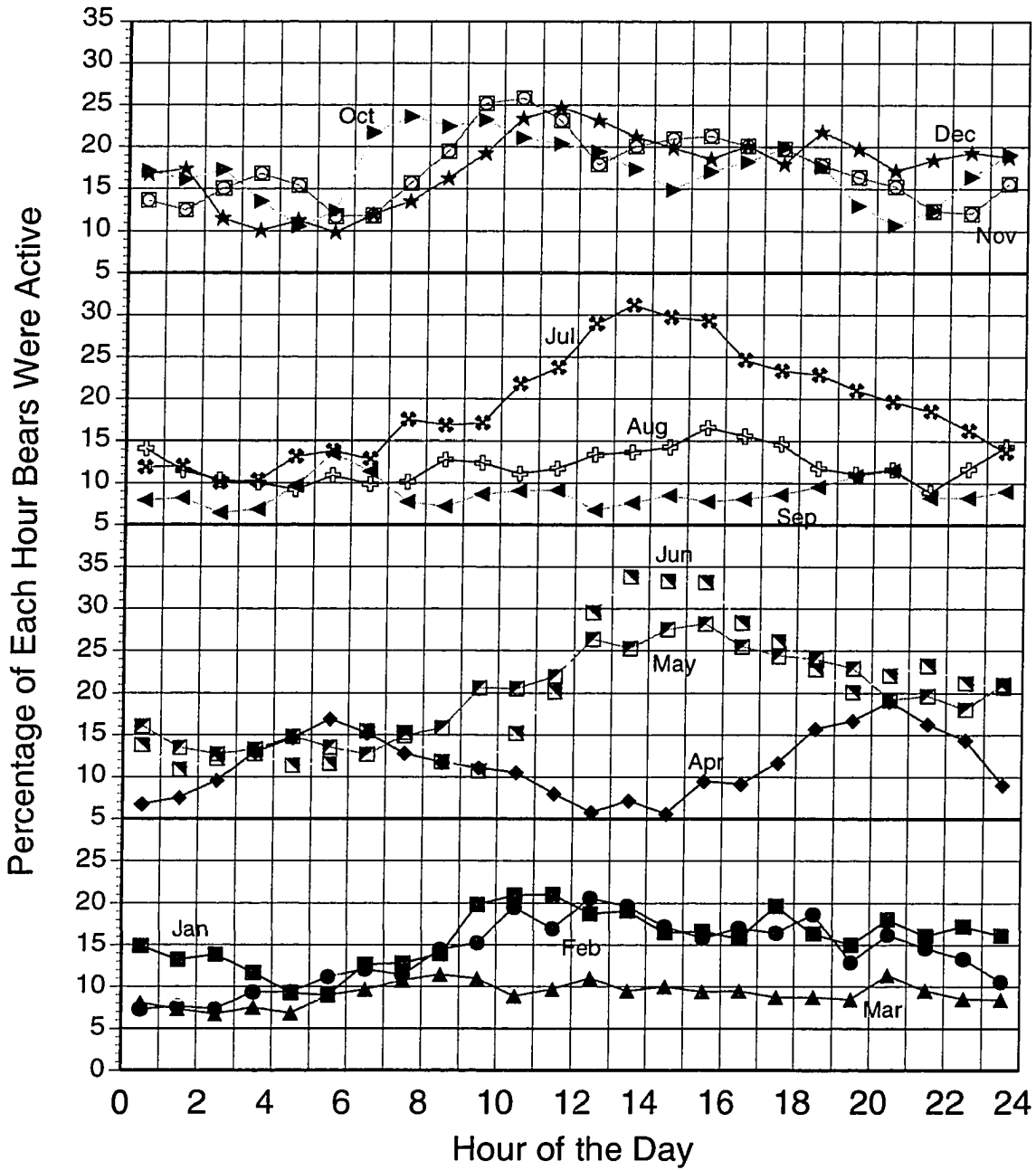
Figure 5. Diel activity patterns (% hour active at each hour) of satellite radio-collared female polar bears accompanied by yearlings in the Beaufort Sea, 1988-93.
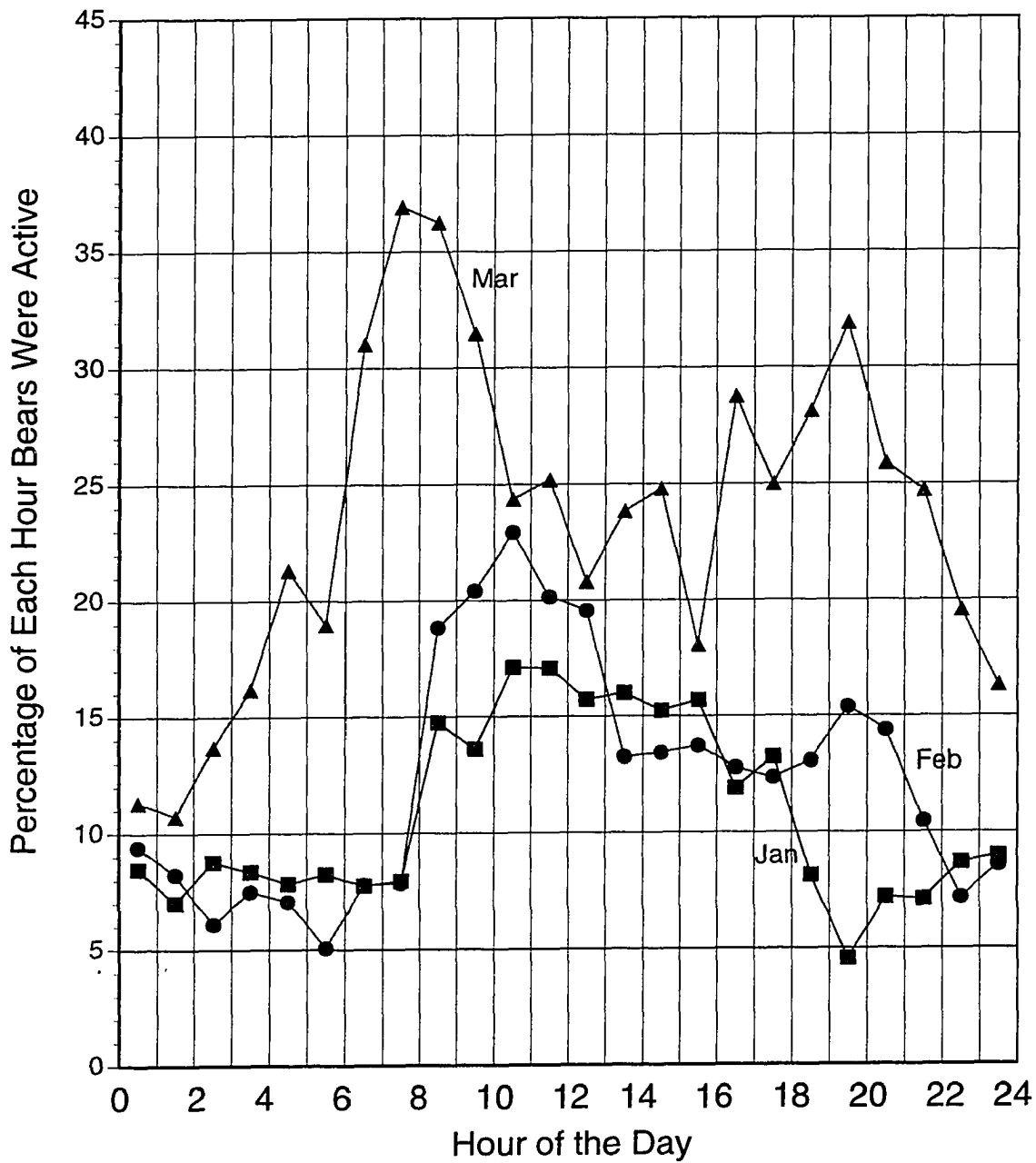
Figure 6. Diel activity patterns (% hour active at each hour) of satellite radio-collared female polar bears accompanied by 2-year-old young in the Beaufort Sea, 1988-93.
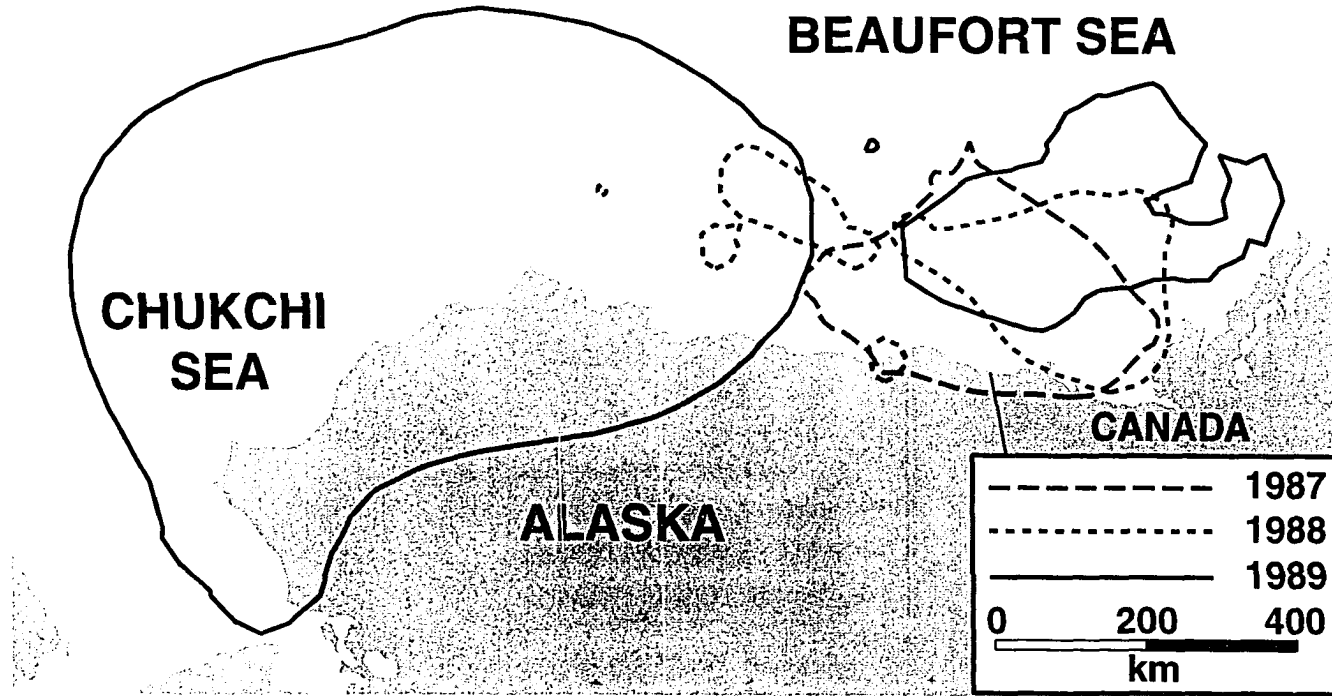
Figure 7. Activity area boundaries calculated with the harmonic mean method for satellite radio-collared polar bear #1734. Boundaries shown enclose 95% of the locations recorded in each year. Note variation in geographic areas occupied among years.
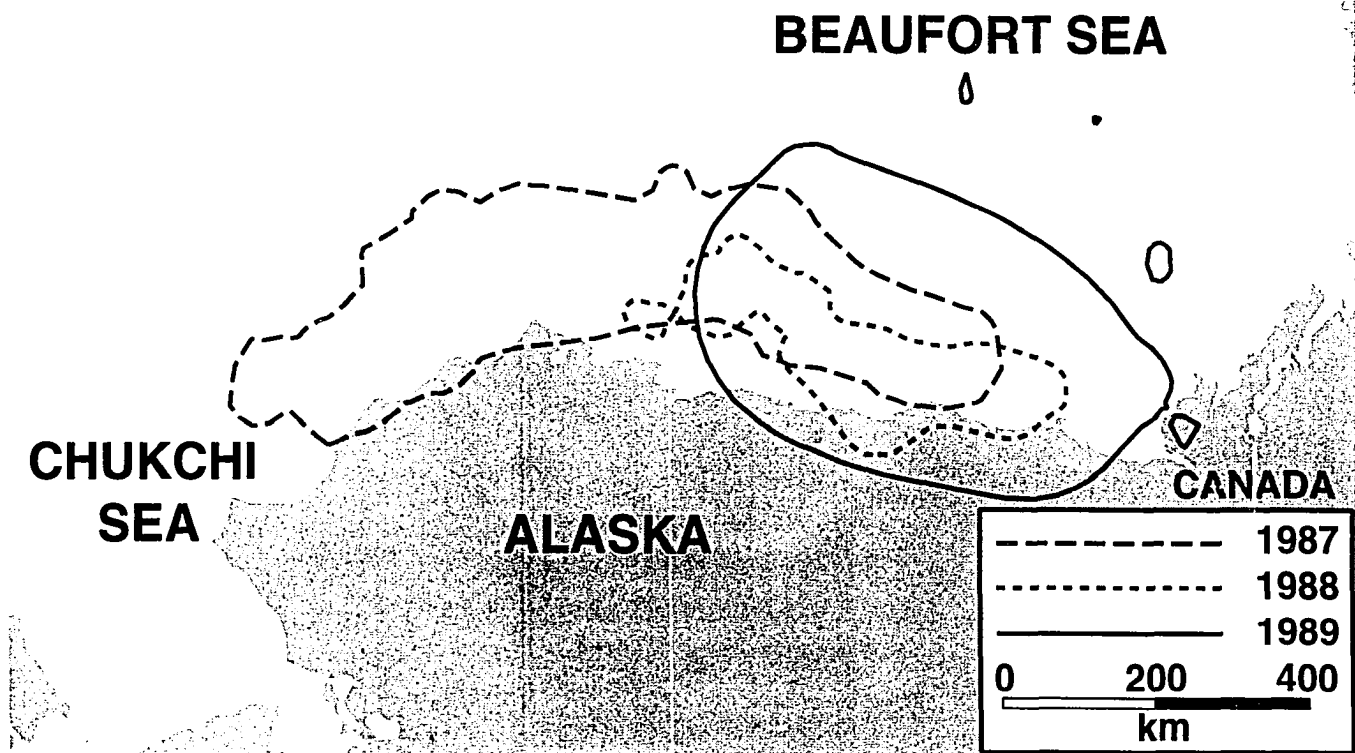
Figure 8. Activity area boundaries calculated with the harmonic mean method for satellite radio-collared polar bear #6201. Boundaries shown enclose 95% of the locations recorded in each year. Note variation in geographic areas occupied among years.

Beaufort Sea

Chukchi

Cape Bathurst ●

Barrow ●

Sea

Prudhoe
● Bay

Kaktovik
●

Tuktoyaktuk

Wainwright ●

Cape
Lisburne
●

● Pt. Hope

Alaska

Canada

● Kotzebue

| 0 | 200 | 400 |

km
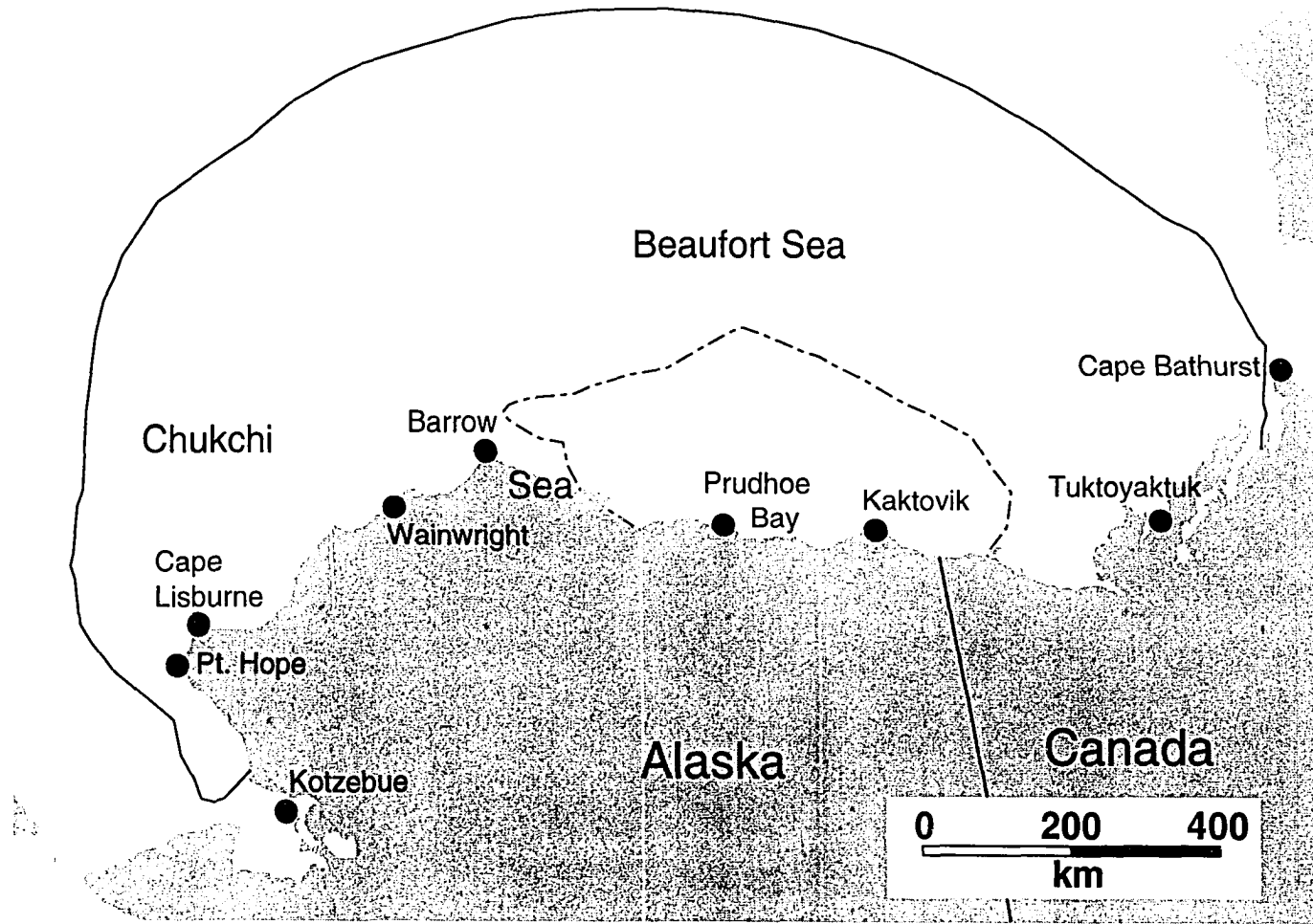
Figure 9. Approximate bounds (95% contour) of the Beaufort Sea polar bear population (solid), and core (50% contour) activity area (dashed) determined by harmonic mean analysis of satellite radio-telemetry data collected 1985-1993. Not including land areas, the population boundary enclosed 939,153 km^2 and the core area enclosed 122,089 km^2. Also shown are place names used in the text.
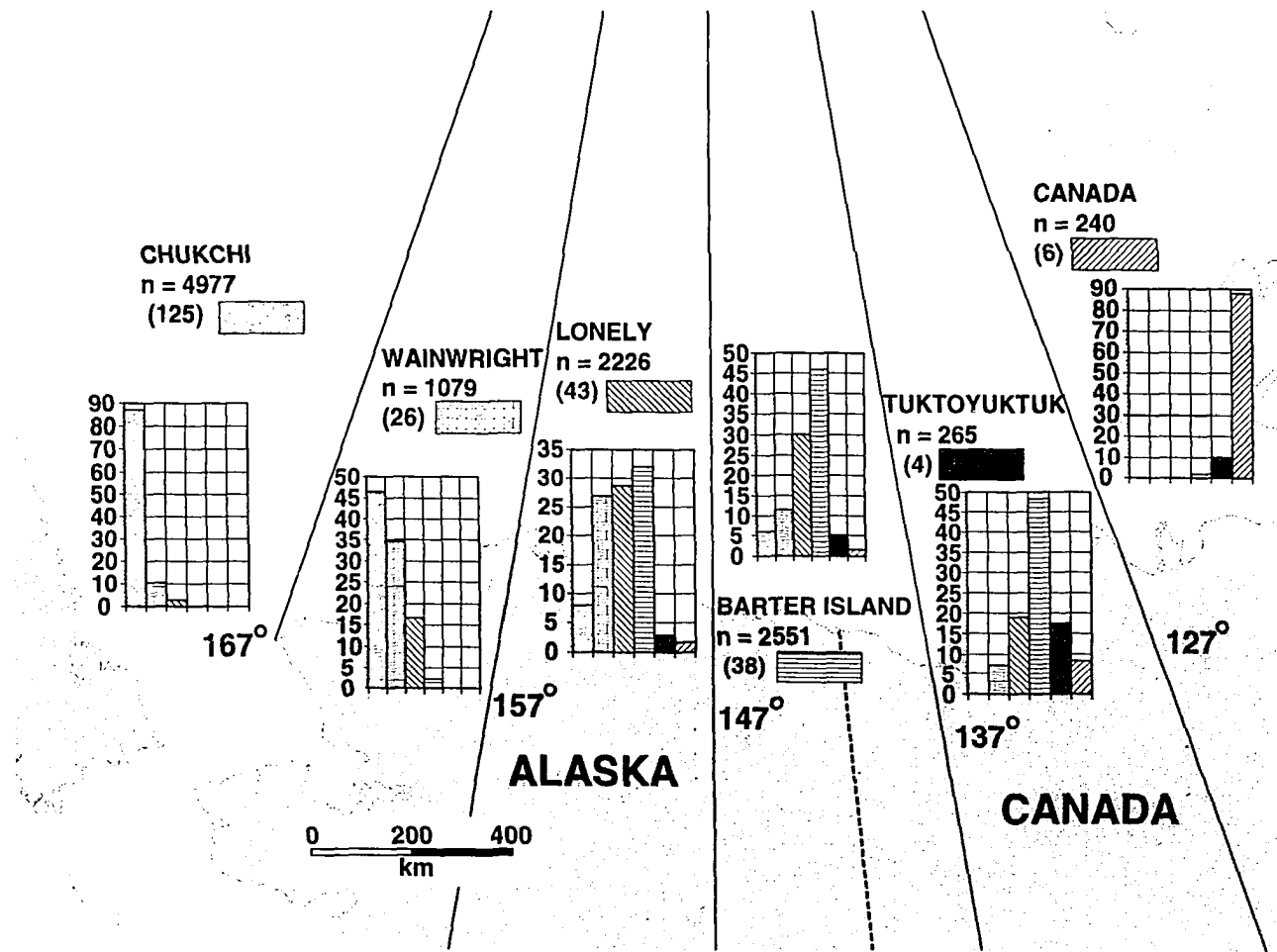
Figure 10. Numbers and positions of relocations (bears) of satellite radio-collared polar bears captured in each of 6 longitudinal zones within the Beaufort Sea. Histograms illustrate proportions of those relocations made in each zone (e.g., 32% of the 2226 relocations of bears originally captured in the Lonely zone were recorded in the Barter Island zone; 47% of the 1079 relocations of bears captured in the Wainwright zone were recorded in the Chukchi zone).
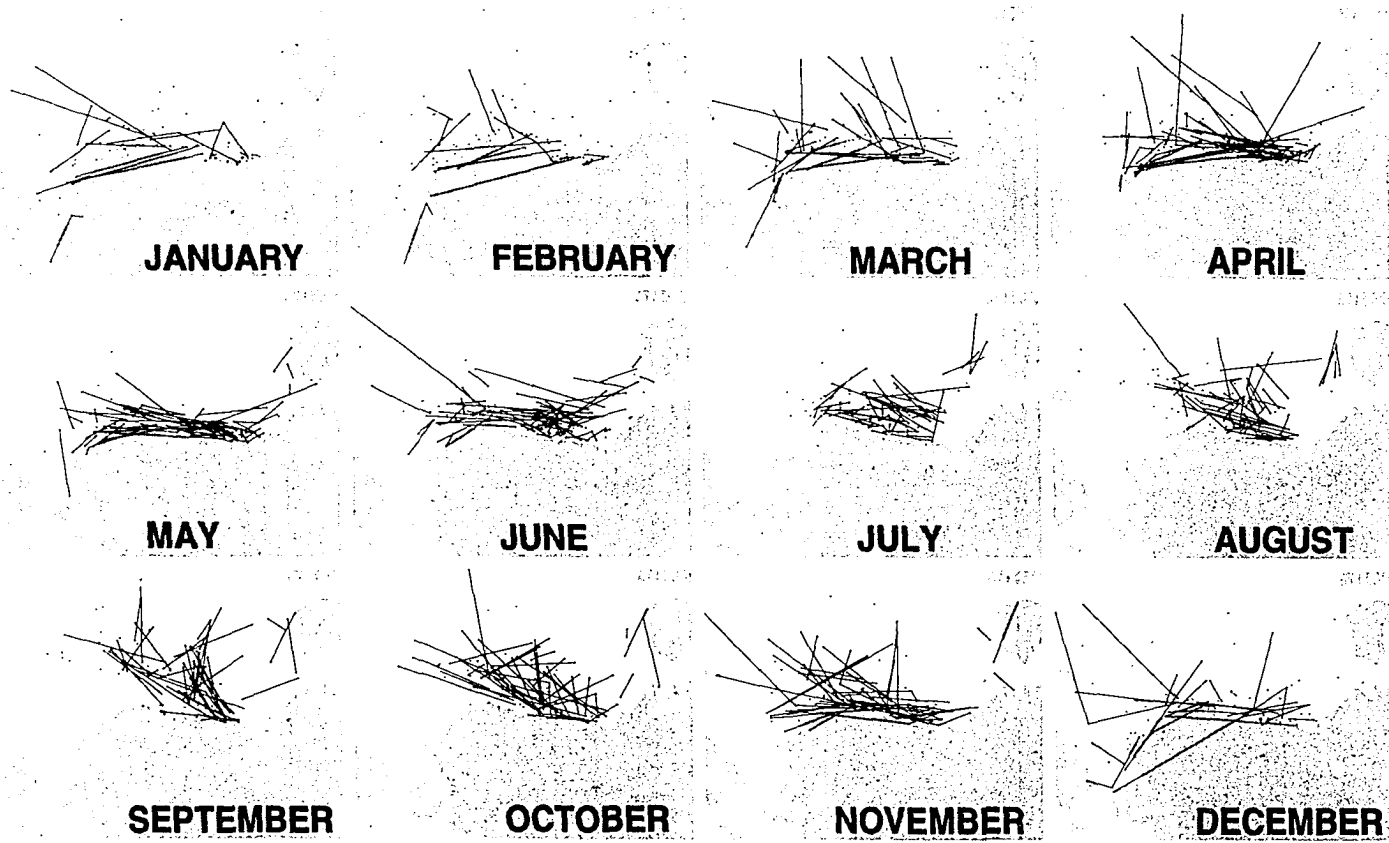
Figure 11. Monthly harmonic mean centers of activity for satellite radio-collared female polar bears in the Beaufort Sea, 1985-93. All bears and all years are grouped by month. Lines connect activity centers from one year to the next for the same individual bears. Note that bears were most likely to return to the vicinity of previous activities during the summer months.
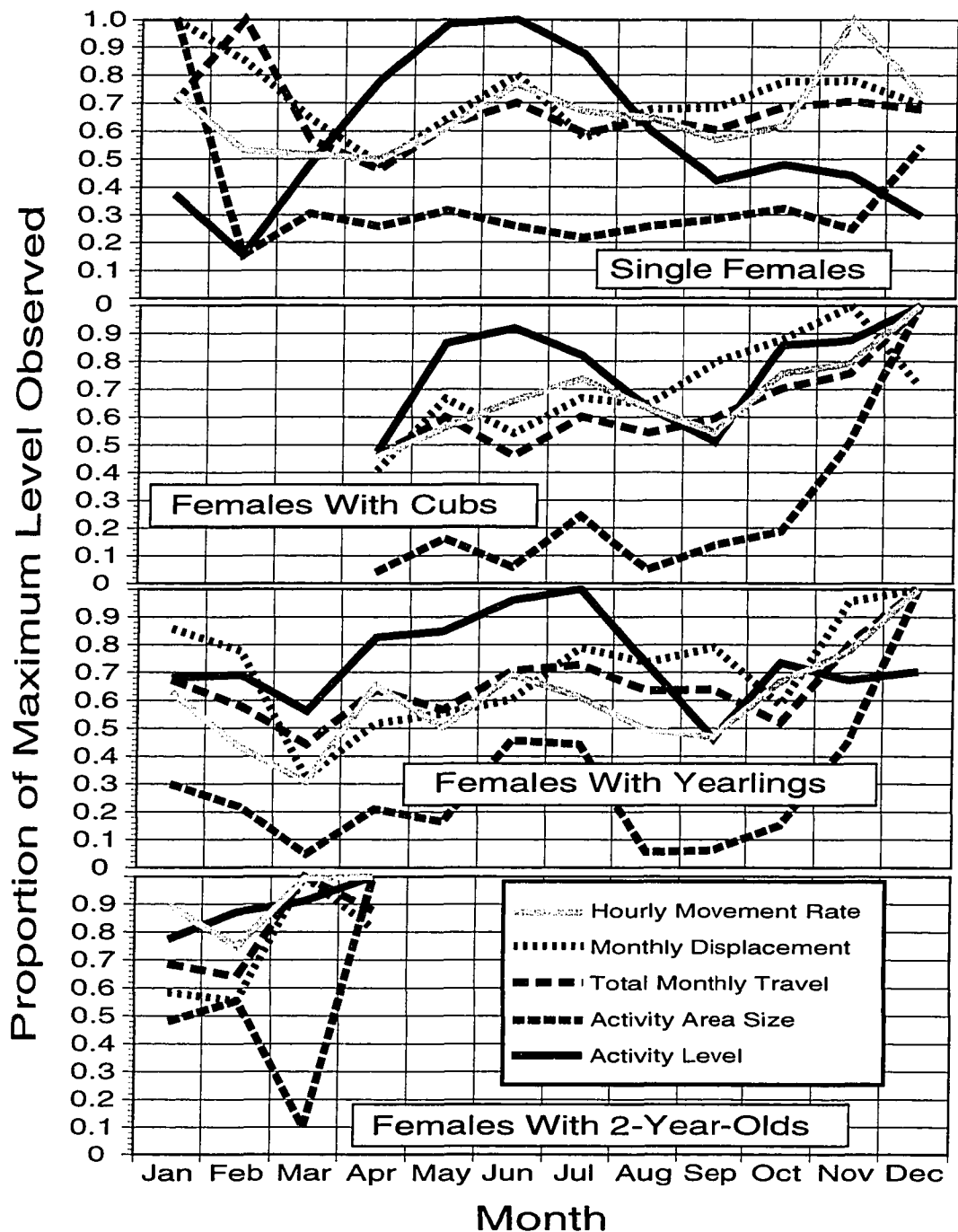
Figure 12. Activity and mobility of satellite radio-collared female
polar bears in the Beaufort Sea, 1985-1993. Note incomplete
concordance of various measurements. Each value is
expressed as a proportion of the maximum.

CHAPTER III

SURVIVAL RATES OF RADIO-COLLARED FEMALE POLAR BEARS AND THEIR DEPENDENT YOUNG[1]

S. C. Amstrup and G. M. Durner

Polar bears (Ursus maritimus) are hunted throughout most of their range. In addition to hunting, polar bears of the Beaufort Sea region are exposed to mineral and hydrocarbon extraction and related human activities such as shipping, road-building, and seismic testing. As human populations increase and demands for polar bears and other arctic resources escalate, reliable estimates of survivorship of polar bears are needed to predict and manage impacts of those activities. We used the Kaplan-Meier model to estimate annual survival (with 95% confidence intervals) for radio-collared female polar bears and their dependent young that were followed during a 12 year study in the Alaskan Beaufort Sea. Survival of adult female polar bears was higher than previously thought $\hat{S}$ = 0.969 (0.952-0.983). If human caused mortalities were deleted, the computed survival rate was $\hat{S}$ = 0.996 (0.990-1.002). Survival of young from den exit to weaning was $\hat{S}$ = 0.676 (0.634-0.701). Survival during the second year of life $\hat{S}$ = 0.860 (0.751-0.903) was substantially higher than that of the first year $\hat{S}$ = 0.651 (0.610-0.675). Shooting by local hunters accounted for 85% of the documented deaths of adult female polar bears. Conversely, 90% of documented losses of young accompanying collared females were not directly caused by humans. Deaths of dependent young were independent of litter size (P = 0.36), indicating that parental investment in single cubs was not different from investment in litters of 2 or more. Precise estimates of survival of independent juveniles and adult males still need to be developed.

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Introduction

Compared with most mammals, polar bears are slow to mature, have long interbirth intervals, and small litters (DeMaster and Stirling 1981; Amstrup and DeMaster 1988). Some specifics of polar bear population dynamics, however, remain unknown. Production of cubs by polar bears, for example, often has been underestimated (Stirling et al. 1975; Lentfer et al. 1980; DeMaster and Stirling 1983; Amstrup et al. 1986). Under-sampling of cubs can prevent accurate descriptions of age structures, and prohibit estimates of survival. In polar bears and other animals that are constrained by their evolutionary histories to long delays in maturation, adult survival is the parameter that has the greatest impact on population growth (Eberhardt and Siniff 1977; Eberhardt 1985; Taylor et al. 1987). However, obtaining useful estimates of survivorship is one of the most difficult challenges in population analysis (Eberhardt 1985). Annual survival rates for adult females in the high 90-percentile range are thought to be necessary to sustain population numbers for large mammals with low reproductive potential (Eberhardt 1985). Previous estimates of survival rates for polar bears, which were derived from age-structure or mark and recapture data, were between 80% and 94% (DeMaster and Stirling 1981; Furnell and Schweinsburg 1984; Amstrup et al. 1986; Amstrup and DeMaster 1988; Ramsay and Stirling 1988; Derocher 1991) and, in most cases, insufficient to maintain polar bear populations if existing estimates of recruitment are accurate. For polar bears, the only useful estimates of age structures are subject to many limitations because they are composites constructed from multi-year data (Spinage 1972; Amstrup et al.

1986). Similarly, heterogeneity in mark and recapture data has reduced accuracy and precision of survival estimates derived from them (Amstrup et al. 1986; Amstrup and DeMaster 1988). We hypothesized that survival rates of polar bears must be higher than indicated by previous estimates.

Polar bears are hunted throughout most of their range. In addition to hunting, polar bears of the Beaufort Sea region are exposed to mineral and hydrocarbon extraction and related human activities such as shipping, road-building, and seismic testing. As human populations increase and demands for polar bears and other arctic resources escalate, reliable estimates of survivorship and reproduction of polar bears are needed to predict and manage impacts of those activities. The objective of this study was to develop reliable estimates of survival of adult and juvenile polar bears in the Beaufort Sea.

Materials and Methods

Field Procedures

We captured and marked polar bears each spring between 1982 and 1992, except for 1990. Bears also were captured in autumns of 1981-86, 1988, and 1989. Autumn captures occurred in October and November each year, and spring captures occurred between March and May. We captured polar bears throughout the Alaskan Beaufort Sea, which extends from Point Barrow, Alaska, at approximately 157°W, to the Canadian border, at 141°W, and in bordering areas to the east and west. We immobilized polar bears by

injecting drugs [phencyclidine hydrochloride (Sernylan®, Park, Davis and Co.), etorphine hydrochloride (M-99®, Lemmon Co.), and tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Co.)] with projectile syringes fired from helicopters (Larsen 1971; Schweinsburg et al. 1982; Stirling et al. 1989). Capture and marking protocols were approved by an independent animal care and welfare committee.

Each year, we collared a limited number ($\bar{x}$ = 27) of adult females with radio transmitters. We attached very high frequency (VHF) radio collars to polar bears between 1981 and 1985 and relocated them approximately 4 times per year with aircraft (Amstrup and Gardner 1994). After autumn 1985, we mostly deployed ultra high frequency platform transmitter terminals (PTT's) that were relocated by satellite. Sensors on PTT's recorded temperature of the collar and 2 indices of activity. Positions of collared animals were determined by sensors on the satellite that interpreted frequency shift patterns caused by changes in relative positions of the satellites and animals (Fancy et al. 1988). Collars carrying PTT's also carried VHF beacons that we located with aircraft. Survival of radio-collared bears was determined by periodic reobservations from aircraft, and by movement and activity patterns discernible from sensors on PTT's. PTT's provided data at least weekly. We attempted to reobserve radio-collared polar bears by aircraft every 2-3 months. Reobservations were not always evenly distributed in time, however, and were most frequent during spring and autumn when the combination of ice conditions and daylight were most suited to visual observations. Hence, we divided reobservations into spring (January-June) and autumn (July-

December) time intervals.

Analyses

Cementum annuli from extracted premolar teeth were counted to estimate ages of radio-collared animals (Hensel and Sorensen 1980; Stirling et al. 1980). Counts were performed at the Laboratory of Polar Bear and Seal Research, University of Alberta, Edmonton, Alberta Canada. Survival rates for adult females and the young accompanying them were estimated by following radio-collared polar bears and determining their fates. Data were analyzed using the Pollock et al. (1989) staggered entry modification of the Kaplan and Meier (1958) survivorship model. We chose this method because of 1) its elegant simplicity (computations similar to those used in life tables), 2) the ease with which the model deals with censored animals (animals that disappear from the study and for which neither subsequent death nor continued life can be documented), and 3) the broad basis in survival theory. Pollock et al. (1989) censored animals (deleted them from numbers at risk) during the first time period in which they were missed by the search effort. Because our time intervals were long (e.g., 2 periods per year) we decided to censor animals during the period in which they were last observed rather than waiting for the first period in which they were not observed. This resulted in lower estimates of survival. With the variation in our reobservation intervals and the long time periods used, however, we felt that the more conservative estimates were safer. Numerous animals left the study when they shed their radios or when their radios failed and then re-entered the study as new

animals at risk when they were recaptured and fitted with new radio collars. Some animals were censored and then found dead several time periods later. These deaths provided information on mortality patterns, but due to the need to be consistent in reporting whether animals died or were censored, we could not use them in calculation of mortality rates.

Pollock et al.'s (1989) model estimates a survival rate and confidence interval on that rate for the telemetry study duration, in our case 12 years. We converted survival estimates for the whole study to the parameter of interest, annual survival, by taking the 12th root of the point and interval estimates. "Total" and "natural" survival were calculated. Computations of total survival included all documented deaths. Natural survival was estimated by censoring animals that died due to human-causes rather than recording them as deaths.

We also calculated survival of young between age 0-1 and 1-2 with the procedure of Trent and Rongstad (1974). That procedure is simply a comparison of the observed losses with binomial expectations (e.g. the mean survival rate for the ith period of monitoring is $\bar{S}_i = \frac{x_i - y_i}{x_i}$, where x_i represents the number of animals monitored in the ith period and y_i represents the numbers of animals dying in the ith period). For dependent young, we examined two time periods: 1. when young were aged "0-1", and 2. when young were aged "1-2". We modified the Trent and Rongstad (1974) procedure by assuming that censored animals died at the same rate as non-censored animals. Those assumed deaths were then added to deaths (y_i) actually observed. For example, if $\bar{S}_i = 0.8$, then 20% of censored animals

were assumed to have died and that 20 was added to the number of known mortalities. Also, rather than estimating confidence intervals from a published table of approximations (Trent and Rongstad 1974), we generated individual binomial distributions with the binomial probability function in SAS version 6.07 (SAS Institute Inc., Cary, NC) to establish our interval estimates. We report survival as "point estimate or mean" followed by 95% confidence interval, when interval estimates were available.

Results

Survival was estimated from attachment of 297 radio collars to adult female polar bears between 1981 and 1992 (Table 1). We estimated survival over the 12-year study period at 0.684 (0.553-0.816). This 12-year survival rate translated into a constant annual survival rate of $\hat{S}$ = 0.969 (0.952-0.983). Radio-collared females ranged in estimated age from 3 to 27 years. Survival estimates for females aged 3-10 were $\hat{S}$ = 0.964 (0.906-0.998) (Table 2). For ages 11-27, the estimates were $\hat{S}$ = 0.962 (0.933-0.984) (Table 3). Although fewer animals died between the ages of 3 and 10 than from 11-27, the 95% confidence intervals around the estimates for each age group overlapped extensively suggesting that the difference was not significant. Deletion of mortalities caused by humans resulted in an estimated natural survivorship of 0.996 (Table 4) with a 95% confidence interval that overlapped unity (0.990-1.002).

Only 26 deaths of radio-collared adult female polar bears were documented during the 12 years of monitoring. These included: 3 natural

deaths, 1 death caused by consumption of ethylene glycol from an unknown source (Amstrup et al. 1989), and 22 bears (85% of the detected mortality) shot by coastal hunters. Six of those deaths (1 natural death plus 5 hunting mortalities) could not be included in Kaplan-Meier calculations because the deaths were not discovered by radio-telemetry, and the animals had been censored, due to radio failure, long before their deaths. Two of the natural deaths of radio-collared polar bears apparently were caused by fatal fights with other bears. The cause of the third natural mortality was not determined due to weather and the distance to the site of death; however human intervention seemed unlikely. During the course of the study, we also were able to determine the causes of deaths of 3 unmarked bears that were serendipitously found dead. One of these, a large male, died of gastric dilatation and volvulus (Amstrup and Nielsen 1989), one adult female died of complications arising from blockage of the bile duct by gall stones, and a third was apparently killed and eaten by a large male. Hence, agonistic behavior was the apparent cause of 3 of the 5 natural deaths we observed.

Survival of young from den exit through the time of weaning was $\hat{S}$ = 0.676 (0.634-0.701) (Table 5). Most of the mortality of young occurred during the first year of life (Table 6), when the annual survival rate was $\hat{S}$ = 0.651 (0.610-0.675). Survival during the second year of life $\hat{S}$ = 0.859 (0.751-0.903) was much higher (Table 7). Binomial estimates of cub ($\bar{x}$ = 0.71; 0.63-0.82) and yearling ($\bar{x}$ = 0.87; 0.85-0.93) survival (Trent and Rongstad 1974) were higher than Kaplan-Meier estimates.

Deaths of five cubs or yearlings were associated with the harvest of their radio-collared mothers. We concluded the 2 yearlings accompanying the radio-collared bear that died of ethylene glycol poisoning also died, but because they were not radio-collared, their remains were not found. The 61 other documented deaths of young of radio-collared females were due to unidentified natural causes. Fifty of 68 documented deaths of young were from litters of 2. We recorded 20 deaths of single young from litters of two, and loss of 15 whole litters of two. Rates of disappearance of young as singles or as whole litters were not significantly different (χ^2 = 0.83, df = 1, $\underline{P}$ = 0.36). Likewise, the rate of loss of litters of single cubs (16 of 102 litters) did not differ from the rate of loss of litters of twin cubs (15 of 106) (χ^2 = 0.072, df = 1, $\underline{P}$ = 0.79).

Discussion

Annual variability in mortality of adult females (Tables 1-3) mainly resulted from annual variation in numbers of bears killed by hunters. Hunter kill was regulated by the availability of bears near coastal settlements. Proximity of radio-collared bears to the coast and hence their vulnerability to harvest, varied with weather and sea-ice conditions, among years. The polar bear's evolutionary strategy of long life would suggest that variations in mortality of adults caused by natural factors will occur infrequently and irregularly, and that annual survival of adults should be treated as a constant (Eberhardt 1977). Hence, an estimate of annual mortality calculated over a period of several years is more useful than shorter-term measurements that

are influenced by serendipity.

These are the first estimates of survival for polar bears that were determined by following known individuals over time. Hence, they are not subject to a variety of assumptions (e.g., stable age structure, equal probability of capture) that can be violated when relying on other methods. Estimates based on age structure analyses can be reliable if the assumptions are met (Caughley 1966; 1967; 1977). However, such methods have dealt with "synthetic cohorts" and are subject to many questions (Spinage 1972) to which we seldom have answers. DeMaster and Stirling (1983) and Larsen (1985) used changes in numbers and sizes of litters seen to estimate survival of young. Age structure estimates are particularly dubious for cubs, because new cubs in the spring, the first group in the age structure, may be under-sampled (Amstrup and DeMaster 1988). Other published estimates of survival of young have been based on mark/recapture data. Reliability of both age structure and mark/recapture data from polar bear studies usually is limited by small sample sizes and heterogeneity of the capture samples.

This study has shown that survival rates of polar bears are higher, at least in the Beaufort Sea, than previous estimates have indicated. Estimated survival rates of adult bears approached 1 when they were unperturbed by humans. These estimates were sufficient to allow the growth in the population that has been observed in recent years (Amstrup unpubl.). Also, these estimates corroborated the conclusions of Eberhardt (1985) that marine mammal populations can be sustained only if survival of adults is in the high

90% range. Even the lower extremes of our interval estimates fall within the range prescribed by Eberhardt (1985).

Two caveats on our estimates of survival rate for adults should be considered. First, if a disproportionate number of censored subjects were undiscovered deaths, our survivorship estimates could be biased upward. Second, the difference between our estimates of total and natural survival does not include the possibility of density-dependent compensation.

We believe our search efforts were successful in preventing survival estimates from becoming significantly biased. If animals dying of natural causes tended to sink, preventing subsequent transmissions, or if all radios quit at the time of death, a bias could have emerged. We discovered many premature failures of the radio hardware, and we discovered many cases of bears shedding their radios at various times after attachment. Simultaneous death and radio failure appeared highly unlikely, and in our experience, bears that die of natural causes are not likely to sink. Bears that were sick sought firm substrates in which to rest and ultimately die (Amstrup et al. 1989; Amstrup and Nielsen 1989; Amstrup unpubl.). If many instrumented animals were dying during this study, we would have found them.

If animals were illegally killed and their collars destroyed they would have been undetected. We are confident that "illegal kills" were not common. The taking of a polar bear is a big event in the coastal villages of the Beaufort Sea and difficult to keep secret. Also, polar bear hunters in the Beaufort Sea make a concerted effort to police themselves (Treseder and Carpenter 1989;

Nageak et al. 1991). Hence, we believe the vast majority of our censored animals were shed radios or radio failures and not undetected deaths, and we feel our estimate of total survival is largely unbiased.

Some compensation in mortality of polar bears in the Beaufort Sea seems likely. Amstrup (unpubl.) reported strong evidence of a density response involving survival of young and stature of adult females. With a population size lower than 2000 and a harvest of approximately 80 (Amstrup et al. 1986; Treseder and Carpenter 1989; Nageak et al. 1991; Amstrup unpubl.) density responses involving even small numbers noticeably could alter estimated rates. Hence, for purposes of simulation, estimates of natural survival rate between 0.969 and 0.996 also should be considered.

We are more confident in the Kaplan-Meier estimates than we are in our binomial (Trent and Rongstad 1974) estimates because of the systematic method in which censored animals are incorporated. Our treatment of censored animals in the binomial model was sensible, but "ad-hoc."

Survivorship of dependent young was independent of the litter sizes of which they were a part. This implies that parental investment does not diminish for single cub litters as suggested by Tait (1980). Polar bears breed in the spring, implantation occurs in the autumn, and birth occurs in mid-winter (Ramsay and Stirling 1988). The altricial young then must be nurtured for months inside a birth lair, and then for up to two years following emergence (Ramsay and Dunbrack 1986). During any reproductive cycle, therefore, many physiological and ecological unknowns could intervene between conception

and birth, and between birth and weaning. A bear with a litter of any size has overcome many of the hurdles it faces in attempts to reproduce. It would make no sense for such a bear, assuming sufficient resources are available to raise the cub, to make a decision to abandon or otherwise reduce investment in a single cub. The next cycle, after all, may be worse from the standpoint of foraging opportunity, snow cover for denning, or even the opportunity to encounter an acceptable mate. Furnell and Schweinsburg (1984) concluded that mortality of dependent young occurred primarily by loss of whole litters. Females that cannot care for 2 young, they reasoned, cannot care for 1. Our data refute that conclusion also. Events that lead to loss of a portion of a litter do not necessarily result in loss of all litter members. In fact, often it may be the case that a female is inadequately nourished to provision for multiple young, but could provide for a single cub.

Eberhardt (1977) observed that juvenile marine mammals were most vulnerable to relative scarcity of resources. Young and Ruff (1982) demonstrated that social interactions in black bears can directly influence recruitment of young to adult age even when food resources are not in short supply. We observed that survival of dependent polar bears improved with age. We were unable, however, to examine survival of independent juveniles (aged 2-3) with radio-telemetry. We have observed juvenile bears scavenging kills of more experienced animals, and Stirling (1974) and Smith (1980) presented evidence of the potential importance of such scavenging to recruitment. We also have observed that larger bears often chase smaller bears away from kills, and sometimes even kill them. This suggests that

successful foraging among independent juveniles, and their survival, may be influenced by social factors as well as availability of seals.

Male polar bears cannot be followed by radio telemetry for extended periods because their necks are larger than their heads, and radio-collars do not stay attached. Hence, we have no radio-telemetry data on survivorship of adult males. Adult males are of course, necessary for population maintenance. Males also may be vectors of population regulation (McCullough 1981; Young and Ruff 1982). Population dynamics of polar bears will be fully understood only with better estimates of survival of independent juveniles and adult males; and with clarification of the possible roles males may play in regulating population size.

Acknowledgments

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Table. 1. Kaplan-Meier survival rate estimates calculated from female polar bears of all ages that were radio-collared in the Beaufort Sea of Alaska and Canada 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $(\hat{S}_t)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e(\hat{S}_t)$ (Krebs 1989).

SEASON	New Radios Applied	Total Number at Risk r_j	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $(\hat{S}_t)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	15	15	13	0	1.000		0.000	1.000	1.000
au81	14	16	1	0	1.000	0.000	0.000	1.000	1.000
sp82	14	29	6	0	1.000	0.000	0.000	1.000	1.000
au82	5	28	6	0	1.000	0.000	0.000	1.000	1.000
sp83	24	46	7	0	1.000	0.000	0.000	1.000	1.000
au83	6	45	12	0	1.000	0.000	0.000	1.000	1.000
sp84	24	57	20	1	0.982	0.018	0.000	0.949	1.016
au84	1	37	10	1	0.956	0.027	0.001	0.891	1.021
sp85	42	68	8	2	0.928	0.030	0.001	0.869	0.987
au85	4	62	8	0	0.928	0.000	0.001	0.866	0.990
sp86	16	70	24	2	0.901	0.029	0.001	0.835	0.968
au86	1	45	11	0	0.901	0.000	0.002	0.819	0.984
sp87	14	48	15	0	0.901	0.000	0.002	0.821	0.981
au87	0	33	2	1	0.874	0.031	0.003	0.768	0.980
sp88	15	45	9	2	0.835	0.045	0.003	0.736	0.934
au88	28	62	2	0	0.835	0.000	0.002	0.751	0.920
sp89	10	70	13	1	0.823	0.014	0.002	0.742	0.904
au89	27	83	17	0	0.823	0.000	0.001	0.749	0.898
sp90	0	66	23	6	0.748	0.095	0.002	0.658	0.839
au90	0	37	3	0	0.748	0.000	0.004	0.627	0.869
sp91	14	48	11	1	0.733	0.021	0.003	0.626	0.840
au91	0	36	7	1	0.712	0.028	0.004	0.588	0.837
sp92	23	51	16	2	0.684	0.040	0.003	0.579	0.790
au92	0	33	33	0	0.684	0.000	0.004	0.553	0.816
Total	297		Annual Survival Rate		0.969			0.952	0.983

Table. 2. Kaplan-Meier survival rate estimates calculated from female polar bears aged 3-10 that were radio-collared in the Beaufort Sea of Alaska and Canada 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $(\hat{S}_t)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e(\hat{S}_t)$ (Krebs 1989).

SEASON	New Radios Applied	Total Number at Risk r_j	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $(\hat{S}_t)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	11	11	10	0	1.000		0.000	1.000	1.000
au81	9	10	5	0	1.000	0.000	0.000	1.000	1.000
sp82	10	15	4	0	1.000	0.000	0.000	1.000	1.000
au82	3	14	5	0	1.000	0.000	0.000	1.000	1.000
sp83	16	25	4	0	1.000	0.000	0.000	1.000	1.000
au83	4	25	8	0	1.000	0.000	0.000	1.000	1.000
sp84	14	31	16	1	0.968	0.033	0.001	0.907	1.029
au84	1	15	7	1	0.903	0.069	0.005	0.761	1.045
sp85	25	32	7	0	0.903	0.000	0.002	0.806	1.001
au85	3	28	5	0	0.903	0.000	0.003	0.799	1.007
sp86	8	31	8	2	0.845	0.067	0.004	0.728	0.962
au86	1	22	10	0	0.845	0.000	0.005	0.706	0.984
sp87	9	21	10	0	0.845	0.000	0.005	0.703	0.987
au87	0	11	1	0	0.845	0.000	0.010	0.648	1.042
sp88	12	22	6	1	0.807	0.047	0.006	0.658	0.955
au88	20	35	3	0	0.807	0.000	0.004	0.689	0.924
sp89	5	37	12	0	0.807	0.000	0.003	0.692	0.921
au89	9	34	18	0	0.807	0.000	0.004	0.687	0.926
sp90	0	16	10	2	0.706	0.134	0.009	0.518	0.893
au90	0	4	1	0	0.706	0.000	0.037	0.331	1.081
sp91	6	9	6	0	0.706	0.000	0.016	0.456	0.956
au91	0	3	1	0	0.706	0.000	0.049	0.273	1.139
sp92	9	11	5	1	0.642	0.095	0.013	0.415	0.869
au92	0	5	8	0	0.642	0.000	0.030	0.305	0.978
Total	175	Annual Survival Rate			0.964			0.906	0.998

Table. 3. Kaplan-Meier survival rate estimates calculated from female polar bears aged 11-27 that were radio-collared in the Beaufort Sea of Alaska and Canada 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $(\hat{S}_t)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e(\hat{S}_t)$ (Krebs 1989).

SEASON	New Radios Applied	Total Number at Risk r_j	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $(\hat{S}_t)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	2	2	1	0	1.000		0.000	1.000	1.000
au81	5	6	0	0	1.000	0.000	0.000	1.000	1.000
sp82	6	12	4	0	1.000	0.000	0.000	1.000	1.000
au82	2	10	3	0	1.000	0.000	0.000	1.000	1.000
sp83	8	15	4	0	1.000	0.000	0.000	1.000	1.000
au83	2	13	3	0	1.000	0.000	0.000	1.000	1.000
sp84	10	20	7	0	1.000	0.000	0.000	1.000	1.000
au84	1	14	2	0	1.000	0.000	0.000	1.000	1.000
sp85	19	31	3	3	0.903	0.102	0.003	0.804	1.002
au85	1	26	4	0	0.903	0.000	0.003	0.795	1.011
sp86	11	33	13	0	0.903	0.000	0.002	0.807	0.999
au86	0	20	3	0	0.903	0.000	0.004	0.780	1.026
sp87	4	21	7	0	0.903	0.000	0.004	0.783	1.023
au87	0	14	0	1	0.839	0.074	0.008	0.662	1.015
sp88	3	16	4	1	0.786	0.065	0.008	0.608	0.964
au88	8	19	2	0	0.786	0.000	0.007	0.623	0.950
sp89	7	24	2	1	0.754	0.043	0.006	0.604	0.903
au89	7	28	4	0	0.754	0.000	0.005	0.615	0.892
sp90	6	30	9	3	0.678	0.105	0.005	0.541	0.816
au90	1	19	1	0	0.678	0.000	0.008	0.505	0.851
sp91	10	28	5	1	0.654	0.036	0.005	0.511	0.796
au91	1	23	6	0	0.654	0.000	0.006	0.497	0.811
sp92	9	26	10	1	0.629	0.039	0.006	0.482	0.776
au92	0	15	14	0	0.629	0.000	0.010	0.435	0.823
Total	123		Annual Survival Rate		0.962			0.933	0.984

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Table. 4. Kaplan-Meier estimates of natural survival rate calculated from female polar bears of all ages that were radio-collared in the Beaufort Sea of Alaska and Canada 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $\left(\hat{S}_t\right)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e\left(\hat{S}_t\right)$ (Krebs 1989). Natural survival rates were calculated by censoring animals that were killed by humans rather than including them as deaths.

SEASON	New Radios Applied	Total Number at Risk r_j	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $\left(\hat{S}_t\right)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	15	15	13	0	1.000		0.000	1.000	1.000
au81	14	16	1	0	1.000	0.000	0.000	1.000	1.000
sp82	14	29	6	0	1.000	0.000	0.000	1.000	1.000
au82	5	28	6	0	1.000	0.000	0.000	1.000	1.000
sp83	24	46	7	0	1.000	0.000	0.000	1.000	1.000
au83	6	45	12	0	1.000	0.000	0.000	1.000	1.000
sp84	24	57	21	0	1.000	0.000	0.000	1.000	1.000
au84	1	37	10	1	0.973	0.027	0.001	0.921	1.025
sp85	42	68	10	0	0.973	0.000	0.000	0.935	1.011
au85	4	62	8	0	0.973	0.000	0.000	0.933	1.013
sp86	16	70	26	0	0.973	0.000	0.000	0.936	1.010
au86	1	45	11	0	0.973	0.000	0.001	0.926	1.020
sp87	14	48	15	0	0.973	0.000	0.001	0.928	1.018
au87	0	33	3	0	0.973	0.000	0.001	0.918	1.028
sp88	15	45	11	0	0.973	0.000	0.001	0.926	1.020
au88	28	62	2	0	0.973	0.000	0.000	0.933	1.013
sp89	10	70	14	0	0.973	0.000	0.000	0.936	1.010
au89	27	83	17	0	0.973	0.000	0.000	0.939	1.007
sp90	0	66	28	1	0.958	0.015	0.001	0.911	1.005
au90	0	37	3	0	0.958	0.000	0.001	0.895	1.021
sp91	14	48	12	0	0.958	0.000	0.001	0.903	1.014
au91	0	36	8	0	0.958	0.000	0.001	0.894	1.022
sp92	23	51	18	0	0.958	0.000	0.001	0.904	1.012
au92	0	33	33	0	0.958	0.000	0.001	0.891	1.025
Total	297		Annual Survival Rate		0.996			0.990	1.002

Table. 5. Kaplan-Meier estimates of survivorship between den emergence and weaning for young of female polar bears that were monitored with radiotelemetry in the Beaufort Sea, 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $(\hat{S}_t)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e(\hat{S}_t)$ (Krebs 1989).

SEASON	Total Number at Risk r_i	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $(\hat{S}_t)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	3	3	0	1.000	0.000	0.000	1.000	1.000
au81	10	5	3	0.700	0.357	0.015	0.462	0.938
sp82	10	3	1	0.630	0.105	0.015	0.392	0.868
au82	10	4	1	0.567	0.105	0.014	0.336	0.798
sp83	6	4	0	0.567	0.000	0.023	0.268	0.866
au83	3	0	0	0.567	0.000	0.046	0.145	0.989
sp84	20	9	4	0.454	0.223	0.006	0.307	0.601
au84	8	3	2	0.340	0.288	0.010	0.149	0.532
sp85	10	3	2	0.272	0.223	0.005	0.128	0.416
au85	7	1	2	0.194	0.336	0.004	0.065	0.324
sp86	23	2	5	0.152	0.245	0.001	0.095	0.209
au86	16	3	1	0.143	0.065	0.001	0.078	0.207
sp87	24	13	1	0.137	0.043	0.001	0.086	0.187
au87	10	0	7	0.041	1.204	0.000	0.016	0.066
sp88	14	4	2	0.035	0.154	0.000	0.017	0.053
au88	34	4	4	0.031	0.125	0.000	0.021	0.041
sp89	42	12	9	0.024	0.241	0.000	0.017	0.032
au89	48	6	2	0.023	0.043	0.000	0.017	0.030
sp90	46	27	10	0.018	0.245	0.000	0.013	0.024
au90	13	4	4	0.013	0.368	0.000	0.006	0.019
sp91	23	5	3	0.011	0.140	0.000	0.007	0.015
au91	17	6	1	0.010	0.061	0.000	0.005	0.015
sp92	34	17	4	0.009	0.125	0.000	0.006	0.012
au92	13	13	0	0.009	0.000	0.000	0.004	0.014
Annual Survival Rate				0.676			0.634	0.701

Table. 6. Kaplan-Meier estimates of survivorship between den emergence and age one for young of female polar bears that were monitored with radiotelemetry in the Beaufort Sea, 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $\left(\hat{S}_t\right)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e\left(\hat{S}_t\right)$ (Krebs 1989).

SEASON	Total Number at Risk r_j	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $\left(\hat{S}_t\right)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	3	3	0	1.000	0.000	0.000	1.000	1.000
au81	10	5	3	0.700	0.357	0.015	0.462	0.938
sp82	10	3	1	0.630	0.105	0.015	0.392	0.868
au82	10	4	1	0.567	0.105	0.014	0.336	0.798
sp83	6	4	0	0.567	0.000	0.023	0.268	0.866
au83	3	0	0	0.567	0.000	0.046	0.145	0.989
sp84	17	6	4	0.434	0.268	0.006	0.278	0.589
au84	8	3	2	0.325	0.288	0.009	0.140	0.510
sp85	10	3	2	0.260	0.223	0.005	0.121	0.399
au85	7	1	2	0.186	0.336	0.004	0.062	0.310
sp86	21	0	5	0.142	0.272	0.001	0.085	0.198
au86	16	3	1	0.133	0.065	0.001	0.072	0.193
sp87	15	4	1	0.124	0.069	0.001	0.065	0.183
au87	10	0	7	0.037	1.204	0.000	0.015	0.060
sp88	11	1	2	0.030	0.201	0.000	0.013	0.048
au88	34	4	4	0.027	0.125	0.000	0.018	0.036
sp89	37	7	9	0.020	0.279	0.000	0.014	0.027
au89	48	6	2	0.019	0.043	0.000	0.014	0.025
sp90	27	8	10	0.012	0.463	0.000	0.008	0.017
au90	13	4	4	0.008	0.368	0.000	0.004	0.013
sp91	20	2	3	0.007	0.163	0.000	0.004	0.010
au91	17	6	1	0.007	0.061	0.000	0.004	0.010
sp92	27	10	4	0.006	0.160	0.000	0.004	0.008
au92	13	13	0	0.006	0.000	0.000	0.003	0.009
Annual Survival Rate				0.651			0.610	0.675

Table. 7. Kaplan-Meier estimates of survivorship between age 1 and age 2 for young of female polar bears that were monitored with radiotelemetry in the Beaufort Sea, 1981-1992. Staggered entry of new animals into the study, and calculation of finite survival rate $\left(\hat{S}_t\right)$ were handled according to Pollock et al. (1989). Instantaneous mortality in each period calculated as $\hat{M} = \log_e\left(\hat{S}_t\right)$ (Krebs 1989).

SEASON	Total Number at Risk r_j	Censored	Deaths d_j	Survival $\hat{S}_t$	Mortality $\hat{M}$	Var $\left(\hat{S}_t\right)$	Minimum 95% Interval on $\hat{S}_t$	Maximum 95% Interval on $\hat{S}_t$
sp81	3	3	0	1.000	0.000	0.000	1.000	1.000
au81	1	1	0	1.000	0.000	0.000	1.000	1.000
sp82	6	3	1	0.833	0.182	0.019	0.561	1.106
au82	4	4	0	0.833	0.000	0.029	0.500	1.167
sp83	5	3	0	0.833	0.000	0.023	0.535	1.132
au83	3	0	0	0.833	0.000	0.039	0.448	1.218
sp84	10	9	1	0.750	0.105	0.014	0.518	0.982
au84	1	1	0	0.750	0.000	0.141	0.015	1.485
sp85	5	3	1	0.600	0.223	0.029	0.267	0.933
au85	3	1	0	0.600	0.000	0.048	0.171	1.029
sp86	14	2	1	0.557	0.074	0.010	0.363	0.751
au86	11	2	0	0.557	0.000	0.012	0.338	0.776
sp87	19	13	1	0.528	0.054	0.007	0.365	0.691
au87	5	0	2	0.317	0.511	0.014	0.087	0.546
sp88	6	4	1	0.264	0.182	0.009	0.083	0.445
au88	7	2	0	0.264	0.000	0.007	0.096	0.432
sp89	28	12	2	0.245	0.074	0.002	0.166	0.324
au89	22	3	0	0.245	0.000	0.002	0.156	0.334
sp90	40	27	6	0.208	0.163	0.001	0.151	0.266
au90	7	4	0	0.208	0.000	0.005	0.071	0.346
sp91	15	3	2	0.181	0.143	0.002	0.098	0.263
au91	10	2	1	0.162	0.105	0.002	0.070	0.255
sp92	19	14	0	0.162	0.000	0.001	0.096	0.229
au92	5	5	0	0.162	0.000	0.004	0.032	0.293
Annual Survival Rate				0.859			0.751	0.903

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CHAPTER IV

POPULATION DYNAMICS OF POLAR BEARS IN THE BEAUFORT SEA[1]

S. C. Amstrup and G. M. Durner

Polar bears (Ursus maritimus) are hunted throughout most of their range. In addition to hunting, polar bears of the Beaufort Sea region are exposed to mineral and hydrocarbon extraction and related human activities such as shipping, road-building, and seismic testing. Yet, population size and status for polar bears in the Beaufort Sea, and reproduction and survival rates—values necessary to manage human perturbations—were not well known at the start of this study. We estimated the size and trend of the polar bear population in the Beaufort Sea. Also, we estimated rates of recruitment and survival, and examined population regulatory factors. This study was divided into a hypothesized over-harvested early period (1967-1974) and a later recovered period (1981-1992). We analyzed archived records of 589 captures of 534 bears from the early period and 1,087 captures of 789 bears obtained in the late period. Also during the late period, we radio-collared 302 adult females and relocated them 1,450 times by aircraft and thousands of times by satellite. The number of polar bears in the Beaufort Sea grew at more than 2% per year through 1992, reaching a population ca.1500 animals. There was a compensatory relationship between total population size and recruitment of subadults (P = 0.02). Population size alone explained 55% of the variation in proportions of 2-and 3-year-olds in annual samples. Large populations recruited proportionately few juveniles, and smaller populations recruited higher proportions of juveniles. Condition of single adult females and those with cubs, as reflected in measurements of axial girth, declined significantly as the population grew ($P \leq 0.003$), and population size alone explained 75% of the variation in axial girth of reproductive age females.

Although numbers of young produced per female when the population was small ($\bar{x}$ = 0.40) and when it was large ($\bar{x}$ = 0.38) were similar (P = 0.88), litters of more than one yearling were more frequent when the population was small (P = 0.06). Temporal differences in sampling during the 2 periods may have prevented comparisons of litter sizes of cubs and 2-year-olds and other comparisons as well. Observed reproductive intervals of 3.4 and 3.7 years in early and late periods were suggestive of change, but not significantly different (P = 0.19). The age structure of the small population was younger than that of the larger population of later years (males: P < 0.001; females: P < 0.001). Survival of adults, as calculated from life tables, was higher and survival of young lower when the population was large. At the close of this study, the population was thought to be approaching carrying capacity. Despite the lack of individual significance in some tests for density effects associated with approaching K, the fact that all 8 changes we evaluated were in the direction predicted by density theory was significant (P = 0.004). Although numbers of bears at the close of the study were relatively large, absolute numbers of bears were small. The additional loss of as few as 30 bears each year might push the total take from the population to maximum sustained yield. Excess take did precipitate a decline in the 1960's and 1970's. Hence, managers must be alert to possible changes in human activities, including hunting and habitat alterations, that could precipitate another decline.

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Introduction

Polar bears residing in the Beaufort Sea of Alaska and Canada have been hunted at varying levels of intensity for decades (Amstrup et al. 1986; Stirling 1986). Recently, polar bears have been exposed to increased potential risks associated with oil and gas exploration and development and mineral extraction (Amstrup et al. 1986; Amstrup et al. 1989; Stirling 1990). As human populations increase and demands for polar bears and other Arctic resources escalate, managers need reliable estimates of breeding rates, reproductive intervals, litter sizes, and survival of young and adults. Survival of adult females is the parameter that has the greatest effect on population growth in polar bears and other animals that are constrained by their evolutionary histories to long delays in maturation (Eberhardt and Siniff 1977; Eberhardt 1985; Taylor et al. 1987). Amstrup and Durner (Chapter III) have developed precise estimates of survival for polar bears in the Beaufort Sea. The meaning of those estimates, however, to population dynamics is not clear without accurate assessments of reproduction and factors regulating population size. Unfortunately, knowledge of polar bear reproduction is inchoate. Denning areas in the Beaufort Sea have only recently been described (Chapter V), and available estimates of litter size, reproductive intervals, and age-specific productivity of females are dated and have not included the whole Beaufort Sea.

Despite the absence of many parameter estimates necessary to determine yield, polar bears long have been hunted throughout most of their range. In the Beaufort Sea, the intensity of hunting varied greatly after the turn

of the century. The highest harvests occurred from 1961-1972 when airborne hunters operating in the Beaufort and Chukchi seas of Alaska killed an average of 260 bears per year (Amstrup et al. 1986). Although managers, at the time thought that the aerial harvest was being sustained (Lentfer et al. 1980), it was later suggested that populations were smaller, and had declined substantially as a result of aerial hunting (Amstrup et al. 1986). For many years prior to the popularizing of aerial hunting, polar bears in Alaska were harvested in limited numbers by subsistence hunters, but otherwise had been unperturbed since the early part of this century (Amstrup and DeMaster 1988). It is reasonable to conclude, therefore, the population prior to aerial hunting was high, possibly near "K-carrying capacity." After 1972, polar bear hunting by airplane was outlawed. The ban on aerial hunting in Alaska followed the 1968 introduction in Canada of harvest quotas, in response to concern about the possibility of over-harvest there (Stirling 1986). Harvests by local indigenous people continue to the present in both countries. Those harvests, however, are thought to be below maximum sustainable yield. We reasoned, therefore, that the population must have grown after 1972. We tested the hypothesis that the size of the population in an early study period (1967-1974) influenced by aerial hunting did not differ from that in a later study period (1981-1992) during which recovery was suspected (Amstrup et al. 1986).

As a population increases, the first negative effect of its own density is presumed to be increased mortality of young (Eberhardt 1977). At still-higher densities, age of maturity increases and then productivity of mature animals declines. Finally, at the highest densities, survival of adults may decline

(Eberhardt 1977). If the population of polar bears in the Beaufort Sea continued to grow into the 1990's, we would expect to see some or all of these density-related changes in population structure. Eberhardt (1977) observed in general, that juvenile marine mammals are the most vulnerable to relative scarcity of resources and that restricted availability of resources will affect survival of juveniles before affecting other population parameters. Polar bears are weaned at 2.3 years, and for up to 2 years thereafter may be more vulnerable to a variety of hazards than older age classes. Stirling (1974) observed that bears seldom consume all of a seal they have killed, and concluded that scavenging the leftovers is important to survival of juveniles, and hence to recruitment. Smith (1980) also documented that polar bears often scavenge kills of other bears. The greatest effect of increased competition for resources, therefore should fall on young, independent polar bears that are still learning survival skills and are most dependent on scavenging. We further reasoned that we might see poorer survival and weaker representation in the age structure of juveniles when population levels were high, and we tested the null hypotheses that survival of litter members and independent juveniles are independent of total population size and numbers of adults.

We observed juvenile bears scavenging kills of more experienced animals. We also observed that larger bears often chase smaller bears away from kills suggesting that successful foraging among independent juveniles, and their survival, may be influenced by social factors as well as relative availability of food resources. If juveniles are most vulnerable to such

incidents (Eberhardt 1977; Young and Ruff 1982), these observations suggest agonistic behavior may be a limiting factor in polar bear populations. If carrying capacity is set by the environment, we should expect to see survival of young in litters decline, and age of first reproduction and reproductive intervals increase. Finally, adult stature will diminish as their condition declines, and production of litters will decline (Eberhardt 1977). If the carrying capacity is not reached because social phenomena intervene, we may see survival of subadults as the principal limiting factor. To evaluate this, we tested the hypothesis that physical stature of female polar bears is not related to population size. We compared reproductive patterns in the early period of study, when the population was low, to the latter period when it was higher, and tested the hypothesis that litter sizes of young do not vary between periods when the population sizes differ. We also tested whether reproductive intervals and age-specific productivity, both of which contribute to production of young, varied between periods when the population was small and when it was larger.

Because sex ratios of young are thought to be indicative of population status (Verme 1969; Trivers and Willard 1973) we tested whether the sex ratio of young differed from even during either lows or highs in the population.

Recovery from the aerial polar bear harvest, should have resulted in significant changes in the age structures and survivorship schedules of male and female polar bears (Amstrup et al. 1986). We examined this by testing the hypothesis that age structures during the period of low numbers did not differ

from that of the period of high numbers.

Materials and Methods

Field Procedures

We captured and marked polar bears each spring between 1982 and 1992, except for 1990. Bears also were captured in autumns of 1981-86, 1988 and 1989. Autumn captures occurred in October and November each year, and spring captures occurred between March and May. We captured polar bears in coastal areas of the southern Beaufort Sea, from Point Barrow, Alaska, at ~157°W, to Cape Bathurst in Canada at ~127°W. Bears also were captured in bordering areas east and west of the Beaufort Sea. We used logistical bases at Barrow, Prudhoe Bay, and Kaktovik, Alaska; and Tuktoyaktuk Northwest Territories, Canada (Fig. 1). We immobilized polar bears by injecting drugs [phencyclidine hydrochloride (Sernylan®, Park, Davis and Co.), etorphine hydrochloride (M-99®, Lemmon Co.), and tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Co.)] with projectile syringes fired from helicopters (Larsen 1971; Schweinsburg et al. 1982; Stirling et al. 1989). Capture and marking protocols were approved by an independent animal care and welfare committee.

We tattooed polar bears on both sides of the upper lip, and tagged their ears with polyethylene tags. Measurements, including axial girth and zygomatic width, were recorded for each captured bear. A vestigial premolar tooth was removed from each captured bear, and cementum annuli were

counted for age determination (Hensel and Sorensen 1980; Stirling et al.
1980). Each year, we tallied new captures and recaptures, and updated
capture and reproductive histories of previously marked animals. We
examined capture data in archives of the U. S. Fish and Wildlife Service for the
period 1967-1980 (Lentfer 1968; Lentfer et al. 1980). Those data were
collected by personnel of the Alaska Department of Fish and Game and the U.
S. Fish and Wildlife Service between 1967 and 1972, and by the U. S. Fish
and Wildlife Service thereafter. Data collected in the Canadian portions of the
southern Beaufort Sea (between 127°—137° west longitude and south of 72°
north latitude) were provided by the Canadian Wildlife Service for the periods
1971-1979, and 1983-1987, 1989, and 1992. Unless otherwise specified,
analyses for any particular period were performed on combined data from the
southern Beaufort Sea of both Canada and Alaska. Latitude and longitude
values used in this manuscript are degrees north and west, respectively.

Each year after 1980, we collared a limited number ($\bar{x}$ = 27) of females
with radio transmitters. We wanted to monitor only adult females, and initially
radio-collared only females with young, those that showed evidence of prior
lactation, or those that appeared to have reached adult size. After 1983, we
radio-collared females with zygomatic widths ≥18 cm. This was the smallest
width we observed for bears accompanied by young, and provided a more
objective assessment of adult stature. We attached very high frequency (VHF)
radio collars to polar bears between 1981 and 1985 and relocated them
approximately 4 times per year with aircraft (Chapter V). After autumn 1985,
we mostly deployed ultra high frequency platform transmitter terminals (PTT's)

that were relocated by satellite. Sensors on PTT's recorded temperature of the collar and 2 indices of activity. Positions of collared animals were determined by sensors on the satellite that interpreted frequency patterns caused by changes in relative positions of the satellites and animals. (Fancy et al. 1988). Collars carrying PTT's also carried VHF beacons that we located with aircraft. Radio tracking often was used to aid recaptures of polar bears. Unless otherwise specified, however, "capture" is used in this paper to describe only those events where polar bears were encountered non-selectively during normal visual searching bouts.

Analyses

Amstrup et al. (1986) reported that evidence of recovery from over-harvest was apparent in the age structure beginning in 1975. From 1975 to 1980, patterns in the age structure were intermediate between those of the over-hunted period and more recent conditions. Hence, age structure data were divided, for comparison, into an early over-hunted period (1967-1974) and a later recovered period (1981-1992). Between 1986 and 1992, a main goal of the capture work was to attach PTT's to adult females. Because of the need to deploy all PTT's that had been purchased each season, we sometimes overflew rather than capture animals that were clearly males. This bias was most strongly associated with the largest of males, and could have altered recapture probabilities and minimized representation of old males in age structures from the late period of study.

Population Size and Trend

   We attempted to estimate population size with Jolly-Seber (Pollock et al. 1990) and log-linear (Cormack 1989) mark and recapture models. Estimates derived from those models, however, varied so greatly among years that they were of no use. Radical fluctuations in the population estimates derived from these models apparently stemmed from capture heterogeneity which resulted in poor estimates of the numbers of marks available in each year (see also page 176: methods of calculating survival). Because of problems with these multi-year models, we estimated population size with the Petersen model (Seber 1973:60). The Petersen model, as conceived, did not provide for births, deaths, immigration, or emigration, and thus was not applicable to multi-year data sets like ours. We modified the procedure, however, for multi-year use by applying independent estimates of survival to determine the numbers of marked animals available for recapture in each year. Age-specific survival rates determined by radio telemetry were weighted by the relative strength of each age class and averaged. The average survival rate was applied iteratively to determine the number of marked animals available for capture in each year. That estimate of the number of animals available for recapture was revised each year and used in a series of independent annual estimates. We further refined the annual estimates of marks available for the early part of the study, by correcting for the proportion of tagged animals unavailable for capture. From 1967-1980, 74% of the polar bears tagged in the southern Beaufort Sea were captured and marked near Barrow between 154° and 160° longitude (Fig. 1). Our satellite-telemetry work

verified that bears captured in that longitude zone spent 47% of their time west

of 160°, where their probability of recapture was nil. Only 2 polar bears

included in this study were captured west of 160° before 1981. Our

modification of the Petersen model relied upon independent estimates of

numbers of marks available and accounted for at least some of the

heterogeneity in capture probabilities. Fluctuations in Petersen estimates

were less severe than estimates from other models, and interval estimates for

some years were tight enough to engender some confidence.

We also examined patterns of population size in the southern Beaufort

Sea, with Leslie (1945; 1948) matrix models. Our projections began with the

population estimate generated by the modified Petersen index for 1975. We

used the southern Beaufort Sea age structure derived for the 1967-1974

period. Numbers of animals aged "0" were determined by dividing observed

numbers of yearlings by the calculated survival from age 0 to 1. Reproductive

input for matrix models was the age-specific production (m_x) of female young.

For age classes 0-17, we used the 1967-1974 rates. For age classes $\geq$18,

which were not present in the early study period, we used rates calculated

from 1981-1992. Survival rate inputs for Beaufort Sea projections were those

calculated from radio-telemetry data for adults, cubs, and yearlings. Survival

of animals aged 2-3 was assumed to be equal to that of cubs and yearlings.

We evaluated the sensitivity of the population to variation in survival rates by

substituting the low point in the 95% confidence interval on survival rates, for

the point estimate. These substitutions were made for all ages, juveniles only,

and adults only. We made matrix projections for polar bears in Hudson Bay,

based on parameter estimates of Derocher (1991) and the same starting number of animals used for Beaufort Sea projections. Age structures and productivity schedules for Hudson Bay in the early 1980's, when reproductive values were thought to be higher, and late 1980's, were used alternately. The best estimate of survival from Hudson Bay (Derocher 1991) was used alternately with our Beaufort sea survival estimate as an added sensitivity test.

We also used the Leslie matrix approach to estimate the maximum rate of increase possible (R_{max}) for this polar bear population (R_m in Caughley and Birch 1971). After determining that most of the documented mortality of polar bears in the southern Beaufort Sea was caused by human activities—principally subsistance hunting, Amstrup and Durner (Chapter III) used the Kaplan-Meier procedure (Pollock et al. 1989) to estimate the "natural" mortality rate for polar bears. We estimated R_{max} by applying that natural survival rate for adult animals to our Leslie matrix model. In addition, because we were interested in the maximum possible rate, we used the upper confidence interval values, rather than the point estimates, for survival of juvenile animals. We used the same values from the Beaufort Sea for recruitment as we used before.

Reproductive Patterns

Sizes of litters captured with adult females in each period and litter sizes observed in autumn and spring were compared with chi-square contingency tables. Numbers of male and female young captured as litter members, and losses of single young relative to losses of whole litters of 2

young, were compared to a hypothesized equal occurrence with chi-square goodness of fit tests. In all chi-square analyses, cells with few occurrences were combined until expected values were at least 1 and fewer than 20% of the cells had expectations less than 5 (Conover 1980:156).

Reproductive interval was calculated from life histories of individually marked polar bears for which recapture intervals allowed verification of reproduction. The minimum successful interval of reproduction was defined as the minimum number of years separating births of cubs that were subsequently weaned. For example, the reproductive interval for a female producing cubs in spring 1985, weaning them in 1987, and producing a new litter in 1988 would be 3 years. Conversely, if a female was first observed with cubs in 1985, her last opportunity to wean young would have been 1984. If she lost the cubs from 1985, produced and lost another litter in 1986 and finally produced a litter in 1987, weaning them in 1989, she would have had a 5 year minimum reproductive interval. Reproductive intervals in early and late periods were compared with the normal approximation to the Mann-Whitney test (Zar 1984:142).

We calculated age-specific productivity (numbers of cubs produced per female) as the number of offspring produced by females in each age group divided by the number of females in that age group (Stirling et al. 1980). Age group representation was from the estimated standing age structure. To increase the numbers of females from which data could be included, females with yearlings as well as females with cubs were included in computations of

productivity as: $m_x = \left(C_x + (Y_{x+1})\left(\frac{1}{\hat{S}_1}\right)\right)\left(\frac{1}{F_x + F_{x+1}}\right)$ where: m_x = specific

productivity at age "x", C_x = no. cubs of females aged "x", Y_{x+1} = no. yearlings

of females aged "$x+1$", $\hat{S}_1$ = estimated survival of young to age 1, F_x = no.

females aged "x", F_{x+1} = no. females aged "$x+1$."

Numbers of yearlings were corrected back to numbers of cubs with

division by an estimate of the survival rate developed from radio-telemetry

data (Chapter III) for cubs between ages of 0 and 1. We felt that the yearling

component of this estimate was reliable, because female polar bears in the

southern Beaufort Sea accompany their young for >2 years after birth. Often,

however, 2-year-olds were weaned before their mothers were encountered in

the spring, so the presence of those animals was not a reliable indicator of

numbers of 2-year-olds, and we did not back-calculate from litters of 2-year-

olds. The number of litters produced at each age was estimated using the

same equation and substituting numbers of litters for numbers of young. The

derived estimate of m_x was divided by 2 to represent the age-specific

production of females (fecundity, assuming an equal sex ratio) as it is used in

life tables or matrix (Leslie 1945; Caughley 1977) projection models. Overall

production of young in early and late periods was compared with the $\underline{Z}$-test for

equality of ratios (Cochran 1977:180).

Survival Patterns

Analysis of the Age Structure

The age structure was analyzed with life table methods (Caughley 1977; Seber 1973). Life tables were constructed from the multi-year capture data for the early and late periods. Numbers of animals each age captured in all years were added together to form approximations of the standing age structures for both study periods. The derived life tables, therefore, were of the composite time-specific type (Seber 1973:400; Amstrup et al. 1986). Cubs, animals aged "0", appeared to be under-sampled in all age structures examined. Hence, we estimated numbers of cubs that must have been present by dividing numbers of yearlings, the first fully represented age group, by the survival rate we estimated for the first year of life. Survival rates used were derived from radio telemetry (Chapter III). Composite age structures were characterized by over-representation of some age classes. That is, more animals in one age group than in the group or groups that preceded it. Such "bumps" in the age structure prevent life table calculations, because higher representation in the Age_{x+1} category than in the Age_x category imply survival rates >1. Therefore, we smoothed the age structure, by first transforming age frequency tallies to their natural logarithms. Then quadratic and cubic least-squares regressions were calculated with Y = In(Age Frequency) and X_1, X_2, and X_3 corresponding to age, age^2, and age^3 (Caughley 1966; 1977). The age frequencies for each life table were smoothed with the polynomial regression providing the greatest adjusted multiple coefficient of determination

(R^2) value. The adjusted R^2 indicates the power of the independent variables to explain patterns in the dependent variables while accounting for the loss of degrees of freedom as additional independent variables are added to regression models (Neter et al. 1985). Shapes of smoothed age structures were strongly affected by the erratic and low representation in older age classes. Hence, we smoothed age structures only through the first year class represented by 1 or 0 observations. We constructed life tables including ages 0-20 whenever sufficient data were available.

Parameters comprising the tables were: the age category "x", the frequency of animals observed in each age group N_x, the smoothed frequency of animals observed in each age group N_x' (which is used in place of N_x for subsequent calculations), the proportion surviving to age x, $l_x = \dfrac{N_x}{N_0}$, proportion dying in each age group, $d_x = l_x - l_{x+1}$, mortality rate at each age $q_x = \dfrac{d_x}{l_x}$, and survival rate at each age $p_x = 1 - q_x$. In addition to the most common life table parameters, the average proportion of animals alive (L_x) in each age interval and the total number of animal-time intervals lived (T_x) also were included in each life table (Seber 1973:394). Population mortality rate,

$$\bar{q} = \frac{N_x}{\sum\limits_{y=x}^{n} N_y}$$, and age-specific life expectancy (e_x) (Caughley 1966; 1967;

1977), as well as the proportion alive in each age interval (C_x) (Eberhardt 1988) also were determined. Population mortality rate $(\bar{q})$ represents the weighted mean mortality rate for animals aged x onward. The age-specific life

expectancy (e_x) represents the number of years of further life expected by animals that have survived to a particular age x. Age-specific survival also was evaluated with $\hat{S}$ the Heincke geometric survival estimate (Seber 1973:415). The Heincke survival estimate is related to Caughley's (1967; 1977) population mortality $(\bar{q})$ as simply $1 - \bar{q}$ and so is compatible with the other life table statistics. Confidence intervals are available for Heincke's $\hat{S}$ but not for Caughley's $\bar{q}$. We used confidence bounds on $\hat{S}$ to test whether age-specific survival rates observed during the early and late study periods were different. We also tested for overall differences in age structures developed for the two time periods and for males and females with "n by 2" chi-square contingency tables (Caughley 1966).

Mark/Recapture Analysis

We attempted to estimate survival rates from capture and recapture patterns of animals marked between 1967 and 1992 using the Jolly-Seber approach (Pollock et al. 1990), and a log-linear model (Cormack 1989). Survival estimates from the Jolly-Seber and log-linear models that were neither realistic nor reasonable apparently resulted because of heterogeneity of capture probabilities. Estimates of annual survival rates fluctuated markedly providing many estimates below the range necessary to sustain populations (Eberhardt 1985), and many estimates greater than unity. Estimates of numbers of marks available for recapture, derived by the Jolly-Seber models, sometimes exceeded the numbers of marks previously attached—an impossible situation. Mark and recapture estimates of survival, therefore, were

not used in subsequent analyses.

Population Regulation

We used step-wise linear least-squares regression to examine the relationships between variations in population composition and total population size (McCullough 1981). Dependent variables we examined included: numbers of cubs/adult, yearlings/adult, 2-year-olds/adult, 3-year-olds/adult, and numbers of 2+3-year-olds/adult. Polar bears 6 years and older were defined, for the purposes of these regressions, as adults. Independent variables were population size estimated from Leslie matrix models, number of adult males, number of adult females, and total number of adults in the annual samples. Finally, we tested whether axial girth, the only measure of stature collected consistently for the entire period of study, was independent of population size and structure. Axial girth is significantly related to body mass (Durner and Amstrup unpubl.; Kolenosky et al. 1989), and thus provided an indication of changes in body condition over time. We averaged both dependent and independent variables over successive 3-year periods beginning with 1967. This reduced the number of time intervals considered (e. g., one data point for 3 years rather than one per year), but it also minimized fluctuations introduced into the data by annually variable sample sizes.

The step-wise procedure first calculated the best one-variable model, then tested all remaining independent variables to establish the best 2-variable model and so on. We were willing to accept multiple regression models only if

the addition of another independent variable resulted in an improved coefficient of determination (adjusted $\underline{R}^2$), and if the partial $\underline{F}$ for that variable was significant at the 0.05 level. We used the sequential Bonferroni procedure to evaluate "table-wide" significance of regression models related to density effects (Rice 1989). The collective significance of observed shifts in reproduction, survival, and physical stature was determined with the sign test (Zar 1984:386).

Statistical analyses were performed on a Data General AVIION 6200 computer (Data General Corp., Westboro, MA) running SAS version 6.07 software (SAS Institute, Inc., Cary, NC). Routine compilations of data, Leslie matrices, and life table computations were performed on a Power Macintosh 7100 computer running Excel version 4.0 software (Microsoft Corp., Redmond, WA). We report actual probabilities of statistical tests performed unless $\underline{P} < 0.001$.

Results

We analyzed 3,243 captures of 2,663 individual polar bears occurring between 1967 and 1992. During the early period (1967-1974), there were 589 captures of 534 individual polar bears. During the late period (1981-1992) there were 1087 captures of 789 bears. During the early and late study periods respectively, an additional 397 captures of 381 bears and 494 captures of 418 bears were recorded in areas adjacent to the southern Beaufort Sea. Capture data from adjacent areas were used only to provide a framework for analyses of the Beaufort Sea data, and were not used in

analyses reported here unless specifically stated. The concentration of marking was heavily weighted toward the western Beaufort Sea through 1980, with 74% of animals captured within ± 3° longitude of Barrow. Capture effort was geographically more evenly distributed between 1981 and 1992 (Fig. 1). Also in the late period, we attached 439 radio-collars to 302 individual female polar bears. We relocated collared bears 1,450 times with aircraft and many thousands of times by satellite. Data collected with different sampling designs (e.g., radio-telemetry vs. mark and recapture) could not always be combined or compared. Also, some measurements were occasionally not obtained. Therefore, sample sizes reported may vary somewhat among different categories of analyses.

Population Size and Trend

Mark and recapture estimates indicated that the polar bear population of the southern Beaufort Sea grew during this study. The most precise Petersen estimates from the early part of the study (835 total animals, and 598 females) were derived in 1976 (Tables 1 and 2). The precision achieved then, apparently resulted from the large number of tags applied in years leading up to and including 1976 (DeMaster et al. 1980). This resulted in many surviving marked animals that were available for capture in 1976. Large numbers of marks available and large sample sizes resulted in tight confidence intervals again in 1985—1987. The population was estimated at 744 females and 1417 total animals in 1986. The estimated instantaneous growth rates, between 1976 and 1986, for females only and the total population, respectively, were

0.022 and 0.053. Projection of the population size to 1992 based upon the range of calculated growth rates through 1986, yielded 887 females, and 2165 males and females combined. If the population really was 60% female (see "analysis of the age structure", this chapter), 887 females would have meant there were 1479 males and females in 1992.

The Leslie (1945) matrix also projected growth of the population during the study period. When matrix inputs included the age structure we observed in the early period, survival schedules (including all sources of mortality) calculated from telemetry, a cub production schedule from the early period for ages ≤17 and from the late period for females aged ≥18; the southern Beaufort Sea population was estimated to have grown to a final population of 883 females by 1992 (Fig. 2). This estimate represented a finite rate of change of 1.024, an instantaneous rate of change of 0.024 (Krebs 1989) and was very near the 0.022 instantaneous growth rate estimated for females by the Petersen procedure (Seber 1973). If the 1992 population was 60% females, the total population size was 1472, which is very close to the population estimated above with the Pedersen procedure (Seber 1973).

The indicated rate of growth was very sensitive to the survival rate estimates applied. For example, if the survival rates for adult ages was lowered to the lower limit of the 0.95 interval, the population grew at a finite rate of only 1.009 for the 16-year period. If survival of young were set at the lower limit of the 0.95 confidence interval, the finite rate of growth was only 1.006. If both values were held at the lower confidence interval limits, the

population declined at a finite rate of 0.988 (Fig. 2). The sensitivity of polar bears to survival estimates also was demonstrated by projections done using age structure, survival, and productivity values estimated from the Hudson Bay region (Derocher 1991). Despite empirical evidence that the Hudson Bay population of polar bears has grown over the past 20 years, projection matrices based upon parameters estimated from that population predicted a finite rate of decline of 0.997. If our higher survival estimates determined from radio telemetry were substituted for those estimated in Hudson Bay, however, the population was projected to grow at a finite rate of 1.029 for the first 16 years of projection (Fig. 2).

The sensitivity of rate of growth to the survival rates chosen also was apparent in our attempt to establish R_{max}. When the natural survival rate was used for adults, and the upper confidence interval values used for juveniles, the instantaneous rate of population growth was projected to be 0.060. This unencumbered rate of growth could be thought of as the maximum sustainable yield (MSY) rate for this population. The maximum number that could be removed would then be the product of this rate and the population size at MSY.

Reproduction

In the early and late periods we captured 102 and 271 females accompanied by young of various ages (Table 3). Small sample sizes may have contributed to variations in estimated age-specific productivity during the early period. In the late period, however, production of cubs appeared to be relatively stable from ages 6-24. The oldest females producing cubs were 17

and 24 years old in the early and late periods respectively. Age-specific

productivity determined from females captured by conventional methods did

not differ from that determined from radio-collared bears ($\underline{Z}$ = 0.18, $\underline{P}$ = 0.86).

Conventional capture and radio-telemetry data, therefore, were pooled to

increase sample size. Mean values for overall cub production in the early

(0.40) and late (0.38) study periods, when the population was small and larger

respectively, did not differ ($\underline{Z}$ = 0.15, $\underline{P}$ = 0.88). Nonetheless, production of

cubs was higher for many year-classes of females in the early period than in

the late period, and the dearth of older females in the early period may have

inhibited comparisons. In the early period when the population was small 2%

of 4-year-old females, 14% of 5-year-old females, and 42% of 6-year-old

females produced cubs. In the late period, when the population was larger,

these values were 2%, 7%, and 24% (Table 3), suggesting some delay in

maturation relative to the earlier period even if differences were not significant.

Mean litter sizes of cubs, yearlings, and 2-year-olds were 1.58, 1.71,

and 1.48 in the early period, and 1.63, 1.49, and 1.38 in the late period (Table

3). Litters of multiple cubs (χ^2 =1.89, df = 1, $\underline{P}$ = 0.17) and 2 year-olds (χ^2 =

0.41, df = 1, $\underline{P}$ = 0.52) were equally frequent in the 2 time periods. Litters

comprised of more than one yearling, however, were marginally more frequent

during the early period than during the late period (χ^2 = 3.48, df = 1, $\underline{P}$ =

0.06). This also may be an indication of a decline in reproductive performance

when the population was larger.

The average minimum interval of successful reproduction calculated

from Alaskan data only was shorter in the early study period when the population was small ($\bar{x}$ =3.36, $\underline{n}$ = 14) than when the population was larger ($\bar{x}$ = 3.68, $\underline{n}$ = 47), but the difference was not significant (Mann-Whitney $\underline{U}$ = 284.5, $\underline{Z}$ = 0.89, $\underline{P}$ = 0.19). The sensitivity of these comparisons also probably was reduced by the divergent sample sizes.

In the early period, spring and autumn litter sizes could not be compared because of inadequate sampling in fall. During the late study period, litters of multiple cubs were more frequent in the spring than they were in the autumn (χ^2 = 7.41, df = 1, $\underline{P}$ = 0.007). Yearling litter sizes, however, did not differ between seasons (χ^2 = 0.12, df = 1, $\underline{P}$ = 0.73; Table 4). More young aged 0-2 were females in both study periods (Table 5), but the ratio of male to female young did not differ significantly from unity (χ^2 = 3.03, df = 5, $\underline{P}$ = 0.70). The average rates of litter production calculated as the inverse of the reproductive interval (Amstrup and DeMaster 1988) were 0.30 and 0.27 in the early and late periods.

Survival Patterns

Analysis of the Age Structure

In the early period, ages of 222 captured males and 361 captured females (62% females) were estimated. Similarly, ages were determined for 432 males and 643 females (60% females) captured in the late period. The oldest age determined for a female polar bear encountered in this study was 27 years. The oldest male was 23. Old animals were more frequent in the late

period than in the early period (Figs. 3 and 4). In the early period, one female

was captured at age 17 and another at 21, and only 7 (2%) were aged 15+.

The oldest male captured in the early period was 17 years old, and only 2

males (1%) were ≥15. This contrasted with the late period, when 44 (10%)

captured males and 78 (12%) captured females were ≥15 years of age. In

both periods, the male age structures were comprised of fewer old animals

than the female age structures (early: χ^2 = 32.8, df = 16, $\underline{P}$ = 0.008; late: χ^2 =

43.5, df = 16, $\underline{P}$ < 0.001). The age structures for both sexes were comprised

of a higher proportion of young and a lower proportion of old animals in the

early period (Figs. 3 and 4) (males: χ^2 = 60.3, df = 16, $\underline{P}$ < 0.001;

females: χ^2 = 75.6, df = 16, $\underline{P}$ < 0.001). Rejection of a hypothesis that age

structure and population size are independent clearly was indicated.

Examination of life tables revealed higher overall survival rate (px) for

both males and females in the late period. Changes in survival, however, were

not consistent across all age groups. For both males and females, periods of

high survival rate (px) of old animals were associated with lower survival rate

(px) of young (Fig. 4). Estimated survival rate (px) of males through age 5 was

lower during the late period than during the early period (Tables 6 and 7). Life

expectancies (e_x) and survivorship ($\hat{S}$ and p_x) of males profoundly increased

from birth into the prime ages of 5-9 during the late study period but declined

after birth during the early period. Survival rates (p_x) for females from 0-4

years of age also were higher in the early period (Tables 8 and 9), and survival

(p_x) of adult females was higher in the late period. As with males, early period

life expectancies (e_x) and measures of survival ($\hat{S}$ and p_x) of females

declined after age 0, and they increased until maturity during the latter study period. According to Heincke's $\hat{S}$, males aged 2-9 survived at significantly higher rates during the latter study period when populations were high than they did when populations were lower (Tables 6 and 7). Females aged 3-13 also survived at significantly higher rates during the period of higher population according to $\hat{S}$. Because $\hat{S}$ incorporates survival of older age classes into the calculation of survival at each age (after all, it is a component of the age-specific life expectancy), it provides an inflated estimate, relative to p_x, of survival for the early ages. Hence, the indication of $\hat{S}$ that survival of 2 and 3-year-olds was higher in the latter period is an artifact. The higher survival of prime age and older animals, however, corroborates the trends in px estimates. Rejection of the hypothesis of independence of survival rates and population size is in order; and higher survival for prime age animals during years of high population is an inescapable conclusion.

Population Regulation

Numbers of young animals in the southern Beaufort Sea polar bear population were inversely related to the total population size, and to numbers of old animals. Although numbers of cubs ($\underline{P}$ = 0.16) and yearlings ($\underline{P}$ = 0.10) were not significantly related to population size or other independent variables, the relationship was strong among independent subadults. In terms of regression, population size alone explained 56% of the variation ($\underline{R}^2$ = 0.56) in the proportion of 2-year-old animals and 55% of the variation in the proportion of 2+3 year-olds (Table 10; Figure 5). Population size alone also explained

75% of the variation in axial girth for adult females with cubs (Figure 6) and for adult females without young of any age. Population size explained 48% of variation in axial girths of females accompanied by yearlings. None of the independent variables other than mean population size both improved the coefficient of determination and provided significant partial regressions; so only simple linear regressions are reported (Table 10).

In previous sections, we predicted that as the polar bear population in the Beaufort Sea increased we would see: 1) age of maturity increase; 2) reproductive interval increase; 3) litter size decline; 4) age specific production of young decline; 5) survival of litter members decline; 6) survival of independent young decline; 7) a shift in age structure to older animals; and 8) a decline in physical stature of adults. Although many of these predictions did not pass tests of individual statistical significance, all 8 predictions were upheld qualitatively. According to the sign test (Zar 1984, Table B.25), the probability that all 8 indices would shift the same direction by chance alone is 0.004. Hence, despite the lack of individual significance in some tests, the collective shift of all 8 indices in the direction predicted by density theory is significant.

Discussion

Population Size and Trend

Available data confirmed that the population of polar bears in the southern Beaufort Sea was higher in the 1981-1992 study period than it had been earlier. Projection matrices and the modified Petersen index both

indicated population growth at a rate of ~2% per year after 1975. The total population size in 1992 apparently was near 1500 animals. Capturing females that could be fitted with radio collars was the main focus of field efforts in Alaska between 1986 and 1990. Adult males can be consistently distinguished from females, even from a helicopter. In order to save time and fuel for capture of more females, many adult males that were encountered during these years, were not captured. Therefore, old males were under-represented in life tables for the latter study period. Hence, survival of prime-age males in the late period may have been higher than we calculated, and differences in proportions of males and females may have been smaller. If the sex composition of the population was closer to 50% females, the total population estimate for 1992 might have been near 1800 animals at the close of this study. Many caveats on population size estimates could be suggested, and absolute numbers could be debated. That the population has been growing, however, is not debatable. Estimates derived from mark-recapture and matrix projections converged on the same range of values, and reports from local residents and oil field workers as well as our casual observations verified substantially more polar bear sightings in coastal regions of the Beaufort Sea in recent years. Because adult males were known to be under-sampled in the latter period of study, the total population size in 1992 may have been higher than 1500. Conversely, the instantaneous growth rate of 0.053 estimated for males and females combined, seems too large, casting doubt on the highest estimate (2165) we obtained. Hence, although using ~1500 is preferred because it assures we manage conservatively, the estimate

of ~1800 may be the most realistic of our estimates.

Although the population has been growing, the margin of growth has been small enough that relatively small changes in population dynamics features, particularly survival, could dramatically alter the growth rate. Even without human interference in survival patterns, R_{max} for polar bear populations is small. Lower estimates of survival than those we calculated with radio telemetry, even with higher estimates of productivity, such as those estimated in Hudson Bay, did not allow us to project population growth. This supports the observation of Eberhardt (1985) that survival for large K-selected animals must be in the high 90% range to allow populations to sustain themselves.

Reproduction

Although we could not reject many hypotheses that reproductive output was independent of population size, most measures of reproductive performance indicated declines between the early and late years of the study. These declines appeared to be related to increases in relative density of polar bears in the Beaufort Sea. For example, onset of reproduction in the Beaufort Sea region appeared to be later now than it was during the period 1967-1974 when the total population size was lower. Higher proportions of 5- and 6-year-olds produced litters when the population was small than they did when the population was larger. Minimum reproductive intervals appeared to be longer, and litter sizes were apparently smaller when the population was high. If production of young is among the last of population parameters to be affected

by increased density (Eberhardt 1977), declines in these measurements, even if individually non-significant, should collectively be considered significant.

Reproduction among female polar bears began as early as age 4 but was not common until age 6 (Table 3). After age 6, reproductive output may be relatively stable beyond age 20. Lentfer et al. (1980) also reported the most common age of first reproduction in Alaska was 6 years, and Stirling et al. (1975) suggested that some 4- and 5-year-olds produce litters, but litter production among polar bears in the eastern Beaufort Sea did not occur commonly until age 6. Many female polar bears in the central Canadian Arctic, Hudson Bay, the Canadian High Arctic, and southeast Baffin Island produced cubs at 5 years of age (Stirling et al. 1980; Furnell and Schweinsburg 1984; Ramsay and Stirling 1988). This could indicate that undersampling of cubs, or other problems in data collection may have caused an overestimate of age of first reproduction in the Beaufort Sea. Our results, however, corroborate those of Stirling et al. (1976), and Lentfer et al. (1980), and confirm that onset of reproduction in the Beaufort Sea is later than in some of those other regions.

Our estimate of cubs produced per female (~0.40), averaged over all ages of reproductive females (Table 3), was lower than rates calculated for some other areas. Derocher (1991) and Ramsay and Stirling (1988) reported production of cubs among all adults at rates of between 0.6 and 0.9 cubs per female. Young are often weaned as yearlings in the Hudson Bay area (Ramsay and Stirling 1988, Derocher 1991). Weaning young as yearlings

would permit a rate of cub production much higher than in the southern Beaufort Sea or most other areas of the Arctic where young are weaned at ages >2. Our estimates of litter sizes also were lower than those estimated for Hudson Bay (Ramsay and Stirling 1988). DeMaster and Stirling (1983) speculated that the average litter size at birth in Alaska is probably very close to 2.0. We calculated a mean litter size of 1.6 from observations made at or near the time of den emergence, however. Perhaps many cubs are lost before they are available to be observed. Post-emergence declines in litter sizes we documented may be a continuation of losses begun in the den. Also, as counts of yearlings suggest, litter sizes could have declined since the study of DeMaster and Stirling (1983).

In lieu of a correction for mortality of young between pre-weaning age classes, estimates of age-specific parturition rates that rely on numbers of young older than cubs (Stirling et al. 1980; Lentfer et al. 1980) may have been too low. Because of that limitation, Furnell and Schweinsburg (1984) concluded parturition rate should be estimated from the proportion of mature females with young-of-the-year litters only. Ramsay and Stirling (1988) discussed other caveats in use of data on yearlings in estimating rates of reproduction. This is a problem particularly in areas, like the Beaufort Sea, where under-sampling of cubs is chronic. Nonetheless, our more reliable estimates of survival of young make quality estimates of cub production or parturition rate possible from captures of yearlings and 2-year-olds, even if cubs are not captured.

Our derived parturition rate (litter production rate) of 0.25 was very close to that calculated as the inverse of the reproductive interval (0.27). Also, the rate of 0.25 multiplied by our observed mean litter size of 1.6 revealed an average production of 0.40 cubs per reproductive age female, equal to the production rate calculated directly from captures of cubs (0.40, Table 3). The reproductive interval for polar bears in the Beaufort Sea is longer than that reported for Hudson Bay, where young are often weaned as yearlings (Ramsay and Stirling 1988; Derocher 1991), but similar to that reported for other high latitude populations (Furnell and Schweinsburg 1984). The long reproductive interval and low rate of cub production we calculated suggest that previous low estimates of reproduction in the Beaufort Sea were not entirely due to sampling problems as suggested by Amstrup and DeMaster (1988). Productivity rates may have been higher than we calculated in the early years of the project because we used the same correction for cub survival as we did in the later years. It seems unlikely that such an underestimate, if real, could account for all of the difference observed. Reproductive output in the Beaufort Sea region does appear to be lower than in many other areas.

Because our analyses of reproductive trends were based on synthetic cohorts developed from composite age structures, they smooth annual variations in recruitment. Clearly, there are annual variations, but long life spans of polar bears mean many age classes are involved in reproduction. Hence variation in recruitment into any particular age class is damped, and errors in assessing variation in rates are likely to be greater than the true variation (Gerrodette 1987). Therefore, our smoothed estimates of

reproductive parameters appear to be appropriate for modeling the polar bear population.

Litters of cubs were under-sampled throughout this study. Information available from radio-collared females (Chapter V) verified that this under-sampling occurred in part, because much field work, especially in the early study period, occurred when cubs were still in dens. This corroborated conclusions of Lentfer et al. (1980) regarding sampling of young. DeMaster and Stirling (1983) also suggested that young of-the-year litters were not randomly sampled. The births of many cubs on pack-ice at high latitudes also may explain some of the under-sampling we observed. Amstrup and Gardner (Chapter V) reported that approximately half of the cubs born to bears inhabiting the southern Beaufort Sea are born on the pack ice. Many of those birth dens were so far offshore they were beyond the normal operation range of helicopters and therefore could not have been detected by researchers.

Different timing of field research in the early and late periods of study may explain why litter sizes of cubs and 2-year-olds in the early and late periods did not differ, while litters of yearlings larger than one were less common in the late period. In the early period, much research was accomplished in March of each year. Many females with cubs were still in dens and not available for capture or observation in March (Chapter V). Also, fewer bears were denning on land at that time (Chapter V). Consequently, relatively few cubs were captured. Conversely, litters of 2-year-olds were still with their mothers in almost all cases. During the late period, most capturing

was done in April. Proportionately less was done in March, and many captures occurred in May. This temporal difference allowed us to catch more cubs than had previously been encountered, but by April, many 2-year-olds had been weaned. Therefore, we probably under-sampled litters of 2-year-olds. Even if there were differences in frequencies of cub and 2-year-old litters or their sizes, the biases in our sampling may have overshadowed them. Because female polar bears in the Beaufort Sea keep yearlings with them all year, and because they do not enter winter dens, the samples of that age group were not biased by temporal differences in capture effort.

Survival Patterns

Analysis of the Age structure

The age structures of both males and females differed between our 2 study periods in ways that corroborate the hypothesis of over-harvest during the first period and recovery during the latter period of study (Tables 6-9). Higher survival of adults and lower apparent survival of young in the period of high population are consistent with apparent changes in a population approaching K—carrying capacity (Eberhardt 1977; McCullough 1981). Higher survival of adults in the latter period of study, by itself, could be explained solely by the removal of the excessive aerial harvest. The relatively sharper decline in proportions of young, however (Figures 3 and 4), could not be explained by removal of hunting pressure alone.

Survival rates of adults during the late period were higher than rates

previously calculated from similar data (Amstrup et al. 1986; DeMaster et al.

1980). A potential problem with our estimates was the use of composite age

structures rather than an observed standing age structure (Caughley 1966;

1967; 1977). Estimation of a standing age structure from a series of time-

specific life tables assumes a stationary population and a stable age structure

(Spinage 1972). If the population is not stationary, the apparent survival rate

is actually the true survival rate divided by the population growth rate

(Eberhardt 1988). Therefore, estimates of survival, over the period from which

the composite was constructed, are low when the population is growing and

high when the population is declining. Because both empirical observations

(e.g., observations of polar bears and various signs of polar bears, by

residents of Beaufort Sea coastal areas and personnel working there) and

projection models indicated population growth during this study, it is

reasonable to conclude that the survival rates we estimated from the age

structure are low. This conclusion is corroborated by radio-telemetry estimates

of survival of adult polar bears that were higher than those indicated in life

tables. Amstrup and Durner (Chapter III) used telemetry to generate point and

95% interval estimates of survival of adult females at $\hat{S}$ = 0.969 (0.952-0.983).

The radio-telemetry estimate of survival during the first year $\hat{S}$ = 0.651 (0.610-

0.675) of life was lower than that estimated from the age structure, but the

telemetry estimate of survival for the second year $\hat{S}$ = 0.860 (0.751-0.903)

was higher.

Population Regulation

Taylor et al. (1987) concluded that density effects on recruitment in polar bears are inconsequential in most circumstances. If this were true, all available females should breed, and birth rates and survival of young should be high regardless of population level. Derocher et al. (1992) found that female polar bears in Hudson Bay continued to breed and get pregnant even as their body condition declined. Such an observation, in itself, may lead to a conclusion that density has minimal effect on reproduction in bears. Pregnancies, however, and even births do not tell the whole recruitment story. Derocher et al. (1992) also noted that full term pregnancies, as indicated by emergence from the den with or without cubs, did decline with declining condition among females, as did apparent survival of cubs after leaving the den. Our observations corroborate those of Derocher et al. (1992). Concomitant with higher numbers and greater survival rates of adults, we observed lower rates of cub production. Litter sizes of yearlings were smaller when the population was larger. Although the differences were not significant, observed inter-birth intervals were longer and parturition rates lower when the population was high. Proportions of young and their survival were negatively correlated with population size. Derocher and Stirling (1992) speculated that declining survival of litter members may be the most prominant effect of increased density in their Hudson Bay study area. Survival of young apparently declined as a result of declining condition of adult females, and the condition of females declined because of relative unavailability of food. Also, there was evidence that age at first reproduction and inter-birth interval may

have increased in Hudson Bay in recent years, just as it has in the Beaufort
Sea (Derocher and Stirling 1992).

We have observed a strong tendency for polar bears to follow the tracks
of other bears. Young polar bears often follow tracks of other bears and
scavenge kills. We have seen adult males drive smaller bears from kills.
Hence, scavenging behavior may increase risks of agonistic encounters with
larger bears at the same time it increases foraging success. This suggests
that successful foraging among independent juveniles, and their survival, may
be influenced by social factors as well as availability of seals and other
resources. Young and Ruff (1982) have shown that social interactions in bears
can directly influence recruitment of young even when food resources are not
in short supply. Also, McCullough (1981) suggested that agonistic behavior of
adult males may be a major regulating factor in some populations. Indeed,
agonistic behavior caused 3 of the 5 natural deaths for which we were able to
determine a cause. These dead were adult animals, but juveniles usually are
more vulnerable to such incidents (Eberhardt 1977; Young and Ruff 1982).
Our observations, nonetheless, do not support the hypothesis that agonistic
behavior is an important limiting factor in the polar bear population of the
southern Beaufort Sea. We did observe large bears drive smaller ones from
kills. Such observations were recorded less than once per year, however, and
even combined with the 3 deaths described above, they account for a small
proportion of the interactions among bears we observed. Also, population size
emerged as the principal independent variable explaining variations in all
dependent variables examined. Further, after population size was in the

models, neither numbers of adult males nor numbers of adult females nor any other independent variable added significant explanatory power. Restricted availability of resources resulting from high relative densities appears to be the main factor limiting the polar bear population in the Southern Beaufort Sea. Derocher and Stirling (1992) drew the same conclusion in regard to the polar bear population of Hudson Bay.

Polar bears in the Beaufort Sea and elsewhere eat mainly ringed seals (Phoca hispida) (Smith and Stirling 1975; Stirling and Archibald 1977; Smith 1980). The distribution of bears is thought to be closely related to the distribution of seals, and changes in the dynamics of polar bear populations in response to transitory changes in ringed seal populations have been documented (DeMaster and Stirling 1981). Hence, ringed seals are the most likely resource to limit polar bear numbers. In a simple predator-prey system such as the one involving polar bears and ringed seals, where the predator is heavily dependent upon one species of prey; equilibrium points with high numbers of predators (e.g., K—carrying capacity) must be characterized by lower numbers of prey than occur at lower densities of predators (Caughley 1979). Data from the Beaufort Sea, with which this hypothesis could be tested, unfortunately are limited.

Surveys of ringed seals in the Beaufort Sea region have documented changes in density and distribution of seals within and among seasons (Burns and Harbo 1972; Stirling et al. 1982; Frost et al. 1988; and Kingsley 1990). Evaluation of long-term trends in seal numbers, however, has been less

clear-cut than assessment of short-term variations. For example, Frost et al. (1988: Table 35, mean of all years and strata) reported that densities of ringed seals, in land-fast ice of the Beaufort Sea, averaged 1.16 seals/km^2. Those surveys were conducted during the time when we determined the population of polar bears was high. The estimate of Frost et al. (1988), contrary to the pattern described by Caughley (1979), was substantially higher than the 0.463 seals/km^2 reported by Burns and Harbo (1972: Table 3, strata III-VI) when the polar bear population was low. On the other hand, the estimated density of 0.354 seals/km^2 (Frost et al. 1988: Table 34, mean of all years and strata) for the pack ice of the Alaskan Beaufort Sea was very similar to estimates for combined pack and fast-ice areas in the Canadian Beaufort Sea (0.345 seals/km^2; Stirling et al. 1982: Table 7, mean of all years and strata). Although they used different platforms for observations, Stirling et al. (1982) and Frost et al. (1988) used similar survey designs, suggesting their results should be more comparable than were those of Burns and Harbo (1972) and Frost et al. (1988) which used much different designs. If those surveys are comparable, they suggest an absence of long-term changes in seal numbers. More realistically, methodologies probably were too insensitive to detect long-term changes in numbers of seals because of vagaries in annual and seasonal conditions, differences in observation platforms, and different areas of survey.

The available survey data may not be precise enough to detect long-term trends in numbers. They may, however, allow a test of whether polar bears, at current densities, could be significantly affecting seal numbers. Ringed seals are thought to be most common in land-fast ice habitats, and in

waters of moderate (50-100 m) depth (Kingsley 1990). Also, they are thought to be much less common at water depths beyond 175 m (Kingsley 1990) than in shallower waters. Land-fast ice in the Beaufort Sea consistently occurs at depths less than 20 m. The surface area of land-fast ice (water depths 0-20 m between Barrow and Cape Bathurst) is ~51,099 km^2. When we doubled the estimated density (1.16 seals/km^2; Frost et al. 1988) of seals in the land-fast ice, to account for seals in the water and hence missed by survey crews, and multiplied that estimate (2.32 seals/km^2) by the area of land-fast ice; we obtained an estimated number of ringed seals in the land-fast ice of 118,550. To estimate numbers of seals in the pack ice, we ignored the preference ringed seals show for water depths less than 175 m (Kingsley 1990), and assumed they are equally numerous to depths of ~2000 m. Then, we doubled the estimated density of seals in the pack ice (0.354 seals/km^2; Frost et al. 1988) and multiplied that number (0.708 seals/km^2) by the 293,798 km^2 of pack ice over waters of 20-2000 m depth to estimate 208,009 ringed seals in the pack ice. The estimated total number of ringed seals in the Beaufort Sea, then, was ~326,560.

Kingsley (1990) estimated that polar bears require approximately 40 seals/year to meet demands of maintenance and reproduction. If our estimate of ~1500 polar bears in the Beaufort Sea is accurate, polar bears annually would consume 60,000 ringed seals. This suggests that polar bears in the Beaufort Sea consume 18% of the seal population annually. Ringed seals do not reproduce until age 6 and produce only one young per year thereafter (Kingsley 1990). Therefore, losses of 18% of the population per year to polar

bears could not be sustained. Perhaps our estimates of energy requirements of polar bears are too high or our estimates of numbers of seals in the Beaufort Sea are too low. Certainly, dealing with average values based upon many assumptions has its limitations. Nonetheless, these calculations may be evidence that numbers of polar bears in the Beaufort Sea are high enough that they could be suppressing growth in ringed seal numbers; which in turn, would invoke density responses among the polar bears. Hammill and Smith (1991) documented levels of predation on ringed seals by polar bears that were great enough, at least in localized areas, to suppress population growth. Our conclusion that polar bears are showing a density response associated with relative unavailability of resources, namely ringed seals, therefore, appears plausible.

McCullough (1981) reported significant negative correlations between numbers of adult grizzly bears (Ursus arctos) and unweaned young. McCullough (1981) attributed this phenomenon to possible infanticide by large males. Cubs and yearlings also are the age classes of polar bears most vulnerable to cannibalism (Stirling 1974; Taylor et al. 1985). We documented some intraspecific killing, but numbers of adult males, when entered into our regression models, did not help explain variation in numbers of young. Hence, agonistic social interactions did not appear to be important regulatory factors in the population of polar bears in the southern Beaufort Sea. Higher relative densities for grizzly bears than for polar bears, larger sizes of activity areas for polar bears, and the inability of polar bears to defend territories all are differences that may reduce infanticide among polar bears. Also, major

portions of the population analyzed by McCullough (1981) regularly used human waste dumps for feeding. Such feeding artificially concentrated bears, and may have led to infanticide that otherwise would not have occurred.

Recently weaned young, ages 2 and 3, are among the fastest and most agile of polar bears, and should be much less likely than litter members to fall victim to cannibalism (Taylor et al. 1985). It was in these earliest ages of independence, however, where we observed the greatest depression in numbers. Differences in the foods and feeding patterns as well as spatial use patterns of grizzly and polar bears may explain this difference. The main foods of grizzly bears are diffused and come in small bundles that are easily handled by small bears (e.g., berries, pine nuts). Also, many grizzly bear foods, although difficult to find, are not difficult to catch. Polar bears, on the other hand, feed on marine mammals, principally seals. These are large parcels of food that are widely dispersed in time and space, and which require learned skills and a threshold physical size to secure (Stirling 1974). The diet of grizzly bears is more similar to that of black bears (Ursus americanus) than it is to the diet of polar bears. Black bears can be self-sufficient at less than 6 months of age (Erickson 1959), suggesting rapid assimilation of the skills necessary to survive. Perhaps the learning curve for young grizzly bears also is steeper than it is for young polar bears. This apparent difference between grizzly bears and polar bears may reflect our observation that infanticide is not a significant regulating factor in polar bear populations.

Conclusion

We learned that the polar bear population of the southern Beaufort Sea adjacent to northern Alaska and northwestern Canada was higher at the close of this study than it had been for many years. Also in this study, we found evidence that those increases in numbers were correlated with changes in the nature of the population itself. During the time when the polar bear population in the southern Beaufort Sea was low, there were few old animals and proportionately more young animals than there were in the latter years of the study when the population was high. Recent survival rates of adults were high, but survival rates of juveniles were lower. Smaller proportions of young females produced cubs when the population was high, suggesting that the onset of reproduction may have been later when the population was relatively high than it was when the population was lower. Minimum reproductive intervals increased and litter sizes may have decreased as the population rose. Numbers of young animals were significantly inversely-related to total population size, and physical stature of reproductive age females declined as the population rose.

These observations, taken collectively, suggested that the population was approaching "K-carrying capacity" by the close of this study in 1992. The changes we observed are precisely those that should occur as a population of K-selected animals approaches carrying capacity (Eberhardt 1977; Derocher and Stirling 1992). Despite the fact that this population is high in relative terms, in absolute terms it is very small. The population of the entire southern Beaufort Sea may have included only 1500 animals at the end of this study. If

the population was growing at a rate of approximately 2% per year, loss of an additional 30 animals, to hunting or other perturbations, would place the annual removal at or near maximum sustainable yield. Hence, room for significant perturbations, beyond those to which the population already is exposed, may be limited. Because the population appears to be near K, however, some density-dependent compensation could occur if perturbations affected only polar bears themselves. Hence, added hunting or direct mortalities related to incidental takes by industry, may have less effect on the population than simple addition or subtraction could predict. Some added takes might simply substitute for deaths that are already occurring. Unfortunately, data suggest that most mortalities of bears in the Beaufort Sea already are human caused (Chapter III), so the number of added takes tolerable might be small indeed. Alterations of habitat that negatively affect numbers or productivity of seals, apparently would not be easily absorbed. Available data indicated that present numbers of polar bears already may be strongly influencing ringed seal populations. Likewise, human activities that disrupt maternal denning or altered survival of dependent young, might not be easily compensated. Managers, therefore, must remain alert for changes in human activities that could precipitate direct mortalities of polar bears. They also must be alert for habitat alterations that could adversely affect maternal denning or the availability of ringed seals. Proposed activities that could have any of these effects should be preceded by studies that more accurately determine numbers of polar bears and ringed seals and the dynamics of the interactions between these two species.

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Table 1. Estimates of numbers of female polar bears in the Beaufort Sea derived from modified Lincoln-Petersen (Seber 1973) procedure. Numbers of marks available each year were estimated by applying the survival rate (determined from radio telemetry) to the estimated number of marks available during the previous year. Availability of marks also was corrected, in years 1967-1981, for the proportion of time marked animals were west of longitude 160° W in areas where they could not be captured.

Year	Number Caught	Number Previously Marked	Number Unmarked	Number Released	Estimated Marks Available	Estimated Population N	Confidence Limit on Pop. $\pm CL$	$\dfrac{CL}{N}$
1967	19	0	19	19	0		0	0.00
1968	58	2	56	58	17	191	300	1.57
1969	18	2	16	18	63	217	356	1.64
1970	39	4	35	39	69	299	403	1.35
1971	37	1	36	36	90	928	1890	2.04
1972	83	6	77	82	109	704	848	1.20
1973	14	4	10	14	161	258	313	1.21
1974	97	11	86	97	149	651	597	0.92
1975	55	10	45	55	204	555	516	0.93
1976	61	11	50	61	217	598	534	0.89
1977	7	1	6	7	232	495	910	1.84
1978	20	3	17	20	207	581	854	1.47
1979	25	1	24	25	195	1356	2757	2.03
1980	25	7	18	25	191	330	331	1.00
1981	26	3	23	26	181	655	985	1.50
1982	45	4	41	45	178	1039	1226	1.18
1983	65	9	56	63	190	923	670	0.73
1984	38	10	28	37	213	628	354	0.56
1985	118	28	90	112	208	799	248	0.31
1986	98	33	65	97	254	744	186	0.25
1987	62	23	39	62	277	730	215	0.29
1988	68	17	51	68	275	1058	395	0.37
1989	72	29	43	72	284	693	177	0.26
1990	0	0	0	0	284	285	0	0.00

Table 2. Estimates of size of the Beaufort Sea polar bear population derived from modified Lincoln-Petersen (Seber 1973) procedure. Numbers of marks available each year were estimated by applying the survival rate (determined from radio telemetry) to the estimated number of marks available during the previous year. Availability of marks also was corrected, in years 1967-1981, for the proportion of time marked animals were west of longitude 160° W in areas where they could not be captured.

Year	Number Caught	Number Previously Marked	Number Unmarked	Number Released	Estimated Marks Available	Estimated Population N	Confidence Limit on Pop. $\pm CL$	$\dfrac{CL}{N}$
1967	32	0	32	32	0		0	0.00
1968	84	3	81	84	28	334	487	1.46
1969	25	3	22	25	95	332	491	1.48
1970	62	6	56	62	102	492	582	1.18
1971	63	1	62	62	137	2355	4884	2.07
1972	131	9	122	128	172	1218	1262	1.04
1973	25	4	21	25	253	703	942	1.34
1974	174	19	155	174	239	1115	808	0.73
1975	113	19	94	112	343	1040	738	0.71
1976	115	27	88	115	379	835	480	0.58
1977	17	5	12	17	406	648	734	1.13
1978	46	8	38	46	364	1011	1049	1.04
1979	48	7	41	48	350	1140	1269	1.11
1980	40	9	31	40	340	742	707	0.95
1981	43	3	40	43	323	1891	2957	1.56
1982	101	18	83	101	315	1071	651	0.61
1983	99	11	88	97	347	2116	1452	0.69
1984	55	13	42	54	376	1253	649	0.52
1985	202	44	158	194	363	1527	392	0.26
1986	186	58	128	185	446	1417	277	0.20
1987	127	43	84	127	499	1453	329	0.23
1988	100	20	80	100	507	2443	890	0.36
1989	92	30	62	92	511	1534	421	0.27
1990	0	0	0	0	498	498	0	0.00

Table 3. Numbers of litters and cubs produced by female polar bears captured at all ages in the Beaufort Sea. Age specific cub production was calculated as: [a] $m_x = \left(C_x + (Y_{x+1})\left(\frac{1}{\hat{S}_i}\right)\right)\left(\frac{1}{F_x + F_{x+1}}\right)$ (To calculate age specific litter production rate, numbers of litters was substituted for yearlings and cubs.). Overall litter sizes are the mean of the products of #'s of litters and litter sizes at each age.

	Early Study Period: 1967-1974									Late Study Period: 1981-1992[b]								
Age	W/Out Young	#Cub Litters	Mean Cub Litter Size	#Yrl. Litters	Mean Yrl. Litter Size	#2Yr. Litters	Mean 2Yr. Litter Size	Age Specific Litters per female	Age Specific Cubs per female	W/Out Young	#Cub Litters	Mean Cub Litter Size	#Yrl. Litters	Mean Yrl. Litter Size	#2Yr. Litters	Mean 2Yr. Litter Size	Age Specific Litters per female	Age Specific Cubs per female
0	18	0	0.00	0	0.00	0	0.00	0.00	0.00	98	0	0.00	0	0.00	0	0.00	0.00	0.00
1	42	0	0.00	0	0.00	0	0.00	0.00	0.00	91	0	0.00	0	0.00	0	0.00	0.00	0.00
2	39	0	0.00	0	0.00	0	0.00	0.00	0.00	66	0	0.00	0	0.00	0	0.00	0.00	0.00
3	40	0	0.00	0	0.00	0	0.00	0.00	0.00	36	0	0.00	0	0.00	0	0.00	0.00	0.00
4	40	0	0.00	0	0.00	0	0.00	0.02	0.02	40	0	0.00	0	0.00	0	0.00	0.02	0.04
5	31	2	1.50	1	1.00	0	0.00	0.14	0.19	40	3	1.33	1	2.00	0	0.00	0.07	0.11
6	12	6	1.17	4	1.25	1	1.00	0.42	0.61	47	11	1.27	3	1.67	0	0.00	0.24	0.31
7	8	2	1.50	8	1.63	3	1.33	0.27	0.45	28	16	1.38	11	1.27	0	0.00	0.35	0.44
8	10	4	1.50	7	1.71	6	1.67	0.28	0.53	24	10	1.90	13	1.15	1	1.00	0.27	0.45
9	7	2	2.00	7	2.00	9	1.44	0.39	0.70	27	11	1.64	12	1.58	8	1.25	0.24	0.36
10	3	1	1.00	9	1.78	3	1.67	0.23	0.38	17	11	1.82	9	1.33	7	1.43	0.23	0.40
11	3	4	2.00	4	1.75	4	1.50	0.26	0.53	18	11	1.73	5	1.60	3	1.00	0.34	0.51
12	3	1	1.00	1	2.00	1	1.00	0.25	0.56	9	8	1.50	7	1.29	3	1.00	0.44	0.62
13	1	1	2.00	1	3.00	1	2.00	0.13	0.25	12	4	1.50	11	1.36	3	1.67	0.30	0.43
14	1	1	2.00	0	0.00	2	1.50	0.51	1.02	9	3	1.67	7	1.43	1	2.00	0.42	0.71
15	0	0	0.00	1	2.00	0	0.00	0.62	0.62	9	5	2.00	10	1.70	0	0.00	0.32	0.58
16	0	1	2.00	2	1.00	1	1.00	0.20	0.40	10	7	1.71	7	1.71	1	2.00	0.27	0.49
17	0	1	2.00	0	0.00	0	0.00	1.00	1.00	8	3	2.00	3	2.00	4	1.50	0.23	0.41
18	0	0	0.00	0	0.00	0	0.00	0.00	0.00	5	5	2.00	3	1.67	2	2.00	0.40	0.80
19	0	0	0.00	0	0.00			0.00		3	2	2.00	3	2.00	1	1.00	0.30	0.60
20	0	0	0.00	0	0.00			0.00		1	2	2.00	2	2.00	3	1.67	0.41	0.73
21	1	0	0.00	0	0.00			0.00		2	3	1.33	3	1.67	0	0.00	0.23	0.31
22										2	2	1.00	0	0.00	1	1.00	0.22	0.22
23										2	1	2.00	0	0.00	1	1.00	0.11	0.22
24										2	3	1.33	0	0.00	0	0.00	0.50	0.62
25										3	0	0.00	1	1.00	0	0.00	0.00	0.00
26										1	0	0.00	0	0.00	0	0.00	0.00	0.00
27										1	0	0.00	0	0.00	0	0.00	0.00	0.00
28										0								
29										0								
30										0								
	259	26	1.58	45	1.71	31	1.48	0.24[c]	0.40[c]	611	121	1.63	111	1.49	39	1.38	0.25[c]	0.38[c]

[a] C_x = # Cubs of females aged "x". Y_{x+1} = # Yearlings of females aged "$x+1$". $\hat{S}_i$ = 0.65 = estimated survival of young to age 1. F_x = # Females aged "x". F_{x+1} = # Females aged "$x+1$".

[b] Conventional capture and radio-telemetry data combined.

[c] Overall cub production (Sum of age specific numbers of cubs/Sum of Age specific numbers of females) did not differ between the 2 periods (Z = 0.11, P = 0.84). means shown here are for ages (4-17) in which reproduction was recorded during early period.

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Table 4. Litter sizes of polar bear young captured or observed in the Beaufort Sea during spring and fall seasons between 1967 and 1992.

1967-1974	Cub Litter Size[a]			Yearling Litter Size[b]			2-Year-Old Litter Size			
	1	2	3	1	2	3	1	2	3	Totals
Spring	11	15	0	17	32	2	18	16	0	111
Fall										0
Sub-Total	11	15	0	17	32	2	18	16	0	111
1981-1992										0
Spring	22	55	2	48	45	1	30	20	0	223
Fall	36	37	0	25	27	0	1	0	0	126
Sub-total	58	92	2	73	72	1	31	20	0	349
Total	69	107	2	90	104	3	49	36	0	460

[a]Litters of more than one cub were more frequent in spring than in fall (χ^2 =7.41, df = 1, P = 0.007), during the late period of study. Other differences in litter size between spring and fall were not significant.

[b]Litters of more than one yearling were marginally more frequent in the early period of study than in the late period (χ^2 =3.48, df = 1, P = 0.06).

Table 5. Sexes of polar bear young captured in the Beaufort Sea, 1967-1974 and 1981-1992. Sex ratios of dependent young did not differ from even (χ^2 =3.03, df = 5, $\underline{P}$ = 0.70).

Offspring Age	1967-1974			1981-1992		
	0	1	2	0	1	2
No. Males	14	45	32	63	71	33
No. Females	18	42	39	74	73	52
Males/Female	0.78	1.07	0.82	0.85	0.97	0.63

Table 6. Composite life table[a] constructed from the sample of male polar bears captured in the Beaufort Sea,1967-1974.

X	$N_x{}^b$	$N_x{}'$	l_x	d_x	q_x	p_x	L_x	T_x	$\bar{q}$	$\hat{S}$	$\hat{S}-$	$\hat{S}+$	e_x	c_x
0	69	57	1.00	0.15	0.15	0.85	0.93	4.30	0.21	0.79	0.74	0.84	4.30	0.21
1	45	49	0.85	0.15	0.18	0.82	0.78	3.37	0.22	0.78	0.72	0.83	3.95	0.18
2	32	40	0.70	0.14	0.21	0.79	0.63	2.59	0.24	0.76	0.70	0.83	3.70	0.15
3	25	32	0.56	0.13	0.23	0.77	0.49	1.96	0.25	0.75	0.68	0.83	3.53	0.12
4	28	25	0.43	0.11	0.25	0.75	0.38	1.47	0.25	0.75	0.66	0.83	3.44	0.09
5	24	19	0.32	0.08	0.26	0.74	0.28	1.10	0.26	0.74	0.65	0.84	3.40	0.07
6	16	14	0.24	0.06	0.27	0.73	0.21	0.82	0.25	0.75	0.63	0.86	3.42	0.05
7	12	10	0.17	0.05	0.27	0.73	0.15	0.61	0.25	0.75	0.61	0.89	3.50	0.04
8	6	7	0.13	0.03	0.28	0.72	0.11	0.46	0.24	0.76	0.59	0.92	3.64	0.03
9	4	5	0.09	0.02	0.27	0.73	0.08	0.35	0.23	0.77	0.58	0.95	3.84	0.02
10	6	4	0.07	0.02	0.27	0.73	0.06	0.27	0.22	0.78	0.58	0.98	4.09	0.01
11	1	3	0.05	0.01	0.26	0.74	0.04	0.21	0.20	0.80	0.55	1.05	4.39	0.01
12	4	2	0.04	0.01	0.24	0.76	0.03	0.17	0.19	0.81	0.55	1.07	4.73	0.01
13	2	2	0.03	0.01	0.22	0.78	0.02	0.14	0.18	0.82	0.48	1.16	5.06	0.01
14	1	1	0.02	0.00	0.20	0.80	0.02	0.12	0.17	0.83	0.40	1.26	5.35	0.00
15	1	1	0.02	0.00	-0.01	1.01	0.02	0.10	0.17	0.83	0.32	1.35	5.54	0.00
16	0	1	0.02	0.00	0.00	1.00	0.02	0.08	0.20	0.80	0.02	1.58	4.50	0.00
17	1	1	0.02	0.00	0.00	1.00	0.02	0.06	0.25	0.75	-0.10	1.60	3.50	0.00
18	0	1	0.02	0.00	0.00	1.00	0.02	0.04	0.33	0.67			2.50	0.00
19	0	1	0.02	0.00	0.00	1.00	0.02	0.03	0.50	0.50			1.50	0.00
20	0	1	0.02	0.02	1.00	0.00	0.01	0.01	1.00	0.00			0.50	0.00

[a] X = age class, N_x = no. each age, $N_x{}'$ = N_x smoothed according to Caughley (1966), l_x = survival to age X, d_x = mortality age X, q_x = mortality rate at X, p_x = $1-q_x$, L_x = average alive in interval X, T_x = number of time intervals lived for animals aged X (Seber 1973:415), $\bar{q}$ = Caughley's (1967) population mortality, $\hat{S}$ = $1-\bar{q}$ = Heincke survival rate (Seber 1973:415), $\hat{S}-$ = lower limit 0.95 CI, $\hat{S}+$ = upper limit 0.95 CI, e_x = age specific life expectancy (Caughley 1966, 1967), c_x = proportion alive at X (Eberhardt 1988).

[b] N_0 calculated by dividing N_1 by the survival rate estimated, for ages 0-1 (0.65), from radio telemetry.

Table 7. Composite life table[a] constructed from the sample of male polar bears captured in the Beaufort Sea,1981-1992.

X	N_x^b	N_x'	l_x	d_x	q_x	p_x	L_x	T_x	$\bar{q}$	$\hat{S}$	$\hat{S}-$	$\hat{S}+$	e_x	c_x
0	109	99	1.00	0.31	0.31	0.69	0.84	4.10	0.22	0.78	0.74	0.82	4.09	0.28
1	71	68	0.69	0.19	0.28	0.72	0.59	3.26	0.19	0.81	0.77	0.85	4.71	0.19
2	33	49	0.50	0.12	0.25	0.75	0.44	2.67	0.17	0.83	0.79	0.87	5.33	0.14
3	37	37	0.37	0.08	0.22	0.78	0.33	2.23	0.16	0.84	0.80	0.89	5.91	0.10
4	43	29	0.29	0.06	0.19	0.81	0.27	1.90	0.14	0.86	0.81	0.90	6.41	0.08
5	29	24	0.24	0.04	0.16	0.84	0.22	1.63	0.14	0.86	0.81	0.91	6.78	0.07
6	11	20	0.20	0.03	0.14	0.86	0.19	1.41	0.13	0.87	0.81	0.92	7.01	0.06
7	16	17	0.17	0.02	0.12	0.88	0.16	1.23	0.13	0.87	0.81	0.92	7.09	0.05
8	21	15	0.15	0.02	0.11	0.89	0.14	1.07	0.13	0.87	0.81	0.93	7.02	0.04
9	13	13	0.13	0.01	0.10	0.90	0.13	0.92	0.14	0.86	0.80	0.93	6.81	0.04
10	11	12	0.12	0.01	0.09	0.91	0.12	0.80	0.14	0.86	0.78	0.93	6.48	0.03
11	15	11	0.11	0.01	0.08	0.92	0.11	0.68	0.15	0.85	0.77	0.93	6.06	0.03
12	7	10	0.10	0.01	0.08	0.92	0.10	0.58	0.16	0.84	0.74	0.93	5.57	0.03
13	11	9	0.09	0.01	0.09	0.91	0.09	0.48	0.18	0.82	0.72	0.92	5.03	0.03
14	7	8	0.08	0.01	0.10	0.90	0.08	0.39	0.20	0.80	0.68	0.92	4.46	0.02
15	6	8	0.08	0.01	0.11	0.89	0.07	0.31	0.23	0.77	0.64	0.91	3.88	0.02
16	9	7	0.07	0.01	0.12	0.88	0.06	0.24	0.26	0.74	0.58	0.89	3.28	0.02
17	10	6	0.06	0.01	0.14	0.86	0.06	0.17	0.32	0.68	0.49	0.88	2.67	0.02
18	2	5	0.05	0.01	0.16	0.84	0.05	0.12	0.40	0.60	0.33	0.88	2.02	0.01
19	4	4	0.04	0.01	0.19	0.81	0.04	0.07	0.55	0.45	0.14	0.76	1.31	0.01
20	6	3	0.04	0.01	0.21	0.79	0.03	0.03	1.00	0.00	0.00	0.00	0.50	0.01

[a] X = age class, N_x = no. each age, N_x' = N_x smoothed according to Caughley (1966), l_x = survival to age X, d_x = mortality age X, q_x = mortality rate at X, p_x = $1-q_x$, L_x = average alive in interval X, T_x = number of time intervals lived for animals aged X (Seber 1973:415), $\bar{q}$ = Caughley's (1967) population mortality, $\hat{S}$ = $1-\bar{q}$ = Heincke survival rate (Seber 1973:415), $\hat{S}-$ = lower limit 0.95 CI, $\hat{S}+$ = upper limit 0.95 CI, e_x = age specific life expectancy (Caughley 1966, 1967), c_x = proportion alive at X (Eberhardt 1988).

[b] N_0 calculated by dividing N_1 by the survival rate estimated, for ages 0-1 (0.65), from radio telemetry.

Table 8. Composite life table[a] constructed from the sample of female polar bears captured in the Beaufort Sea,1967-1974.

X	N_x^b	N_x'	l_x	d_x	q_x	p_x	L_x	T_x	$\bar{q}$	$\hat{S}$	$\hat{S}-$	$\hat{S}+$	e_x	c_x
0	65	50	1.00	0.03	0.03	0.97	0.99	7.55	0.12	0.88	0.84	0.91	7.55	0.12
1	42	49	0.97	0.05	0.05	0.95	0.95	6.57	0.14	0.86	0.83	0.90	6.74	0.12
2	39	46	0.93	0.07	0.07	0.93	0.89	5.62	0.15	0.85	0.81	0.89	6.06	0.12
3	40	43	0.86	0.08	0.09	0.91	0.82	4.72	0.17	0.83	0.79	0.88	5.49	0.11
4	40	39	0.78	0.09	0.11	0.89	0.73	3.90	0.18	0.82	0.77	0.87	5.01	0.10
5	34	34	0.69	0.09	0.14	0.86	0.64	3.17	0.20	0.80	0.75	0.86	4.59	0.09
6	23	30	0.60	0.09	0.16	0.84	0.55	2.52	0.21	0.79	0.72	0.85	4.23	0.07
7	21	25	0.50	0.09	0.18	0.82	0.46	1.97	0.23	0.77	0.70	0.85	3.92	0.06
8	27	21	0.41	0.08	0.20	0.80	0.37	1.52	0.24	0.76	0.68	0.84	3.66	0.05
9	25	17	0.33	0.07	0.21	0.79	0.30	1.14	0.25	0.75	0.65	0.84	3.42	0.04
10	16	13	0.26	0.06	0.23	0.77	0.23	0.84	0.27	0.73	0.61	0.85	3.22	0.03
11	15	10	0.20	0.05	0.25	0.75	0.18	0.61	0.28	0.72	0.57	0.87	3.05	0.02
12	6	8	0.15	0.04	0.27	0.73	0.13	0.44	0.29	0.71	0.51	0.91	2.90	0.02
13	4	5	0.11	0.03	0.29	0.71	0.09	0.31	0.30	0.70	0.45	0.94	2.79	0.01
14	4	4	0.08	0.02	0.30	0.70	0.07	0.21	0.31	0.69	0.40	0.97	2.70	0.01
15	1	3	0.05	0.02	0.32	0.68	0.05	0.15	0.32	0.68	0.31	1.06	2.66	0.01
16	4	2	0.04	0.01	0.34	0.66	0.03	0.10	0.32	0.68	0.28	1.09	2.67	0.00
17	1	1	0.02	0.01	0.35	0.65	0.02	0.07	0.31	0.69	-0.21	1.60	2.77	0.00
18	0	1	0.02	0.00	-0.25	1.25	0.02	0.05	0.29	0.71			3.00	0.00
19	0	1	0.02	0.00	0.00	1.00	0.02	0.03	0.50	0.50			1.50	0.00
20	0	1	0.02	0.02	1.00	0.00	0.01	0.01	1.00	0.00			0.50	0.00

[a] $X=$ age class, $N_x=$ no. each age, $N_x' = N_x$ smoothed according to Caughley (1966), $l_x =$ survival to age X, $d_x =$ mortality age X, $q_x =$ mortality rate at X, $p_x = 1-q_x$, $L_x =$ average alive in interval X, $T_x =$ number of time intervals lived for animals aged X (Seber 1973:415), $\bar{q} =$ Caughley's (1967) population mortality, $\hat{S} = 1-\bar{q} =$ Heincke survival rate (Seber 1973:415), $\hat{S} - =$ lower limit 0.95 CI, $\hat{S} + =$ upper limit 0.95 CI, $e_x =$ age specific life expectancy (Caughley 1966, 1967), $c_x =$ proportion alive at X (Eberhardt 1988).

[b] N_0 calculated by dividing N_1 by the survival rate estimated, for ages 0-1 (0.65), from radio telemetry.

Table 9. Composite life table[a] constructed from the sample of female polar bears captured in the Beaufort Sea, 1981-1992.

X	N_x^b	N_x'	l_x	d_x	q_x	p_x	L_x	T_x	$\bar{q}$	$\hat{S}$	$\hat{S}-$	$\hat{S}+$	e_x	c_x
0	112	95	1.00	0.24	0.24	0.76	0.88	6.44	0.14	0.86	0.83	0.88	6.43	0.14
1	73	72	0.76	0.15	0.20	0.80	0.69	5.56	0.13	0.87	0.84	0.90	7.25	0.11
2	52	58	0.61	0.10	0.16	0.84	0.56	4.87	0.12	0.88	0.85	0.91	7.93	0.09
3	35	48	0.51	0.07	0.13	0.87	0.48	4.31	0.11	0.89	0.86	0.92	8.39	0.07
4	37	42	0.44	0.05	0.11	0.89	0.42	3.83	0.11	0.89	0.86	0.92	8.61	0.06
5	34	37	0.40	0.03	0.09	0.91	0.38	3.41	0.11	0.89	0.86	0.92	8.59	0.06
6	50	34	0.36	0.03	0.07	0.93	0.35	3.03	0.11	0.89	0.85	0.92	8.35	0.05
7	37	32	0.34	0.02	0.06	0.94	0.33	2.68	0.12	0.88	0.84	0.92	7.94	0.05
8	33	30	0.32	0.02	0.05	0.95	0.31	2.36	0.13	0.87	0.83	0.92	7.40	0.05
9	38	28	0.30	0.02	0.05	0.95	0.29	2.05	0.14	0.86	0.82	0.91	6.79	0.04
10	27	27	0.28	0.02	0.06	0.94	0.28	1.76	0.15	0.85	0.80	0.90	6.13	0.04
11	23	25	0.27	0.02	0.07	0.93	0.26	1.48	0.17	0.83	0.77	0.89	5.48	0.04
12	17	24	0.25	0.02	0.08	0.92	0.24	1.22	0.19	0.81	0.74	0.88	4.84	0.04
13	22	22	0.23	0.02	0.11	0.89	0.22	0.98	0.21	0.79	0.71	0.87	4.25	0.03
14	13	19	0.20	0.03	0.13	0.87	0.19	0.77	0.24	0.76	0.67	0.86	3.69	0.03
15	18	17	0.18	0.03	0.16	0.84	0.16	0.58	0.27	0.73	0.62	0.83	3.17	0.03
16	18	14	0.15	0.03	0.19	0.81	0.13	0.41	0.31	0.69	0.55	0.82	2.68	0.02
17	10	11	0.12	0.03	0.23	0.77	0.11	0.28	0.37	0.63	0.46	0.80	2.21	0.02
18	9	9	0.09	0.02	0.27	0.73	0.08	0.17	0.45	0.55	0.33	0.77	1.73	0.01
19	7	6	0.07	0.02	0.31	0.69	0.06	0.09	0.59	0.41	0.12	0.70	1.19	0.01
20	4	4	0.05	0.02	0.36	0.64	0.04	0.04	1.00	0.00	0.00	0.00	0.50	0.01

[a] X = age class, N_x = no. each age, N_x' = N_x smoothed according to Caughley (1966), l_x = survival to age X, d_x = mortality age X, q_x = mortality rate at X, p_x = 1-q_x, L_x = average alive in interval X, T_x = number of time intervals lived for animals aged X (Seber 1973:415), $\bar{q}$ = Caughley's (1967) population mortality, $\hat{S}$ = 1-$\bar{q}$ = Heincke survival rate (Seber 1973:415), $\hat{S}-$ = lower limit 0.95 CI, $\hat{S}+$ = upper limit 0.95 CI, e_x = age specific life expectancy (Caughley 1966, 1967), c_x = proportion alive at X (Eberhardt 1988).

[b] N_0 calculated by dividing N_1 by the survival rate estimated, for ages 0-1 (0.65), from radio telemetry.

Table 10. Relationships in the capture samples, between population size of polar bears in the Beaufort Sea, proportion of young in the population, and axial girth of females in various reproductive stages.

Dependent Variable [a]	Independent Variable [a]	Coefficient Value [b]	Mean Square		r^2 [b]	$\underline{p}$ [c]
2-year-olds/Adult	Intercept	0.681	Model	0.0867		
	Population Size	-0.0007	Error	0.010	0.56	0.021
3-year-olds/Adult	Intercept	.485	model	0.038		
	Population size	-0.0005	Error	0.007	0.42	0.059
2+3-year-olds/Adult	Intercept	1.17	Model	5.23		
	Population Size	-0.001	Error	0.161	0.55	0.023
Axial Girth for Females with Cubs	Intercept	142.76	Model	228.9		
	Population Size	-0.040	Error	10.7	0.75	0.002[d]
Axial Girth for Single Females	Intercept	136.75	Model	121.8		
	Population Size	-0.037	Error	5.9	0.75	0.003[d]
Axial Girth for Females with Yearlings	Intercept	142.03	Model	182.9		
	Population Size	-0.033	Error	27.8	0.48	0.037

[a] To minimize "noise" introduced by annually variable capture samples, we averaged observations for 3 year periods.
[b] Simple coefficients of determination are shown.
[c] Significance level of individual $\underline{F}$ tests. Addition of other independent variables resulted in significant partial $\underline{F}$ tests, so only simple regression models were used.
[d] These tests significant at "table-wide" probability levels of 0.05 (Rice 1989).
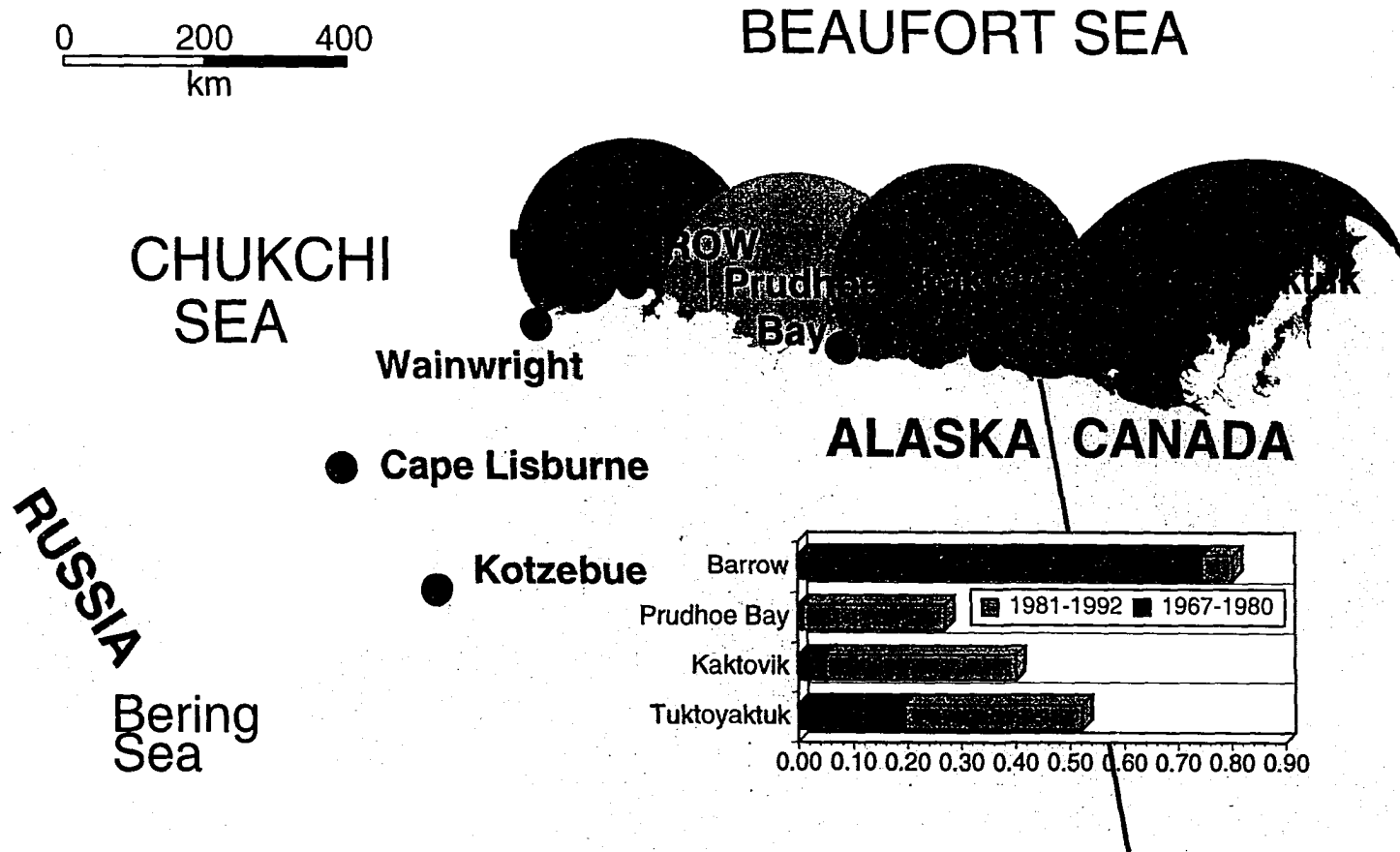
Figure 1. Logistical bases, sampling areas, and relative effort for polar bear capture and marking, 1967-1992. Shaded areas show approximate aerial distribution of sampling near each base. Histogram shows relative marking effort near each base before and after 1981. The Canada-Alaska border lies along 141° W longitude and Pt. Barrow lies at ca. 157° W. Other place names used in text also are shown.
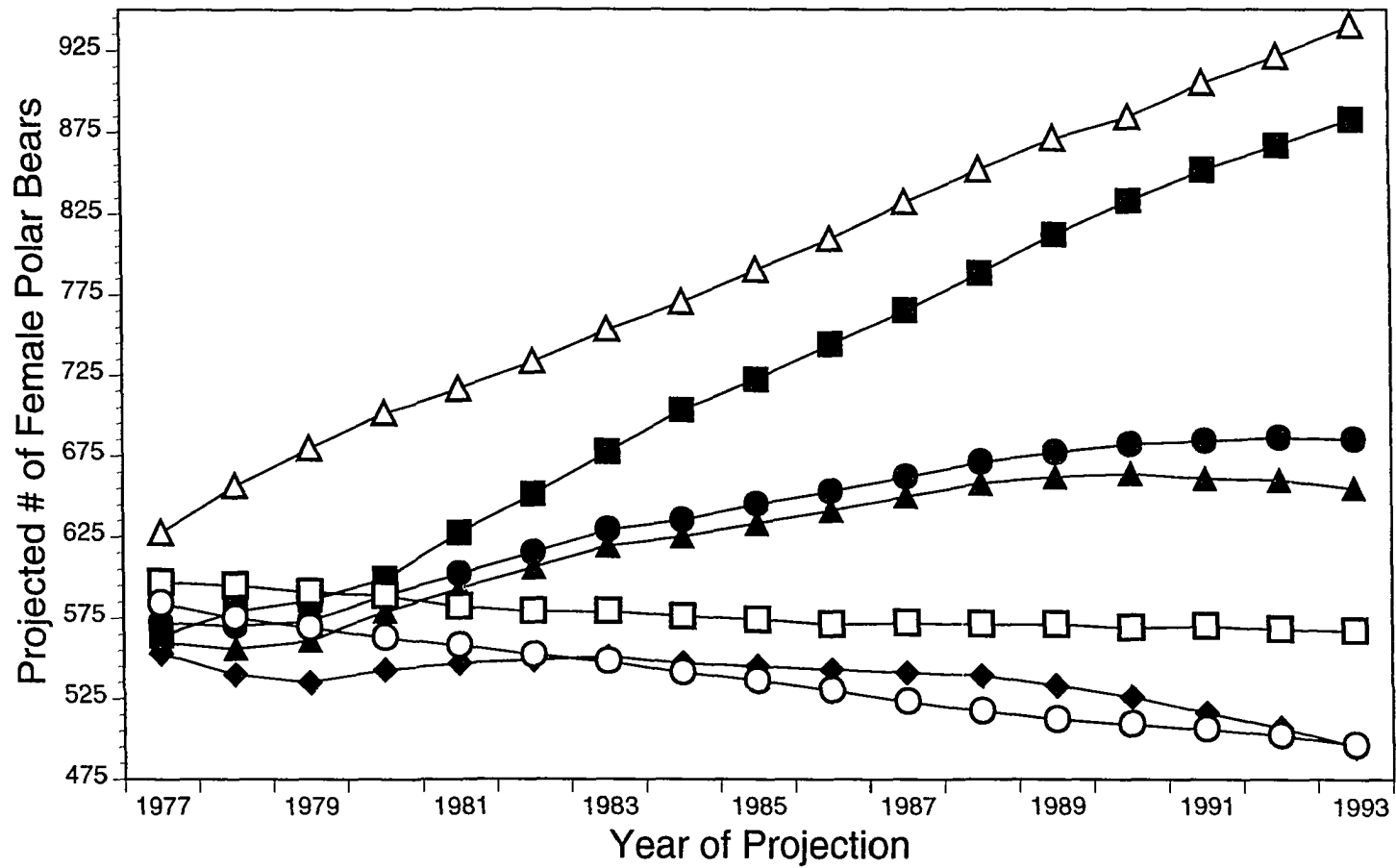
Figure 2. Leslie matrix population projections for female polar bears. Solid shapes indicate age structure and productivity values from the Beaufort Sea (BS). Survival rates for the BS were estimated with radio-telemetry for ages 0,1 and 4-30; rates for ages 2,3 were assumed to be equivalent to those for ages 0,1. Hollow shapes indicate survival and productivity values and age structure derived in Hudson Bay (HB, Derocher 1991). Starting population size in each projection was 598 females. ■=point survival estimates, ●=lower 95% interval survival estimate for adults, ▲=lower 95% interval estimate for young, ◆=lower 95% interval estimate for all ages, □=early 1980's HB productivity estimates, O=late 1980's HB productivity estimates, △=early 1980's productivity estimates plus BS point estimates of survival.
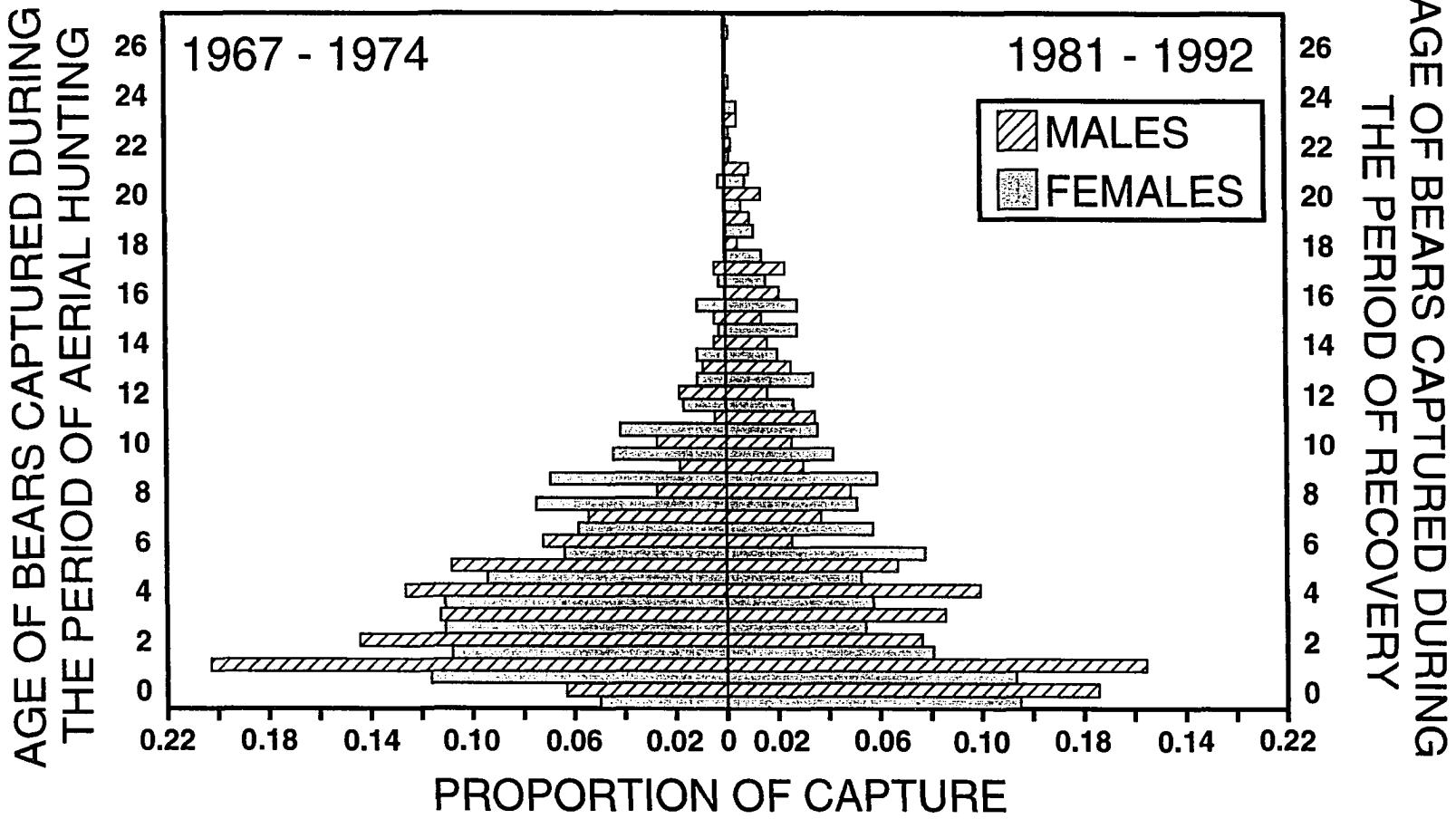
Figure 3. Proportions of polar bears in each age group captured in the Beaufort Sea during the period affected by aerial hunting (1967—1974) and in the period of recovery from that hunting (1981—1992). Note the weaker representation of post-weaning animals and the stronger representation of old animals in the 1981-1992 period. Note that the weak representation of zero age animals in the early study period resulted because sampling was done in early spring before many cubs emerged from dens.
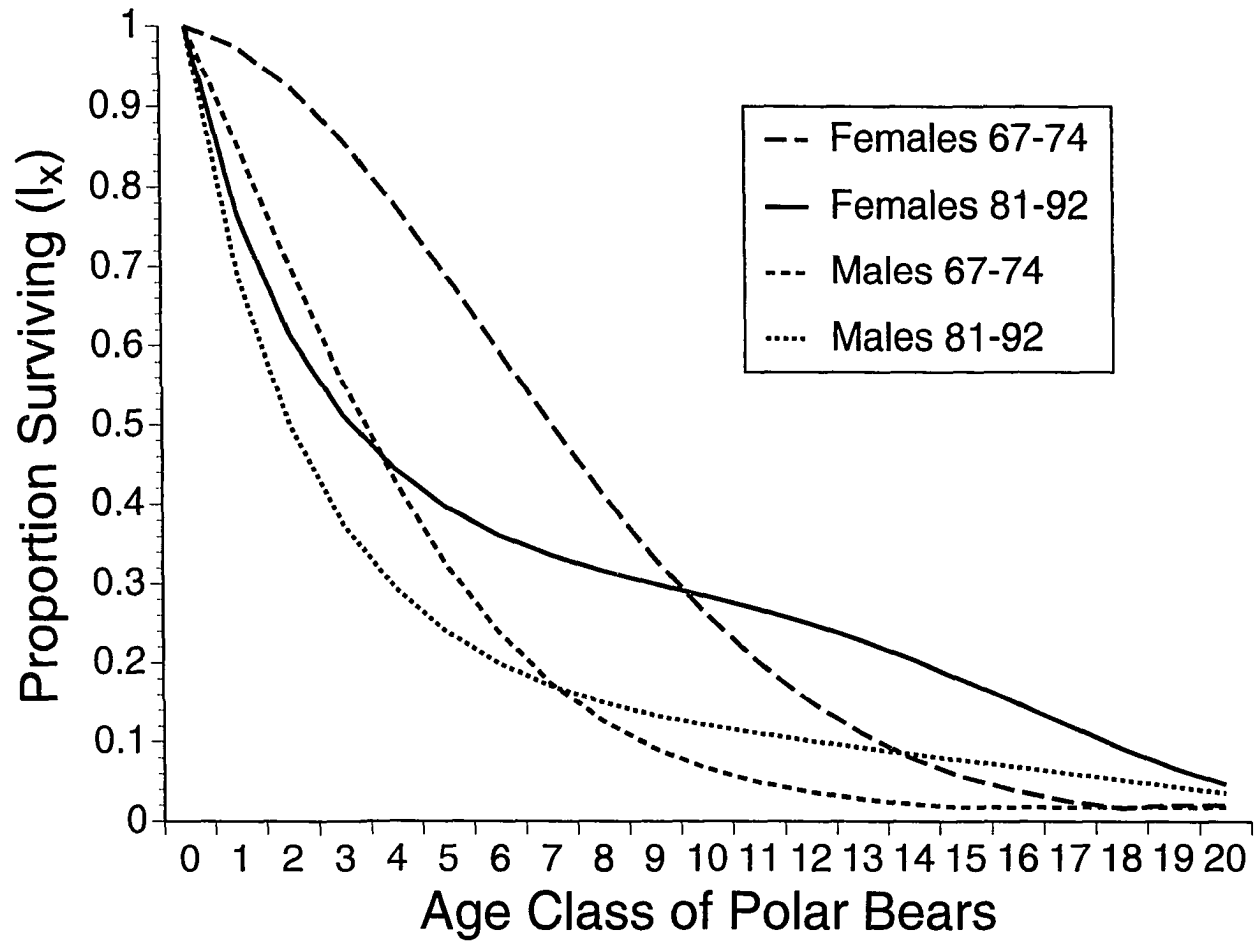
Figure 4. Smoothed (Caughley 1977) l_x curves for polar bears in the Beaufort Sea during 1967-1974 and 1981-1992 study periods. Note that survival early in life was poorer and survival later in life greater during the 1981-1992 study period.
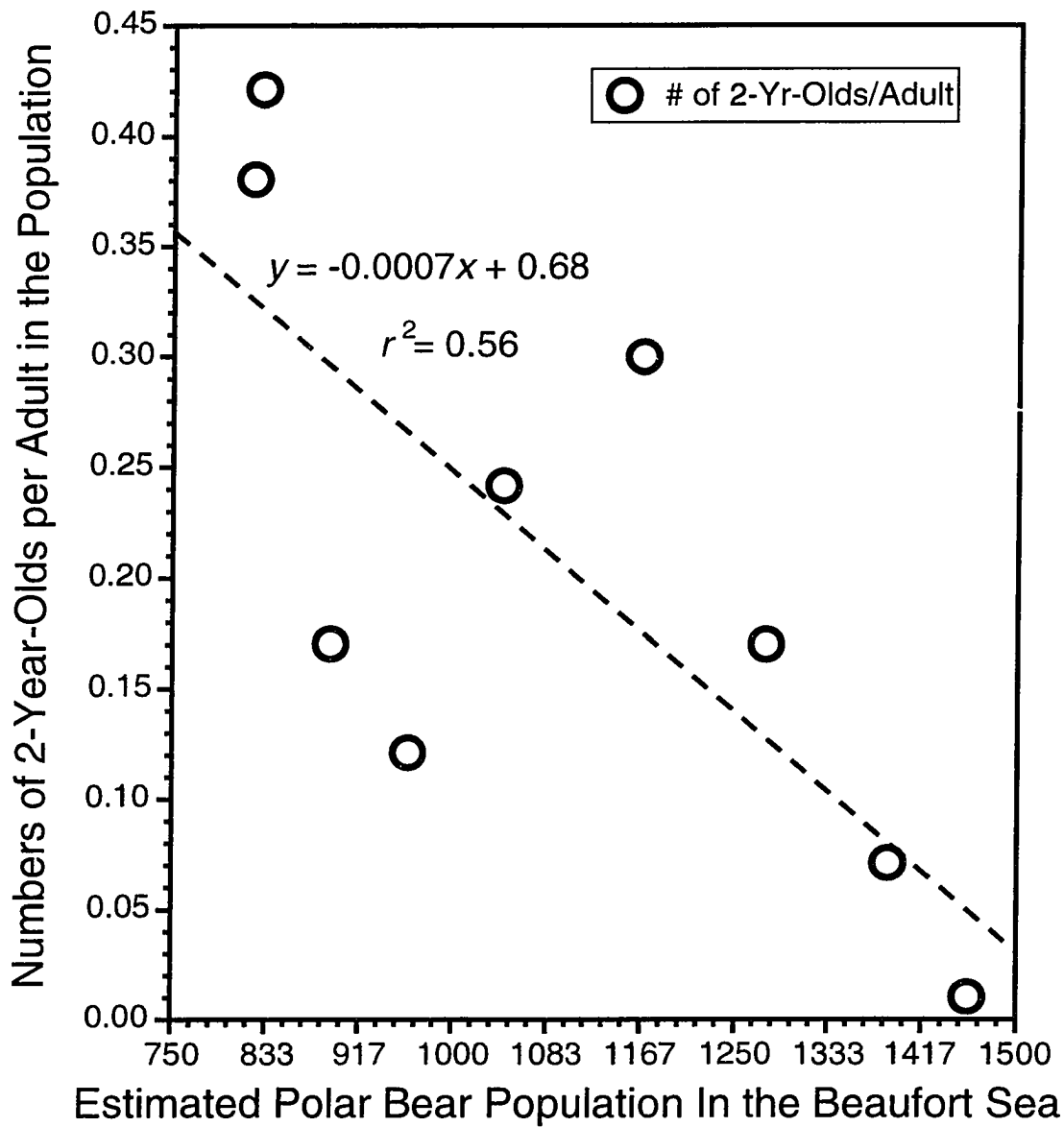
Figure 5. Relationship between estimated size of the Beaufort Sea polar bear population and numbers of 2-year-old young per adult in the population, 1967-1992. Adults were defined as animals aged ≥ 6 years. The fitted line was significantly different from "0" ($\underline{P}$ = 0.02). An $\underline{r}^2$ of 0.56 means that 56% of variation in the proportion of 2-year-olds was explained by population size alone.
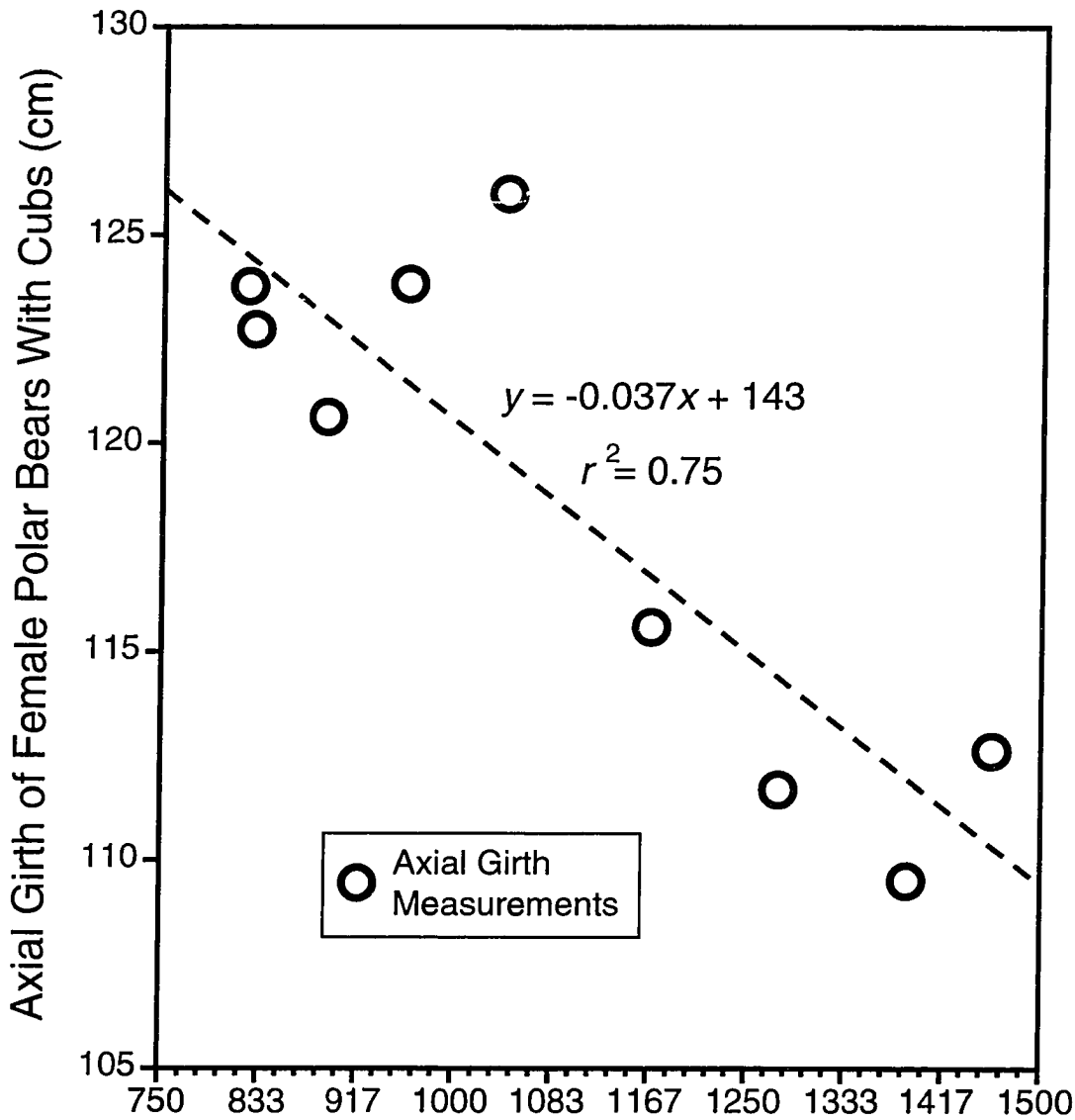
Figure 6. Relationship between estimated size of the Beaufort Sea polar bear population and axial girth of female polar bears accompanied by cubs of the year, 1967-1992. The fitted line was significantly different from "0" ($\underline{P}$ = 0.002). An $\underline{r}^2$ of 0.75 means that 75% of the variation in axial girth was explained by population size alone.

CHAPTER V

POLAR BEAR MATERNITY DENNING IN THE BEAUFORT SEA[1]

S. C. Amstrup and C. Gardner

POLAR BEAR MATERNITY DENNING IN THE BEAUFORT SEA

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Abstract: The distribution of polar bears (Ursus maritimus) is circumpolar in the Northern Hemisphere, but known locations of maternal dens are concentrated in relatively few, widely scattered locations. Denning is either uncommon or unknown within gaps between known denning concentration areas. The Beaufort Sea region of Alaska and Canada lies in the largest of those gaps. To understand effects of industrial development and proposed increases in hunting, the temporal and spatial distribution of denning in the Beaufort Sea must be known. We captured and radiocollared polar bears between 1981 and 1991 and determined that denning in the Beaufort Sea region was sufficient to account for the estimated population there. Of 90 dens, 48 were on drifting pack ice, 38 on land, and 4 on land-fast ice. The proportion of dens on land was higher (P = 0.029) in the last half of the study. Bears denning on pack ice drifted as far as 997 km ($\bar{x}$ = 385 km) while in dens. There was no difference in cub production by bears denning on land and pack ice (P = 0.66). Mean entry and exit dates were 11 November and 5 April for land dens and 22 November and 26 March for pack-ice dens. Female polar bears captured in the Beaufort Sea appeared to be isolated from those caught east of Cape Bathurst in Canada. Of 35 polar bears that denned along the mainland coast of Alaska and Canada 80% denned between 137°00'W

and 146°59'W. Bears followed to >1 den did not reuse sites and consecutive dens were 20-1,304 km apart. However, radio-collared bears were largely faithful to substrate (pack-ice, land, land-fast ice) and the general geographic area of previous dens. Bears denning on land may be vulnerable to human activities such as hunting and industrial development. However, predictable denning chronology and lack of site fidelity indicate that many potential impacts on denning polar bears could be mitigated.

Polar bears inhabit most ice-covered seas of the Northern Hemisphere (Amstrup and DeMaster 1988). Their distribution is circumpolar, and they normally occur in low densities (1 bear/141-269 km^2) (DeMaster and Stirling 1981, Amstrup et al. 1986, Amstrup and DeMaster 1988). Known locations of maternal birth dens are concentrated in a few, widely scattered locations (Harington 1968, Ramsay and Andriashek 1986). Among the best known denning concentration areas are the Svalbard Archipelago, north of Norway (Larsen 1985); Franz Josef Land, Novaya Zemlya, and Wrangel Island, in Russia (Uspenski and Chernyavski 1965, Uspenski and Kistchinski 1972); and the west coast of Hudson Bay in Canada (Ramsay and Stirling 1990).

Denning is either uncommon or has been overlooked in gaps between known denning concentration areas. The Beaufort Sea region of northern Alaska and Canada lies in the largest of those gaps (Harington 1968:Fig. 2).

As many as 2,000 polar bears occur in the Beaufort Sea throughout the year, and ≥140 females should seek dens there each fall (Amstrup et al. 1986). Yet, 11 years of study, plus analysis of historic sightings dating from 1910, revealed only 35 dens (U.S. Fish and Wildlife Service, unpubl. data). Lentfer and Hensel (1980) suggested that suitable denning habitat along Alaska's north coast was limited. Polar bears are hunted by local native people in Canada and Alaska, and Canadian hunters believed that the harvest in Alaska was being sustained by production of polar bears in Canada (Stirling and Andriashek 1992). Recently, hunting along the nearby Russian coast, where it was banned in 1956 (Uspenski and Belikov 1991), has been proposed. Therefore, the sources of the bears frequenting the Beaufort Sea is an international management concern.

Known denning areas at the start of this project were on land. Lentfer (1975a) and Lentfer and Hensel (1980) reported 2 dens and observations of cubs and cub footprints on the pack ice north of Alaska. Larsen et al. (1983) also observed footprints of females with cubs on the pack ice far from land. However, the possibility that polar bears might commonly den on pack ice had not been proposed as an explanation for the dearth of dens between known land-denning areas. In addition, fidelity to denning areas, presumably an indication of limited availability of necessary habitats, has been assumed (Ramsay and Andriashek 1986) but not verified.

Polar bears in dens cannot be legally hunted in Canada, and hunting of bears in dens is discouraged in Alaska. Also, hunting seasons in Canada usually begin after female bears are thought to enter dens (Treseder and

Carpenter 1989). Industrial activities are a potential threat to polar bears, especially as they might affect bears in dens (Stirling 1990, Stirling and Andriashek 1992). Temporal as well as spatial management of hunting and industrial activities may be critical to coexistence of polar bears and humans. Yet, knowledge of den entry and emergence and the duration of denning is limited (Lønø 1970, Lentfer and Hensel 1980, Kolenosky and Prevett 1983, Larsen 1985, Messier et al. 1992).

Our objectives were to determine the (1) origin of polar bears occurring in the Beaufort Sea, (2) frequency of denning on pack ice relative to land, (3) relative production of females using land and pack-ice dens, (4) polar bear geographic preferences for and fidelity to den sites, and (5) denning chronology.

This manuscript was prepared in partial fulfillment of the requirements of S. C. Amstrup for a Ph.D. from the Department of Biology and Wildlife, University of Alaska Fairbanks. Amstrup directed and performed all aspects of the research including collection and analysis of data. Gardner worked as field and office assistant to Amstrup, and aided with collection of data and some of the initial analyses. Principal funding was provided by the U.S. Fish and Wildlife Service. The Minerals Management Service, U.S. Department of Interior; the National Oceanic and Atmospheric Administration, U.S. Department of Commerce; AMOCO Inc.; ARCO Alaska, Inc.; BP Exploration Alaska, Inc.; Dome Petroleum Ltd.; Beaudrill/Gulf Canada Ltd.; and the Northern Oil and Gas Assessment Program of Canada (through cooperation with the Departments of Renewable Resources of the Northwest Territories

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METHODS

Field Procedures

We captured polar bears by injecting immobilizing drugs (phencyclidine hydrocholoride [Sernylan®, Park, Davis and Co.], etorphine hydrochloride [M-99®, Lemmon Co.], and tiletamine hydrochloride plus zolazepam hydrochloride [Telazol®, Warner-Lambert Co.]) with projectile syringes fired from helicopters (Larsen 1971, Schweinsburg et al. 1982). Capture protocols were approved by an independent animal care and welfare committee. Up to 47 ($\bar{\underline{x}}$ = 30) female polar bears were captured and radiocollared annually during spring (Mar-May) or autumn (Oct-Nov) from 1981-91. We captured bears throughout the Beaufort Sea, which extends from Point Barrow, Alaska, at approximately 157°W, to Cape Bathurst, Northwest Territories, Canada, at approximately 127°W, and in bordering areas to the east and west. Canadian cooperators captured and radiocollared bears (for us to radiotrack) in the Canadian Beaufort Sea and Amundsen Gulf east of Cape Bathurst. Analyses were concentrated on bears that were captured and denned within the

Beaufort Sea and adjacent land areas.

We attached very high frequency (VHF) radio collars to polar bears between 1981 and 1985 and relocated them with aircraft (Fig. 1). After autumn 1985, we mostly deployed ultra high frequency platform transmitter terminals (PTTs) that were relocated by satellite. Sensors on PTTs recorded the animal's location, temperature of the collar, and 2 indices of activity (Fancy et al. 1988). A short-term activity counter recorded the number of seconds of movement during the minute prior to transmission. A long-term activity counter recorded the proportion of time the bear was moving in the 72 hours prior to transmission. Collars carrying PTTs also carried VHF beacons that we located with aircraft.

We located dens of radio-collared polar bears with satellite position fixes, aircraft radio tracking, and visual sightings. Den locations were placed in 3 substrate categories: land, either offshore islands or the mainland coast of Alaska and Canada; land-fast ice, sea ice that was frozen to the ocean bottom or attached to ice that was frozen to the bottom, and generally did not move (Parkinson et al. 1987); and drifting pack ice, which was in constant motion. In analyses, dens on land-fast ice were included with land dens. Den locations on land were plotted on 1:63,360 topographic maps. We used Loran-C, or very low frequency positioning devices to plot dens found with aircraft on pack ice. Locations recorded for pack-ice dens were those observed at the time of den entry. Dates of den occupation were determined by low-level aerial telemetry and visual observation or by changes in temperature and activity sensors on the PTTs. When a bear entered her den, transmitter temperature

increased and remained above 0 C (10-40 C warmer than ambient) and both activity counts declined. When a bear left her den, location changed, transmitter temperature decreased, and activity increased. Whenever possible, den locations of bears fitted with PTTs were also verified by aerial telemetry. Unless otherwise stated, we reported results only for dens that were confirmed by consistent PTT temperature and activity output, repeated radio tracking and visual observations, or both. Unconfirmed locations were classified as suspected dens.

We located dens of bears without radio collars (incidental dens) by searching coastal areas, with light aircraft, for openings in the snow. Searches consisted of opportunistic flights related to capture activities during spring and autumn 1981-91. We also flew aerial transect den surveys between Herschel Island, Yukon Territory (69°30'N, 139°30'W) and the Colville River delta (70°30'N, 150°30'W), in spring 1988, 1989, and 1990. A pilot and 1 observer conducted the survey in 1989, and a pilot and 2 observers did the 1988 and 1990 surveys. We flew at altitudes of 50-150 m and speeds of 110-150 km/h. We scheduled surveys according to previously observed peak periods of emergence from dens. Surveys were divided into areas of high and low probability of encounter based upon the 1965-88 distribution of maternal dens and the availability of habitats with snow-catching topography. We flew a transect along the beach and a series of transects parallel to the beach extending 20 km inland. Transects were separated by 0.8 km in high- and 1.6 km in low-probability areas. The mainland coastal bluffs, river channels, and barrier islands were surveyed by flying parallel to the relief features and

deviating to search connecting features. We also recorded dens observed by local residents and other scientists.

We determined whether a denning attempt was successful (emergence of ≥1 cub) by locating and observing radio-collared females within 30 days of emergence from the den. Success of unmarked bears was determined by observation at the den site or by counting footprints in the snow left by the bears as they abandoned the den.

Analyses

We used 2 methods to test whether the distribution of our capture effort biased the distribution of dens we located by radio telemetry. First, we divided the study area into 4 longitudinal zones and compared the distribution of captures in each zone to the distribution of subsequent denning attempts in each zone with a Chi-square contingency table. Second, we compared locations where bears were captured to locations where they denned with the distribution free Multi-Response Permutation Procedure (MRPP) (Mielke et al. 1981, Biondini et al. 1988).

We evaluated selection of substrate or geographic areas by denning polar bears by comparing the observed distribution of dens on land and on pack ice, and in each of 4 longitudinal zones along the coast, with Chi-square goodness-of-fit tests. Annual variations in denning substrate, differences in distributions of incidental dens and dens located by radio telemetry, fidelity of denning bears to substrate, and fidelity to either the eastern or western half of the study area were examined with Chi-square contingency tables. We tested for deviations from randomness among den entry and emergence dates with

the non-parametric runs test (Zar 1984:419). We used the Student's t-test to compare distances between sequential land and pack-ice dens. To evaluate long-term fidelity we used Student's t to compare latitudes and longitudes of incidental dens we found with dens found in the 1970s (Lentfer and Hensel 1980). We compared entry and exit dates and durations in dens for bears on land and pack ice with a 2-factor ANOVA. We report actual significance levels resulting from statistical tests performed except where P < 0.001 and where test statistics calculated for the runs test exceeded tabled values (Zar 1984:627-635). Differences were significant at P ≤ 0.05.

RESULTS

Between 1981 and 1991, radio-collared polar bears were followed to 125 suspected maternity dens (Fig. 2). We confirmed 90 of those dens and evaluated success for 59. During the same time interval, we located 31 suspected incidental dens, confirmed 26, and evaluated success for 17. We examined 14 dens on the ground. All were constructed of ice and snow only, and both single- and multiple-chambered dens were observed. Half of examined dens and many others were in areas of minimal topographic relief, where denning might not have been suspected without the aid of radio telemetry.

The longitudinal distribution of locations where bears were captured and radiocollared was different than the distribution of locations where they denned (χ^2 = 49.35, 9 df, P < 0.001; MRPP: P < 0.001). Thus, locations of dens we found were not biased by capture efforts.

Den Distribution by Substrate

We confirmed 48 (53%) dens of radio-collared bears on drifting pack ice, 38 (42%) on land, and 4 (4%) on land-fast ice. When all years were considered, numbers of dens on pack ice and land were not different (χ^2 = 0.25, 1 df, $\underline{P}$ = 0.62). Numbers of dens on land and pack ice appeared to vary among years (Fig. 3). Variations among all years were not significant (χ^2 = 13.2, 9 df, $\underline{P}$ = 0.16), but the proportion of land dens found from 1986-90 was higher than that found from 1981-85 (χ^2 = 4.74, 1 df, $\underline{P}$ = 0.029).

Productivity

We observed 28 radio-collared bears within 30 days of emergence from pack-ice dens. Of those, 16 produced 26 cubs ($\bar{\underline{x}}$ = 0.93/den, SD = 0.90). Twenty-one of 31 land-denning bears, observed within 30 days of emergence, produced 33 cubs ($\bar{\underline{x}}$ = 1.1/den, SD = 0.85). Productivity of females that used pack-ice dens and that of females that denned on land was not different (χ^2 = 0.81, 2 df, $\underline{P}$ = 0.66). The power of this test, however, was only 0.11 because of small sample size.

Geographic Distribution of Dens

Radio-collared polar bears denned between Victoria Island in Canada, and Wrangel Island in Russia (Fig. 2). Only 3 bears, enroute to dens, moved between the Beaufort Sea and points east of 127°W. Thirteen bears captured in the Beaufort Sea denned west of 157°W, but only 1 denned on Russian soil.

Dens on land were concentrated in far northeastern Alaska and the northern Yukon Territory of Canada, including Herschel Island. Of 42 land dens, 35 (mainland dens) were along the mainland coast between 127°W and

167°W. The distribution of mainland dens (Table 1) was different among 10° longitude zones (χ^2 = 56.7, 3 df, $\underline{P}$ < 0.001).

Of 26 incidental dens known to be on land, 11 were observed from 137°00'W to 146°59'W, 6 were observed from 147°00'W to 156°59'W, and 9 were west of 157°W. This distribution was different from that observed by radio telemetry (χ^2 = 11.3, 3 df, $\underline{P}$ = 0.01), reflecting the higher frequency of incidental dens in western Alaska.

Whereas dens on land were located in a narrow band ranging inland 0.02-61 km, the south and north extremes of pack-ice dens were over 700 km apart. The latitudinal range of pack-ice dens was 70°12'N to 77°48'N ($\bar{x}$ = 73°05'N, $\underline{n}$ = 48), and 37 dens (77%) were north of 72°00'N, including 22 (46%) north of 73°00'N. Bears captured in the Beaufort Sea entered dens on pack ice as far east as 117°18'W and as far west as 178°54'W ($\bar{x}$ = 146°33'W, $\underline{n}$ = 48). Polar bears drifted 19-997 km ($\bar{x}$ = 357 km, SD = 246 km, $\underline{n}$ = 37) while in dens on pack ice. Successful females drifted 114-816 km ($\bar{x}$ = 385 km, SD = 218 km, $\underline{n}$ = 16). Drift bearings for 34 of 37 dens, for which complete drift information was available, ranged 226-350°. Drifting with the sea ice imparted some risks to denning bears. In winter 1985-86, 6 polar bears in pack-ice dens were swept past Point Barrow and southwest into the Chukchi Sea, due to unusually unstable ice. Only 1 denned successfully.

Den Site Fidelity

We followed 27 polar bears to >1 suspected or confirmed maternity den. One radio-collared polar bear was followed to 4 maternal denning sites, 7 were followed to 3 dens each, and 19 to 2 dens. Confirmed sequential dens were

separated from their precursors by a mean of 308 km (SD = 262, n = 30).

Distances separating sequential land dens were not different from those

separating sequential pack-ice dens (t = 0.5, 19 df, P = 0.62).

Bears that denned once on pack ice were more likely to den on pack ice

than on land in subsequent years, and vice versa (χ^2 = 4.9, 1 df, P = 0.03).

Similarly, bears that denned once east of 146°59'W, the midpoint of the

longitudinal range of mainland dens, were more likely to den there than to the

west in subsequent years (χ^2 = 5.5, 1 df, P = 0.02). Also, neither latitudes (t =

0.05, P = 0.96) nor longitudes (t = 0.75, P = 0.46) of incidental dens we found

in northern Alaska differed from those reported in the 1970s (Lentfer and

Hensel 1980; U.S. Fish and Wildl. Serv., unpubl. data).

Denning Chronology

Successful land-denning bears entered dens between 8 October and 24

November and emerged between 13 March and 18 April, for durations of 96-

183 days. Successful pack-ice denning bears entered dens between 17

October and 13 December and emerged between 4 March and 29 April, for

durations of 81-164 days (Table 2). Duration of land denning did not differ

from that of pack-ice denning (F = 0.31, 1 df, P = 0.58), and there was no

interaction between success and substrate (F = 1.42, 1 df, P = 0.24).

However, successful bears remained in dens longer than bears that did not

produce cubs (F = 9.41, 1 df, P = 0.004). Also, entry (n_1 = 16, n_2 = 16, μ = 8, P

= 0.005) and exit (n_1 = 16, n_2 = 18, μ = 11, P = 0.05) dates varied in a non-

random pattern that probably reflected annual variations in weather. However,

data were not sufficient to confirm that relationship.

DISCUSSION

Polar bears commonly den in the Beaufort Sea region. We found over 10 dens/year by annually radiocollaring 1.5% of the population (Amstrup et al. 1986). Extrapolation to the estimated population size would account for the total numbers of dens projected for the Beaufort Sea, indicating a population that is not dependent on reproduction from other known denning areas.

Distribution of Dens by Substrate

Our data suggest denning on pack ice occurs frequently. Lentfer and Hensel (1980) recognized the occurrence of dens on pack ice but suggested that denning on pack ice was limited to bears that could not make it to shore. Larsen et al. (1983) reported footprints of new cubs deep in the pack ice between Greenland and Svalbard but did not discuss whether those cubs might have been born in dens on the pack ice, and Harington (1968) concluded that denning on ice was not preferred.

Radio-collared bears denned on land more often in the latter half of this study than in the first half. Because sample sizes were small, variation in denning substrate we observed among years could be due to chance. We believe, however, that the higher proportion of land denning late in the study is real. We found more incidental land dens than earlier investigators despite their greater search effort (Lentfer and Hensel 1980; U.S. Fish and Wildl. Serv., unpubl. data). Also, researchers working in the Canadian Beaufort Sea found more dens and evidence of dens on land in the 1980s than during studies conducted there in the 1970s (Stirling et al. 1988, Stirling and Andriashek 1992). The apparent absence of onshore denning for many years

before this study may have resulted from hunting that began with Yankee whalers in the late 1800s and early 1900s (Hanna 1920, Mowat 1984), and continued, after modern firearms became available to local residents, until the 1960s (Leffingwell 1919, Van de Velde 1957, 1971, Stirling and Andriashek 1992). Because polar bears reproduce slowly (DeMaster and Stirling 1981, Taylor et al. 1987, Amstrup and DeMaster 1988), and are largely faithful to denning substrate, even a limited continuing harvest in the early and mid-1900s could have prevented the re-establishment of land denning until now. Increases in numbers of polar bears in the western Chukchi Sea (Uspenski and Belikov 1991) and the large numbers of bears recently reported denning on the mainland Chukchi Sea coast of Russia (Stishov 1991) support the hypothesis of increasing numbers of land dens in Alaska and adjacent areas.

Lentfer and Hensel (1980) concluded that suitable denning habitat along Alaska's north coast is limited due to the lack of topographic relief. Our observations refute that conclusion. If polar bears in the Beaufort Sea region moved as far inland to den as bears do in Hudson Bay (Ramsay and Stirling 1990), they would find substantial variation in elevations, slopes, and aspects. Further, in many areas of the Alaskan North Slope micro-relief is adequate to catch the snow needed for denning. Finally, factors other than topographic relief apparently affect capture of snow. Several dens were found, only because of telemetry, in an almost imperceptible series of swales, 30 km west of Kaktovik.

Productivity

Reported polar bear litter sizes have varied from 1.58 to 1.9 (Harington

1968, Stirling et al. 1977, Lentfer et al. 1980, Larsen 1985, Ramsay and Stirling 1988). By comparison, production in our study area of about 1 cub per den seems low. However, previous estimates of litter size did not include unsuccessful reproductive attempts. After excluding unsuccessful females, litter sizes we observed within 1 month of den exit averaged 1.6.

Harington (1968), Lønø (1970), and Lentfer and Hensel (1980) suggested that risks in denning on pack ice should make it a less preferred habitat for denning. A polar bear entering a den in pack ice cannot know the nature of habitat, availability of food, or geographic location where she will emerge months later. Also, currents, winds, or other factors related to the dynamics of pack ice can disrupt bears in dens. Polar bears using dens on the pack ice were subjected to risks caused by ice instability and movement, but we did not find that those risks reduced productivity. Low power of the Chi-square tests we performed indicated that conclusions regarding productivity of bears denning on land and pack ice must be viewed with caution.

Geographic Distribution of Dens

Patterns of polar bear denning we observed indicate that polar bears occurring across the mainland coast of the Beaufort Sea in Alaska and Canada are from the same population, but female bears occurring east of 127°W may be segregated from those in the Beaufort Sea. Lentfer (1975b) concluded that polar bears occurring along Alaska's west coast were members of a population discrete from that along the northern coast. Our data indicated that segregation between bears of northern and western Alaska is less distinct than the segregation at the eastern end of the Beaufort Sea.

The northeastern corner of Alaska and adjacent Yukon Territory coast of northwestern Canada comprised 23% of the longitudinal range of the mainland denning area but accounted for 80% of the total mainland dens. The higher-than-expected use of this area raises management concerns because this part of the Arctic holds promise of large recoverable reserves of hydrocarbons (Weeks and Weller 1984). Overlap of exploration and development activities with polar bear denning and other activities has already occurred, and many of those activities have potential to disrupt polar bear denning (Stirling 1990, Stirling and Andriashek 1992).

Fidelity to Den Sites

The large and predictable concentrations of dens in some regions (Uspenski and Chernyavski 1965, Uspenski and Kistchinski 1972, Larsen 1985, Ramsay and Andriashek 1986, Ramsay and Stirling 1990) indicate high fidelity to maternity denning areas. Polar bears we followed by radio telemetry were faithful to denning substrate and to general geographic areas. They were not faithful, however, to particular places. Our data on den distribution and fidelity of females to denning areas indicated there are both pack-ice and land-denning bears. Den substrate switching appeared to be limited. This segregation may have begun when some females were prevented from reaching land in the fall. They continued to den on pack ice because of the philopatry we observed.

When all years were considered, denning polar bears preferred some areas over others, but no areas were used by collared bears in all years. Weather, ice conditions, and prey availability, all of which varied annually,

probably determined where bears denned. Those annual variations and the long-distance movements of polar bears (Amstrup 1986, Garner et al. 1990) made seasonal recurrence at exactly the same location unlikely.

Limited data indicate that polar bears denning on the west shore of Hudson Bay have higher fidelity to previous denning sites than we observed (Ramsay and Stirling 1990). Polar bears in Hudson Bay are forced to remain on land between July and October of each year because sea ice there melts completely (Stirling et al. 1977, Ramsay and Andriashek 1986). While landlocked, they cannot forage and have much time to seek preferred denning locations. Because polar bears at higher latitudes continue to forage on the drifting pack ice until just before den entry, their locations at den entry time are less predictable.

Denning Chronology

Little information on den entry or emergence dates of polar bears has been available. Larsen (1985) reported that most dens on Svalbard were opened in late March and vacated by mid-April. Lentfer and Hensel (1980) reported late March and early April departure times in Alaska. Kolenosky and Prevett (1983) and Ramsay and Andriashek (1986) reported emergence in late February and early March in Hudson Bay. Lentfer and Hensel (1980) reported polar bears came ashore to den in late October and early November. Messier et al. (1992) reported den entry dates in early September and emergence in March and April for polar bears in the high Canadian Arctic. Those data may indicate a more protracted denning period at higher latitudes than we recorded (Table 2), but Messier et al. (1992) observed only 5 bears,

and neither den occupancy nor outcome were visually confirmed.

Initiation of denning depends on sufficient snow accumulation to allow excavation of a den cavity. Timing of sea ice formation can also alter the onset of denning on land or sea ice. For dens on pack ice, entrance times and physical locations are especially dependent on ice type and consolidation. Dens must be in ice stable enough to stay intact for 81-164 days while being pushed by currents for hundreds of kilometers.

MANAGEMENT IMPLICATIONS

Contrary to previous hypotheses (Stirling and Andriashek 1992), substantial polar bear denning occurs in the Beaufort Sea region of northern Alaska and adjacent Canada. Bears that den on pack ice are subject to risks not encountered by bears that den on land. Unstable, moving ice caused early abandonment of dens and, apparently, loss of cubs. However, the persistence of pack-ice denning indicated that those risks are not overwhelming. Conversely, human perturbations, such as hunting or industrial activities, may have a disproportionately high influence on land-denning bears.

Most bears that denned on land selected sites in the northeastern corner of Alaska or adjacent Canada where oil and gas exploration has occurred or is likely (Weeks and Weller 1984, Stirling 1990). Fidelity to denning substrate suggests bear population recovery from perturbations that unequally affect either land or pack-ice dens will be slow. For example, the increase we observed in land denning may have resulted from a decline in hunting of denning areas that began decades ago. The potential for disruptions of denning areas, therefore, should be of concern to managers of proposed

developments. The absence of site fidelity, however, indicated that denning

habitats are not limiting. The chronology of denning is predictable. Therefore,

temporal and spatial management of hunting and industrial developments

should mitigate many human impacts on denning bears.

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Table 1. Geographic distribution of polar bear maternal dens, located and confirmed by radio telemetry, along the mainland coast of the Beaufort Sea and adjacent northwestern Alaska, 1981-91.

Longitudinal zones where dens were located	Denning substrates		
	Land[a]	Pack ice	Total[b]
127°00' — 136°59'	1	8	9
137°00' — 146°59'	28	15	43
147°00' — 156°59'	3	14	17
157°00' — 166°59'	3	8	11

[a]Includes dens on land fast ice.

[b]Ten dens east or west of the 127°00'-166°59' mainland zone are not included.

Table 2. Entry and exit dates of polar bears radiotracked to confirmed dens in the Beaufort Sea region (1981-1991). Included are bears for which success (production of ≥ 1 cub) was evaluated within 1 month of den emergence.

Substrate	Success	Den entry dates			Den exit dates			Duration in den		
		n	x̄	SD	n	x̄	SD	n	x̄	SD
Land	No	8	25 Nov	17.1	8	11 Mar	25.3	8	106	34.1
Land	Yes	20	11 Nov	22.1	18	5 Apr	8.8	18	147	22.3
Pack ice	No	12	19 Nov	22.3	10	8 Mar	35.7	10	112	43.7
Pack ice	Yes	16	22 Nov	20.7	10	26 Mar	13.1	10	130	27.5
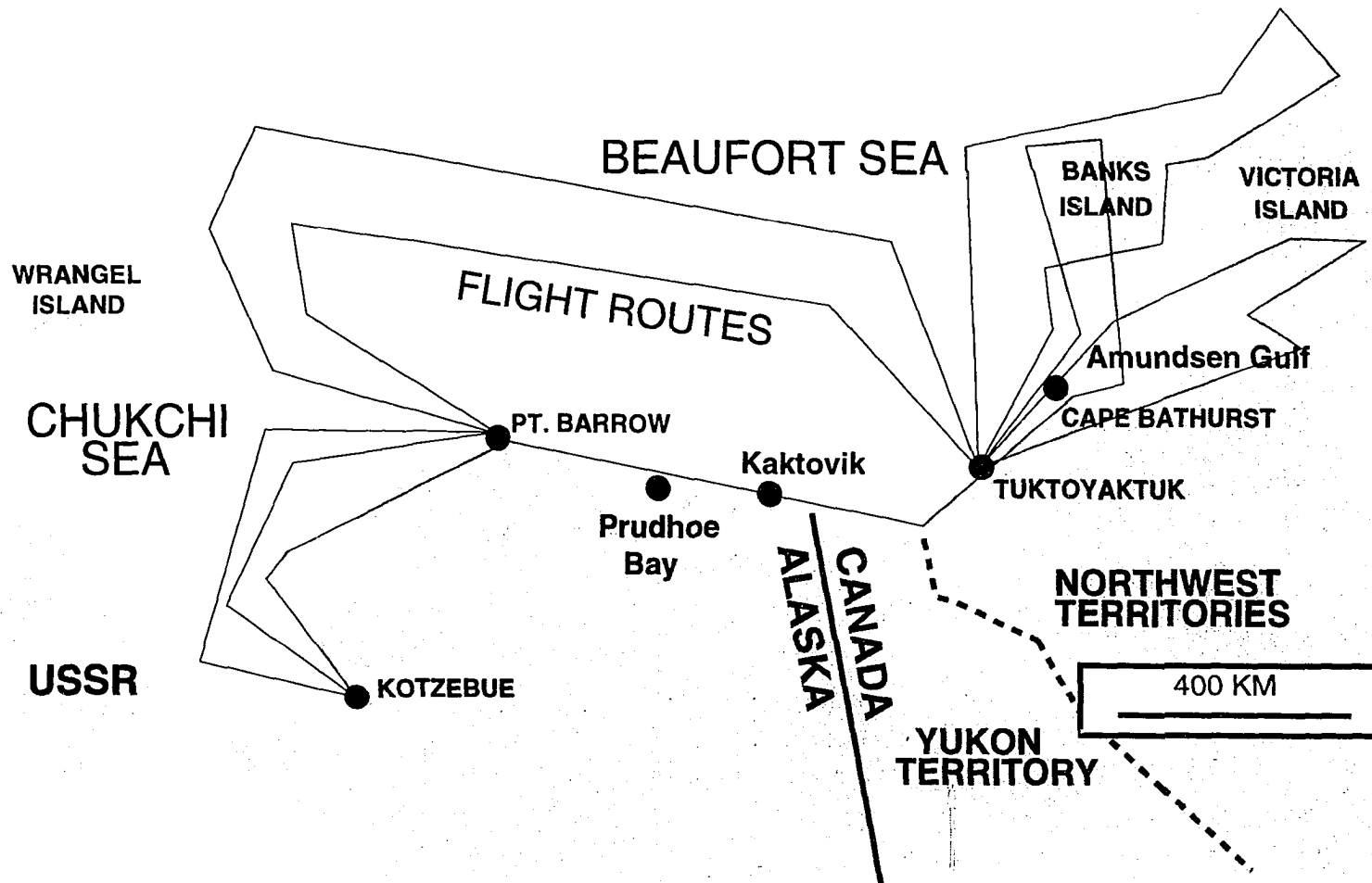
Figure 1. Approximate radio-tracking routes for polar bears flown 4 times per year, 1983-1987, and twice per year, 1988-1991. Also shown are place names used in the text.
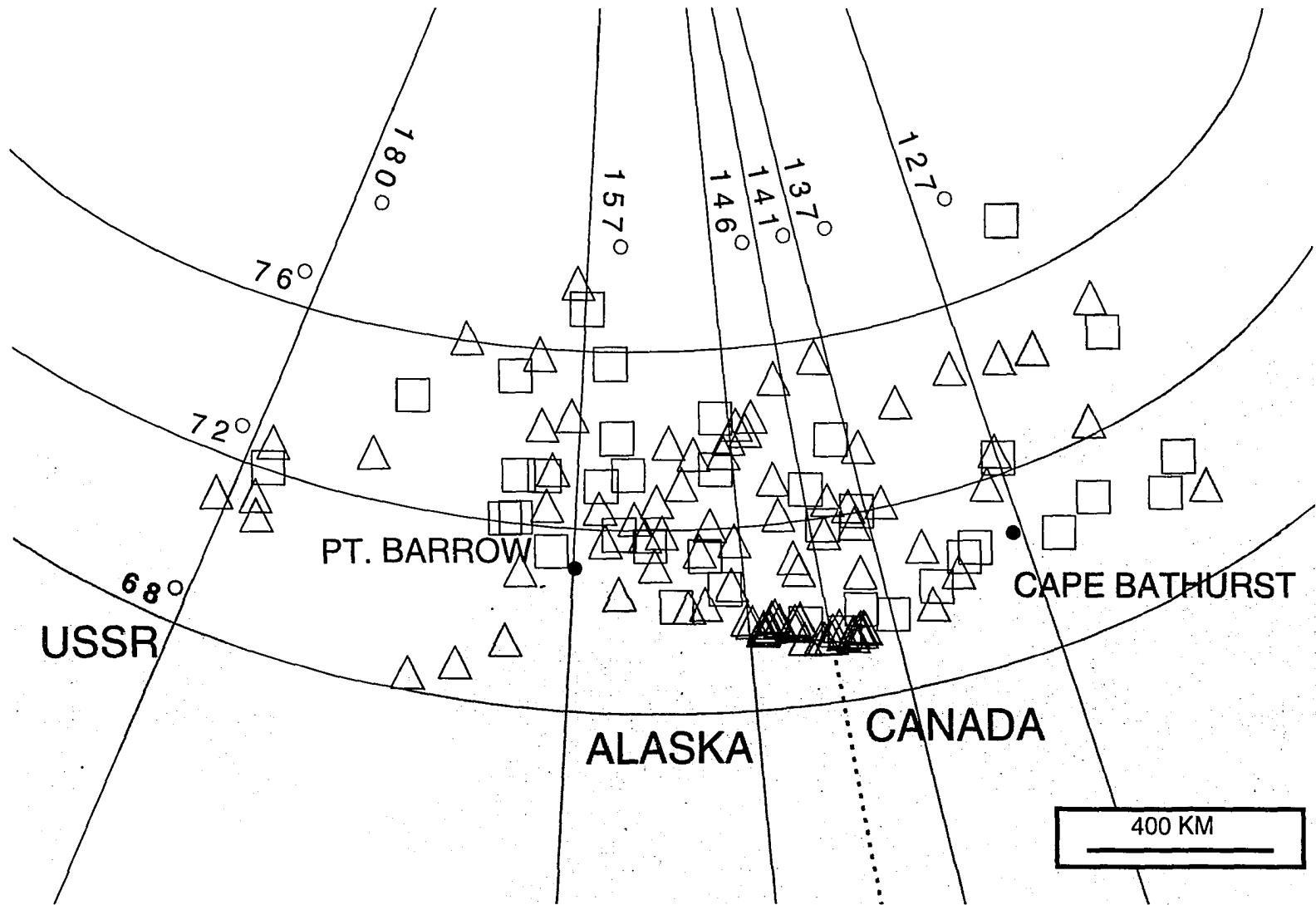
Figure 2. Suspected (squares) and confirmed (triangles) polar bear maternity dens located by radio telemetry, 1981-91.
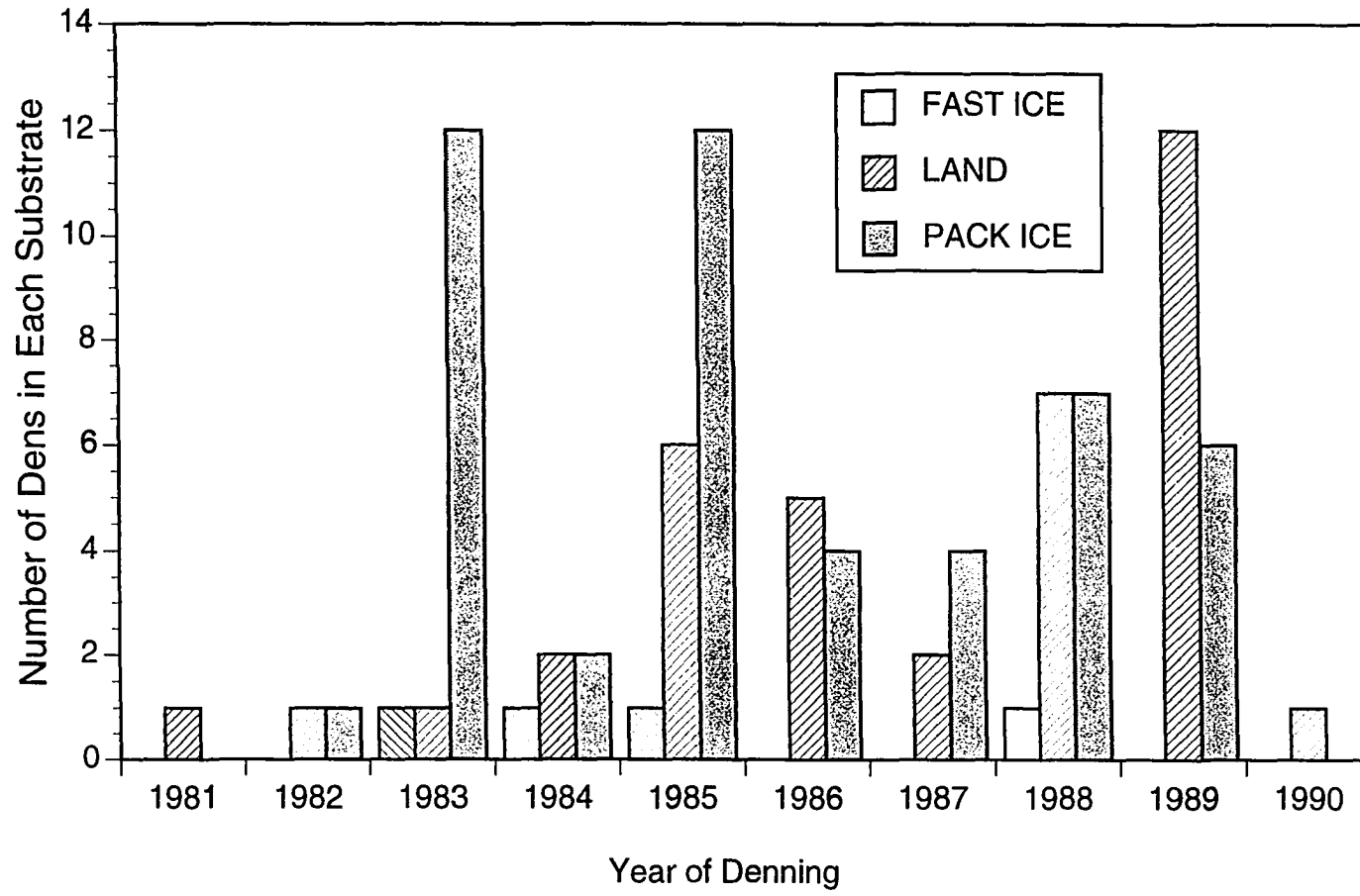
Figure 3. Numbers of radio-collared polar bears entering confirmed dens on

land, fast ice, and pack ice in arctic Alaska and Canada, 1981-1990. Years

shown are those in which bears entered their dens.

CHAPTER VI

HUMAN DISTURBANCES OF DENNING POLAR BEARS IN ALASKA[1]

S. C. Amstrup

Human Disturbances of Denning Polar Bears In Alaska

STEVEN C. AMSTRUP

Abstract: Polar bears (<u>Ursus</u> <u>maritimus</u>) give birth in dens of snow and ice. The altricial neonates cannot leave the den for >2 months post-partum, and are potentially vulnerable to disturbances near dens. The coastal plain (1002) area of Alaska's Arctic National Wildlife Refuge (ANWR) lies in a region of known polar bear denning, and also may contain >9 billion barrels of recoverable oil. Polar bears in dens could be affected in many ways by hydrocarbon development, but neither the distribution of dens nor the sensitivity of bears in dens has been known. I documented the distribution of dens on ANWR between 1981 and 1992, and observed responses of bears in dens to various anthropogenic disturbances. Of 44 dens located by radiotelemetry on the mainland coast of Alaska and Canada, 20 (45%) were on ANWR and 15 (34%) were within the 1002 area. Thus, development of ANWR will increase the potential that denning polar bears are disturbed by human activities. However, perturbations resulting from capture, marking, and radiotracking maternal bears did not affect litter sizes or stature of cubs produced. Likewise, 10 of 12 denned polar bears tolerated exposure to exceptional levels of activity. This tolerance and the fact that investment in the denning effort increases through the winter, indicated spatial and temporal restrictions on developments could prevent the potential for many disruptions of denned bears from being realized.

Key Words: Alaska, ANWR, Arctic, denning, disturbance, impact, oil

development, polar bear, reproduction, Ursus maritimus

INTRODUCTION

Pregnant polar bears excavate dens of snow and ice in early winter (Harington, 1968; Lentfer and Hensel, 1980; Ramsay and Stirling, 1990), and give birth in December or early January (Kostyan, 1954; Harington, 1968; Ramsay and Dunbrack, 1986). The altricial neonates need to remain in the protective den for >2 months post-partum and therefore, are potentially vulnerable to disturbances near dens. Section 1002 of the Alaska National Interest Lands Conservation Act (ANILCA) set aside 600,000 ha of the coastal plain of ANWR in northeastern Alaska for special study. This "1002" area may contain >9 billion barrels of recoverable oil, and may be the most promising onshore oil and gas exploration area in the United States (U. S. Dep. Interior, 1987). Lentfer and Hensel (1980) and Amstrup et al. (1986) suggested many ways bears in dens might be impacted by hydrocarbon related activities, and Amstrup and Gardner [1994 (Chapter V)] reported that polar bears denned most commonly along the northeastern coast of Alaska. Despite speculation, however, neither the distribution of dens on ANWR nor the sensitivity of bears to disturbances near their dens has been known.

This report documents the use of ANWR for denning by polar bears between 1981 and 1992. Also, it summarizes information on responses of polar bears in dens to aircraft, over-snow vehicles, and foot traffic.

METHODS

Dens of female polar bears were located by satellite telemetry, very high

frequency (VHF) aircraft telemetry, and aerial sightings of opened dens in fall and spring. The nature and frequency of exposures of bears at den sites to human activities were recorded, and notes were kept on responses by bears and the subsequent outcome of the denning event. Responses of unmarked bears to various human activities were recorded opportunistically. These observations were few, but some disturbances caused by researchers were similar to those that might accompany industrial development and other endeavors. Therefore, responses of denned polar bears to research activities also were recorded.

The ultimate measure of den-site disturbances is reproductive output. Therefore, I compared numbers (determined by observation, capture, or by counting footprints in the snow), weights, and skull measurements (the sum of condylobasal length and zygomatic width) of cubs produced by radiocollared, marked, and new females captured after leaving dens. New females were subjected to no human disturbances prior to their capture upon emergence from the den in early spring. Marked and radiocollared females were exposed to one or more capture by helicopter darting [Amstrup and Gardner, 1994 (Chapter V)] prior to denning and subsequent recapture in the spring with new cubs. Radiocollared females were exposed, while in dens, to several overhead passes and circles with helicopters or fixed-wing aircraft in order to pinpoint their locations. Flights were conducted at altitudes of 150 m to 500 m (unless otherwise stated), depending on weather conditions and topography. Activity levels of denned bears were determined, during aerial monitoring, by fluctuations in rate and strength of pulsed transmissions. Once den sites were

accurately known, continued occupation of dens of radiocollared females was confirmed with more distant flights or activity and temperature data recorded by satellite radiocollars [Amstrup and Gardner, 1994 (Chapter V)].

Litter sizes of cubs produced by new, marked, and radiocollared females were compared with chi-squared-contingency-tables, and measurements of cubs were compared with the chi-squared approximation of the Kruskal-Wallis (KW) test (Conover, 1980). Statistical analyses were performed on a Data General AVIION 6200 computer (Data General Corp., Westboro, MA) running SAS version 6.07 software (SAS Institute, Inc., Cary, NC).

RESULTS

DEN LOCATIONS

Using radiotelemetry between 1981 and 1992, I located 44 dens on land or land fast ice along the mainland coast of Alaska and Canada. Of those, 20 (45%) were within the bounds of ANWR, and 15 (34%) were within the bounds of the 1002 area (Fig. 1). The ANWR and 1002 coasts comprise only 13% and 10% of the longitudinal range over which mainland dens were observed. In addition to the 20 dens within ANWR, 1 was on lands controlled by the Village of Kaktovik and surrounded by ANWR lands, and 2 others were just offshore of the 1002 area on land fast ice. Numerous dens also were found in Canada just east of ANWR (Fig. 1).

POTENTIAL DISTURBANCES AT DENS

Litters of 38 radiocollared bears (including #s 3, 4, 9, and 11 below), 28 marked bears, and 52 new bears were captured after emergence from maternity dens in the spring (Table 1). Four denned bears were exposed to

more intense than usual aircraft activity associated with this study, and 8 were

exposed to activities of persons engaged in other endeavors (Table 2).

Responses to Aircraft

We recorded 40 cases (including #s 1-4 below) of potential disruptions of

denning by research aircraft. Motions detectable among collared bears within

dens did not appear to be elevated during telemetry flights, and only bears #1

and #3 left their dens. Production of cubs (Table 1) by radiocollared, marked

and new bears did not differ ($\chi^2 = 1.31$, df = 2, P = 0.519). Likewise, skull

measurements (KW, $\chi^2 = 4.1$, df = 2, P = 0.13) and body weights (KW, $\chi^2 =$

2.79, 2 df, P = 0.25) of cubs born to females in each group did not differ.

Responses of 4 denned bears exposed to greater than usual levels of

aircraft disturbance during this study were mixed. Bear #1 was seen digging

her den in a deep snow bank when the helicopter flew over her, on 30 October

1984, at an altitude of approximately 100 m. She fled, but was captured,

instrumented, and released adjacent to her excavation. After recovery, #1

wandered extensively until 2 December when she was relocated in another

den 64 km west of her capture.

Bear #2 was observed in her open den on 19 October 1981. She came to

the entrance when the helicopter hovered 300 m in front of and 100 m over her

den. Bear #2 was observed in the entrance of her den 3 more times before 28

October when blowing snow closed the den for the winter. Those sightings

included a slow 50 m high overhead flight that occurred by accident on 26

October. Because bear #2 was an unmarked bear, her presence through the

winter was not verified. However, a female with 2 cubs was observed by a

local resident at the den site on 22 March 1982.

Bear #3 ran from her open den on 5 November 1983 (the third day she had been seen there) when the helicopter hovered 100 m overhead and 100 m in front of her den. She was caught and released adjacent to her den, but traveled as far away as 120 km before entering a second den 20 km from her first. Bear #3 was monitored by radiotelemetry through the winter, and emerged from her den in the spring with 2 cubs.

The closed den of bear #4 was first located on 19 March 1991 by several 200 m high overhead flights, with a twin engine turboprop aircraft. The transmitter signal indicated no detectable activity of the bear in the den during these flights. On 27 March no signal was heard, despite numerous passes at 30-50 m altitudes. I assumed #4 had left her den, but learned later the radio receiver had malfunctioned. On 5 April the den was open and polar bear footprints led from the den to a point 100 m to the south and then returned to the den. On 7 April, more footprints leading away from and back to the den were observed. Also, snow machine tracks circled the polar bear footprints and approached to within 10 m of the den exit. Bear #4 left the den on 13 April 1991, and was recaptured with a single cub 5 km north of the den. Bear #4 remained in her den despite numerous exposures to low-level aircraft and the close approach of a snow machine, and emerged later, presumably without human influence.

Unmarked bear #5 was exposed to humans on foot as well as aircraft. On 8 March 1981, B. P. Kelly observed a den opening on a north shore barrier island. On approaching the den (by helicopter) to investigate, bear #5 and a

single cub emerged and fled north onto the sea ice. The helicopter landed at the den site. Kelly entered the den, recorded some notes regarding its structure, made a sketch, and departed. On 11 March 1981, Kelly returned to the den site by helicopter, landed and walked to the den to make more notes, but bear #5 was back. Bear #5 and cub were observed, by helicopter, to occupy the den area until 13 March. Kelly did not visit the den thereafter.

Exposure to Over-Snow Vehicles and Activities

The sealed den of bear #6 was radio located on a Canadian north shore island on 12 January and 9 March 1984. She left the den shortly thereafter, however, and was next observed without cubs in June 1984. A local resident hunter later reported seeing a running polar bear, in late March, near the draw where the den of #6 was located. The hunter thought the bear had just come from a den, but he did not investigate whether cubs may have been left behind. The bear he observed might have been #6, and it is possible that the passing of his snow machine induced her to abandon her den.

Two maternity dens (bears 7 and 8) were found on the south shore of a barrier island in spring 1991 within 2.8 km of an oil production plant employing 80-90 people. Vehicle traffic, human activity and associated noises were constant throughout the denning period. Bear #8 was followed from her den, captured, and radiocollared. Her 2 cubs were known to survive at least 6 months thereafter. Tracks of 2 cubs emerged from the den of #7, but their survival after leaving the den was not known.

Bear #1, which had been disturbed by helicopter at her first den site in fall of 1984, may have been disturbed from the site to which she relocated. She

was in her second den on 2 and 27 December 1984, but on 11 February 1985 she was alone on the sea ice near Barrow. Examination of her den location revealed a single Rollagon tractor (Crowley All-Terrain Corp., Anchorage, AK) path within 250 m of the den site, and a well-traveled Rollagon path parallel to the coast at a distance of 450-500 m from the den site. Rollagon tractors weigh approximately 27,000 kg, and trailers weigh between 17,000 and 20,000 kg. Both tractors and trailers ride on tall, wide, low pressure tires, and ground impact is 0.30 kg/cm^2 (4.2 psi).

Two denning animals were exposed to 3-dimensional seismic exploration (Yilmaz, 1987) and Rollagon traffic during the winter of 1988-1989. A satellite radiocollared bear (#9) denned on a north coast barrier island on 20 October 1988, and an unmarked bear (#10) was observed in a den just east of the den of #9 on 1 November 1988. The eastern most receiver line of the seismic grid was 1000 m west of the den of #9 and 2000 m west of the den of #10. The parallel seismic lines were approximately 10 km long, spaced at intervals of 50 m, and extended 27 km east to west. The Rollagon traffic approached to within 2500 m and 3400 m of the dens of #10 and #9 respectively.

Bear #9 and her 2 cubs remained in their sealed den as the Rollagon units passed and during the time the seismic crews were nearest (1000 m). Temperature and activity data relayed from the satellite radiocollar of #9 suggested she opened her den between 8 and 11 February when seismic testing was done on source lines 1900 to 2500 meters west of her den, and left her den on 12 March when activity occurred 6300 m west of her. Bear #9 was captured with 2 cubs of the year on 9 April 1989, 29 days after leaving the

den. Footprints of a female and two cubs at the den of bear #10, on 1 April, may be evidence that she left the den with cubs, but her success was not substantiated by subsequent observations.

A heavily-used ice road passed 400 m in front of the den of Bear #11 when her opened den was located on 22 March 1992. Footprints around the den exit indicated #11 and cubs had been in and out of the den several times by 22 March. Road construction started 22 December 1991, and was concluded 28 January 1992. Drilling, 6 km down the road from the den, began on 7 February, and was completed in April. At least 6 light vehicles and 1 large truck passed in front of the den every other day, and at least 4 runs each day were made by both a blade type snow plow and a rotary snow blower. Traffic was heavier during and after snow or wind storms, and during construction. The mean den entry date recorded for the Beaufort Sea area was 20 November, and all bears that produced cubs entered dens on land before 24 November [Amstrup and Gardner, 1994 (Chapter V)]. Therefore, bear #11 must have been in her den when construction work began. Workers on the road and drilling project were unaware of the presence of the bear, and the bear apparently tolerated the relative nearness of the construction activities and traffic. On 25 March, #11 took her 2 cubs north across the ice road and onto the sea ice.

Unmarked bear #12 emerged from and reentered her open den as a survey party traveling in a 7000 kg tracked vehicle and 2 light snow machines approached to within 65 m on the morning of 19 March 1993. The survey party, which was staking seismic shot lines, withdrew, and ceased operations.

Subsequent observations from a 400-500 m high Cessna 185 aircraft and a knoll 680 m from the den, verified that #12 and her 2 cubs used the area around the den and the den itself until the morning of 21 March, when they walked north to the sea ice. Records verified that the same survey crew passed within 46 m of the den, which was closed then, on 9 March 1993. They also surveyed the lines 270 m and 135 m from the den on 13 and 18 March, respectively. Thus, #12 tolerated several close approaches to her den and left later, in the absence of human activity.

DISCUSSION

Polar bears denned on ANWR and the 1002 area more frequently than would have been expected if they denned uniformly along the mainland coast. Amstrup and Gardner [1994 (Chapter V)] documented that the preponderance of dens in the northeastern coastal area of Alaska represented a statistically significant preference. The potential for disruption of dens in that area, therefore, must be taken seriously.

On the other hand, most bears in this study showed substantial tolerance for human activities. Pinpointing the locations of the dens of radiocollared polar bears by aircraft required more overhead flights, at lower altitudes, than most other kinds of aircraft travel. Also, live capture and marking, were probably more disruptive to bears than other possible perturbations. Yet, recruitment of cubs through the time of emergence from the den and sizes of cubs were not affected by those disruptions. Ramsay and Stirling (1986) reported that capturing and handling female polar bears in Canada did not negatively affect numbers or sizes of cubs.

Interactions of denned polar bears and industrial activities have not been reported elsewhere. However, observations of grizzly bears (Ursus arctos), which are closely related to polar bears, also suggested substantial tolerance of such activities. McLellan and Shackleton (1989) found that summer active grizzly bears were not displaced from the immediate vicinity of seismic testing supported by helicopters. Reynolds et al. (1986) reported some movements and possible increased heart rates when denned grizzly bears were exposed to seismic testing activities. However, they also observed that similar movements and heart rate patterns sometimes occurred in absence of human activities, and they concluded that "effects on the bears were probably minimal" (Reynolds et al., 1986:174).

After studying sounds and vibrations detectable in artificial dens, Blix and Lentfer (1992) observed that only seismic testing less than 100 m from a den, and a helicopter taking off at a distance of 3 m produced noises inside the dens that were notably above background levels. Blix and Lentfer (1992) also concluded that a polar bear in its den is unlikely to feel vibrations unless the source is very close. They did not address, however, the formation of ice and the increasing density of snow that occurs when a den is occupied all winter and which would reduce insulation quality of the snow. Nor did they address the great individual variation in behaviors of polar bears.

Many questions about how bears in "real dens" are affected by disturbances remain unanswered. Bear #s 2, 4, 5, and 7-12 tolerated various activities near their dens, and bears exposed to research-related disturbances were not negatively affected. These observations corroborated the conclusion

of Blix and Lentfer (1992) that bears in dens are well insulated from outside sounds and vibrations. The possible den abandonment by bears #1 and #6 may be evidence to the contrary. However, during this study, 22 radiocollared bears, not exposed to human disturbances, abandoned their dens without cubs. Thus, although I cannot rule out a cause and effect relationship, it is equally likely the departures of #1 and #6 were unrelated to human activities. Kelly et al. (1988) demonstrated that efforts generating large sample sizes that lend themselves to hypothesis testing can quantify effects of industrial disturbances. Unequivocal conclusions regarding sensitivities of denned polar bears to industrial disturbances will be available only from similar controlled studies.

Polar bears may be more willing to abandon dens in fall than later in the denning period. Belikov (1976) reported that polar bears were easily disturbed from their dens in the fall, and I observed 2 bears (#1 and #3) abandon their fall dens in response to disturbances that appeared less severe than those tolerated by some bears in the spring. Also, evidence for the 2 cases (bears #1,#6) of possible human-induced abandonment of dens in spring was only circumstantial.

Bears have less to lose by leaving a den in the fall than they do by leaving nearer the time of parturition or afterward. Amstrup and Gardner [1994 (Chapter V)] confirmed that the survival of cubs prematurely forced out of their dens, by movements of the sea ice, was poor. They also concluded that individual polar bears have strong ties to general areas and substrata, but not to particular denning sites and that most bears enter dens in November. It is

less expensive for a bear that is looking for a den site to find an alternate location than it is to abandon an occupied den and create another elsewhere. Therefore, initiation of intense human activities in October or November, would give bears enroute to land dens the opportunity to den in less disturbed areas. Also, bears already in dens could relocate more easily when parental investment is low. The 2 bears I captured at dens in the fall reentered dens at other locations, and 3 bears disturbed from dens near Hudson Bay in autumn also relocated to other den sites (Ramsay and Stirling, 1986).

CONCLUSIONS

Polar bears preferred to den on and near ANWR, and if hydrocarbon development occurs there, the potential for disturbance of denning polar bears will increase. Loss of a large portion of the present productivity of polar bears denning on ANWR would undermine recruitment in the Beaufort Sea population. However, data indicate that many denned bears exposed to human activities are likely not to be affected in ways that aiter their productivity. Also, rigorous adherence to flexible management strategies, including spatial and temporal restrictions of developments, could prevent the potential for many disruptions of dens from being realized.

ACKNOWLEDGMENTS

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Table 1. Litter sizes, skull measurements, and weights of cubs captured with female polar bears after emerging from maternity dens in the spring. Differences among classes of females were not significant.

Female class[2]	Litter size			Skull sizes(cm)[1]			Weight (kg)		
	N	Mean	St. dev.	N	Mean	St. dev.	N	Mean	St. dev.
New	52	1.65	0.48	19	26.43	2.07	23	29.48	6.65
Marked	28	1.53	0.51	23	27.43	1.87	18	35.78	11.29
Radiocollared	38	1.66	0.48	36	27.41	1.87	34	30.59	9.95

[1]Skull measurements shown are the sum of condylobasal length and zygomatic width.

[2]"New" females had never been captured before; "Marked" females were captured and marked or radio-collared prior to entering their dens, but were not located in dens by aircraft radio telemetry; "Radio-collared" females were captured and radio-collared prior to denning and located in their dens by low-altitude aircraft radio telemetry.

Table 2. Summary of observations of polar bears exposed to human activities while in dens. Numbers of cubs observed upon emergence and subsequent survival of those cubs are shown.

| Bear No.	Possible Perturbation	Time of Disturbance	Distance To Disturbance	Behavioral Response	No. Cubs	Minimum Survival
1	Aircraft, Capture	30 Oct	100 m	Redenned	N/A	N/A
1	Rollagon Train	Early Jan	250 m	Left Den?	0	N/A
2	Aircraft Overflight	19 Oct	<50 m	None	2	Unknown
3	Aircraft, Capture	5 Nov	100 m	Redenned	2	Weaned
4	Aircraft, Snow Machine	Mar-Apr	< 50 m	None	1	<6 months
5	Aircraft, Foot Traffic	8-11 Mar	<50 m	Left & Returned	1	Unknown
6	Snow Machine	Late Mar	~200 m	Left Den?	0	N/A
7	Oil Field Operations	Continuous	2.8 km	None	2	Unknown
8	Oil Field Operations	Continuous	2.8 km	None	2	>6 months
9	Seismic Survey	Jan-Apr	1000 m	None	2	<6 Months
10	Seismic Survey	Jan-Apr	2 km	None	2	>1 month
11	Oil Field Operations	Dec-Apr	~400 m	None	2	>1 month
12	Field Survey	9-19 Mar	46 m	None	2	N/A
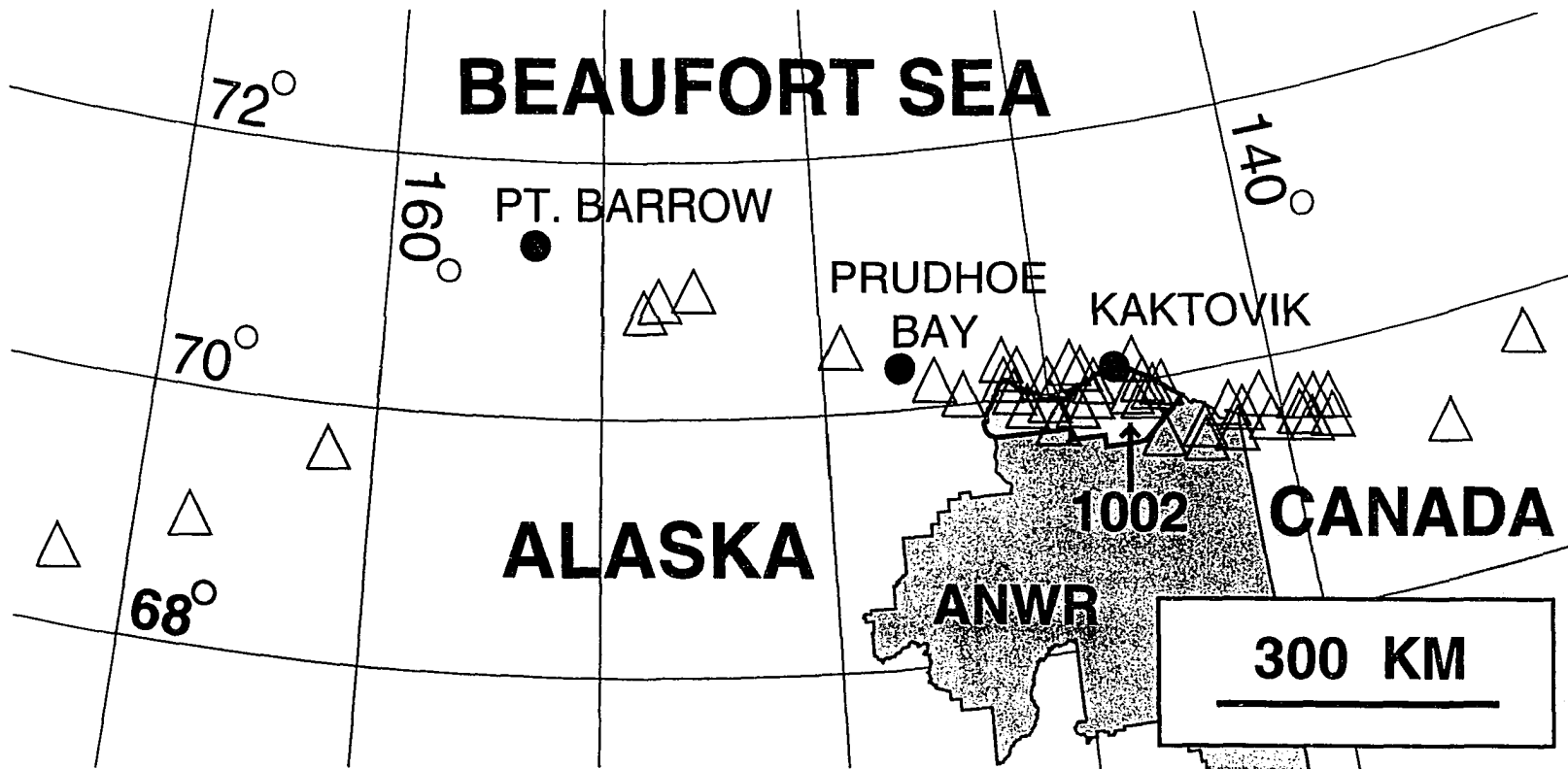
Figure 1. Locations of dens found by radiotelemetry along the Alaskan and Canadian mainland coasts between 1981 and 1992 (modified from Amstrup and Gardner, 1994: Fig. 2). Of the Dens Located, 45 and 34 % were on ANWR and the 1002 area. Also shown are place names used in the text.

CHAPTER VII

SUMMARY AND CONCLUSIONS

S. C. Amstrup

Few researchers are afforded the opportunity to spend over a decade in continuous study of a single species. Fewer still are able to focus such an opportunity onto a species like the polar bear, which by virtue of its distribution and population dynamics can only be understood through very long-term research (Derocher and Stirling 1992). I am fortunate to have had such an opportunity. I am doubly fortunate that I had access to data collected in the Alaska Beaufort Sea by other researchers for more than a decade before my studies began—a period during which the population was severely over-harvested. I also had access to data collected by colleagues in the Canadian Beaufort Sea and in the Chukchi Sea. This study could not have been so successful without those data. Finally, I was fortunate to have access to advanced radio-telemetry technologies that gave me the ability to follow large numbers of individuals over time.

The above factors allowed me to describe the movements of many individuals and determine bounds of the population of polar bears occupying the Beaufort Sea. They allowed me to estimate numbers of animals and compare the status of the population in the late 1980's and early 1990's to what it had been 20 years earlier. Finally, I was able to determine where Beaufort Sea polar bears are born; erasing a long standing mystery surrounding this population. The result was a much better understanding of polar bears now than we had at the outset of this study.

Movements and Activities of Polar Bears

I have shown that there is a population of polar bears that resides largely within the confines of the Beaufort Sea. Bears of this stock or population almost never move eastward of Cape Bathurst, the point of land separating the Beaufort Sea from Amundsen Gulf to the east. Although they do make frequent seasonal movements into the eastern Chukchi Sea, most return to the Beaufort Sea when the sea ice extent is reduced each summer. Members of this population probably are not genetically isolated from members of adjacent populations, or probably from any other polar bear population (Cronin et al. 1991). However, the rapid numerical response to locally-applied pressures suggests they should be managed as a separate Beaufort Sea population.

I was able to confirm, with large sample sizes, the great mobility of polar bears. Some bears made linear movements of over 5,000 km annually, and sustained movement rates of over 4 km/hr. Polar bears were not nomads, however. Those that were followed for periods of 2 or more years demonstrated seasonal fidelity, particularly in summer (albeit to large geographic areas), and occupied definable activity areas.

The travel rates of female polar bears varied according to both the time of the year and reproductive status, and I can speculate about some of those variations. As might have been expected, females with cubs traveled at slower rates than those with older young or those not encumbered by young, but were more active. The lowest movement rates generally occurred in late winter, when suitable foraging habitats are fewest and when many bears may have

restricted movements to conserve energy (Messier et al. 1992; 1994), or when bears may have figured out the best places to be in the relatively stable ice of late winter. Highest movement rates were in early winter when the greater volatility of sea ice may have necessitated higher levels of mobility among bears looking for favored foraging locations.

My descriptions of movements and activities have raised as many questions as they have answered. Additional information, not collected in this study will be necessary, however, to answer those questions. For example, I recorded that bears shifted their geographic positions to the north through the summer months and back to the south in winter. Summer movements corresponded with ablation of sea-ice in shallow coastal waters, and the fall movements corresponded with refreezing of that ice. Movements of polar bears from the central Beaufort Sea toward the east and west in winter, may be related to the persistent leads that develop where the sea ice is influenced by the Chukchi Gyre to the west, and the MacKenzie River to the east. Movements of bears back to the central Beaufort Sea in summer appeared to coincide with the earlier deterioration of sea ice in those easterly and westerly areas. Unfortunately, patterns in the sea ice of the Beaufort Sea have been described only generally (Stirling and Cleator 1981; Gloersen et al. 1992). Hence, I can only speculate about explanations of these movements.

Polar bears in the Beaufort Sea eat mainly ringed (Phoca hispida) and bearded (Erignathus barbatus) seals, and the distribution of bears is thought to be closely related to the distribution of seals (DeMaster and Stirling 1981). The distribution and availability of seals, in turn, must ultimately be controlled

by the movements and condition of the sea ice. The southerly shift in geographic location among most bears during October, for example, may have brought bears summering on the persistent pack ice back into the annual ice zone nearer shore, where seal densities are thought to be higher. Also, polar bears can have a significant impact on ringed seal populations (Hammill and Smith 1991). Predation by bears has modified the behaviors of northern hemisphere ice seals (Stirling 1977), and may have modified distribution of seals. High levels of activity among polar bears in late morning and afternoon, during the summer, might correspond with times when seals are hauled out in their subnivian lairs or on the surface of the ice and thus more available to bears (Kelly and Quakenbush 1990). Unfortunately, little is known about the distribution, abundance, and activities of seals; and explanations of interactions between bears and seals are lacking.

As a result of this study, I was able to provide the best yet descriptions of movements and activities of polar bears for the Beaufort Sea. If we are to explain movements and activities of polar bears, however, we need to learn the details of the predator/prey interactions between bears and seals, and understand how that interaction is mediated by the volatile sea ice platform upon which both seals and bears depend. Many logistical difficulties will make understanding seals, sea ice, and the movements of polar bears a formidable task. Given the fact that polar bears may be important indicators of the welfare of the Arctic and the world (Stirling and Derocher 1993), overcoming the obstacles will be worth it.

Another topic not addressed in this study is movements of male polar

bears. The necks of adult male polar bears are larger than their heads, and at present there is no satisfactory method of long term attachment of transmitters to males. Consequently, I have no information on movements or activities of male bears. Males may move much differently than females (Derocher and Stirling 1990), or they may move similarly (Lentfer 1983). Not knowing what males do is a limitation, because males are necessary to maintenance of the population, and because they also may play a role in limiting population size (McCullough 1981; Young and Ruff 1982; Stringham 1983). Males also appear to be more vulnerable to hunters. Polar bear populations apparently can sustain higher takes of males than of females (Taylor et al. 1987); but population effects of sexual biases in the take are not understood. Clearly, then, future research must more carefully consider the movements, distributions and behaviors of male members of polar bear populations as well as the effects those members have on the rest of the population.

Population Dynamics of Polar Bears

Amstrup et al. (1986) suggested the Beaufort Sea population had declined substantially by the early 1970's due to over-hunting. This study corroborated that decline. Also during this study, the population of the Beaufort Sea region was shown to grow at a rate of at least 2% per year. That is near the maximum that could be expected given the population is still subjected to some harvest (Taylor et al. 1987). The close agreement of 2 largely independent estimates engendered confidence that the growth rate I estimated was real, and that the population estimate was reasonable.

Major changes in population size often provide important opportunities to

understand population dynamics (McCullough 1979). My observations of changes in numbers, for example, allow the status of the population relative to K, and therefore K, to be estimated. Amstrup et al. (1986) presented evidence that the population in the early 1980's was approximately the same size as it had been in the late 1950's—the early years of aerial hunting. Amstrup et al. (1986) also indicated that the population had been much lower during the intervening period as a result of that aerial hunting. Prior to the popularizing of aerial hunting, polar bears in Alaska were largely unperturbed, with a harvest limited to small numbers taken by subsistence hunters (Amstrup and DeMaster 1988). Hence, it is reasonable to conclude the population prior to aerial hunting was high, and probably near K. The population has continued to grow since the estimate made in the early 1980's. Therefore, at the end of this study the Beaufort Sea population must have been as large or larger than it was before aerial hunting became popular in the 1950's when it should have been near K. That the Beaufort Sea population is now near K is substantiated by the fact that changes in age structure, reproduction, and survival, such as those I observed, occur mainly at population levels very near K (Fowler 1981).

In this study, I found evidence that density was suppressing survival of young and indications that reproduction also may have been affected. During the time when the polar bear population in the Beaufort Sea was low, there were few old animals and proportionately more young animals than there were in the latter years of the study. Recent survival rates of adults, as evidenced by radio telemetry and the age structure, are high, but survival rates of juveniles are lower. Numbers of young animals were significantly

inversely-related to total population size and estimated numbers of adults. Newly independent young, that would be expected to feel the brunt of density related competition for resources, appeared to be the most influenced by population size. Litters of more than one yearling, however, also were significantly less frequent late in the study than they were earlier. Derocher and Stirling (1992) speculated that production and survival of litter members may be the feature most affected by increased density in their Hudson Bay study area. They also reported that age at first reproduction and inter-birth interval may have increased as the population grew (Derocher and Stirling 1992).

As a population increases toward K, the first negative effect of its own density is increased mortality of young (Eberhardt 1977). At still-higher densities, age of maturity increases and then productivity of mature animals declines. Finally, at the highest densities, survival of adults may decline (Eberhardt 1977). The changes in population composition, survival, and recruitment I observed, follow that pattern and appear to be typical signs of a population approaching K-carrying capacity (Eberhardt and Siniff 1977; McCullough 1979). Also, they are similar to patterns recently reported in Hudson Bay where the polar bear population also has grown (Derocher and Stirling 1992).

Although I observed density effects on the population, I was not able to learn how density influenced reproduction or survival. In terrestrial bears, harassment, or infanticide by large males may be a principal mechanism of density dependent population regulation (Young and Ruff 1982; McCullough

1981; Stringham 1983). Harassment of subadults by adult males at scavenging sites (Smith 1980) may be an important regulating factor among polar bears. Any effect male polar bears have on their population, however, is yet to be confirmed.

Their life history features, and my observations, suggest that polar bears should be among the most K-selected of wild animals. They are not completely invulnerable to short-term perturbations of their environment, however. Survival and production of young in the Beaufort Sea population dropped dramatically in response to abnormally harsh winter conditions in 1974-75 (DeMaster et al. 1980). That response occurred in a density independent fashion and at a time when population size was low (Rogers 1987; DeMaster 1981). An understanding of predator/prey interactions and how those interactions are mediated by weather and sea-ice conditions is needed to understand the population dynamics of polar bears.

One of the most significant contributions of this study was the improved estimate of survival rates of litter members and adult polar bears. Reliable estimates of survival rates in polar bears were not available at the start of my research, and in general, obtaining reliable estimates of survival is a major obstacle to population dynamics analyses (Eberhardt 1985). I estimated, with 95% confidence, that annual survival of adult female polar bears is between 0.946 and 0.980. This is higher than any previous estimate, and in line with what appears to be needed to sustain populations of large mammals (Eberhardt 1985). My estimates of survival of litter members were much lower, but eminently reasonable. It was these survival estimates and knowledge of

the movements of bears, gathered by radio telemetry, that allowed me to determine the size and trend of the Beaufort Sea polar bear population.

Polar bears in the Beaufort Sea now appear to be at or near K, and are showing significant density-related effects. The fact of density-dependent responses in reproduction and survival and the effect of those responses on management decisions, however, may be quite different. The degree to which density dependent responses are useful in managing a species depends upon the height and shape of the "yield curve." A tall yield curve, that is nearly symmetrical, such as is characteristic of white-tailed deer (McCullough 1979) means that many more young are produced when a population is near maximum sustained yield (MSY) than when it is near K. Less fecund species, like polar bears have a shorter yield curve that is strongly skewed to the left (Fowler 1981). Such a curve indicates that total numbers of young produced by a population at K are nearly as numerous as the total number produced at MSY, and that recovery of the population after over-exploitation necessarily will be slow. If the difference in yield is small, the relative gains in harvestable numbers are not great enough for managers to take the risks of managing at MSY. The growth rate I observed, and the growth rate potential for polar bears (Taylor et al. 1987), suggest that managing at MSY might yield relatively few additional harvestable animals. The risks of destabalizing the population if it were pushed below MSY (McCullough 1979) and the long recovery period that would be necessary, then, might be too great to justify MSY as a management target.

Because the Beaufort Sea population of polar bears has grown over the

last 2 decades, it is clear that the existing harvest is within sustained yield. If an increased harvest, to a stable point (fixed removal yield; McCullough 1979) near MSY becomes the management objective, much better and more timely estimates of population size and K will be needed.

Denning Ecology of Polar Bears

In all recorded history before this project started, only 35 locations of polar bear maternity dens in Alaska were published (Lentfer and Hensel 1980). Many of those 35 were known only approximately, from reports of local residents and early explorers, and the degree of confirmation was highly variable. This dearth of records of dens led many to wonder what was going on, and others to speculate that "Alaska's" polar bears were really not "Alaska's" but visitors from breeding areas in other countries. I found over 100 dens during this study, and verified that there are sufficient numbers of dens in the Beaufort Sea region of Alaska and Northwest Canada to account for the estimated population size here. Over 1/2 of the denning in this region is on offshore sea ice, a discovery that was not expected, and may help explain the failure of earlier workers to find sufficient numbers of dens. The discovery of offshore denning also may explain why cubs of the year were chronically under-sampled in early capture studies.

In addition to the discovery of large numbers of maternal dens in the off-shore sea-ice, I discovered that polar bears, contrary to popular beliefs, did not den in the same place each time they were pregnant. Polar bears were largely faithful to the substrates of previous dens, either land or sea-ice, but faithful only to general geographic areas of previous dens. That is, a bear that

denned once along the eastern Alaska coast of the Beaufort Sea was likely to den in eastern Alaska or Western Canada the next time, but not at the same site. Most bears entered their dens in mid-November (11 and 22 November for land and pack ice dens). They appeared to continue foraging right up to the time of den entry. Then, they denned near where they happened to be foraging. The fact that polar bears of the Beaufort Sea den only in ice and snow, rather than in the soil under the snow, combined with the annually variable autumn snow and ice conditions undoubtedly mediated where bears denned each year.

I found more dens at sea than on land, but land denning along the Beaufort Sea coast appeared to be increasing through the duration of the study. The sea ice is a less stable platform for denning than land. Bears that denned at sea drifted up to nearly 1000 km during the winter. Hence, even if the den remained intact through the winter, the predictability of resources upon emergence of the female and her new cubs from their den was limited. I observed that natural phenomena sometimes disrupted dens. The production of cubs from dens at sea, however, was not significantly different than that from dens on land; and dens on land were more vulnerable to a variety of human-caused disruptions.

In addition to questions of the security of animals while in dens, the phenomenon of pack ice denning also suggests questions about navigation capabilities of polar bears . No other vertebrate is passively transported this far "in the blind." So, not only do polar bears range far and wide, they are able to determine where they are and return to previously used areas after long

distances of passive transport. How polar bears accomplish this is unknown.

The preferred region for land denning was the northeast corner of Alaska and adjacent Canada. This region, which includes the "1002 area" of the Arctic National Wildlife Refuge, also holds the highest potential for discovery of commercial hydrocarbon deposits in the U. S. Loss of a large portion of the productivity of the dens from this area could undermine recruitment of polar bears into the Beaufort Sea. Clearly, there is the potential for many disruptions of dens in this region. Observations of polar bear dens that were exposed to varying levels of human disturbance, however, indicated that many denned bears that are exposed to human activities will not be exposed in ways that alter their productivity. The low density of dens in the Beaufort Sea region and the nature of proposed human activities also indicated that many dens simply would not be exposed. Rigorous adherence to flexible management of human activities, including spatial and temporal restrictions, should prevent the potential for many disruptions of dens from being realized.

The general distribution of dens in the Beaufort Sea region is now known, but it is largely unexplained. Why, for example, more bears chose to den in the far-eastern corner of Alaska and adjacent Canada, is unknown. The influences of slope, aspect, and elevation are not understood, although we do know that some bears make mistakes in their choices (Clarkson and Irish 1991). Why more than half of the bears I monitored, denned at sea when sea-ice denning is unknown right next door in the Canadian High Arctic (Messier et al. 1994), also is unknown. For the present, it may be sufficient to know where polar bears tend to den, and that they are not as sensitive to disturbance as

previously thought (Belikov 1976). If pressures on other resources of the Arctic increase, however, we also will need to know why they den there.

Conclusion

With reasonable management flexibility, the welfare of the polar bear population occupying the Beaufort Sea seems assured. Members of the population range widely within the Beaufort Sea, but seldom move far into adjacent areas. The population is relatively high, perhaps near carrying capacity. Denning is widely scattered in remote areas, and much of the known denning occurs on the pack ice where human interference is unlikely. It appears that only major local perturbations, or widespread changes such as global warming can adversely affect polar bears of this region in the immediate future. On the other hand; although the population is relatively high, it is small in absolute terms. Effects of perturbations lowering survival or recruitment could occur swiftly. Conversely, detecting those effects and responding to them with management actions likely will be slow. The biological potential for recovery from any perturbation is low because of the low reproductive rate of polar bears in the Beaufort Sea. Hence, vigilance is mandatory despite the relatively optimistic outlook.

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