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Long-term Trends in the Population Ecology of Polar Bears in Western Hudson Bay in Relation to Climatic Change

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ABSTRACT. From 1981 through 1998, the condition of adult male and female polar bears has declined significantly in western Hudson Bay, as have natality and the proportion of yearling cubs caught during the open water period that were independent at the time of capture. Over this same period, the breakup of the sea ice on western Hudson Bay has been occurring earlier. There was a significant positive relationship between the time of breakup and the condition of adult females (i.e., the earlier the breakup, the poorer the condition of the bears). The trend toward earlier breakup was also correlated with rising spring air temperatures over the study area from 1950 to 1990. We suggest that the proximate cause of the decline in physical and reproductive parameters of polar bears in western Hudson Bay over the last 19 years has been a trend toward earlier breakup, which has caused the bears to come ashore in progressively poorer condition. The ultimate factor responsible for the earlier breakup in western Hudson Bay appears to be a long-term warming trend in April–June atmospheric temperatures.

Key words: climatic change, Hudson Bay, polar bear, sea ice

RÉSUMÉ. De 1981 à la fin de 1998, la condition physique de l'ours polaire adulte, mâle et femelle, s'est détériorée de façon importante dans l'ouest de la baie d'Hudson, tout comme le nombre de naissances et la proportion d'oursons de l'année pris durant la période d'eau libre, et qui étaient indépendants au moment de leur capture. Au cours de la même période, la débâcle de la banquise sur l'ouest de la baie d'Hudson s'est produite plus tôt. Il existait un lien très marqué entre le moment de la débâcle et la condition physique des femelles adultes (c.-à-d. que plus la débâcle se produisait tôt, plus les ourses étaient en mauvaise condition physique). La tendance à une débâcle précoce était également corrélée à l'augmentation de la température ambiante printanière dans la zone d'étude de 1950 à 1990. On suggère que la cause immédiate du déclin des paramètres physiques et reproducteurs de l'ours polaire dans l'ouest de la baie d'Hudson au cours des derniers 19 ans a été une tendance à une débâcle précoce, ce qui amené les ours à venir sur la terre ferme dans un état de plus en plus mauvais. Le facteur responsable de la débâcle précoce dans la baie d'Hudson semble être en fin de compte la tendance au réchauffement à long terme de l'atmosphère en avril et en juin.

Mots clés: changements climatiques, baie d'Hudson, ours polaire, banquise

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INTRODUCTION

Polar bears are distributed throughout the circumpolar Arctic in relatively discrete populations. Throughout their range, polar bears feed predominantly on ringed seals (*Phoca hispida*) and to a lesser degree on bearded seals (*Erignathus barbatus*) (Stirling and Archibald, 1977; Smith, 1980). Ringed seal pups are born in early April and are weaned at six weeks of age (McLaren, 1958), by which time they are approximately 50% fat by wet weight (Stirling and McEwan, 1975; Lydersen et al., 1992). From shortly after their birth until breakup of the annual ice in early summer, ringed seal pups are abundant and probably easier to catch than older seals because they are less experienced; they represent a high caloric return per unit of energy expended by a hunting polar bear. When seals are unavailable (as during the open water season in western Hudson Bay from late July to early November) or simply less accessible (as during periods of intense cold and inclement weather in mid-winter; Latour, 1981; Messier et al., 1994), polar bears become inactive. They also fast, relying on their fat reserves in a hibernation-like physiological state for up to several months at a time (Nelson et al., 1983; Derocher et al., 1990). Polar bears reach their lightest weights of the year in late March, just before the birth of the next cohort of ringed seal pups. This fact suggests it is the success of their hunting in spring and early summer that enables them to maximize the body reserves necessary for survival, reproduction, and nursing of cubs through the rest of the year. Thus, factors that influence the distribution and annual duration of sea ice have the potential for profound influence on the population ecology of the polar bear (Stirling and Derocher, 1993).

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Since 1981, the condition of adult male and female polar bears has declined significantly in western Hudson Bay, as have natality and the proportion of independent yearling cubs caught during the open water period (Derocher and Stirling, 1992; Stirling and Lunn, 1997). In this paper, we relate our data from the past 19 years on the population ecology of polar bears in western Hudson Bay to long-term climatic warming in this area (Skinner et al., 1998) and its possible effects on the timing of breakup and, thus, polar bears' access to seals.

MATERIALS AND METHODS

Determination of the Study Area for the Western Hudson Bay Polar Bear Population

We used the management boundaries of the western Hudson Bay polar bear population (WH) to define our study area, which included the coastal areas of Ontario, Manitoba, and Nunavut, bounded by 63˚10′ N and 88˚30′ W (Fig. 1). These borders were initially established because several analyses of the movements of bears tagged during late summer and fall, when bears were on land or on ice near the coast, showed that they returned to the same areas at the same season in subsequent years (Stirling et al., 1977; Derocher and Stirling, 1990; Ramsay and Stirling, 1990; Taylor and Lee, 1995). Later analyses using conventional and satellite radio telemetry data were generally consistent with the results from the mark-recapture data (Fig. 2).

To determine whether variation in ecological parameters such as the timing of breakup significantly influenced the condition of the animals in fall, natality, and cub survival, we needed to understand the distribution and movements of polar bears on the sea ice until spring. Thus, we plotted 46 bear-years of movement data, recorded from 41 individual adult female polar bears on which satellite radio collars (Telonics Inc., Mesa, Arizona) were deployed between 1991 and 1998, to evaluate where the bears we captured and measured during the ice-free period were distributed on the sea ice during the winter and spring.

Annual Duration and Extent of Ice Cover for Hudson Bay

Data on the extent of sea-ice cover (in km^2) for the combined area of Hudson Bay, Foxe Basin, and Hudson Strait are available from the National Ice Center (Washington, D.C.) as single values for ice extent for each week from 1979 through 1994 (National Ice Center, 1998). Since the area of Hudson Bay, Foxe Basin, and Hudson Strait is geographically contained, we could calculate annual estimates of sea-ice extent over the whole area, as a proportion of a fixed maximum, to determine whether there was any detectable temporal trend in the total annual amount of ice cover.

We also calculated the extent of ice cover for Hudson Bay alone (excluding James Bay) using data from the National Snow and Ice Data Center at the University of Colorado (Boulder, Colorado). These data consisted of monthly sea-ice concentrations for the Arctic from 1960 to 1994, digitized on a standard 1˚ grid (cylindrical projection). The ice concentrations (recorded in tenths) were converted to extent data (km^2) by multiplying the concentration value for each cell by the area of water contained in each cell. We totalled the extent data for all cells to obtain monthly values for ice extent and then summed the monthly values for a calendar year to obtain annual ice-extent estimates for Hudson Bay.

Analysis of Dates of Breakup and Freeze-up of the Annual Ice in Western Hudson Bay

Following Etkin (1991), we defined breakup of the annual ice as the date by which half the total cover had disintegrated during the spring melt period to give a total ice cover of 5/10. Data for estimation of the time of breakup from 1979 through 1998 were taken from the weekly regional ice analysis maps for Hudson Bay produced by the Canadian Ice Service. We used a 10-week period, extending from mid-June through mid-August, to incorporate the dates from the beginning of breakup to the date when annual ice was absent from the study area.

A grid of sampling points at intervals of 0.5˚ latitude and longitude was overlaid onto the weekly ice concentration maps for the study area. Individual ice concentration values were obtained from all 128 points on the grid and then averaged. The values for the 10-week period were then plotted. The date at which the total ice coverage was equal to 5/10, interpolated from the graph, represented the date of breakup for this study.

Freeze-up in the study area was defined as the date by which the ice cover was equal to 5/10 concentration during the period of ice formation and consolidation. The time period over which data were analyzed extended from October through December (1979–97) and included the period from the initial formation of ice on the bay to the date when the area was completely covered by ice. The methodology paralleled that used to determine the date of breakup.

Skinner et al. (1998: Fig. 2) demonstrated that between 1950 and 1990, mean air temperatures in May and June in western Hudson Bay were warming at a rate of 0.2–0.3˚C per decade, while on the eastern side they were cooling at a similar rate. From their Figures 2a and 2b, we estimated a mid-line between the areas that were warming and cooling (roughly from Cape Henrietta Maria in northeastern Ontario to Rankin Inlet on the northwestern coast of Hudson Bay) to divide Hudson Bay into eastern and western sections. We then used the same methodology outlined above to estimate breakup and freeze-up times for both sections.

Mean Dates of Polar Bears' Coming Ashore in Relation to Time of Breakup

We used satellite telemetry to determine the locations of adult females and thus estimate the dates they came ashore from 1991 through 1998. Forty-six separate deployments of radios on 41 individuals were made during this period. The configuration of the collars varied from year to year, but all collars transmitted for 4 to 6 hours at intervals of 2 to 10 days. While over 5000 locations were received, we selected only one location per day per bear from all available locations on the basis of quality indices provided by Service Argos (Landover, Maryland). The date that each bear came ashore was defined as the date of its first location on land. We were able to estimate the date ashore on 40 separate occasions for 34 individuals (range: 1–9 bears/year). Dates ashore could not be estimated for all deployments, either because of collar malfunctions or because the satellites were unable to determine collar locations for all transmission periods.

To evaluate whether or not the timing of breakup influenced when bears with satellite collars came ashore, we calculated the time of breakup each year (using the methods described above) for an area of similar but variable boundaries of latitude to the north and longitude to the east that included a minimum of 90% of the locations of bears while on the sea ice. The mean dates on which the bears came ashore each year were plotted against the dates of breakup of the sea ice in the defined area.

Comparison of Condition of Adult Polar Bears in Western Hudson Bay between Years

Bears were sampled nonselectively and immobilized with Telazol®, and a series of standard measurements was taken (Stirling et al., 1989). To evaluate variability in condition of adult males and females fasting on land in western Hudson Bay in fall, we used the formula $C = (W/L^2)$, where C = index of condition (Quetelet Index), W = weight in kg, and L = body length in metres (Ganong, 1991). To control for variation between years in the timing of sampling periods, we scaled weights to a constant capture date of 21 September. For each bear, we corrected the weight by 0.85 kg for each day between its capture and 21 September, subtracting for capture dates before 21 September and adding for those after (Derocher and Stirling, 1992). We presented condition as three-year running means, because the variability that characterizes annual values sometimes obscures the trends we were interested in examining.

Comparison of Condition of Adult Male and Female Polar Bears in the Study Area and in Southeastern Hudson Bay

To make a preliminary assessment of whether the trends we recorded in the study area might be occurring over the whole of Hudson Bay, we compared the condition of adult male and female polar bears captured in the study area in 1997 and 1998 to that of a sample of adult male and female polar bears available from only those same two years in southeastern Hudson Bay (SH) (M. Obbard, pers. comm. 1998), scaling data to the same capture date. The weights of adult females accompanied by either cubs-of-the-year or yearling cubs were pooled because previous analyses had shown they were not significantly different (Derocher and Stirling, 1992).

Definitions and Calculation of Reproductive Parameters

All polar bears were assumed to be born on 1 January. Cubs-of-the-year are bears less than one year of age. Yearling cubs are between one and two years of age, and two-year-old cubs are between two and three years of age but still with their mother. Subadults were independent bears between two and three years of age. Four-year-old female bears were defined as adults because that is the age at which most breed for the first time.

We used data from captured female polar bears, alone or accompanied by cubs of different ages, to estimate their age-specific natality (Ramsay and Stirling, 1988). Three-year running means were calculated to estimate natality in western Hudson Bay from 1980 to 1998.

Survival of Cubs for the First Six Months after Leaving the Maternity Den

In February-March of all springs from 1981 through 1998 (except 1985 and 1986), we attached HF radio collars to between 4 and 20 adult female polar bears, either at their maternity dens or within a few days of their return to the sea ice. These females were relocated approximately six months later, when they returned to shore to fast during the open water season. At that time, we counted the number of accompanying cubs to estimate survivorship through that initial period.

Proportion of Yearlings Caught Alone

A unique aspect of the population ecology of polar bears in western Hudson Bay is that in some years a significant proportion of yearlings (18–20 months old) in the capture sample are independent because they have already been weaned. In all other areas of the Arctic reported on to date, cubs remain with their mothers until they are 2.5 years of age (Ramsay and Stirling, 1988). As the weaning of yearlings is such a departure from the typical pattern, we monitored the number that were caught alone as a proportion of the total number of yearlings in the capture sample each year. We suspected this parameter might be sensitive to ecological change.

Statistics

Statistical analyses followed procedures presented by Sokal and Rohlf (1995). Nonparametric tests were used

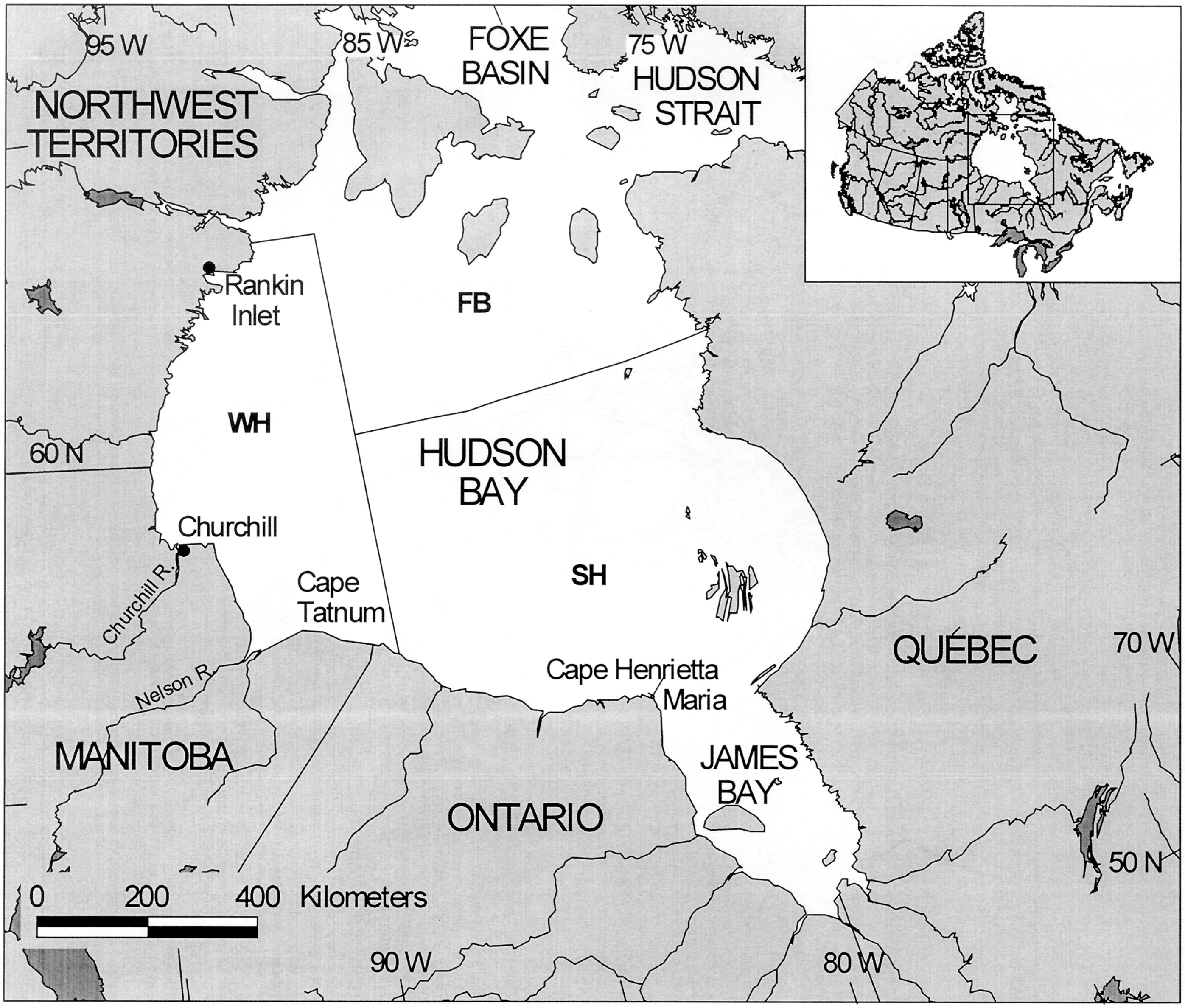

FIG. 1. Map of the study area and the management boundaries for the polar bear populations of western Hudson Bay (WH), southern Hudson Bay (SH), and Foxe Basin (FB).

where the data were not normally distributed. Unless otherwise stated, statistical tests were considered significant at $p = 0.05$. Means are presented with one standard error.

RESULTS

Area Occupied by the Western Hudson Bay Polar Bear Population

Of 1620 locations recorded from bears on the sea ice, 70.7% (1146) were within the management boundary of the study area (Fig. 2). The occurrence of about 30% of the total number of locations outside the study area was a consequence of three factors. First, at some time during the winter, most bears spent at least a brief period up to 100 km or more to the east of the study area. Second, in some years, the ice breaks up in such a way that a large proportion of the last remaining ice is carried farther to the southeast than usual by wind or currents and eventually disintegrates there. Finally, one individual captured in the Cape Tatnam area in 1994 spent most of her time outside the study area in south-central Hudson Bay and James Bay. Of the 474 locations recorded east of the study area, 120 (25.3%) were recorded in 1994. This was a direct consequence of two events: the last ice to break up drifted further to the east than usual, and the one female radio-collared in that year was there.

Although some of the winter movements of the radio-collared adult female bears extended past the eastern boundary of the management zone, such variations did not

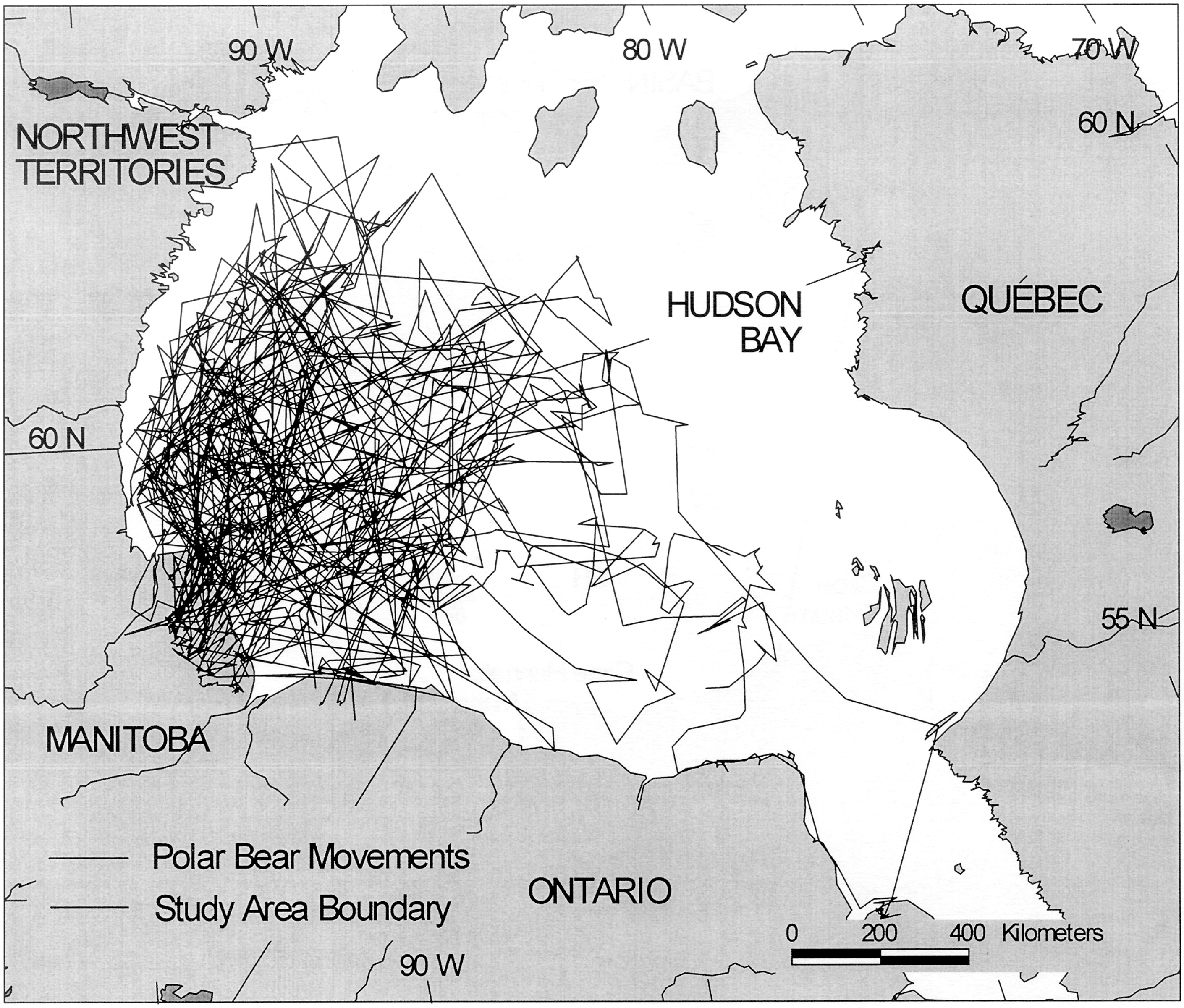

FIG. 2. Movements of 41 adult female polar bears through a total of 46 bear years, between 1991 and 1998.

affect the overall fidelity of adult females to the study area. Of 632 locations recorded on land, only 35 (5.5%) were outside the study area. Moreover, 29 (82.9%) of those 35 locations originated from the same bear that spent so much of her time on the sea ice to the east of the study area in 1994.

Trends in Ice Cover and Breakup in Hudson Bay

Analysis of data from the National Ice Center on the total ice cover for the combined area of Hudson Bay, Foxe Basin, and Hudson Strait showed considerable interannual variability. A long-term, but nonsignificant, trend was increasing total ice cover from 1972 to 1994 (Pearson product moment correlation, r = 0.158; df = 22; p = 0.47). In contrast, the analysis of total ice extent from 1960 through 1994 for Hudson Bay alone indicated a long-term, but also nonsignificant, decline in total ice cover (r = -0.256; df = 34; p = 0.07). Variation in the total extent of ice cover between years resulted from changes in the timing of breakup, freeze-up, or both. Thus, in years with a large ice extent, the date of breakup tended to be later while the date of freeze-up was earlier. The opposite occurred in years with a relatively low ice extent.

The analysis of the timing of breakup in the study area in western Hudson Bay (the area occupied by our study population of polar bears) for the 20-year period 1979–98 indicated an overall trend that approached significance (r = -0.413, df = 19, p = 0.07) for breakup to occur at an earlier date (Fig. 3a). There was no trend in the time of freeze-up in the 19 years between 1979 and 1997 (Fig. 3b; r = -0.124; df = 18; p = 0.61). The overall consequence of these results was an increase, albeit not statistically significant, in the annual total

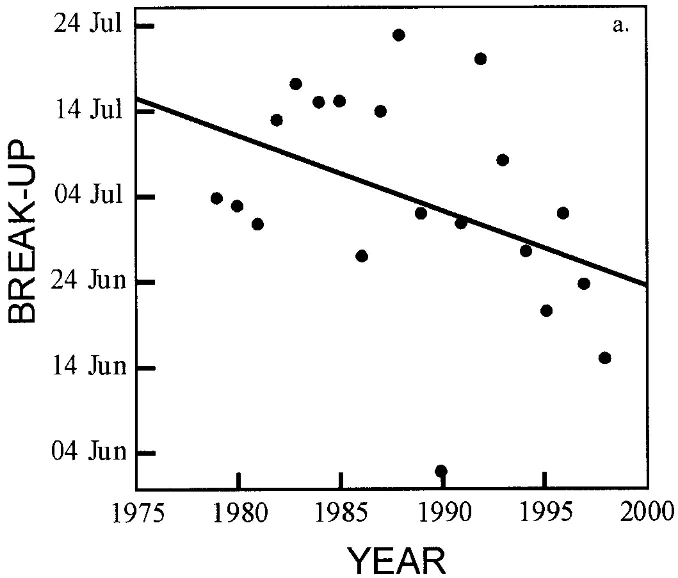

FIG. 3a. Dates of breakup (1979–98) in the study area.

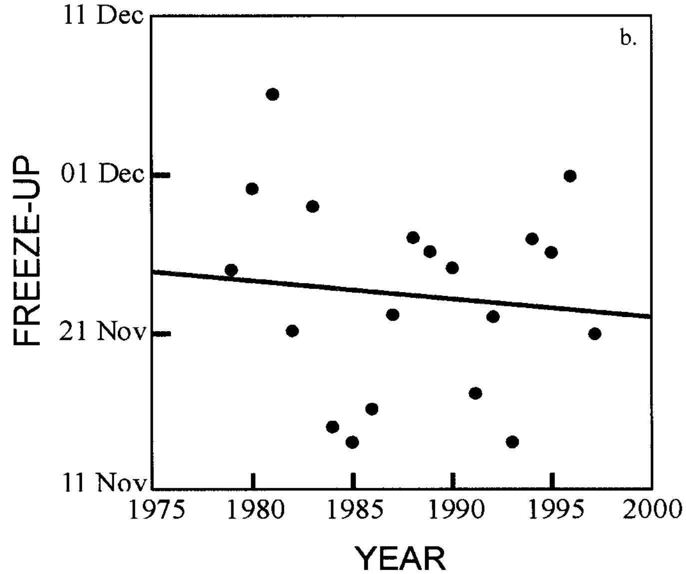

FIG. 3b. Dates of freeze-up (1979–97) in the study area.

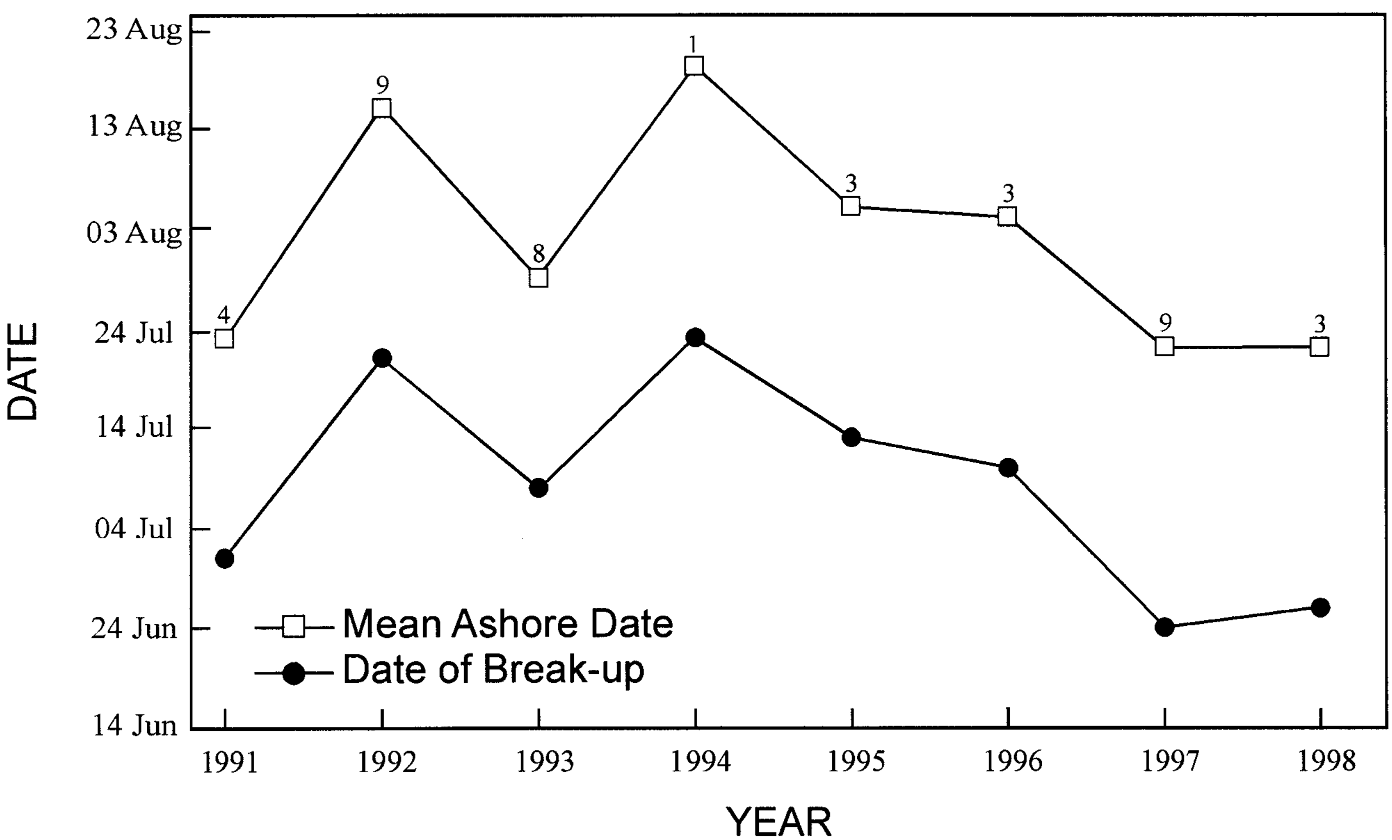

FIG. 4. Mean date of breakup in the area of sea ice where female polar bears with satellite collars spent at least 90% of their time each year (1991–98) and the mean dates the bears came ashore in those years. (Numbers above upper line = sample size).

number of ice-free days through the duration of our study, due mainly to the trend for an earlier breakup. Comparing decades, the mean Julian date of breakup was significantly later (t-test, t = 2.455, df = 17, $p < 0.05$) in the 1980s (191.3 ± 2.7, n = 10, range = 178–205) than it was in the 1990s (177.8 ± 4.7, n = 9, range = 153–202).

Date Ashore and Ice Conditions

The correlation between the mean date on which female polar bears with satellite radio collars came ashore and the timing of breakup in the area, which was adjusted to include a minimum of 90% of the locations, was highly significant (Fig. 4, r = 0.975; df = 7; $p < 0.001$). Between

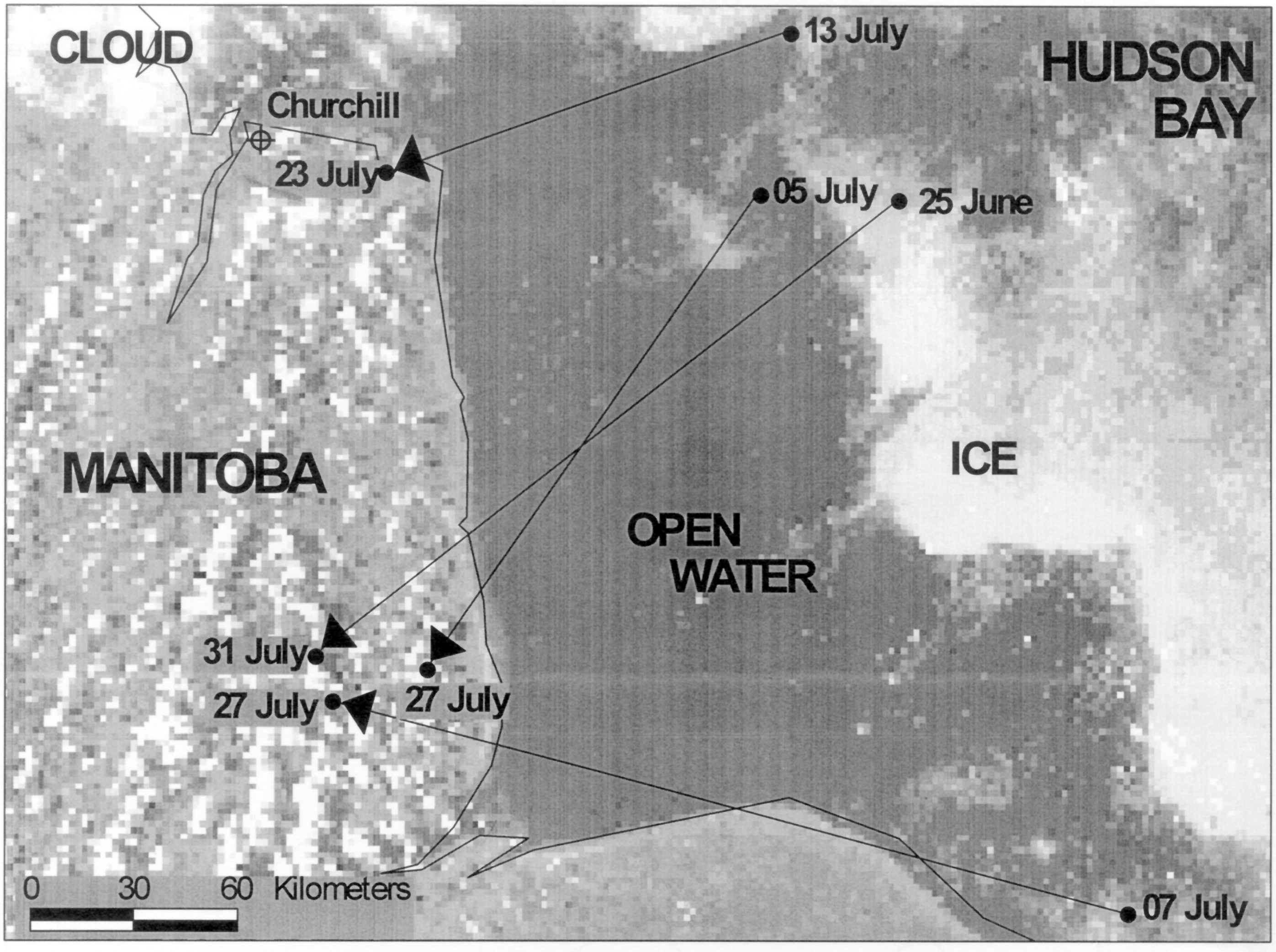

FIG. 5. Satellite photo of sea ice in western Hudson Bay on 8 July 1997, and the locations of 5 individual adult females with satellite radio collars. The photo shows that individual females from the study area show fidelity to that area by continuing to hunt in patches of disintegrating sea ice, or by simply going ashore, rather than moving to the southeast to find the last remaining ice.

1991 and 1998, female bears with radio collars came ashore an average of 24.6 ± 0.87 days after breakup (range = 21–28 days), indicating that they remained on the ice to continue to hunt seals well after a significant reduction in total cover (Fig. 5).

Condition of Adult Males and Females and Natality

Since the early 1980s, there has been a significant decline in the condition of adult polar bears, both females (r = -0.799, n = 17, $p < 0.001$) and males (r = -0.732, n = 17, $p < 0.001$) (Fig. 6). This decline was interrupted by increased values for both sexes in 1992 and 1993, after which condition again declined (Derocher and Stirling, 1992; Stirling and Lunn, 1997). There was also a statistically significant relationship over the 19 years of this study between the date of breakup and the condition of the adult female polar bears when they came ashore to fast through the open water season. The earlier the breakup, the poorer the condition of the females (r = 0.559, $p < 0.05$, n = 18). Natality followed a similar pattern (Spearman rank correlation, $r_s = -0.543$, n = 17, $p < 0.05$). Throughout the study period, the size of the population remained essentially unchanged (Lunn et al., 1997).

Average Condition of Adult Male and Female Polar Bears in the Study Area and in Southeastern Hudson Bay in 1997 and 1998

In 1997 and 1998, in southeastern Hudson Bay, both adult male polar bears and females accompanied by cubs-of-the-year or yearling cubs were in significantly better condition on average than were their counterparts in our study area. The mean values for the Quetelet Condition Index (weight over body length squared; Ganong, 1991) were as follows: adult males, SH, 81.1 $kg/m^2 \pm 3.5$, n = 15; WH, 64.5 $kg/m^2 \pm 1.4$, n = 80 (t = 4.717, df = 93, $p < 0.001$); adult females, SH, 67.3 $kg/m^2 \pm 3.4$, n = 17; WH, 44.2 $kg/m^2 \pm 1.0$, n = 60 (t = 9.047, df = 75, $p < 0.001$).

Survival of Cubs for the First Six Months after Leaving the Maternity den

The survival of cubs from early March (when they left the dens) to the following August-September (when the radio-collared females and accompanying cubs were resighted) also varied over the study period. From 60–65% in the early 1980s, it fell to just over 50% through the late 1980s and early 1990s and then increased to 70–80% through the mid-to-late 1990s (Fig. 7).

Lone Yearlings

The proportion of yearlings that were independent in the annual capture samples fluctuated widely at 3–4 year intervals, but overall the maximum proportions have declined from about 60% in 1982 to 15–20% since 1991 (Fig. 6). There was no statistically significant relationship between the proportion of lone yearlings and the time of breakup in the same year ($r = -0.205$, $n = 14$, $p = 0.46$).

DISCUSSION

Area Occupied by the Western Hudson Bay Population

Although most (70.7%) of the offshore locations recorded from the adult female polar bears with satellite radio collars were within the defined study area, 29.3% were to the east. Figure 2 shows that most of the locations outside the study area resulted from movements of bears offshore from the coastline of Nunavut and Manitoba, south of Rankin Inlet and north of the Nelson River. Such movements do not represent emigration of animals from the study area but simply a winter distribution that extends offshore to the east beyond the current management boundary. This conclusion is confirmed by the finding that 94.5% (597/632) of the data points recorded on land over the eight-year period were within the study area.

The greatest number of locations outside the study area, comprising 25.3% (120/474) of the locations on ice and 82.9% (29/35) of those on land, was recorded in 1994, all from the same bear. This bear's movements may have been influenced by the fact that the last sea ice broke up further east in 1994 than in most other years. However, as this bear was captured for instrumentation in the southern portion of the study area, between the Nelson River and the Manitoba border, it may be that she was simply at the western end of her normal home range. Overall, however, the data clearly indicated that the bears had a high degree of fidelity to the terrestrial portion of the study area during the ice-free period. They spent most of their time on the sea ice within the study area or in the adjacent area to the east.

To date, we lack comparative data on movements of adult males on the sea ice; since the diameter of their necks exceeds that of their heads, they do not retain collars. However, limited preliminary analyses of mark-recapture data in other areas indicate movements of similar distances by bears of both sexes, both within and between seasons (Stirling et al., 1980; 1984). For management purposes, consequently, the unstated assumption to date (e.g., Taylor and Lee, 1995) has been that the home ranges of bears are similar in size for both sexes, although this hypothesis remains largely untested. Thus, for this paper, we retained 88˚30′W as the eastern boundary of our study area (Fig. 1), and we assumed that this boundary affected adult males and females similarly.

Total Ice Cover and the Timing of Breakup and Freeze-up

Overall, the total extent of sea ice in the Arctic has been decreasing at an annual rate of approximately 3–5% over the past two decades (Gloersen and Campbell, 1991; Johannessen et al., 1995; Maslanik et al., 1996; Bjørgo et al., 1997). To date, most of this decrease has occurred in the Siberian sector of the Arctic (Maslanik et al., 1996). Meanwhile, for the combined area of Hudson Bay, Foxe Basin, and Hudson Strait, the total extent of sea ice was reported to be increasing between 1978 and 1987 (Parkinson and Cavalieri, 1989). Our analysis of total ice cover for the combined area of Hudson Bay, Foxe Basin, and Hudson Strait, which we extended from 1972 through 1994 by using data from the National Ice Center, indicated a similarly increasing (though nonsignificant) trend. Analysis of total ice cover for Hudson Bay alone showed a nonsignificant declining trend.

From 1979 through 1998, the trend toward an earlier breakup in the study area approached statistical significance ($p = 0.07$), whereas the mean time of freeze-up did not change (Figs. 3a and 3b). Because Hudson Bay is essentially a closed system, atmospheric conditions (i.e., surface air temperatures) are the principal factors affecting ice conditions (Etkin, 1991). By analyzing the mean monthly surface air temperatures in April, May, and June from 1950 to 1990, Skinner et al. (1998) demonstrated that the average temperatures for western Hudson Bay have been increasing at a rate of 0.2–0.3˚C per decade. Thus, this increasing mean spring temperature is probably largely responsible for the observed trend towards an earlier breakup in western Hudson Bay. In contrast, in eastern Hudson Bay, where temperatures have been gradually cooling over the same period (Skinner et al., 1998), there has been neither a trend nor a significant change in timing of breakup. The possible effects of other factors, such as wind direction, snowfall, ocean temperature, and currents, are unknown to us.

Relationship between the Timing of Breakup and When Adult Females Come Ashore

The strong correlation ($p = 0.001$) between the dates of breakup and coming ashore in the areas where bears spent 90% of their time (Fig. 5), and the narrow range of variation in those two dates between years (21–28 days),

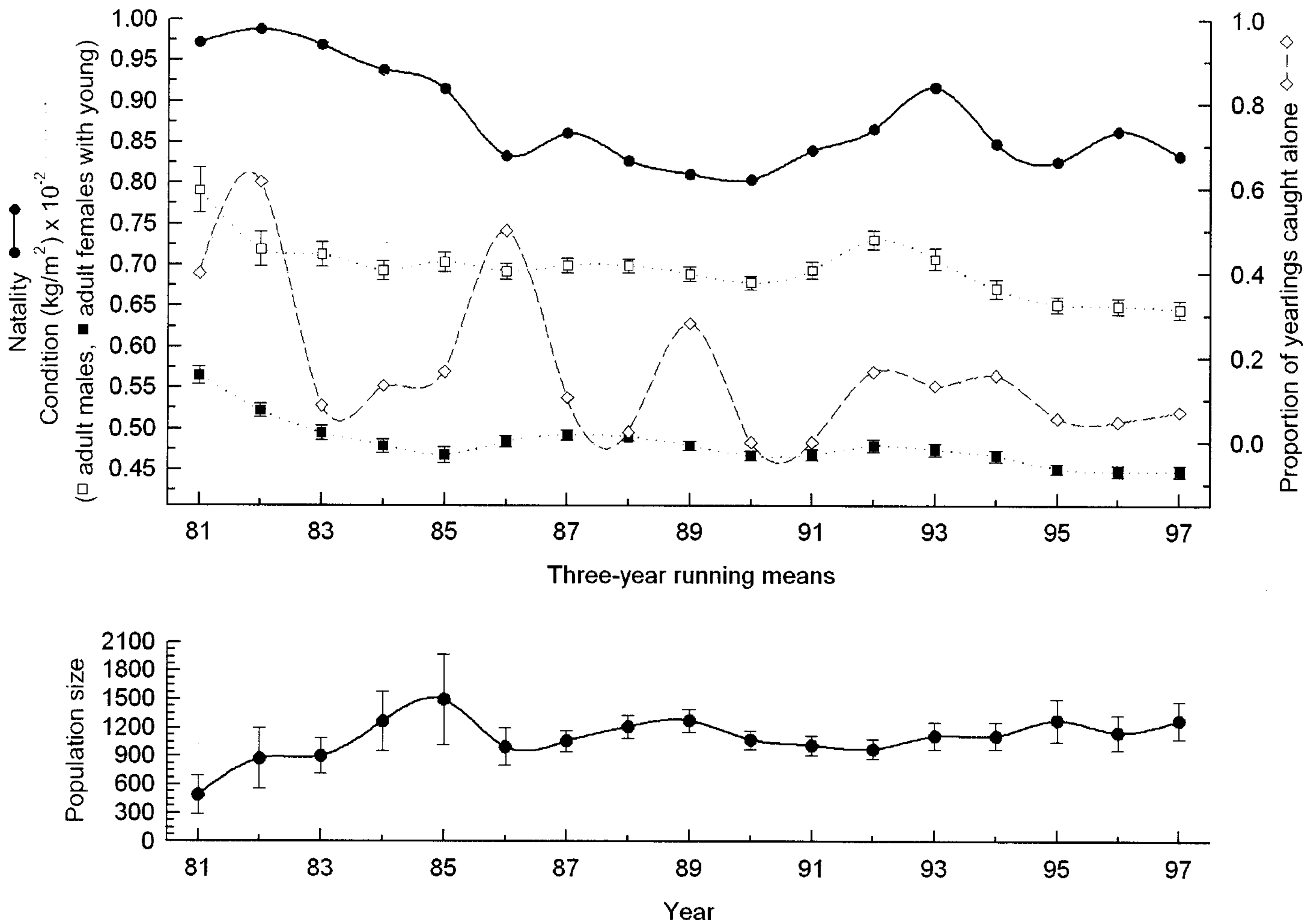

FIG. 6. Trends in natality and condition of adult male and female polar bears, expressed as three-year running means; the proportion of yearlings that were alone when captured in the fall; and population size (1981–97).

indicate an optimum length of time that bears remain on the sea ice before it disintegrates.

It is informative to examine the behaviour of bears in years when the timing of breakup differed the most from the average. In 1992 and 1994, the bears arrived on shore later than in other years (Fig. 4). In 1992, breakup in western Hudson Bay was three weeks or so later than usual, most probably as a consequence of the simultaneous occurrence of the Mount Pinatubo eruption in the Philippines and an El Niño event. The eruption of Mount Pinatubo in 1991 ejected millions of tonnes of sulphur dioxide into the atmosphere, producing a haze that redirected part of the incoming solar radiation and ultimately produced colder-than-normal global temperatures the following year. The maximum decrease in temperature was about 2˚C for one to four years after the eruption, depending on the area of the globe (NASA Goddard Institute for Space Studies, 1998). Plots of spring (March-April-May) and summer (June-July-August) temperature departures from normal for western Hudson Bay reveal that the temperature in 1992 was on average 2˚C lower (Climate Research Branch, 1998). The decline in temperature in western Hudson Bay may also have been influenced by the moderate El Niño event in 1991–92. Analysis of 23 strong-to-moderate El Niño events between 1900 and 1990 suggests that such events produce a subsequent positive temperature anomaly over western Hudson Bay in the spring (Shabbar and Khandekar, 1996). Thus it is possible, though not confirmed, that the 1991–92 El Niño could have accentuated the temperature anomaly produced by the eruption of Mount Pinatubo. Regardless, the delay in breakup of the sea ice was clear and well documented.

In 1994, the late dates of breakup and arrival on shore were more a consequence of the distribution and movements of the single bear from which we received an adequate data set than of a climatically induced change in the timing of breakup. This individual bear spent more time along the southeastern edge of Hudson Bay, where the last ice usually melts later than in the study area. Nevertheless, the tightness of the correlation between the dates of breakup and the arrival on shore of nine female bears in 1992 (when breakup in the study area really was late) or 1994 (when data were available from only one animal, which was in an area where the lateness of breakup was a local event) clearly indicates the importance of using the areas defined by the animals.

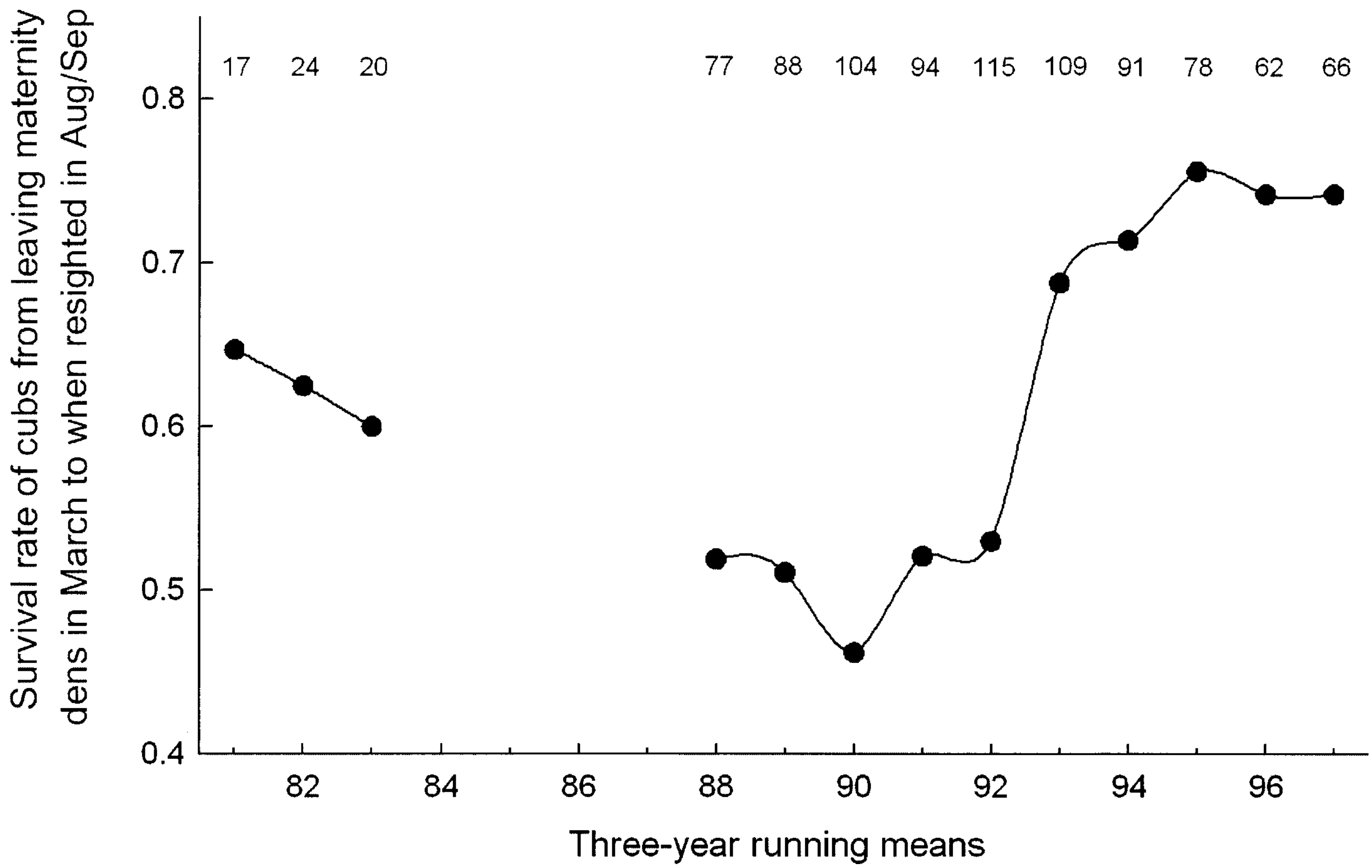

FIG. 7. Survival rate of cubs between their departure from the maternity den in late February-early March and the time when they were resighted on land in August-September. (Numbers represent cubs seen in the spring.)

Factors Influencing Changes in Physical and Reproductive Characteristics of Polar Bears

Polar bears require sea ice to provide a platform from which to hunt ringed seals. The most important hunting period is the late spring, when fat, recently weaned, and naive ringed seal pups are abundant. Such pups may be up to 50% fat by wet weight (Stirling and McEwan, 1975; Stirling and Øritsland, 1995). Nevertheless, regardless of the year, the timing of breakup, or the sample size of female polar bears being tracked, the range in the mean interval after breakup that bears with satellite radio-collars came ashore was only 21 to 28 days. A major factor determining the tightness of the relationship between the dates of breakup and when the adult female bears finally come ashore (Fig. 4) was that individual bears showed strong fidelity to a particular area of coast. The movements of the four females illustrated in Figure 5 support this conclusion. Their last recorded positions on the sea ice and their first recorded positions on land clearly indicate that their fidelity to a particular land area took precedence over moving further to the southeast, where a substantial amount of sea ice was still present. Thus, even though the last ice to melt in southern Hudson Bay usually does so off the Ontario coast, the bears originally captured in the study area in Manitoba, north of the Nelson River, retained a strong fidelity to that area (Fig. 2). They did not simply drift passively to the southeast where the last remaining ice melted each year. Taken together, these observations suggest a balance between the length of time that bears can remain on the ice (hunting seals to accumulate energy stores for the open water period) before there is no longer enough ice to make seal hunting energetically cost-effective, and the amount of energy the bears would have to expend walking back along the coast if they were passively carried away from the study area on the drifting pack. This balance may be critical for pregnant females returning to den in specific known areas of suitable maternity denning habitat because they must fast for eight months and nurse their cubs (from about 0.6 kg at birth to about 10–12 kg) before leaving their dens.

The biological significance of maximizing mass prior to returning to shore to fast is demonstrated by the positive relationship between the mass of females with cubs and the survival of their cubs (Derocher and Stirling, 1996; 1998). Clearly, it is critical to the reproductive success of a pregnant adult female, and to the survival of both independent bears and females with cubs, to maximize the number of days they can spend on the sea ice feeding before they come ashore to fast through the open water season. This fact probably explains the small variation in the interval between breakup and when the bears come ashore each year (Fig. 4), regardless of the variation between years in the timing of breakup.

The major divergence from the pattern of declining physical and reproductive parameters occurred following the 1991 eruption of Mount Pinatubo, when cooling over the northern hemisphere (McCormick et al., 1995) delayed the breakup of ice in western Hudson Bay by three weeks or more (Stirling and Derocher, 1993). Apparently because they could feed for three weeks longer, both males and females came ashore in better condition. In the following year, the females' natality and the survival of their cubs were significantly greater than in previous years (Stirling and Lunn, 1997; this study, Fig. 7). After about 1993, the condition of males and females, natality rates, and the proportion of lone yearlings in the capture sample began to decline again. In contrast, the survival of cubs through the first six months after leaving the den remained high even after 1994, when the condition of females and their natality had already declined. The reason for this apparent anomaly is not clear at this time.

To summarize, in western Hudson Bay, the condition of adult female polar bears coming ashore to fast through the open water season appeared to be determined by the timing of breakup (i.e., the earlier the breakup, the poorer the condition of the females). There was also a correlation between the trend toward earlier breakup and a decadal-scale pattern of warming of spring air temperatures over the study area between 1950 and 1990 (Skinner et al., 1998). In eastern Hudson Bay, in contrast, no significant change in breakup date occurred; there was a decadal-scale pattern of cooling of mean air temperature in spring; and the average condition of both adult male polar bears and females accompanied by cubs-of-the-year or yearling cubs was significantly greater than in the study area. All these data taken together suggest that the proximate cause of the decline in physical and reproductive parameters of polar bears in western Hudson Bay over the last 19 years has been a trend toward earlier breakup, which has resulted in the bears coming ashore in progressively poorer condition. The ultimate factor responsible for the earlier breakup in western Hudson Bay appears to have been a long-term warming trend in spring atmospheric temperatures.

Status of Polar Bears in Western Hudson Bay

In the early to mid-1980s, the natality of female polar bears in western Hudson Bay was the highest recorded anywhere in polar bear range. In some of those years, females successfully weaned up to about 40% of their cubs at 1.5 years of age instead of the normal 2.5 years (Ramsay and Stirling, 1988). Consequently, to understand why several physical and reproductive parameters have declined, it is important to understand how natality could have been sustained at a level so much higher than that of other polar bear populations in the first place. What facilitated the successful weaning of yearlings in western Hudson Bay, but nowhere else in their range? And how could females manage these physiological feats in a habitat where pregnant females must also fast for eight months or more?

Subsequently, through the late 1980s and 1990s, a long-term decline in natality and in condition of both male and female adult polar bears was documented (Derocher and Stirling, 1992; Stirling and Lunn, 1997; this study). Except during the brief post-Pinatubo period, this decline has continued to the present. To date, this declining trend does not constitute a threat to the population: even in the late 1980s, when natality was at its lowest, the rates were still higher than the upper range of values reported for bears elsewhere in the Arctic (e.g., Stirling et al., 1976, 1980). For about the last 12 years, estimates of population size have remained relatively constant (Lunn et al., 1997; this study), indicating that the declines in condition and natality have not yet led to a decline in population. However, it is equally clear that if the trends continue in the same direction, they will eventually have a detrimental effect on the ability of the population to sustain itself.

A concurrent problem for humans, if condition of the bears declines to the point where they have difficulty sustaining themselves through the open water period, is that bears will become progressively more likely to enter areas of human habitation in search of food, threatening human life and property. For example, in 1995 (when breakup was late) there were 62 calls to the Polar Bear Alert program in Churchill, while in 1996 (when breakup was early) there were 151 (C. Elliott, pers. comm. 1998).

Although there is considerable uncertainty about future trends in global climate, some models have predicted that the temperature for Hudson Bay will increase on average 2–6˚C over the next 55–100 years (Maxwell, 1997). Etkin (1991) speculated that an increase in mean air temperature of 1˚C could advance breakup by about a week in western Hudson Bay and two weeks in eastern Hudson Bay. Other models have made similar predictions for the Arctic as a whole (Etkin, 1990; IPCC, 1996). If these predictions are borne out, then bears may come ashore lighter than at present, while needing to fast for a longer period.

Other Factors

In this paper, we have focused on the relationship between time of ice breakup, long-term trends in spring air temperatures, and physical and reproductive parameters of adult female polar bears. There are no data with which to consider the possible impact of such factors on other components of the food chain, such as ringed seals. For example, might warmer spring temperatures cause the premature collapse of subnivean lairs excavated by ringed seals to hide their pups during the first few weeks of life, and thus result in increased predation by polar bears?

Major hydroelectric developments have also been completed within the Hudson Bay-James Bay watershed. These developments have significantly altered the freshwater input into both James Bay and Hudson Bay by affecting the seasonal cycle of runoff. In Hudson Bay, runoff has increased by 52% during winter (November to April) and decreased by 6% during summer (May to October) (Prinsenberg, 1980). This represents an additional 3 cm layer of freshwater over the entire Bay. The modification of the pattern of runoff, especially during May through July, might also affect the timing of breakup and freeze-up. Although we suspect this factor is likely secondary to the influence of atmospheric temperature in spring, its possible additive importance warrants further study.

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REFERENCES

BJØRGO, E., JOHANNESSEN, O.M., and MILES, M.W. 1997. Analysis of merged SMMR-SSMI time series of Arctic and Antarctic sea ice parameters 1978–1995. Geophysical Research Letters 24:413–416.

CLIMATE RESEARCH BRANCH, ENVIRONMENT CANADA. 1998. El Niño: The Canadian Perspective. Available at: http://www1.tor.ec.gc.ca/elnino/canadian/all/index_e.cfm

DEROCHER, A.E., and STIRLING, I. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Canadian Journal of Zoology 68:1395–1403.

———. 1992. The population dynamics of polar bears in western Hudson Bay. In: McCullough, D.R., and Barrett, R.H., eds. Wildlife 2001: Populations. London: Elsevier Applied Science. 1150–1159.

———. 1996. Aspects of survival in juvenile polar bears. Canadian Journal of Zoology 74:1246–1252.

———. 1998. Offspring size and maternal investment in polar bears (*Ursus maritimus*). Journal of Zoology (London) 245: 253–260.

DEROCHER, A.E., NELSON, R.A., STIRLING, I., and RAMSAY, M.A. 1990. Effects of fasting and feeding on serum urea and serum creatinine levels in polar bears. Marine Mammal Science 6:196–203.

ETKIN, D.A. 1990. Greenhouse warming: Consequences for Arctic climates. Journal of Cold Regions Engineering 4:54–66.

———. 1991. Break-up in Hudson Bay: its sensitivity to air temperatures and implications for climate warming. Climatological Bulletin 25(1):21–34.

GANONG, W.F. 1991. Review of medical physiology. 15th ed. Norwalk, Connecticut: Appleton and Lange.

GLOERSEN, P., and CAMPBELL, W.J. 1991. Recent variations in Arctic and Antarctic sea-ice covers. Nature 352:33–36.

IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE). Houghton, J.T., Jenks, G.J., and Ephraums, J.J., eds. 1996. Climate Change: The IPCC Assessment. Cambridge, England: Cambridge University Press.

JOHANNESSEN, O.M., MILES, M.W., and BJØRGO, E. 1995. The Arctic's shrinking sea ice. Nature 376:126–127.

LATOUR, P.B. 1981. Spatial relationships and behaviour of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. Canadian Journal of Zoology 59:1763–1764.

LUNN, N.J., STIRLING, I., ANDRIASHEK, D., and KOLENOSKY, G.B. 1997. Re-estimating the size of the polar bear population in western Hudson Bay. Arctic 50:234–240.

LYDERSEN, C., HAMMILL, M.O., and RYG, M.S. 1992. Water flux and mass gain during lactation in free-living ringed seal (*Phoca hispida*) pups. Journal of Zoology (London) 228: 361–369.

MASLANIK, J.A., SERREZE, M.C., and BARRY, R.G. 1996. Recent decreases in Arctic summer ice cover and linkages to atmospheric circulation anomalies. Geophysical Research Letters 23(13):1677–1680.

MAXWELL, B. 1997. Responding to global climate change in Canada's Arctic. Vol. 2. In: The Canada country study: Climate impacts and adaptation. Downsview, Ontario: Environment Canada. 82 p.

McCORMICK, P.M., THOMASON, L.W., and TREPTE, C.R. 1995. Atmospheric effects of the Mt. Pinatubo eruption. Nature 373:399–404.

McLAREN, I.A. 1958. The economics of seals in the eastern Canadian Arctic. Journal of the Fisheries Research Board of Canada, Arctic Unit Circular 1. 94 p.

MESSIER, F., TAYLOR, M.K., and RAMSAY, M.A. 1994. Denning ecology of polar bears in the Canadian Arctic Archipelago. Journal of Mammalogy 75:420–430.

NASA GODDARD INSTITUTE FOR SPACE STUDIES. 1998. Pinatubo Climate Investigation. Available at: http://www.giss.nasa.gov/research/intro/hansen.02/index.html

NATIONAL ICE CENTER. 1998. Sea Ice Gridded Climatology [SIGC] Narrative. Available at: http://www.natice.noaa.gov/index.htm

NELSON, R.A., FOLK, G.E., Jr., PFEIFFER, E.W., CRAIGHEAD, J.J., JONKEL, C.J., and STEIGER, D.L. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management 5:284–290.

PARKINSON, C.L., and CAVALIERI, D.J. 1989. Arctic sea ice 1973–1987: Seasonal, regional and interannual variability. Journal of Geophysical Research 94:14499–14523.

PRINSENBERG, S.J. 1980. Man-made changes in the freshwater input rates of Hudson and James Bays. Canadian Journal of Fisheries and Aquatic Sciences 37:1101–1110.

RAMSAY, M.A., and STIRLING, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). Journal of Zoology (London) Series A 214:601–634.

———. 1990. Fidelity of polar bears to winter den sites. Journal of Mammalogy 71:233–236.

SHABBAR, A., and KHANDEKAR, M. 1996. The impact of El Niño-Southern Oscillation on the temperature field over Canada. Atmosphere-Ocean 34(2):401–416.

SKINNER, W.R., JEFFERIES, R.L., CARLETON, T.J., ROCKWELL, R.F., and ABRAHAM, K.F. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Change Biology 4:3–16.

SMITH, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology 58:2201–2209.

SOKOL, R.R., and ROHLF, F.J. 1995. Biometry: The principles and practice of statistics in biological research. 3rd ed. San Francisco, California: W.H. Freeman and Company.

STIRLING, I., and ARCHIBALD, W.R. 1977. Aspects of predation of seals by polar bears. Journal of the Fisheries Research Board of Canada 34:1126–1129.

STIRLING, I., and DEROCHER, A.E. 1993. Possible impacts of climatic warming on polar bears. Arctic 46:240–245.

STIRLING, I., and LUNN, N.J. 1997. Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. In: Woodin, S.J., and Marquiss, M., eds. Ecology of Arctic environments. Oxford: Blackwell Science Ltd. 167–181.

STIRLING, I., and McEWAN, E.H. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behaviour. Canadian Journal of Zoology 53:1021–1027.

STIRLING, I., and ØRITSLAND, N.A. 1995. Relationships between estimates of ringed seal and polar bear populations in the Canadian Arctic. Canadian Journal of Fisheries and Aquatic Sciences 52:2594–2612.

STIRLING, I., PEARSON, A.M., and BUNNELL, F.L. 1976. Population ecology studies of polar and grizzly bears in northern Canada. Transactions of the North American Wildlife and Natural Resources Conference 41:421–429.

STIRLING, I., JONKEL, C., SMITH, P., ROBERTSON, R., and CROSS, D. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Canadian Wildlife Service Occasional Paper 33. Ottawa: Canadian Wildlife Service. 64 p.

STIRLING, I., CALVERT, W., and ANDRIASHEK, D. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. Canadian Wildlife Service Occasional Paper 44. Ottawa: Canadian Wildlife Service. 30 p.

———. 1984. Polar bear ecology and environmental considerations in the Canadian High Arctic. In: Olson, R., Geddes, F., and Hastings. R., eds. Northern ecology and resource management. Edmonton, Alberta: University of Alberta Press. 201–222.

STIRLING, I., SPENCER, C., and ANDRIASHEK, D. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. Journal of Wildlife Diseases 25: 159–168.

TAYLOR, M.K., and LEE, L.J. 1995. Distribution and abundance of Canadian polar bear populations: A management perspective. Arctic 48:147–154.