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Polar Bears and Seals in the Eastern Beaufort Sea and Amundsen Gulf: A Synthesis of Population Trends and Ecological Relationships over Three Decades

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ABSTRACT. In the eastern Beaufort Sea and Amundsen Gulf, research on polar bear populations and their ecological interrelationships with seals and sea ice conditions began in the fall of 1970. Analysis of movement data from mark-recapture studies and tracking of adult female bears with satellite radio collars indicated that there are two populations of polar bears in the area, one that inhabits the west coast of Banks Island and Amundsen Gulf and a second that is resident along the mainland coast from about Baillie Islands in Canada to approximately Icy Cape in Alaska. Polar bears throughout the Beaufort Sea and Amundsen Gulf were severely overharvested before the establishment of quotas in Canada in 1968 and the cessation of all but subsistence polar bear hunting in Alaska in 1972. Since then, both populations have recovered, and the population estimates currently used for management purposes are 1200 and 1800 for the Northern and Southern Beaufort populations, respectively. However, these population estimates are now dated and should be redone. Most female polar bears in the Beaufort Sea breed for the first time at 5 years of age, compared to 4 years of age in most other populations, and cubs normally remain with their mothers for 2.5 years prior to weaning. Heavy ice conditions in the mid-1970s and mid-1980s caused significant declines in productivity of ringed seals, each of which lasted about 3 years and caused similar declines in the natality of polar bears and survival of subadults, after which reproductive success and survival of both species increased again. The changes in the sea ice environment, and their consequent effects on polar bears, are demonstrable in parallel fluctuations in the mean ages of polar bears killed each year by Inuit hunters. In 1989, the decadal-scale pattern in fluctuations of ice conditions in the eastern Beaufort Sea changed in response to oceanographic and climatic factors, and this change has resulted in greater amounts of open water in recent years. In addition, climatic warming will be a major environmental factor if greenhouse gas emissions continue to increase. It is unknown whether the ecosystem will return to the pattern of decadal-scale change exhibited in previous decades, or how polar bears and seals will respond to ecological changes in the future, but research on these topics is a high priority.

Key words: polar bear, ringed seal, Beaufort Sea, harvest, climatic fluctuation

RÉSUMÉ. C'est à l'automne de 1970 qu'a débuté, dans la mer de Beaufort orientale et le golfe Amundsen, la recherche sur les populations d'ours polaires et leurs interactions écologiques avec les phoques et l'état de la glace marine. Une analyse des données de déplacement obtenues à partir d'études effectuées selon la méthode marquage-recapture et à partir de la localisation d'ourses adultes munies de colliers émetteurs en liaison avec un satellite a révélé qu'il existait deux populations d'ours polaires dans la région, l'une habitant le rivage ouest de l'île Banks et le golfe Amundsen et l'autre la côte continentale depuis environ les îles Baillie situées au Canada jusqu'à Icy Cape en Alaska. Avant l'établissement de quotas au Canada en 1968 et la suspension de la chasse à l'ours polaire en Alaska en 1972 – à l'exception de la chasse de subsistance –, ces animaux faisaient l'objet d'une surexploitation intense dans l'ensemble de la mer de Beaufort et du golfe Amundsen. On a assisté depuis à un rétablissement des deux populations, et les estimations servant actuellement à des fins de gestion sont respectivement de 1200 et de 1800 pour les populations du nord et du sud de la mer de Beaufort. Ces estimations remontent cependant à un certain temps et elles devraient être recalculées. La plupart des ourses polaires dans la mer de Beaufort s'accouplent pour la première fois à l'âge de cinq ans alors que, pour la plupart des autres populations, l'âge est de quatre ans, et les oursons restent normalement avec leur mère deux ans et demi avant le sevrage. Au milieu des années 70 et 80, des conditions de glace épaisse ont provoqué d'importantes baisses dans la productivité des phoques annelés, chaque épisode durant environ trois ans et résultant en des baisses similaires de la natalité des ours polaires et de la survie des jeunes adultes, après quoi le succès de reproduction et la survie des deux espèces augmentaient à nouveau. Des fluctuations parallèles dans l'âge moyen des ours polaires tués chaque année par les chasseurs inuits font état des changements dans le milieu de la glace de mer et des effets qui en ont découlé sur les ours polaires. En 1989, le schéma à l'échelle de temps décennale dans les fluctuations des conditions de glace marine dans la mer de Beaufort orientale a changé en réponse à des facteurs océanographiques et climatiques, et ce changement a résulté en une plus grande surface d'eau libre au cours des dernières années. Le réchauffement climatique sera en outre un facteur environnemental majeur si les émissions de gaz à effet de serre continuent d'augmenter. On ne sait pas si l'écosystème reviendra au schéma de changement décennal tel qu'il s'est manifesté durant les décennies précédentes, ou quelle sera la réponse des ours polaires et des phoques aux changements écologiques dans le futur, mais la recherche dans ces domaines s'avère une priorité.

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Mots clés: ours polaire, phoque annelé, mer de Beaufort, prélèvement, fluctuation climatique

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INTRODUCTION

Research on the population ecology of polar bears (*Ursus maritimus*) in the eastern Beaufort Sea and Amundsen Gulf was initiated in the fall of 1970 as part of the Canadian response to worldwide concern about the conservation of polar bears, which began about 40 years ago. Through the 1950s, and particularly during the 1960s, there was a rapid rise in the recorded number of polar bears killed, probably because of higher prices being paid for polar bear hides and the increasing use of oversnow machines, aircraft, and boats for hunting (Stirling, 1988; Prestrud and Stirling, 1994). In Canada, for example, the recorded harvest fluctuated between 350 and 550 during 1953–64, but rose suddenly to 726 in 1967 (Schweinsburg, 1981). In Alaska, meanwhile, trophy kills alone increased from 139 bears in 1961 to 399 in 1966 (Lentfer, 1970), and there was a similar pattern in Greenland and Svalbard (Lønø, 1970; Larsen, 1986; Born, 1991). Uspenski (1977) estimated that more than 150 000 polar bears had been killed or captured in Eurasia since the beginning of the 18th century. In Russia, all legal hunting of polar bears ceased in 1956. The size of the unrecorded harvest of polar bears throughout the circumpolar Arctic will never be known, but clearly it was substantial.

Concern about polar bears culminated in the first international meeting on the conservation of the polar bear in Fairbanks, Alaska, in 1965 (Anon., 1966). Among other things, the five "polar bear" nations agreed to conduct a polar bear research program within their respective territories and to exchange information freely. The cooperative spirit that emerged from that first meeting later led to the Agreement on the Conservation of Polar Bears that was signed in Oslo, Norway, in 1973 (Stirling, 1988: Appendix I). Among other things, the signatory countries agreed on three issues of particular relevance both to Canada and to subsequent studies of polar bears in the Western Canadian Arctic: 1) to prohibit all taking (including hunting, killing, and capturing) of polar bears except for specific exceptions, such as traditional hunting, defence, and research (Articles I and III); 2) to protect the ecosystems of which polar bears are a part (Article II); and 3) to conduct national research programs on polar bears (Article VII). The Agreement specifically allows for hunting and capturing of bears "by local people using traditional methods in the exercise of their traditional rights and according to the law of that Party; or wherever polar bears have or might have been subject to taking by traditional means by its nationals" (Article III, d and e).

In the 1960s, there was no information on how many polar bears there were anywhere in Canada, on whether they were part of a single worldwide population as suggested by Pedersen (1945), or whether there were several separate subpopulations that would have to be managed independently. The Government of the Northwest Territories (NWT), faced with a rapidly increasing harvest, but no idea at what level it could be sustained, responded by establishing arbitrary interim quotas for each community in 1968, with the understanding those quotas would be revised as new data became available (Kwaterowsky, 1967; Schweinsburg, 1981).

Thus, in 1970, the initial objectives of the new research on polar bears in the eastern Beaufort Sea and Amundsen Gulf were quite straightforward: to determine the size and discreteness of the resident polar bear population, its longevity and reproductive rates, and the location of the most important denning areas, and to estimate the sustainable level of harvest so the quotas could be adjusted accordingly. In addition, because of the unique aspect of the Agreement on the Conservation of Polar Bears that requires signatories "to conserve the ecosystems of which polar bears are a part," it was also important to focus attention on the ecological relationships between polar bears, the seals they preyed upon, and their sea ice habitat.

I have attempted here to: 1) give an integrated overview of what we have learned about population trends and ecological relationships of polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf over the past three decades; 2) comment on the conservation of polar bears and seals within an ecosystem context; and 3) make some suggestions about future priorities and possible concerns in the new millennium.

METHODS

The Study Area

The study area was defined as the eastern Beaufort Sea east of 141° W and south of 75° N, including Amundsen Gulf (Fig. 1; Ayles and Snow, 2002). The distribution of sea ice, leads, and polynyas and the chronology of freeze-up and breakup are determined by marine currents, wind, temperature, seasonal climate changes, and movement of the polar pack ice. A defining feature of the marine ecosystem of the eastern Beaufort Sea is that it borders on the Arctic Ocean, from which it receives a steady inflow of cold and relatively unproductive polar water (Pomeroy, 1997) via a continuous clockwise current (the Beaufort Gyre). This current flows south from the polar basin along the west coast of Banks Island through the Cape Bathurst polynya, where it mixes with westerly currents from Amundsen Gulf, passes westward along the Alaskan coast, and then flows back north toward the pole (Wilson, 1974). In almost all months, there is at least some open water in the shore lead and polynya system that parallels the coast

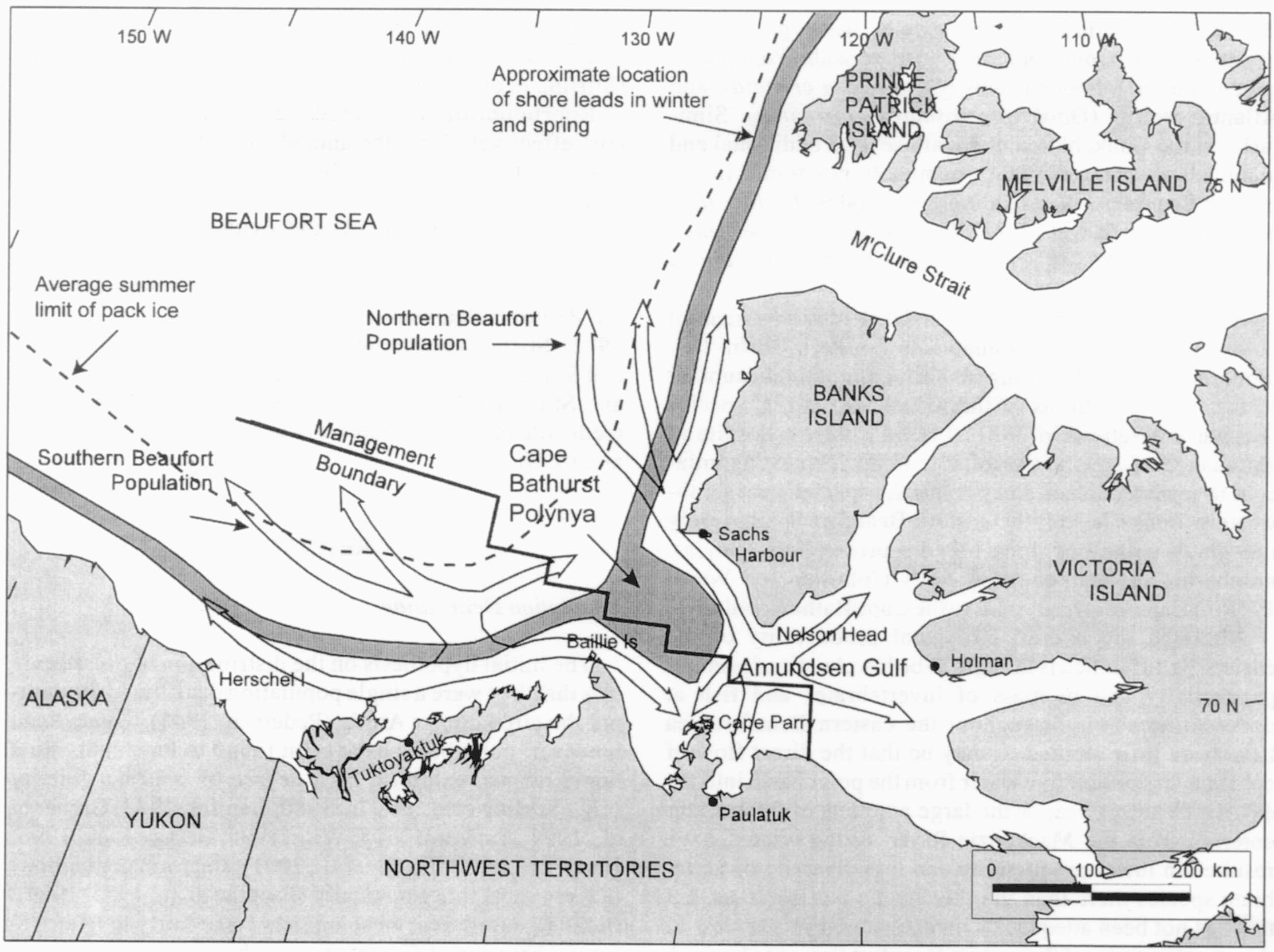

FIG. 1. Map of the Beaufort Sea showing the approximate distribution and seasonal movement patterns of polar bears from the Northern Beaufort and Southern Beaufort populations in relation to the major shore leads, the Cape Bathurst polynya, and the southern extent of pack ice during summer. The southerly and easterly arrows indicate the direction of movements of bears in late fall from the offshore multi-year pack to winter and spring feeding areas, and the northerly arrows indicate the movements of bears in late spring back to summering areas in the offshore pack.

from Prince Patrick Island south through the Cape Bathurst polynya and west along the mainland coast (Smith and Rigby, 1981). The distribution of seals (and consequently of the polar bears that hunt them) is strongly influenced by the distribution of shore leads, polynyas, and areas of annual and multi-year ice, and by both short- and longer-term variations in the pattern of freeze-up and breakup.

Freeze-up of the open water between the land and the offshore multi-year ice usually occurs between mid-October and mid-November, while breakup occurs between late May and late June (Smith and Rigby, 1981). In late summer along the mainland coast, the sea may be ice-free for up to 250–350 km offshore or, in occasional years, as little as a few kilometres (Lindsay, 1975, 1977; Gloerson et al., 1992). However, because of the constant presence of multi-year pack ice to the north, polar bears in the Beaufort Sea can simply move farther offshore to remain on ice during the open water season in summer and fall (Fig. 1). They are not forced ashore to fast on their stored fat reserves for extended periods as bears are in other places, such as Hudson Bay or southeastern Baffin Island (Stirling et al., 1977a, 1980; Ferguson et al., 1997).

There is generally more relief along the south and southeastern coast of Banks Island and western Victoria Island than along the coast of the Tuktoyaktuk Peninsula and western Banks Island. The width of the continental shelf is variable along the west coast of Banks Island and the mainland coast. It is widest off the Tuktoyaktuk Peninsula and narrowest along the Yukon coast. The seaward boundary of the winter landfast ice along the Tuktoyaktuk Peninsula coincides roughly with the 20 m depth contour (Cooper, 1974).

The diversity of marine mammals and seabirds in the eastern Beaufort Sea is significantly lower than in some other parts of the maritime Arctic, such as Baffin Bay to the east or the Chukchi Sea to the west. In the eastern Beaufort Sea, marine mammal diversity is restricted to polar bears, ringed seals (*Phoca hispida*), bearded seals (*Erignathus barbatus*), bowhead whales (*Balaena mysticetus*), and white whales (*Dephinapterus leucas*).

Baffin Bay, in addition to these species, has large numbers of narwhals (*Monodon monoceros*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), and Atlantic walrus (*Odobenus rosmarus rosmarus*). Similarly, in the Chukchi Sea, there are several additional and abundant species of marine mammals not found in the eastern Beaufort Sea, including grey whales (*Eschrichtius robustus*), Pacific walrus (*Odobenus rosmarus divergens)*, spotted seals (*Phoca largha*), and ribbon seals (*Phoca fasciata*).

A comparison of the numbers and distribution of seabird colonies is even more dramatic. In northern Baffin Bay alone, colonial cliff-nesting seabirds cumulatively number in the tens of millions of individuals of several species (Brown and Nettleship, 1981). In stark contrast, despite an abundance of apparently suitable cliffs for nesting adjacent to recurrent leads and polynyas, especially on southwestern Banks Island, the eastern Beaufort Sea has only one small colony of thick-billed murres (*Uria lomvia*), numbering fewer than 1000 birds (Johnson and Ward, 1985) at Cape Parry, adjacent to the Cape Bathurst polynya.

Although the overall biological productivity of the eastern Beaufort Sea is thought to be low, levels of primary productivity and biomass of invertebrates and fish at different locations throughout the eastern Beaufort Sea have been little studied. It may be that the direct flow of cold and less productive water from the polar basin into the eastern Beaufort Sea, or the large amounts of fresh water entering from the Mackenzie River during winter, have resulted in lower productivity and less diversity of vertebrate species there than in other Arctic marine areas, but this has not been adequately investigated. For a review of the oceanography of the eastern Beaufort Sea, see Carmack and Macdonald (2002).

Field Techniques

Details of the field methods and data collected in population studies of polar bears during 1971–79, 1985–87, and 1992–94 are summarized by Stirling et al. (1980, 1993) and Stirling and Lunn (1997). Briefly, however, delineation of the boundaries of the north and south Beaufort polar bear populations was based on analyses of data on the movements of tagged male and female polar bears and tracking of adult females with conventional and satellite radios (Amstrup, 1986; Stirling et al., 1988; Taylor and Lee, 1995; Bethke et al., 1996; Amstrup et al., 2000). There are no comparable tracking data for adult males because their necks are larger than their heads, and radio collars will not stay on. Estimates of polar bear population size were based on analyses of mark-and-recapture data gathered in both Canada and Alaska (DeMaster et al., 1980; Amstrup et al., 1986, 2001a). A vestigial premolar tooth was collected from all captured bears and from most bears killed by Inuvialuit hunters to determine the age structure of the harvest and capture samples (Calvert and Ramsay, 1998). Age- and year-specific reproductive parameters of polar bears were calculated from data collected on adult females captured with and without cubs (Stirling et al., 1980).

Reproduction of ringed seals can be monitored cost-effectively from the annual harvest taken during the open water season by Inuit hunters. In a normal population, at least 30–40% of the seals taken are young-of-the-year (YOY), and ovulation rates of adult females normally exceed 80% (McLaren, 1958; Smith, 1987). Data on ringed seal abundance and reproduction in the Beaufort Sea were taken from Stirling et al. (1977b, 1982), Stirling and Archibald (1977), Smith (1987), Smith and Stirling (1978), Kingsley and Byers (1998), Harwood and Stirling (1992), and Harwood et al. (2000). Canine teeth collected from seals were aged following Stewart et al. (1996).

RESULTS

Population Delineation

The initial hypothesis on the distribution of polar bears was that they were a single population distributed throughout the circumpolar Arctic (Pedersen, 1945). Since then, however, polar bears have been found to have individual home ranges, exhibit a high degree of seasonal fidelity (e.g., Stirling et al., 1977a, 1980; Lentfer, 1983; Garner et al., 1994; Amstrup, 1995; Wiig, 1995; Bethke et al., 1996; Born et al., 1997; Taylor et al., 2001), and form populations that are separable genetically (Paetkau et al., 1995, 1999). In the Beaufort Sea, most animals make fairly long movements between different geographic areas at different seasons of the year. Thus, in summer, they are well offshore in the multi-year pack of the Beaufort Sea or off the northern coast of Banks Island, while in winter they move south toward the shoreline of the mainland coast or Amundsen Gulf. They show fidelity to each area in the same season of different years. Thus the distance between original capture locations and re-capture locations is shorter for animals caught in the same season of different years (because they tend to be back in the same area) than for bears caught in a particular season of one year and in a different season in a subsequent year (because the two locations will normally be in different areas and likely distant from each other). Thus, one of our first findings was that bears captured in the eastern Beaufort Sea and Amundsen Gulf or near Barrow, Alaska, in spring and recaptured or shot by hunters in the spring of a subsequent year tended to be in the same general areas where they were first caught (Stirling et al., 1975; Lentfer, 1983). Bears tagged in one season and recaptured in another (e.g., spring to fall) moved farther between those two points than those caught in the same season of different years, but few bears were recorded moving between Barrow, Alaska, and Canada in the 1970s. Thus, at that time, when our sample sizes were still relatively small, we thought that polar

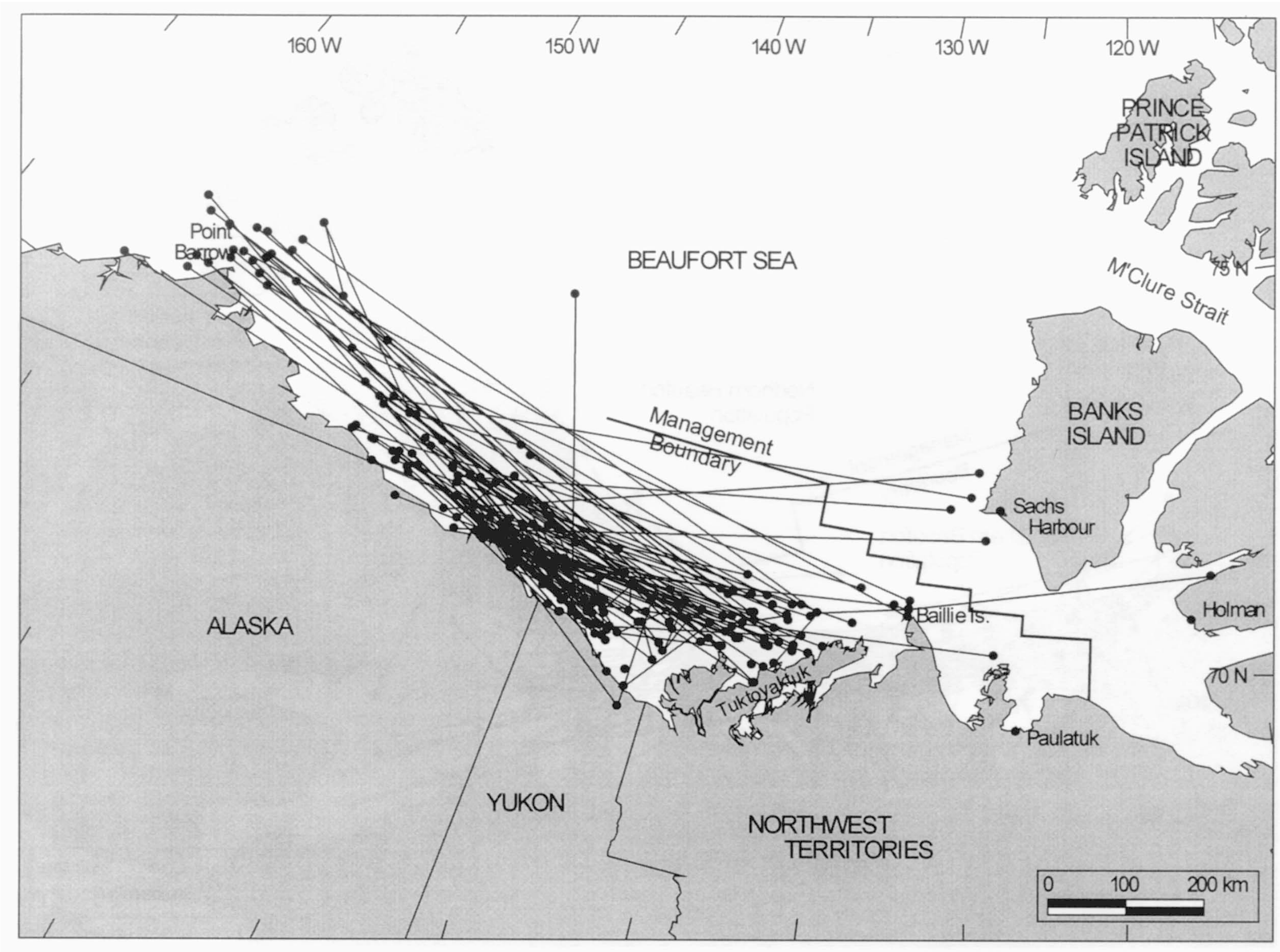

FIG. 2. Movements of polar bears from where they were first caught in Canada and recaptured or shot in Alaska, and vice versa, between 1968 and 1994.

bears from the western and eastern Beaufort Sea did not mix extensively (Stirling et al., 1975; Lentfer, 1983), so that, for management purposes at least, they could be considered separately.

By the 1980s, much larger samples of bears were being tagged throughout the eastern Beaufort Sea, and the tagging effort in Alaska was distributed east from Barrow to the Canadian border. From the movements of bears tagged in Canada and recovered in Alaska and vice versa (Fig. 2), and from tracking individual adult females fitted with conventional VHF radio collars (Amstrup, 1986), it appeared that the bears found along the mainland coast from west of Barrow, Alaska, to about Baillie Islands, NWT, formed a single population, currently known as the Southern Beaufort population. After the capture effort became distributed across the entire coast of the southern Beaufort Sea, from Barrow to Baillie Islands, Amstrup (1995: Fig. 10) demonstrated that, because of the relatively high degree of seasonal fidelity, the probability of a bear that was first tagged in a particular area of the mainland coast being recaptured in the same season in subsequent years declined steadily with distance from the original capture site. Since the bears' movements and home ranges are essentially independent of one another, subpopulations are concentrations of polar bears with independent but overlapping home ranges that are separated from each other to varying degrees by geographic barriers or seasonal patterns of breakup and freeze-up (Stirling, 1988). Thus, it became clear that the distribution of bears throughout the southern Beaufort Sea formed a continuum of home ranges of variable density, and that the earlier conclusion that polar bears in the Canadian and Alaskan areas of the Beaufort Sea were independent was simply a reflection of an incomplete distribution of tagging and search effort. Largely in response to the accumulated data on movements of polar bears, the Inuvialuit of Canada and the Inupiat of Alaska developed an agreement for the co-management of the southern Beaufort Sea polar bear population (Stirling, 1988: Appendix II; Nageak et al., 1991; Brower et al., in press). This co-management agreement, first signed in 1988, was formally revised and reaffirmed in 1990.

Similarly, an examination of the subsequent movements of polar bears first tagged in either the southern or the

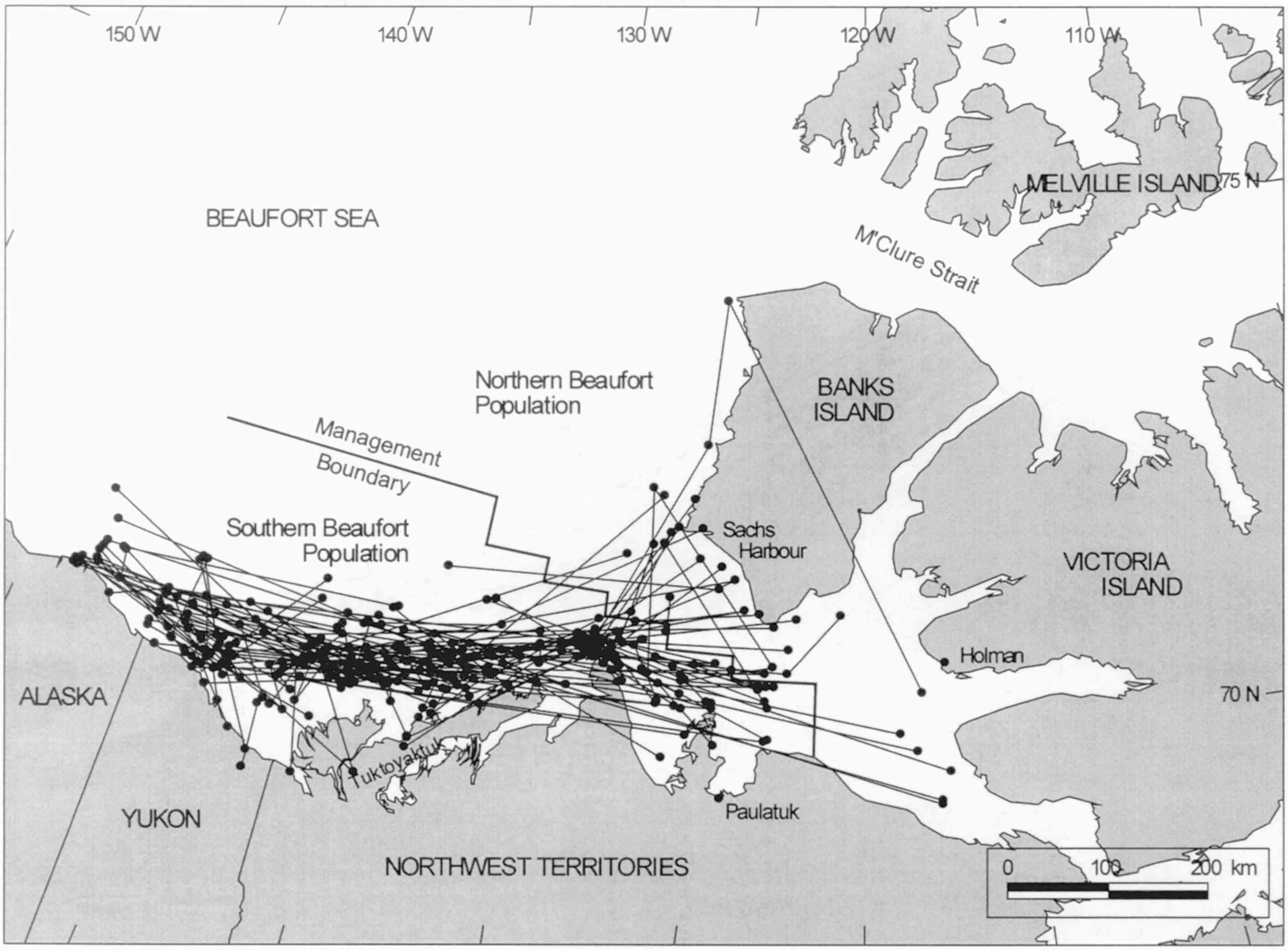

FIG. 3. Movements of polar bears from where they were first tagged in the Canadian portion of the Southern Beaufort Sea population to where they were recaptured or shot, in Canada or near the Canadian border in Alaska, 1970–98.

northeastern area of the Beaufort Sea indicates that, while there is overlap around the area of the Cape Bathurst polynya, there is enough separation of the two populations (now called the Southern Beaufort and Northern Beaufort) to warrant independent management (Figs. 3 and 4). The later addition of data from tracking of females with satellite radios (Bethke et al., 1996; Amstrup et al., 2000) further confirmed the separation of the Northern Beaufort and Southern Beaufort populations. These two populations appear to be kept apart largely by seasonal patterns of breakup and freeze-up of the ice (particularly in the area adjacent to the Cape Bathurst polynya) that influence their seasonal movements (Fig. 1; Stirling, 1990). Finally, in a recent analysis of specimens from bears captured in the Southern and Northern Beaufort Sea, Paetkau et al. (1995, 1999) detected a genetic difference between bears from the Northern Beaufort and Southern Beaufort populations (albeit at a level that was not statistically significant). This finding also supports the conclusion that these populations can be considered independently for management purposes. Local, population-specific management agreements with the government of the Northwest Territories, modelled on the Inuvialuit-Inupiat Polar Bear Management Agreement for the Southern Beaufort Sea, were then developed and signed in 1991 by the hunters and trappers committees from all the communities that harvest polar bears from these Beaufort populations (Calvert et al., 1995).

Additional satellite radios need to be deployed in the area between the Tuktoyaktuk Peninsula and Nelson Head and south to Cape Parry to further refine details of bear movements in the area of overlap between the Northern and Southern Beaufort polar bear populations, although it seems unlikely that further studies will result in major changes to the population boundaries. The most recent analysis of satellite tracking data from the Canadian and Alaskan Beaufort Sea (Amstrup et al., 2000) indicates the possibility of two subgroups within the area formerly considered to contain the Southern Beaufort population, as well as the previously identified populations to the west in the Chukchi Sea and to the north in the northern Beaufort Sea. However, until reassessment of population size in the entire Beaufort Sea and Amundsen Gulf region has been

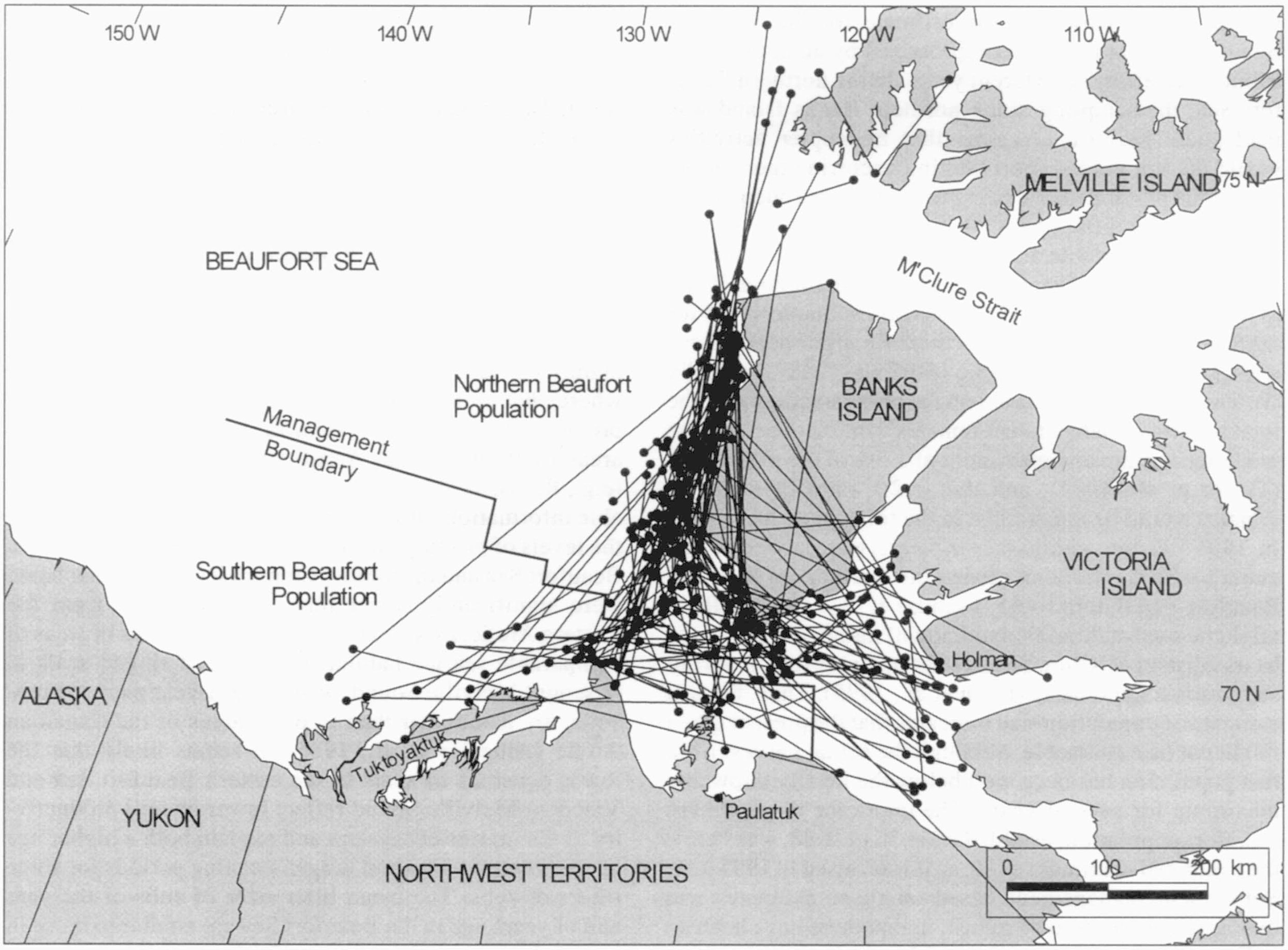

FIG. 4. Movements of polar bears first tagged in the Northern Beaufort Sea population to where they were recaptured or shot, 1971–98.

completed, these new findings are not expected to result in significant changes to how the Southern Beaufort population is managed.

Although some satellite collars were deployed along the west coast of Banks Island (Lunn et al., 1995) and in M'Clure Strait (Bethke et al., 1996), the resulting movement data were insufficient to clarify where the northern boundary of the Northern Beaufort population might be, though it may be toward the northern end of Prince Patrick Island. This is important to know because it will affect the distribution of search effort for any future attempt to estimate population size. From 1992 to 1994, we tracked eight adult females for one year and three for two years and found, for the most part, that bears resident around the western entrance to M'Clure Strait and western Prince Patrick Island did not mix extensively with those on the west coast of Banks Island (Lunn et al., 1995). Most bears remained to the west of Prince Patrick Island, but some travelled northeast along the shore lead system all the way to East Greenland. Paetkau et al. (1999), using genetic data, also demonstrated that the populations most closely related to the Northern Beaufort were the Southern Beaufort and East Greenland populations. These lie to the southwest and northeast, respectively, along the system of shore leads and polynyas that runs parallel to the coast (Smith and Rigby, 1981) and most affects the movement patterns of the bears.

Population Assessment and Demographic Parameters

When the first population study began, there was no information on the size of the population. Because the initial conclusion from mark-recapture studies was that the bears throughout the eastern Beaufort Sea and Amundsen Gulf constituted a single population, the first estimate of 1800, made in the 1970s, referred only to the Canadian sector of the eastern Beaufort Sea and Amundsen Gulf (DeMaster et al., 1980). Following the realization that there were two populations, separate estimates were made of approximately 1800 for the Southern Beaufort and 1200 for the Northern Beaufort (Amstrup et al., 1986, 2001a; Stirling et al., 1988; IUCN Polar Bear Specialist

Group, 1998). However, the estimate for the Southern Beaufort population was compromised by an uneven distribution of effort in different years. In the northern Beaufort Sea, the sampling along northern Banks Island was inadequate because concerns that helicopter activities would disrupt guided sport hunting occurring there at the same time precluded searching the entire area adequately.

The estimates of population size were based on the best information available at the time, and in 1988, when the Inuvialuit-Inupiat Management Agreement for Polar Bears in the Southern Beaufort Sea was signed, quotas of 76 for the Southern and 59 for the Northern Beaufort populations were judged to be sustainable (Stirling, 1988: Appendix II). These quotas were based on the understanding that the total harvest of independent females would not exceed the modelled sustainable maximum of 1.5% of the population (Taylor et al., 1987), and that a 2:1 ratio of males to females would be maintained in the total quota harvested. In 1991–92, an additional six bears were added to the quota for Sachs Harbour, raising the total for the Northern Beaufort population to 65, because it was thought there might be a substantial (but unknown) number of unhunted bears north of M'Clure Strait. Subsequent research did not support this hypothesis (Lunn et al., 1995). Thus, the last estimate of population size indicates that the present quota might not be sustainable, although the actual harvest from this population has been well below the legally allowable maximum for several years. The quota for the Southern Beaufort population, established at 76 in 1988, was below the estimated maximum of 80, so it was raised in 1995–96. Subsequent management based on those estimates and quotas still appears to be robust, in that there have been no indications of overharvest from either the harvest monitoring study or local knowledge. In Canada, the harvest from both the Northern and Southern Beaufort populations has also been below the allowable quota in recent years, mainly because not all the tags allocated to guided sport hunters were used each year, and rough ice conditions and open water in late winter and spring have made it more difficult for hunters to reach the bears in some years (Brower et al., in press).

Baseline Demographic and Reproductive Parameters

The maximum recorded ages were 31 years for both male and female polar bears from the Northern Beaufort Sea population and 26 years for males and 29 years for females from the Southern Beaufort population. These ages are similar to the maximum longevity found in other areas, such as western Hudson Bay, where the populations were not overharvested at the time they were sampled (Derocher et al., 1997).

The age of first breeding of most female polar bears in the Beaufort Sea is 5 years (Stirling et al., 1976; Lentfer et al., 1980) and they produce their first cubs at the age of 6, a year later than in most other areas (Furnell and Schweinsburg, 1984; Stirling et al., 1984; Ramsay and Stirling, 1988). Most cubs in the study area are weaned at 2.5 years of age, as they are in most other areas except western Hudson Bay, where some cubs are successfully weaned at 1.5 years of age (Ramsay and Stirling, 1988). In contrast, in areas such as Viscount Melville Sound, where multi-year ice prevails and seal densities are low, some females may not wean their cubs until they are 3.5 years old (F. Messier and M.K. Taylor, pers. comm. 1999). Two females from the Northern Beaufort population, accompanied by 3.5-year-old cubs, were also captured on the west coast of Banks Island (Stirling et al., 1975).

It is uncertain why female polar bears reach sexual maturity a full year later in the Beaufort Sea than elsewhere, but it may be a consequence of lower overall productivity in the ecosystem in comparison with other areas of the Canadian Arctic such as Lancaster Sound (e.g., Roots, 1980). In a preliminary comparison of available information, Stirling and Øritsland (1995) found that the levels of primary production reported from the eastern Beaufort Sea and the multi-year pack ice of the polar basin were significantly lower than those reported from the Eastern Arctic, as were densities of ringed seals in areas of comparable sea ice habitat. Densities of ringed seals in Viscount Melville Sound, where multi-year pack ice prevails, are also lower than in other areas of the Canadian Arctic (Kingsley et al., 1985). It seems likely that the lower densities of seals in the eastern Beaufort Sea and Viscount Melville Sound reflect lower overall productivity in the marine ecosystem and explain both a higher age of first reproduction and longer weaning periods for some litters of cubs. The mean litter sizes of cubs-of-the-year and of yearlings in the Beaufort Sea are similar to those in most other areas of the Arctic (Stirling, 1988).

Maternity Denning

Identification and protection of core denning areas was a priority agreed to at the first international meeting on polar bears held in Alaska in 1965 (Anon. 1966) and reiterated in Article II of the Agreement on the Conservation of Polar Bears (Stirling, 1988: Appendix I). At first, we thought it would be straightforward to identify denning areas in the eastern Beaufort Sea and Amundsen Gulf because indigenous people had travelled extensively on the land throughout the area during winter and spring for many years. However, when we summarized information from hunters on where maternity denning was known to occur and not to occur, and did additional surveys ourselves, most dens reported were on the western and southern coasts of Banks Island, and there were few occurrences along the Canadian mainland coast and nearby islands (Stirling and Andriashek, 1992).

Meanwhile, extensive searches along the Alaskan coast resulted in discovery of very few additional maternity dens (Lentfer et al., 1980; Amstrup and Gardner, 1991). Some Inuvialuit hunters in Canada, being aware of the paucity of dens in coastal Alaska, had concluded that Alaskans, including those using aircraft prior to the passage of the Marine Mammal Protection Act in 1972, must be hunting bears that originated from the well-known denning areas on western and southern Banks Island. The first significant clue to what was really happening came when Lentfer (1975) found a maternity den and family group with young cubs just out of the den so far offshore across open leads that he concluded they must have denned on the multi-year pack ice. Although one Inuvialuit hunter reported finding a female with cubs in a maternity den on a multi-year ice floe south of Nelson Head in the early 1970s (J. Memorana, pers. comm. 1975), extensive maternity denning in offshore ice was not an idea that I heard suggested by any hunters. Amstrup (1986) and Amstrup and Gardner (1994) subsequently reported that 53% of 90 polar bear maternity dens found by deploying satellite radio collars on adult females captured along the mainland coast of northern Alaska and Canada were in the multi-year pack ice up to about 300 km offshore. Although there is no way of knowing whether female polar bears have always denned offshore in the southern Beaufort Sea, it is clear that they do so now.

The reasons why such a high proportion of the female polar bears in the Southern Beaufort population den offshore, in habitat so different from that preferred by bears in other areas, appear to be a mixture of natural and anthropogenic factors (Stirling and Andriashek, 1992). The first is the distribution of pack ice adjacent to the coast of the eastern Beaufort Sea in late October and early November, when most pregnant females enter their dens (Harington, 1968). The landfast ice freezing out from the coast first connects the mainland with the offshore pack ice in the vicinity of Herschel Island, and then progresses east to the northwestern coast of Banks Island and spreads south from there (Lindsay, 1975, 1977). The Cape Bathurst polynya, to the northeast of the Tuktoyaktuk Peninsula, is the last area to consolidate, and in some years, large areas of open water may persist until late winter (Smith and Rigby, 1981). Consequently, the pattern of freeze-up facilitates pregnant female polar bears' reaching the Yukon coast or the small offshore islands west of the Tuktoyaktuk Peninsula, while open water may make their access to the land farther east more difficult in some years. Lentfer et al. (1980) reported that the first shorefast ice along the mainland coast of Alaska forms between the Colville River and the Canadian border. They suggested that this ice facilitates pregnant female polar bears' reaching the land from the drifting pack and explains the greater prevalence of maternity dens there than elsewhere in Alaska. They further speculated that in years when the pack ice does not reach the coast until later in the winter, female polar bears may not be able to reach the coast or offshore islands and could be forced to den on the drifting pack instead. In contrast, the drifting pack ice lies relatively close to the west coast of Banks Island in fall in most years (Lindsay, 1975, 1977), and therefore pregnant females are able to reach land to establish maternity dens.

The second factor that probably contributed to the low numbers of denning female polar bears observed along the mainland coast of the southern Beaufort Sea is that the area from the Tuktoyaktuk Peninsula to western Alaska has been inhabited for over 100 years by whalers and aboriginal hunters equipped with firearms. Because adult female polar bears appear to show fidelity to maternity denning areas (Ramsay and Stirling, 1990), they form locally stable populations that are highly vulnerable to extirpation if they are hunted there. Thus, those that regularly returned to the mainland coast to den would have been more vulnerable to hunters and could have been eliminated as the use of firearms became widespread. This hypothesis is supported by Leffingwell's (1919:63) report that, "The natives in the vicinity [Canning River in the Alaskan sector of the Beaufort Sea] shot perhaps a dozen [polar bears] each year, mostly females that were giving birth to young in snow caves under high banks of the land." Although the hunting of polar bears in the Canadian Beaufort Sea area prior to about 30 years ago is not well documented, it is clear from discussion with older hunters that hunting female bears in maternity dens was a common practice throughout the region, including the west coast of Banks Island, until the late 1960s.

As a result of the continuing protection given to bears in dens and female polar bears accompanied by cubs-of-the-year for the last 25 years or so in both Alaska and Canada, it appears that maternity denning on the mainland coast between eastern Alaska and about Baillie Islands has begun to recover and will likely continue to do so (Stirling and Andriashek, 1992; Amstrup and Gardner, 1994).

Ecological Relationships between Seals and Polar Bears

The Agreement on the Conservation of Polar Bears requires signatory countries to manage polar bears according to "sound conservation practices" and to "protect the ecosystems of which polar bears are a part." Thus, we and others conducted a series of interrelated studies on polar bears, the seals they prey upon, and the influence of ice conditions. Many of the results have been published elsewhere (Stirling and McEwan, 1975; Stirling et al., 1977b, 1982, 1993; Smith and Stirling, 1978; Smith, 1987; Harwood and Stirling, 1992; Stirling and Øritsland, 1995; Stirling and Lunn, 1997; Kingsley and Byers, 1998), but an overview of the most important results and some new data in relation to the Beaufort Sea are relevant here.

Throughout their range, polar bears feed predominantly on ringed seals and, to a lesser degree, on bearded seals. Most important, however, is that, although polar bears are capable of catching seals of all age classes, young-of-the-year form the bulk of their diet. Ringed seal pups are born in early April and are weaned at about six weeks of age, by which time they are approximately 50% fat by wet weight. Polar bears prefer fat to other parts of a seal. From shortly after the ringed seal pups are born until breakup of the annual ice in early summer, when they become less accessible to polar bears, the pups are abundant, probably easier to catch because they are less experienced, and represent a high caloric return per unit of energy expended by a hunting polar bear. From analyses of specimens collected from seals killed by bears on the sea ice, it is clear that a very large proportion of the animals they depend on, possibly as high as 80%, are young-of-the-year. Polar bears reach their lightest weights in late March, just before the birth of the next cohort of ringed seal pups, which also suggests it is the success of their hunting in spring and early summer that determines whether or not bears are able to accumulate the body reserves necessary for survival, reproduction, and nursing of cubs through the rest of the year. Thus, if major fluctuations in the biological productivity of Arctic marine ecosystems occur, they will affect the production and survival of ringed seal pups, which in turn will be reflected in the reproductive performance of polar bears and survival of their young.

In the eastern Beaufort Sea, in years during and following heavy ice conditions in spring, we found a marked reduction in production of ringed seal pups and consequently in the natality of polar bears (Stirling and Lunn, 1997). The effect appeared to last for about three years, after which productivity of both seals and bears increased again. These clear and major reductions in productivity of ringed seals in relation to ice conditions occurred at decadal-scale intervals in the mid-1970s and 1980s (Fig. 5) and, on the basis of less complete data, probably in the mid-1960s as well (Stirling et al., 1977b; Stirling and Lunn, 1997). Recent analyses of ice anomalies in the Beaufort Sea have now also confirmed the existence of an approximately 10-year cycle in the region (Mysak, 1999) that is roughly in phase with a similar decadal-scale oscillation in the runoff from the Mackenzie River (Bjornsson et al., 1995).

Another way to demonstrate the effect of lowered production and survival of polar bear cubs is to compare the strength of the year-classes born in 1971–73, when production of ringed seal pups was high, with that of those born in 1974–76, when seal productivity was low. Because of natural mortality, there should usually be more bears in younger age classes than in older ones. However, in every year from 1975 through 1979, bears in the 1971–73 year-classes outnumbered those born in 1974–76 (Table 1), despite having experienced an additional three years of mortality.

In a related analysis, Stirling and Øritsland (1995) demonstrated a significant correlation between the estimated sizes of ringed seal and polar bear populations in seven independent groupings of large-scale strata from the Canadian Arctic and adjoining areas of Greenland and Canada. Kingsley (1998) subsequently made a similar analysis of the relationship between ringed seals and predation by polar bears in Baffin Bay, using slightly different assumptions and data, and came to the same conclusions. There was a significant relationship between the densities of seals and bears in the same areas, indicating that relatively larger or smaller estimates of population sizes were not simply a linear function of the size of the areas compared (Stirling and Øritsland, 1995). Stirling and Øritsland (1995) also estimated that, on average, each bear requires an average of about 43 seals per year, which indicates that the 1800 or so bears in the eastern Beaufort Sea and Amundsen Gulf would require a population of 360 000 ringed seals (or ringed seal equivalents, if bearded seals and occasional belugas are eaten as well). The implication for the polar bear populations of the Beaufort Sea and Amundsen Gulf, which have been in recovery for most of the last 20–25 years, is that there are probably not enough seals in the area to facilitate much growth past their current sizes.

Past Harvest Levels and Indicators from Monitoring the Harvest

In a review of the available harvest records for Northwest Territories settlements between 1962 and 1971, Smith and Taylor (1977) reported maximum annual numbers of polar bear hides traded that significantly exceeded the current estimates of sustainable quotas for the following settlements (current quotas are in parentheses): Holman, 55 (20); Tuktoyaktuk, 37 (26); Sachs Harbour, 48 (28); Coppermine, 38 (6); for a total of 178 (80). No similar data were provided for Paulatuk or Yukon, where polar bear hunting also occurred throughout the same time period. Similarly, anecdotes abound about large numbers of hides being sold to employees of the DEW line stations (which at one time were located at intervals of about 80 km along the whole northern coast of Canada) and then shipped directly to southern Canada and the United States, but these are difficult to confirm. However, in the late 1950s, T.W. Barry (pers. comm. 1975), a former Canadian Wildlife Service (CWS) biologist, visited a single family living near one of the intermediate DEW line sites and recorded they had 24 hides for sale at that time. In 1954, one hunter from Holman killed 54 bears in one winter on the northern coast of Victoria Island (J. Memorana, pers. comm. 1973). Taken together, these data suggest the reported numbers of polar bear hides traded in the eastern Beaufort Sea prior to about 1970 significantly underestimate the actual size of the harvest, probably because many additional animals were used locally or sold directly to individual customers and not through trading posts where records were kept. When compared to current estimates of the size of the sustainable polar bear harvest, these records and anecdotes also suggest that polar bears in the Canadian sector of the Beaufort Sea were being overharvested, at least through the 1960s and likely in the late 1950s as well.

The primary reason for establishing interim quotas for polar bears throughout the Northwest Territories in 1968, and starting population assessments in the early 1970s, was the incomplete but nevertheless convincing documentation of a rapid rise in the number of polar bears being killed, which suggested the likelihood of serious overharvesting (Prestrud and Stirling, 1994). Therefore, the Game Management Service of the Department of Indian and Northern

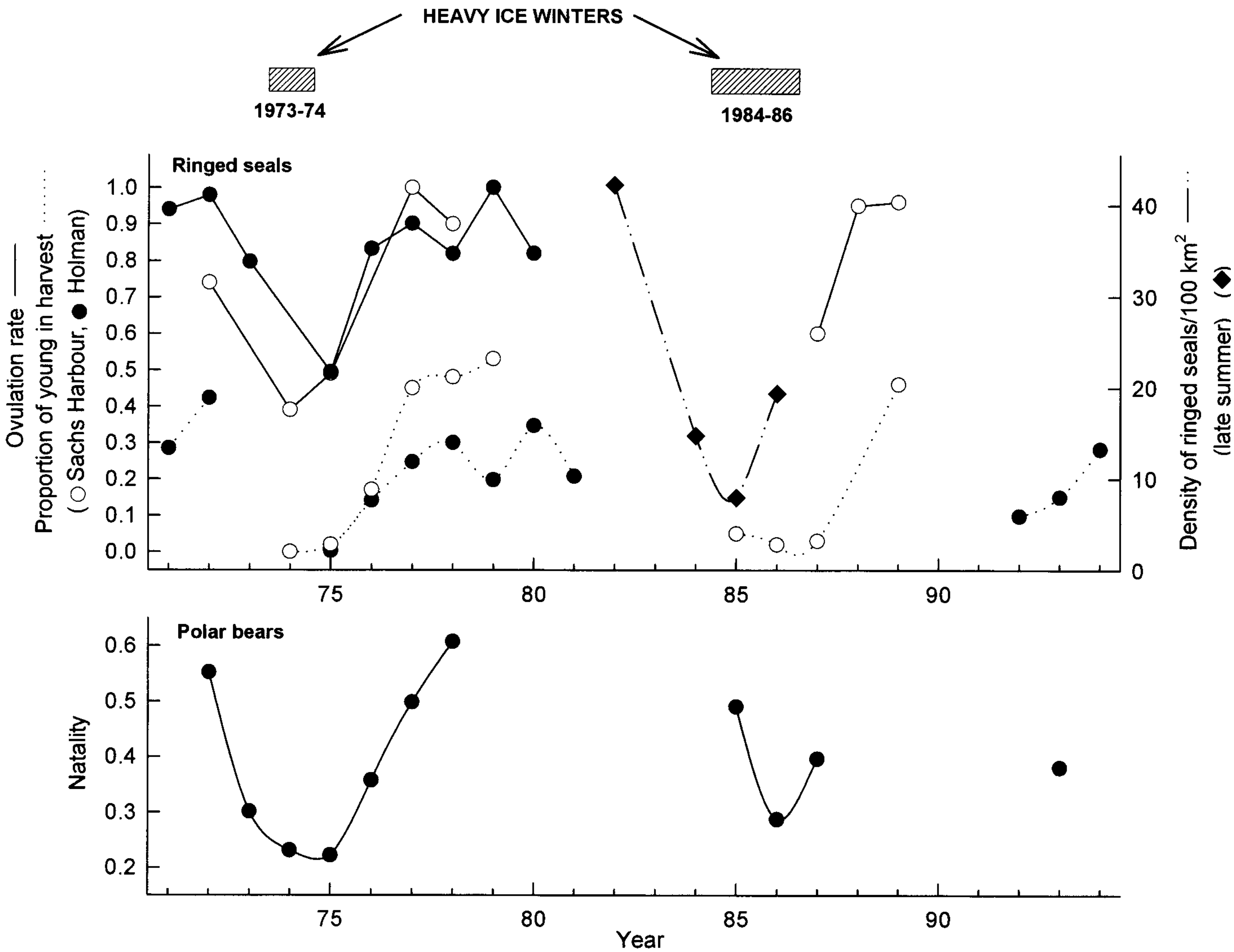

FIG. 5. Changes in indices of productivity of ringed seals and polar bears in relation to winters of particularly heavy ice in the eastern Beaufort Sea from 1971 through 1994. (Data on seals, polar bears, and ice conditions taken from Stirling and Archibald, 1977; Smith and Stirling, 1978; Stirling et al., 1982; Smith, 1987; Kingsley and Byers, 1998; Harwood and Stirling, 1992; Melling, 1996; Stirling and Lunn, 1997; Harwood et al., 2000.)

Affairs, which had the responsibility for polar bear management in the Northwest Territories at the time, established interim quotas for all the settlements. In the absence of scientific information on the size of any polar bear populations, the average of the previous three years' harvests was calculated separately for each village and, to be conservative, a slightly lower level was set as the quota (Kwaterowsky, 1967). It was explained at the time that this was an interim measure and that in due course all settlement quotas would be adjusted up or down in response to population studies when they were eventually completed (Stirling, 1988). Initially, harvest levels decreased in most areas, which concerned Inuit hunters because it directly affected their potential income from selling hides. In 1970, partly in response to that concern, the government of the Northwest Territories introduced guided sport hunting for polar bears to provide a new opportunity for realizing an increased income from the smaller number of animals allowed under the new quota system.

Along with the establishment of quotas, a harvest-monitoring program began that has continued to the present. Initially, data and specimens from the polar bear harvest in the Western Arctic were collected by the Canadian Wildlife Service. Later, this function was taken over by the Northwest Territories Department of Renewable Resources (now the Department of Resources, Wildlife, and Economic Development). Harvest and mark-recapture data from all sources are maintained in a National Polar Bear Data Base managed by the CWS in Edmonton. At first, data were not collected from all the bears killed, but over time, as the hunters became more familiar with the objectives of the program and supported it, the quality of the information improved.

It is informative to examine the data on the sex-specific age structure of bears sampled both in the harvest management program and in the research programs from the early 1970s to the present. Although the patterns were similar, the average ages of captured females and males in the

TABLE 1. Number of polar bears of each age class up to 8 years captured or recaptured between March and July from 1971 through 1979. Brackets on left side of ages in bold type indicate cubs born from 1971 to 1973, while brackets on the right side of ages in italics indicate cubs born from 1974 to 1976.

	Year of Capture								
Age	1971	1972	1973	1974	1975	1976	1977	1978	1979
0	[**0**	[**0**	[**8**	*9*]	*10*]	*3*]	10	6	16
1	2	[**3**	[**10**	[**6**	*5*]	*7*]	*2*]	7	7
2	4	6	[**10**	[**4**	[**11**	*4*]	*0*]	*0*]	3
3	3	7	11	[**11**	[**22**	[**2**	*1*]	*3*]	*1*]
4	3	0	10	17	[**20**	[**8**	[**4**	*1*]	*0*]
5	2	5	7	7	25	[**7**	[**2**	[**3**	*2*]
6	2	4	2	9	19	5	[**3**	[**5**	[**5**
7	2	5	2	3	7	9	3	[**4**	[**6**
8	0	4	2	6	14	4	3	3	[**9**
≥ 9	5	11	27	17	33	14	8	12	20
Unaged	6	3	3	2	1	–	–	–	–
Total	29	48	92	91	167	63	36	44	69

1970s and mid-1980s were consistently higher than those of harvested animals. (The average ages are presented as three-year running means because the variability that characterizes annual values sometimes obscures the longer-term trends that I was interested in examining.) This is because older animals, especially males, tend to prefer the prime hunting habitat in the moving ice adjacent to and offshore from the landfast ice, where seals are abundant, while subadult bears and females accompanied by cubs up to two years of age occur more frequently nearer to the edge of the landfast ice (Stirling et al., 1993) and therefore nearer the coast and the villages. For example, of 45 bears killed by hunters between 1970–71 and 1972–73, only one (2%) was 10 or more years of age, while of 195 bears captured through the same period, 33 (17%) were 10 years or more of age, a difference that was statistically significant ($\chi^2 = 12.7$; $p < 0.05$). On average, shore-based hunters kill bears younger than those in the capture sample because hunters can only reach the floe edge, and occasionally the adjacent pack ice when conditions are favourable, while all offshore habitats out to 160 km or so are accessible by helicopter. Although the average ages of the bears killed by hunters in the eastern Beaufort Sea are clearly indicative of trends in the population, it is important to note that they will usually be slightly lower than those of the population as a whole.

The average ages of both male and female harvested bears were less than 5 years in the early 1970s, slowly increased to about 7 years for males and 9 years for females by the late 1970s, and then fluctuated on roughly a decadal scale between the mid-1970s and mid-1980s (Fig. 6). These patterns reflect three distinct influences: overharvest, recovery, and large-scale environmental fluctuations.

The harvest of polar bears in the Beaufort Sea was unregulated prior to the establishment of quotas in Canada in 1968 and the closing of sport hunting in Alaska in 1972

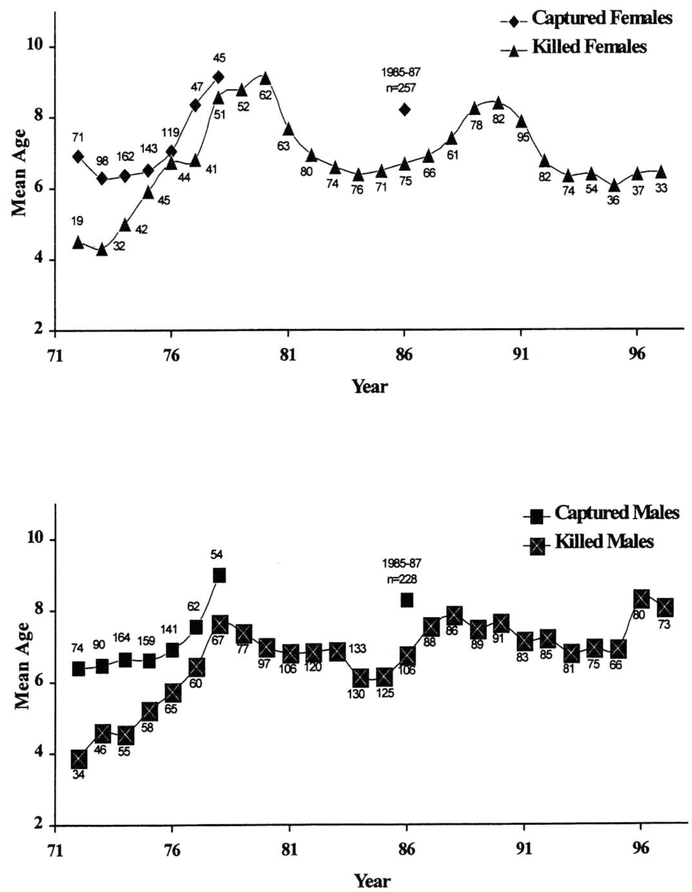

FIG. 6. Average ages of female and male polar bears one year of age and older captured or recaptured or killed by Inuvialuit hunters in the eastern Beaufort Sea and Amundsen Gulf from 1971 through 1998, presented as three-year running means.

(Prestrud and Stirling, 1994). In Alaska, between 1950 and 1972, trophy hunters took 85–90% of the kill. Much of their effort involved extensive use of aircraft to hunt in the offshore pack ice and focused on the largest males that could be located (Amstrup et al., 1986; Prestrud and Stirling, 1994). As a result of the unregulated hunting, polar bears in both the Beaufort Sea populations became severely overharvested. At the beginning of our research, older bears were poorly represented simply because they did not exist. For example, in the Alaskan portion of the Southern Beaufort population, the average ages of male and female bears killed by hunters declined from 8.8 and 6.9 years respectively in 1966 to 5.7 and 5.4 years in 1972 (Amstrup et al., 1986). The average ages of bears killed by shore-based Inuvialuit hunters in Canada in the early 1970s reached similar low levels. Following regulation of the harvest, the polar bear population began to recover fairly quickly, as evidenced by a steady increase in the average ages of both male and female bears taken by hunters in Canada through the 1970s (Fig. 6).

Another indicator of whether a population may be overharvested is the relative presence of older animals, because they tend to be rare in overharvested populations. The three-year running means of the proportion of the harvest of female and male bears that were 10 years of age

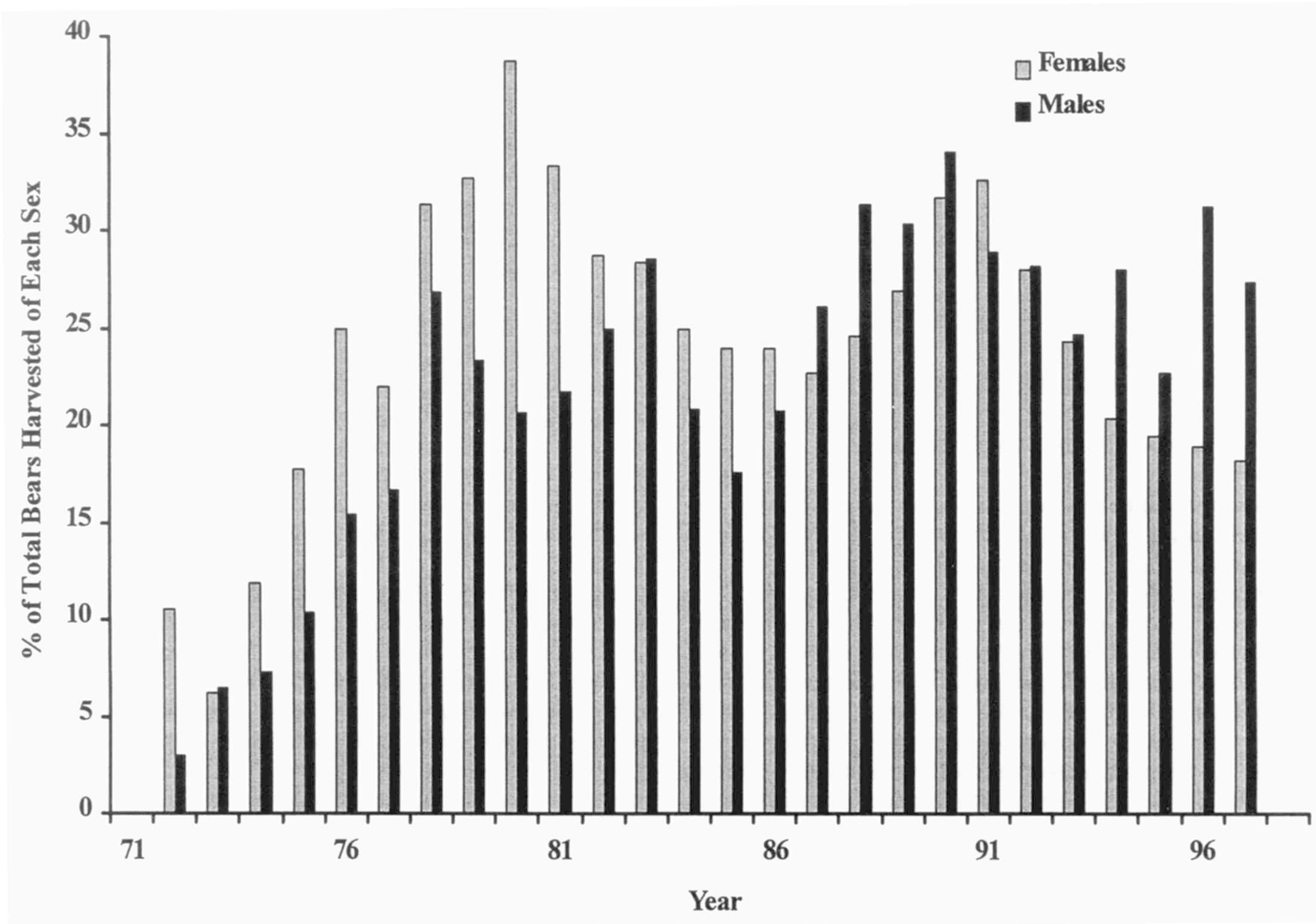

FIG. 7. Proportion of female and male polar bears 10 years of age and older killed by Inuvialuit hunters in the eastern Beaufort Sea and Amundsen Gulf from 1971 through 1998, presented as three-year running means.

or greater from 1971 through 1998 (Fig. 7) show a similar pattern to the mean ages of all harvested bears one year of age or more (Fig. 6). Taken together, the data in Figures 6 and 7 show that the old animals are still abundant in the population when the average age declines, which clarifies that the change is occurring because of an influx of young animals (including higher survival of cubs), and not because large numbers of older ones died. Note that through the early 1970s in particular, animals aged 10 years or more were poorly represented. In the harvest between 1970–71 and 1972–73, the oldest animal recorded was only 11 years old, and the next oldest bears were both 8 years old. By the late 1970s, the proportion of bears 10 years of age or older had increased to 20–30% for males and slightly more for females, with a decadal-scale fluctuation similar to that in Figure 6. The pattern was more distinct in females than in males, probably because older males tend to be farther offshore and are harvested less frequently. In the 1990s, the average age of harvested males and the proportion over 10 years of age did not decline to the same degree as those of females, which may reflect the influence of an increasing amount of sport hunting, in which hunters tend to select for larger, and thus older, males. Alternatively, the lack of a decline in the age of harvested males may indicate that the decadal-scale fluctuations in ice conditions referred to earlier (Mysak, 1999; this study) have been interrupted by the oceanographic regime shift in currents that started in 1989 (Macdonald et al., 1999).

As discussed above, periods of heavy ice through the winter and spring in both the mid-1970s and the mid-1980s (Melling, 1996; Mysak, 1999) caused a significant decline in the productivity of ringed seals for three years or more (Stirling et al., 1977b; Stirling and Lunn, 1997; Kingsley and Byers, 1998). Consequently, the natality rate of polar bears declined as well (Fig. 5), and the frequency of occurrence of cubs born from 1974 to 1976 in the age structure of the capture sample was abnormally low (Table 1). Because younger animals were less abundant in the late 1970s and 1980s, older animals were more predominant in the annual harvest, and thus the average age of animals killed increased (Fig. 6). Subsequently, in the early 1980s and early 1990s, immediately after the periods when ringed seal productivity recovered, both the natality of polar bears and the survival of younger animals increased. Since more younger bears were now available to be harvested, the annual average age of the animals taken, particularly in the subsistence hunt, declined (Fig. 6). However, the drop in the average age of the bears taken did not approach the low levels of the early 1970s, when the population was being overharvested. Thus, the age structure of harvested polar bears can reflect short-term fluctuations in the ecosystem as well as the overall long-term status of the population in relation to harvesting.

FUTURE PRIORITIES AND CONCERNS

Assessment of the Polar Bear Populations

Although it appears that both the Northern and Southern Beaufort polar bear populations have recovered from overharvesting and are continuing to fluctuate in relation to decadal-scale environmental factors, it has been 15 years since the last population studies of polar bears were conducted in the Canadian Beaufort Sea and Amundsen Gulf. Further, the data upon which the current estimates are based were compromised by uneven sampling, which in turn affected the confidence intervals (Amstrup et al., 2001a). Users and managers agree that within the next few years, before further management strategies are initiated, both the Northern and Southern Beaufort polar bear populations should be re-assessed simultaneously, and that fieldwork should be coordinated with Alaska.

A related problem is that, to date, the delineation of polar bear populations for management purposes has been based primarily on mark-recapture data and the movements of adult females (e.g., Bethke et al., 1996; Amstrup et al., 2000; Taylor et al., 2001). There are no comparable data on the seasonal movements of adult males because their necks are too large in relation to their heads to retain radio collars. Although preliminary analyses of mark-recapture data suggest the distances moved by males and females are similar (e.g., Stirling et al., 1984, 1988; Amstrup et al., 2001b), this hypothesis needs to be tested more rigorously because if the movements of males over large areas were substantially different from those of females, it might influence the applicability of the assumption of equal vulnerability to capture inherent in models for analysis of mark-recapture data.

Monitoring the Effects of Changes in Climate and Other Environmental Factors

Beginning in 1989, there was a major shift in the Arctic Oscillation Index, a subsequent shift toward less anticyclonic wind forcing over the Arctic Ocean, and a record minimum ice extent (Macdonald et al., 1999). The change in the wind field means that the ice situated to the north of the Canadian Arctic Archipelago no longer enters the Beaufort Gyre to flow south along the west coast of Banks Island into the southern Beaufort Sea. Instead, most of the multi-year ice now flows northeast and exits the polar basin through Fram Strait. More open pack and less multi-year ice in the southern Beaufort Sea both lead to greater melting and thinning of the annual ice, resulting in more open water since 1989 (C. Parkinson, quoted pers. comm. in Macdonald et al., 1999). In addition, mean air temperatures in April, May, and June in the eastern Beaufort Sea have increased steadily over the last 40–50 years (Skinner et al., 1998: Fig. 2) and, as a result of the change in direction of the wind field and shallower keels below the pressure ridges in the annual ice along the mainland coast during winter, fresh water from rivers and from sea ice melt extends farther north into the Beaufort Sea than was the case in earlier decades (Macdonald et al., 1999). Finally, Melling (1998) has shown that between 1989 and 1996, the upper halocline in the Canada Basin has warmed 0.15˚C, an amount sufficient to account for the melting of 0.7 m of sea ice.

How, or whether, these recent regional-scale changes in ecological conditions have affected the reproduction and survival of young ringed seals and polar bears through the 1990s is not clear. In part, this is because fewer widespread and comprehensive data have been collected from independent studies of both seals and bears over the last decade than was the case in the 1970s and 1980s. Curiously, the productivity of ringed seals in Amundsen Gulf in the early 1990s (as measured by the proportion of young-of-the-year in the open water harvest) appeared to be low, even though ovulation rates were high (Fig. 5; Harwood et al., 2000). Similarly, the natality rate of polar bears sampled in the most northerly portion of the area in 1992–94 was at an intermediate level in the range that tends to prevail in the study area (Fig. 5). Whether or not there could be a relationship between the reproductive data on the bears and seals is uncertain. However, the average ages of harvested polar bears remained lower than in years when heavy ice prevailed, suggesting that, so far at least, reproduction and survival of younger bears are probably still strong.

While direct effects of climatic warming on polar bears or seals have not yet been confirmed in the Beaufort Sea area, warmer temperatures in western Hudson Bay from April through June (Skinner et al., 1998) have been shown to cause breakup to be earlier and the bears to come ashore in poorer condition and with lower natality rates (Stirling et al., 1999). Stirling and Derocher (1993) also reported anecdotal observations of unseasonably warm weather and rain in late winter or early spring that were capable of causing maternity dens of female polar bears to collapse and kill the occupants (Clarkson and Irish, 1991) and washing away the roofs of the subnivean birth lairs of ringed seals, leaving the occupants vulnerable to both inclement weather and unusually high levels of predation. More recently, Smith and Harwood (2000) reported additional mortality of ringed seal pups in some areas of eastern Amundsen Gulf as a result of an unusually early breakup in spring 1999. While the risks of such weather events to polar bears and seals are potentially serious, there are few data available to date with which to quantify or project their importance.

The most important alternative prey species for the polar bear in the Beaufort Sea is the bearded seal, although quantitative data on its consumption by bears are limited. Polar bears have also been recorded killing walruses, belugas, and several other species (see summary in Stirling and Øritsland, 1995), although not in the Beaufort Sea. Stirling and Derocher (1993) predicted that warmer winters in western Hudson Bay would result in more open water during winter and, if so, that numbers of bearded and spotted seals (*Phoca largha*) might increase and become more important in the diet of polar bears. Data gained through monitoring the Inuit harvest of seals at Arviat, Nunavut, indicate this may be happening in western Hudson Bay. (Stirling, unpubl. data). Thus, it seems possible that if open water becomes more extensive in the southern Beaufort Sea in the coming years, numbers of bearded seals may increase, and spotted seals (already known to occur in very small numbers) may also increase. How shifts in the distribution of these or other species in the eastern Beaufort Sea might influence polar bear numbers is unknown, but in the short term, at least, the potential benefits to smaller bears of scavenging on the carcasses of larger prey species might be significant. Similarly, it is possible that, in the short term, more open water might enhance primary productivity. However, in a recent re-evaluation of the data in the Third Assessment Report of the Intergovernmental Panel on Climate Change, Wigley and Raper (2001) conclude that in the absence of climate-mitigation policies, there is a 90% probability that between 1990 and 2100 the world's climate will warm between 1.7˚ and 4.9˚C. That amount of climatic warming is enormous and, if unabated, will have large-scale effects on the climate, ice, and biota of the Beaufort Sea. Consequently, it is of immediate and significant scientific importance to re-establish baseline parameters for polar bears and their prey species that will permit us to evaluate change and develop appropriate responses for conservation and management of marine mammals in the Beaufort Sea.

DEDICATION

This paper is dedicated to the memory of the late Nelson Green. Through his long-term participation on the Inuvialuit Game Council, he was one of the first and strongest advocates of applying the benefits of scientific research studies, in combination with local knowledge, to the management and conservation of polar bears in the Western Canadian Arctic.

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