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ORIGINAL PAPER

Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes

A. S. Fischbach · S. C. Amstrup · D. C. Douglas

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Abstract Polar bears *(Ursus maritimus)* in the northern Alaska region den in coastal areas and on offshore drifting ice. We evaluated changes in the distribution of polar bear maternal dens between 1985 and 2005, using satellite telemetry. We determined the distribution of maternal dens occupied by 89 satellite collared female polar bears between 137°W and 167°W longitude. The proportion of dens on pack ice declined from 62% in 1985–1994 to 37% in 1998–2004 ($P = 0.044$) and among pack ice dens fewer occurred in the western Beaufort Sea after 1998. We evaluated whether hunting, attraction to bowhead whale remains, or changes in sea ice could explain changes in den distribution. We concluded that denning distribution changed in response to reductions in stable old ice, increases in unconsolidated ice, and lengthening of the melt season. In consort, these changes have likely reduced the availability and quality of pack ice denning habitat. Further declines in sea ice availability are predicted. Therefore, we expect the proportion of polar bears denning in coastal areas will continue to increase, until such time as the autumn ice retreats far enough from shore that it precludes offshore pregnant females from reaching the Alaska coast in advance of denning.

A. S. Fischbach (✉)
USGS Alaska Science Center, 4230 University Drive,
Anchorage, AK 99508, USA
e-mail: afischbach@usgs.gov

S. C. Amstrup
USGS Alaska Science Center, 1011 E Tudor Road,
Anchorage, AK 99503, USA
e-mail: samstrup@usgs.gov

D. C. Douglas
USGS Alaska Science Center,
3100 National Park Road, Juneau, AK 99801, USA
e-mail: ddouglas@usgs.gov

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Introduction

Unlike other temperate and Arctic bear species that hibernate when foods are unavailable, polar bears (*Ursus maritimus*) are not required to den because they are able to forage for seals on the pack ice throughout the winter (Amstrup 2003). Pregnant polar bears, however, establish maternal snow dens in autumn or early winter, give birth in mid-winter, and nurture their young until they are able to leave the thermal security of the den in spring (Watts and Hansen 1987; Amstrup and Gardner 1994). Throughout most of their range, polar bears den mainly on land (Amstrup 2003). Historically, many polar bears in the northern Alaska region also have denned on land, land-fast ice (hereafter called fast ice), and drifting pack ice (Amstrup and Gardner 1994).

Denning polar bears subjected to human disturbances may abandon dens before their altricial young can survive the rigors of the Arctic winter (Amstrup 1993). Most human activities that could disrupt dens (e.g., hunting, industrial development, tourism) occur on land and near shore on fast ice (Amstrup 1993). Exploration and extraction of hydrocarbons is expanding in the coastal regions of northern Alaska and proposed in adjacent Canada (National Research Council 2003). In addition, the dynamics (Rigor et al. 2002), seasonal extent (Stroeve et al. 2005), age-composition (Belchansky et al. 2005) and thickness (Rothrock et al. 2003) of the Arctic ice pack have recently changed with climate warming (Comiso 2006; Richter-Menge et al. 2006). These changes emphasize the importance of under-standing the relative frequencies with which polar bears occupy dens on the pack ice and on fast ice and land.

To quantify the denning distributions of polar bears in the northern Alaskan region, VHF radio telemetry and very long-distance offshore tracking flights were used between 1983 and 1991 (Amstrup and Gardner 1994). Although data collected in this manner were spatially expansive, the extended survey flights over the Arctic Ocean were expensive and potentially dangerous, and were discontinued after loss of a tracking plane and crew in 1990 (Sasse 2003). In 1985 we began collaring polar bears in northern Alaska with transmitters that could be relocated by satellite (Amstrup et al. 2000). Most of the satellite transmitters we deployed also transmitted temperature and activity sensor data (Harris et al. 1990). The variable accuracy and intermittent frequency of satellite telemetry relocations (Rodgers 2001) usually necessitates data filtering before analyzing animal movements (Amstrup et al. 2000), but because the physical structure of maternal dens attenuates radio transmissions, we postulated that diminished relocation frequency and accuracy could in itself provide information about the occurrence of polar bear denning activity.

Here, we used an assessment of satellite telemetry location frequency and quality as well as temperature and activity sensor data to distinguish between denning and non-denning adult female polar bears. We validated our methodology using independent field observations and assessed its spatial robustness by comparing den distributions revealed by this method to that obtained by the VHF radio tracking missions of Amstrup and Gardner (1994). We applied the satellite telemetry method to evaluate the status and trends of polar bear denning distribution in the northern Alaskan region. We then examined whether environmental factors that changed during this study explained changes in denning distribution.

Methods

Data collection

We acquired satellite telemetry data between April 1985 and June 2005 from 383 adult female polar bears instrumented with satellite radio collars ($n = 489$, Telonics, Inc., Meza, Arizona, USA) by the United States Geological Survey (USGS) Alaska Science Center and collaborators. The radio transmitters were built to conserve battery life by transmitting for 6–8 h every 3–7 days. Transmissions (401.65 MHz) received by NOAA polar-orbiting satellites were relayed to Service Argos, Inc. (Toulouse, France and Largo, Maryland, USA). Geographic locations of instrumented polar bears were calculated from Doppler shift in transmission frequency and satellite overpass geometry (Service Argos 1996). Service Argos disseminated the location estimates together with an index of location quality and accompanying sensor data ($n = 413{,}283$ satellite overpass records).

The majority of transmitters ($n = 408$) provided temperature and activity sensor data in addition to location information. Temperature was measured by a thermistor inside the radio collar. While body heat conducted into the collar introduces a variably warm bias depending on the animal's activity and posture, internal temperature of a deployed collar generally tracks ambient conditions (Harris et al. 1990). We compared the radio-collar temperatures with the daily mean ambient air temperature at Barrow, Alaska (National Oceanic and Atmospheric Administration 2005) to help determine behavior of instrumented polar bears. Activity was monitored by a mercury tip-switch inside the collar that counted state changes at 1-s intervals. State changes were summed over 24, 72, or 120 h periods to index the animal's activity level. Although activity sensor data were accumulated over three different periods, assessments of relative activity changes within individual bears remained robust because the same sensor was used throughout any given transmitter deployment.

Service Argos changed its convention for reporting location quality indices twice during the course of this study (Rodgers 2001). Because consistent interpretation of location quality was critical to our analyses, we developed a standardized index by cross-walking older indices to the convention used after June 1994. Our standardized numeric index ranks location quality from highest to lowest (3, 2, 1, 0.5, 0.3, 0.2, and 0.1) to facilitate plotting on a scalar axis, and conforms to the post-June-1994 alphanumeric Argos location classes 3, 2, 1, 0, A, B, and Z, respectively.

Classifying bear winter behavior as denning or non-denning

To develop a systematic classification of winter behavior of instrumented polar bears as either denning or non-denning, we first sorted the satellite telemetry data for each bear chronologically from 1 July to 30 June, hereafter termed a "bear-winter". We analyzed 585 bear-winters by examining scatter plots of the activity index, internal collar temperature, surface air temperature at Barrow, and the standardized location quality index. We classified seasonal behavior for all bear-winters that extended through 31 December or that exhibited a clear and persistent denning signature anytime during the den entrance season of October through December (Amstrup and Gardner 1994). Because parturition occurs by early January (Amstrup 2003) denning-like signatures beginning in January or later were deemed to be too late to indicate maternal denning and were not classified as a denning attempt.

Variations in the Argos location quality index are attributable to several factors including the transmitter's geographic position relative to the satellite overpass, stability of the transmitter's oscillator, transmitter power, antenna condition and orientation, animal behavior, and habitat features. Variable satellite viewing geometries introduce unbiased noise in the chronology of the location quality index. A persistent shift in the location quality index, however, indicates a persistent change in habitat or behavior (assuming constant transmitter integrity). For example, when a radio collar is placed on a polar bear, mass of the bear attenuates the transmissions through the standing wave impedance phenomenon (Carr 2001). If the collar detaches, the lower impedance results in increased signal strength, location quality, and relocation frequency. We also have observed similarly improved signal quality when a bear dies, even if the collar remains attached. Concurrent with the collar detachment or the bear's death, recorded collar temperatures track ambient temperatures and become less variable, and activity abruptly falls to zero (Fig. 1a).

The telemetry signature of a denning bear is characterized by a persistent drop in the quality and frequency of relocations upon den entrance, and a return to pre-denning characteristics upon emergence (Fig. 1b). When a bear enters a den, the radio signal is degraded because (1) snow and ice surrounding the den reduce strength of the propagating signal, (2) earthen banks associated with land dens and pressure ridges associated with sea ice dens partially block line-of-sight communication to the satellites, and (3) the antenna can become covered by the bear's body as it lies in the den. Dens on both land and sea ice impose sufficient signal degradation to distinguish a clear drop in transmitter performance during denning, so the identification of denning behavior by signal degradation is unlikely to be biased by den substrate. For transmitters that collect temperature and activity data, the denning signature is further substantiated by a persistent rise in temperature to near or above freezing (distinctly higher than ambient conditions) and a concurrent drop in activity (although some short bouts of high activity may occur). A tracking path, connecting consecutive polar bear relocations, that pauses for extended periods on land or fast ice may also reveal denning behavior.

Telemetry signatures of bears that remain active in winter (non-denning) do not possess an abrupt or prolonged reduction in location quality and frequency (Fig. 1c), aside from a possible steady decline attributable to battery decay. The temperature patterns of radio collars on active bears track ambient surface air temperature, showing substantial variation and positive bias, but no persistent deviation. Activity levels of non-denning bears fluctuate over time and extended periods of low activity are uncommon.

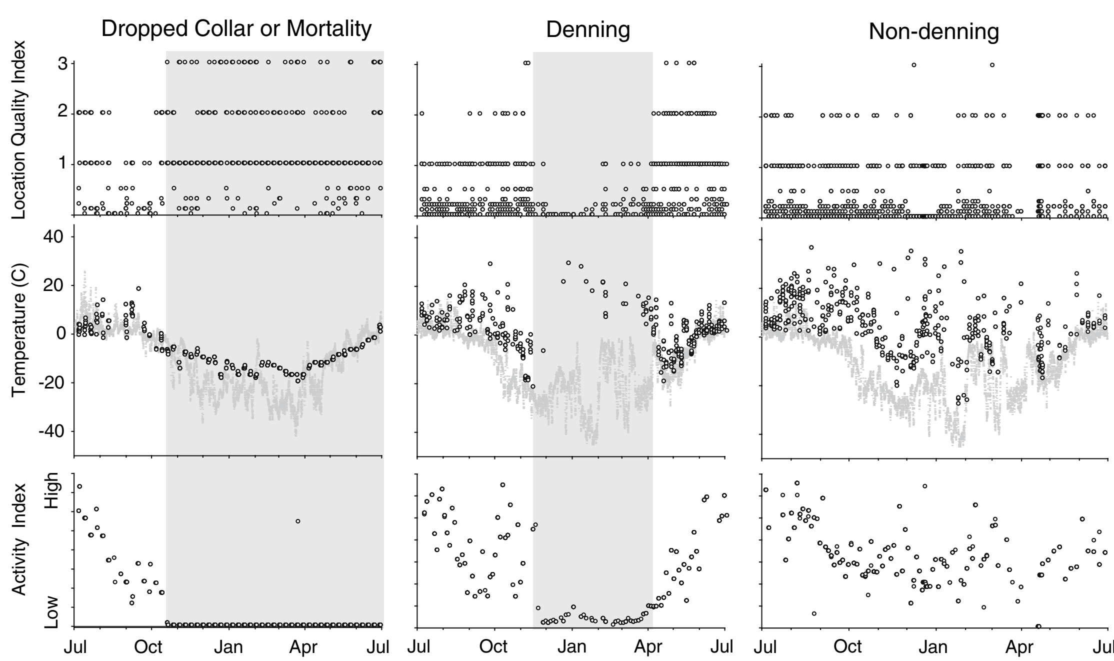

Fig. 1 Examples of three polar bear satellite telemetry data records illustrating three behavioral wintertime signatures: **a** dropped collar or animal mortality; **b** denning; and **c** non-denning. Location quality index is a numerical standardization of the Argos location class indices in use since 1985. Transmitter temperature (*black*) is plotted together with surface air temperature at Barrow, Alaska (*gray*). *Activity index* indicates relative counts per unit time from a mercury tip switch inside the radio collar. *Outlier values* in the sensor records are likely due to parity errors in satellite reception of the modulated signal. *Light gray shading in panel A* denotes time after the inferred dropped collar or mortality event and in *panel B* denotes time when bear behavior was classified as denning

Field validation

Visual observations of collared bears by polar bear researchers and subsistence hunters were used to validate behavior classifications made from satellite data analysis. The field observation data were used in this study only to quantify the accuracy of our telemetry-based classifications, a posteriori. Polar bear research was conducted by the USGS in northern and western Alaska, and by the Canadian Wildlife Service east of Alaska. Observations of subsistence hunters were conveyed by harvest monitoring programs conducted by the US Fish and Wildlife Service and the Government of the Northwest Territories (Department of Resources, Wildlife, and Economic Development). Observations of female polar bears with young-of-the-year confirmed denning the previous winter, observations of females with older offspring confirmed non-denning status during the previous winter, and observations of females with offspring of any age in the autumn confirmed non-denning behavior during the following winter. We confirmed mortalities from hunting by reviewing harvest reporting documents. Dropped collars were confirmed by observation during field research and by recapture of previously collared bears without collars.

Denning distribution

We restricted our analysis of denning distribution to a "core study area" comprising the lands and waters between 137°W and 167°W. The core study area was defined to allow comparison with the previous study of den distributions by Amstrup and Gardner (1994), and because the area has had high levels of polar bear research effort after 1985 (although satellite telemetry data were not collected during 1995–1997). The core study area included the geographic region occupied by the Southern Beaufort Sea polar bear stock, the eastern portion of the Chukchi Sea polar bear stock and the western portion of the Northern Beaufort Sea stock (Amstrup et al. 2004).

We used a linear mixed-effects model (Kenward and Roger 1997) to assess change in the proportion of polar bears denning on pack ice between the early (autumn years 1985–1994) and latter (autumn years 1997–2004) sampling periods. Linear mixed-effects modeling was necessary because Amstrup and Gardner (1994) reported evidence of multi-year fidelity to substrates, despite the annual variation in precipitation, sea ice dynamics and snowdrift patterns. The linear mixed-effects model accounted for possible autocorrelation in den substrate selection by including substrate fidelity of individual bears as a random effect in the model. We also suspected that dens discovered in the same autumn as a radio application could possess a landward bias because radios were attached to bears that were captured within helicopter range of coastal logistic bases. Therefore, we incorporated autumn radio application in the model as a possible interaction with study period.

We hypothesized that sea ice changes may have reduced the availability or degraded the quality of offshore denning habitats and altered the spatial distribution of denning. In recent years, Arctic pack ice has formed progressively later, melted earlier, and lost much of its older and thicker multiyear component (Comiso 2002; Belchansky et al. 2004a, 2005; Stone et al. 2005; Stroeve et al. 2005). We examined ice conditions in the core study area on 1 September. This date was chosen because it just precedes freeze-up and also precedes selection of denning sites by polar bears. We defined total ice extent as the area identified by passive microwave satellite imagery (Comiso 1999) having at least 15% ice cover. We defined marginal ice habitat in the autumn as the proportion identified by passive microwave imagery (Comiso 1999) to have 15–75% ice cover. The fraction of multiyear ice, which also lends inference about ice stability, was defined in winter when satellite microwave observations are most reliable for discriminating ice age (Belchansky et al. 2004b).

We assessed the hypotheses that changes in polar bear harvests or recent increases in the availability of bowhead whale (*Balaena mysticetus*) remains could have influenced the distribution of polar bear maternal dens. Polar bear harvest restrictions have been proposed as causes of changed denning patterns in the 1980s (Stirling and Andriashek 1992; Amstrup and Gardner 1994). Therefore we reviewed reported polar bear harvest patterns to assess whether they may have influenced the distribution of maternal denning during our study. Subsistence bowhead whale harvests in northern Alaska increased during our study (Suydam and George 2004; Koski et al. 2005; North Slope Borough Department of Wildlife Biology unpublished data provided to the authors 24 August 2005), which has led to greater predictability in the presence of whale remains along the Alaska coast. If polar bears come ashore to eat whale remains as a way to fatten before denning, they might simply stay ashore when it is time to enter a den. More predictably available whale remains, therefore, could be a cause for increased coastal denning. Therefore we examined whether evidence of polar bear use of whale remains in the autumn could explain shifts in denning distribution. Although satellite tracking data cannot determine feeding activity, we classified bears as having potential for autumn use of whale remains when the bear's tracking path before 31 December included any standard class Argos location (estimated 1-σ error radius <1.5 km) within 5 km of a whale harvest site.

We hypothesized that den distributions determined from satellite telemetry are spatially representative of denning in the core study area. The aerial radio tracking flights of Amstrup and Gardner (1994) are hypothesized to be spatially representative within the core study area, because they included extensive reconnaissance beyond the eastern and western margins of the core study area as well as up to 700 km offshore. We compared the distribution of dens in the core study area that were determined from satellite telemetry with the distribution determined from the aerial telemetry study of Amstrup and Gardner (1994) during 6 years (1985–1990) in which the two studies overlapped.

Results

Behavior classification

We classified behavior for 481 of the 585 bear-winter satellite telemetry records as either denning ($N = 222$) or non-denning ($N = 259$). The accuracy of our method was confirmed by independent field observations which verified 57 non-denning and 83 denning bear-winters with no misclassifications. We also found the distribution of dens revealed by satellite telemetry agreed with that revealed by extensive aerial radio tracking. During 6 years of coinciding data collection (1985–1990), extensive aerial radio-tracking found 63% of 43 dens on pack ice in the core study area (data extracted from Amstrup and Gardner 1994), while 60% of the 53 dens identified by satellite data analysis were on pack ice (excluding those determined by tracking path alone). The proportions of dens found on and offshore by these two methods did not differ significantly ($\chi^2 = 0.657$, $df = 1$, $P = 0.418$).

Our inability to classify behavior for 104 of the 585 bear-winter records was due to (1) data temporally insufficient or too sparse to distinguish a signature ($n = 75$); (2) data interrupted by a dropped collar or mortality event ($n = 26$); or (3) discordant patterns among the temperature, activity, location quality and location path signatures ($n = 3$). Sparse data were typical of declining transmitter performance near the end of expected battery life. Cold temperatures during the winter season exacerbated battery declines. Subsequent field observations corroborated three of the dropped collar or mortality events identified by the satellite data analysis. The three bear-winters with discordant data involved one temperature sensor that may have been mis-calibrated, and two bears instrumented in Russia that wintered along the west coast of Novaya Zemlya in the Barents Sea where they may have encountered temperature regimes very different from the reference ambient temperatures at Barrow, Alaska.

Trends in denning distribution

During this 20-year study (autumn years of 1985–2004) we identified the denning substrate of 129 denning events within the core study area. We restricted our examination of trends in denning distribution to 124 dens (Figs. 2, 3), occupied by 89 bears, that were classified by satellite telemetry indices other than tracking path alone. This restriction was applied because lack of movement can indicate denning on coastal habitats, but may not reveal denning on drifting pack ice which is in constant motion.

Pack ice denning decreased from 62.3% (SE 8.5%) to 37.1% (SE 8.4%) between the early (1985–1994) and latter (1997–2004) study periods ($F = 1.29$, $df = 120$, $P = 0.0438$). There was no evidence instrumenting some bears close to the time of denning in autumn biased our findings ($F = 0.98$, $df = 120$, $P = 0.323$) or that it affected the observed changes between study periods ($F = 0.02$, $df = 120$, $P = 0.885$).

The patterns of fidelity among bears followed to more than one den also indicated a landward denning shift. The majority of bears for which denning locations were known (62 of 89) were followed to a single den in a single year. Among bears followed to dens in more than one year ($n = 27$), bears showed greater fidelity to substrate in the latter period than the early period. Of the 10 bears followed to multiple dens in the latter period, 9 were faithful to the coastal substrates. In contrast, only 11 of 17 bears followed to multiple dens in the early period were faithful to substrate, and the fidelity was distributed proportionately to the over-all den distribution (4 were faithful to coastal habitats and 7 to pack ice). In both study periods more bears shifted from pack ice to coastal substrates ($n = 4$ early period; $n = 1$ latter period) in subsequent dens than shifted from coastal to pack ice substrates ($n = 2$ early period). The observed shift in fidelity pattern (more bears faithful to land in the latter period and more bears shifting to land in both study periods) suggests a shift in substrate preference whether or not den substrate choice is independent for each pregnancy.

Dens entered on pack ice shifted to the east in the latter period. None of the 20 bears using pack ice dens entered their dens west of 157°W longitude (the approximate longitude of Barrow, Fig. 2) in the latter period, while 15 of 41 pack ice dens were entered west of 157°W longitude in early period. The proportion of pack ice dens entered in the western half of the core study area (west of 152°W longitude) dropped from 54% (SE 9.6%) to 25% (SE 11%) between study periods (Linear mixed-effects model $F = 3.81$, $df = 59$, $P = 0.056$). In contrast, there was no latitudinal shift in offshore denning between the early and latter periods. Equivalent proportions of pack ice dens were entered north and south of the middle latitude (73°N) of the core study area during both periods (Linear mixed-effects model $F = 0.08$, $df = 59$, $P = 0.781$).

We evaluated the observed changes in denning distribution against changes in the extent and nature of sea ice. Autumn sea ice has become less extensive and less consoli-

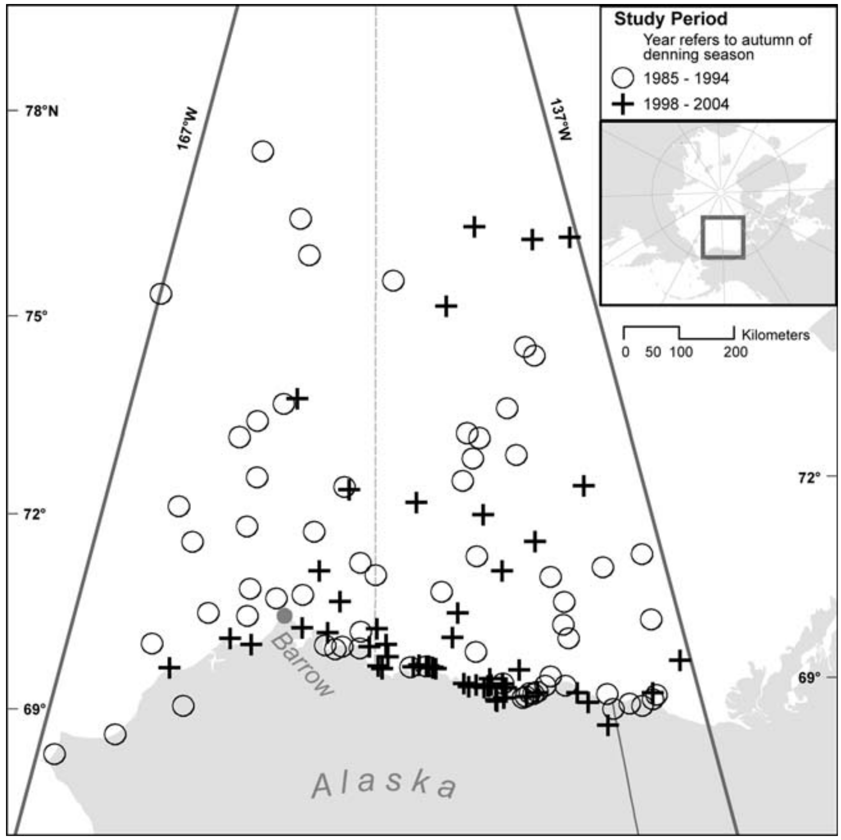

Fig. 2 Distribution of polar bear den entrance locations determined by interpretation of satellite telemetry data in the core study area (137°W–167°W). Dens identified by examination of telemetry relocation path alone are excluded. Note that no pack ice denning bears entered dens west of 157°W (the approximate longitude of Barrow) during the latter period. The *dashed line* indicates the longitudinal center of the core study area

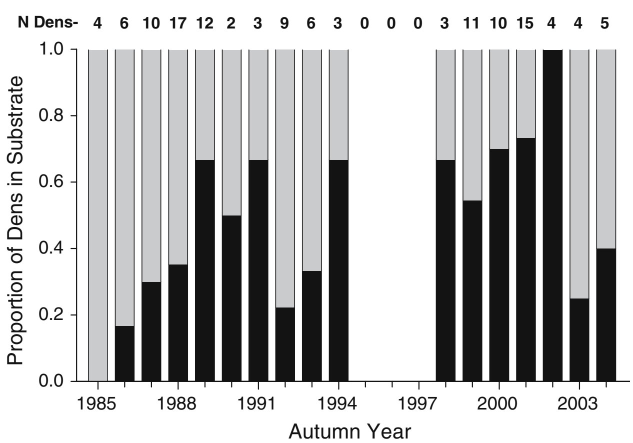

Fig. 3 Annual proportions of polar bear dens in two substrate classes, pack ice (*gray*) and coastal habitats (*black*), within the core study area (137°W–167°W). *Numbers* above each histogram indicated the annual number of denning events determined by interpretation of satellite telemetry indices other than movement path alone. *Year* denotes autumn of the denning season

dated within the core study area during the latter period (Fig. 4a, b). Updated observations from Belchansky et al. (2004b) also revealed a significant decline in mid-winter multiyear sea ice area (Fig. 4c) in the latter period. Furthermore, the rates of sea ice change appeared more pronounced in the western half of the core study area than in the eastern half (Fig. 5a–c). We tested for differences in the rate of change of sea ice between the east and west regions by regressing the differences in each of three ice metrics between the western and eastern areas against time since start of the satellite record in 1979 (Fig. 5d–f). Differences in total ice cover and in multiyear ice area between the eastern and western areas (west minus east) became significantly greater ($P = 0.004$ and 0.013, respectively) with negative slopes (Fig. 5d–f), indicating greater ice losses in the west compared to the east. An increasing trend in the proportion of marginal ice in the western area compared to the east (Fig. 5e) was nearly significant ($P = 0.078$). Hence all three metrics corroborate accelerated sea ice deterioration in the western portion of the study area.

Hunting pressure declined dramatically in the core study area when sport hunting came under a quota system in Canada in 1968 and was banned in Alaska in 1972. Although a low level of hunting continues in both Alaska and Canada, no substantial change in hunting has been reported since the Canadian quota system was established (Brower et al. 2002) and a harvest monitoring program was instituted in Alaska in 1980 (Brower et al. 2002; Schliebe et al. 2002; Schliebe et al. 2006). Since harvest levels have been relatively low and stable for over 30 years, we conclude that reduced hunting pressure was not a determining factor in the landward denning distribution shift.

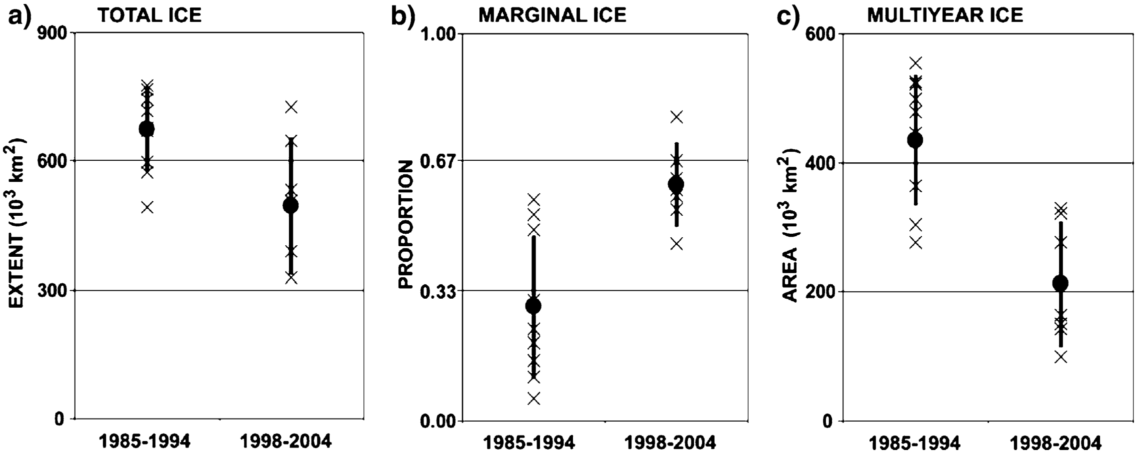

Fig. 4 Mean (±1 SD) sea ice characteristics in the core study area contrasting the early and latter periods: **a** total extent of ice 15–100% concentration on 01 September ($t = 3.0$, $P = 0.009$); **b** proportion of 01 September ice extent comprised of marginal (15–75% concentration) ice ($t = -4.14$, $P < 0.001$); and **c** mid-winter (January) multiyear sea ice area ($t = 4.66$, $P < 0.001$)

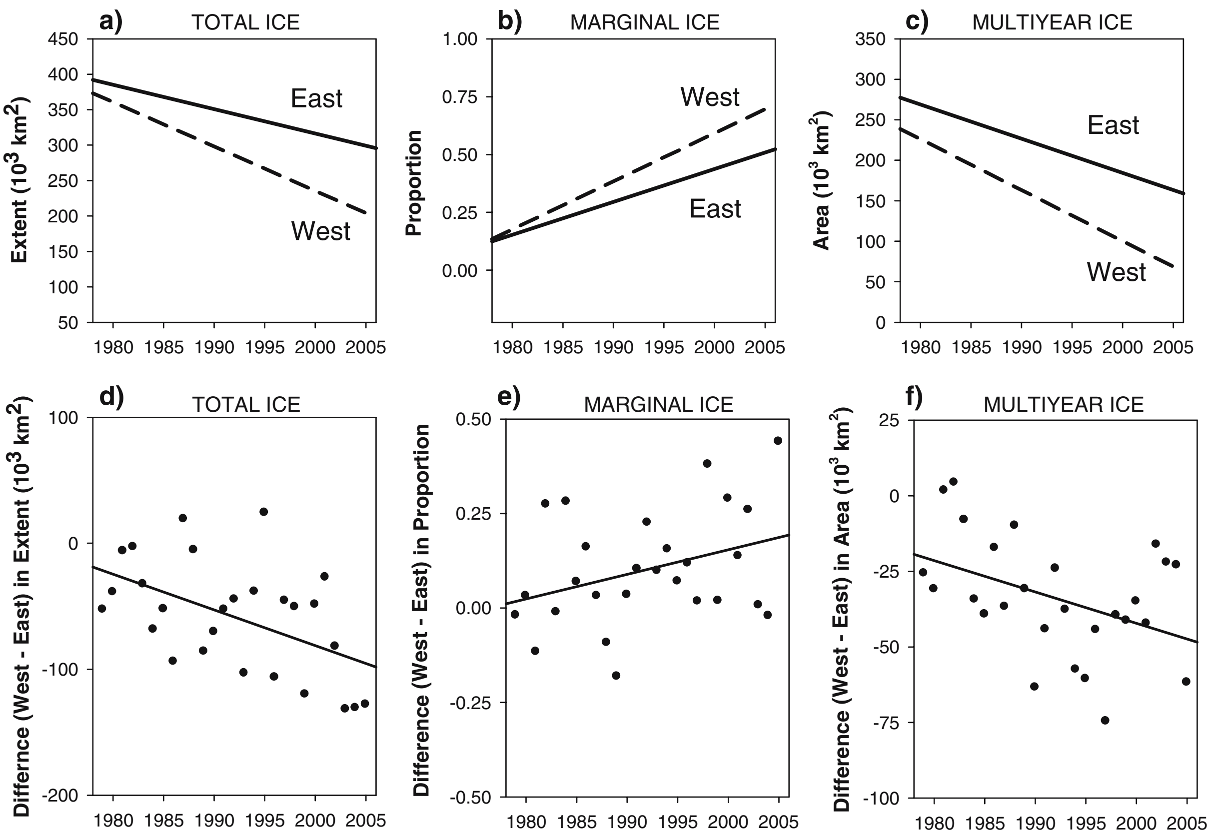

Fig. 5 Linear trends (1979–2005) in the eastern (*solid*) and western (*dashed*) halves (divided at the 152°W meridian) of the core study area in the **a** total extent of ice 15–100% concentration on 01 September, **b** the proportion of total ice on 01 September comprised of marginal (15–75% concentrations) ice, and **c** average multiyear sea ice area in January: all regressions were statistically significant ($P \leq 0.013$). Linear trends in the annual difference (western study half minus eastern study half) in the **d** total extent of ice 15–100% concentration on 01 September ($P = 0.007$), **e** the proportion of total ice on 01 September comprised of marginal ice ($P = 0.078$), and **f** average multiyear sea ice area in January ($P = 0.029$)

Our tracking data indicated that pregnant polar bears made little use of whale remains and that use was not associated with coastal denning. Complete autumn tracking paths ($n = 201$) were available from 123 individual bears in the core study area. Among the complete autumn tracking paths (113 denning and 88 non-denning bear winters), 31 tracks passed close enough that bears could have visited the whale harvest site. Of these, 6 tracks were pre-denning (5.3% of 113 pre-denning tracks) and 25 were of bears which did not subsequently enter a den (28.4% of 88 non-denning tracks). Two individual bears accounted for 11 (10 non-denning and 1 denning) of the 31 tracking paths that could have allowed a whale harvest site visitation. These two bears were known recidivists at the harvest site. The contrast between these two bears and others which may or may not have used the harvest site even though it was nearby, indicate variation among bears in their propensity to utilize whale remains as well as repeated use by some individuals. Nevertheless, it was apparent that females preparing to den were far less likely to use whale harvest sites than non-denning females. Although use of whale harvest sites among pre-denning bears increased in the latter period, from 1.5% (1 of 64) to 10.2% (5 of 49), the vast majority of pre-denning bears never visited a harvest site and the few that did subsequently denned on both pack ice and coastal substrates. Hence, we conclude that increased bowhead whale harvest was not a determining factor in the recent landward shift in polar bear denning.

Discussion

Behavior classification

We were able to identify denning attempts with high accuracy by systematically examining seasonal patterns in location quality, relocation frequency, collar temperature, activity level, and movement path. Independent field observations fully corroborated our behavioral classifications. The den substrate utilization determined by satellite telemetry was statistically indistinguishable from that determined by the long-distance aerial VHF radio tracking (Amstrup and Gardner 1994), during the 6 years that the studies coincided, indicating that the satellite telemetry is an accurate and safe substitute for extensive offshore radiotracking. Although activity sensors on collars were useful for identifying dropped collar and mortality events, they were less useful for classifying behavior. Some denning bears had intermittent bouts of high activity or prolonged bouts of moderate activity, while a few non-denning bears exhibited long periods of low activity. Temperature data, however, typically resolved misleading or ambiguous activity signatures. In the future, including daily average temperature and its variance in the sensor record could improve the ability to discriminate denning behavior, especially when data are sparse, because diurnal averages would be more robust than instantaneous measurements for indicating a long-term sustained behavior like denning.

Trends in denning distribution

The changing nature of the sea ice in the northern Alaska region appeared to be the major factor influencing the changing distribution of polar bear maternal denning that we observed. The significant landward shift from the early to latter periods appeared to be driven by reduced suitability of the pack ice as a denning substrate. Autumn sea ice extent has declined in recent years, and changes in the age-structure and degree of consolidation of the remaining ice are consistent with reduced suitability of sea ice as a stable denning platform. The higher rates of sea ice change in the western portion of the study area also are consistent with the eastward shift of pack ice denning bears. Offshore denning requires pack ice that is available in the autumn and early winter, drifted with sufficient snow to accommodate a den, and stable enough to maintain its integrity for the duration of denning. Unstable ice has been observed to lead to failure of on-ice denning attempts (Amstrup and Gardner 1994), and unconsolidated sea ice is probably less stable during autumn and winter storms. The reductions in sea ice extent create greater open water fetch which can destabilize sea ice even during moderate storms (Atkinson et al. 2006). Similarly, greater fetch coupled with later freeze could restrict access to land denning habitats. Numbers of dens on Hopen, the most southern denning island in the Svalbard Archipelago, are dependent upon the timing of freeze-up. When sea ice freezes too late, bears do not den on Hopen (Derocher et al. 2004).

With the longer melt seasons of recent years (Stroeve et al. 2005) more autumn precipitation may fall as rain rather than snow. Analysis of snow cover over Arctic pack ice from the 1950s through the 1990s showed a decreasing trend (Warren et al. 1999). Hence, the sea ice may not only be less stable, but covered with less snow for den construction. To accumulate snowdrifts sufficient for polar bear denning, the sea ice surface must be deformed by pressure ridges created by wind-driven convergent stresses on relatively thick ice that extends to the coast (Reimnitz et al. 1999; Richter-Menge et al. 2002). Because autumn sea ice is now thinner and extends to the coast later in the season, autumn pressure ridge formation may be more limited than in the past. Pressure ridges that form during mid-winter when consolidated sea ice extends to the coast must survive at least one summer to be available for denning habitat the following autumn. Yet, recent climate patterns have tended to reduce summer ice survival.

The degree of convergence and deformation in the Beaufort Sea ice pack is directly associated with strength and position of the anticyclonic Beaufort Gyre (Rigor et al. 2002). The Beaufort Gyre compresses sea ice against the Canadian Archipelago in the northern Beaufort Sea, shears Beaufort Sea pack ice against northern Alaskan fast ice and facilitates southward advection of multiyear ice into the southern Beaufort and Chukchi Seas. In 1989 and 1990, atmospheric pressure in the Arctic shifted to a low-pressure regime and a weakened and more easterly Beaufort Gyre. Strength of the Beaufort Gyre has not since returned to levels of the persistent high-pressure regime in the 1980s. A weaker and more easterly Beaufort Gyre, together with declining summer ice extent, would tend to reduce the coverage of multi-year ice and convergent ice motion in the western Arctic. Hence in recent years, the conditions necessary to form and keep pressure ridges—a critical element of pack ice denning habitat—in the western portion of the study area have likely been reduced relative to the eastern Beaufort Sea.

We conclude that recent sea ice changes have collectively reduced the availability and quality of offshore denning habitat, and that these changes have been greater in the western portion of the study area. In our judgment, sea ice changes offer the most plausible explanation for the observed decline and eastward shift in pack ice denning. Similar changes in Arctic sea ice are predicted to continue in coming decades (Overpeck et al. 2005; Zhang and Walsh 2006).

Although reduced hunting pressure has been suggested as an explanation for increases in on-shore denning (Stirling and Andriashek 1992; Amstrup and Gardner 1994), our data indicate changes in polar bear hunting patterns were not a determining factor in the landward denning shift we recorded. Reported harvest levels were low and stable throughout this study and had persisted for 25 years prior to the shifts in den distribution we observed. Some other human activities also can be ruled out as a cause for the changed distribution we observed. Hydrocarbon exploration and development expanded in northern Alaska—especially during the latter half of our study (National Research Council 2003). These activities have not occurred on the pack ice, and with the exception of a couple of near shore sites have been limited to terrestrial habitats. Yet during our study, bears chose increasingly to den on land.

Our data did not support the hypothesis that increased availability of bowhead whale remains was responsible for the landward denning shift. Satellite tracking paths indicated that only a small fraction of pregnant bears in the study area visited whale harvest sites, and the few that did denned both near shore and on the pack ice. Hence, we conclude that the increased availability of whale harvest remains on Alaska's north coast was not a significant contributing factor to the recent landward shift in denning distribution.

Implications to population ecology

Historically, most polar bears throughout the polar basin including the Beaufort Sea reside on the sea ice throughout the summer (Amstrup et al. 2000; Amstrup 2003). In recent years, sea ice retreat has forced many polar bears over very deep waters that are presumed to be of low productivity (Pomeroy 1997). Polar bears may alternatively strand on land, and increasing numbers of bears have recently been observed on the Alaska coast during summer and autumn (Schliebe et al. 2006). If adequately nourished before coming ashore, pregnant females could simply den on land rather than returning to the ice after the autumn freeze. This is the pre-denning behavior for bears in Hudson Bay where the sea ice melts entirely in summer forcing the whole population onto land, and where polar bears are able to accumulate large energy stores before the sea ice melts (Stirling et al. 1977). In contrast, polar bears in the Beaufort Sea typically reach peak weights in late autumn and early winter (Durner and Amstrup 1996), not in summer as they do in Hudson Bay. Most Beaufort Sea bears probably are not fat enough in mid-summer to fast for months and then den successfully without first returning to the sea ice to feed. This is substantiated by our satellite tracking data. None of the bears followed to dens in the core study area for which we had complete autumn tracking paths ($n = 113$) spent time loitering on land before entering their dens for the winter. Hence, in contrast to the Hudson Bay population, bears occupying the polar basin may be less capable of maintaining long-term reproductive viability by denning on land after a prolonged summer and autumn fast.

Whether they are forced onto land or far offshore by the recent changes in the sea ice, polar bear foraging opportunities in the Alaska region appear reduced from earlier times. The physical stature of adult male polar bears and cubs has recently declined in the southern Beaufort Sea region, as has the survival of cubs (Regehr et al. 2006). Furthermore, offshore pregnant bears that choose to den on land must wait longer for new sea ice to form, or they must cross greater expanses of open water (Derocher et al. 2004). Although polar bears are strong swimmers, recent observations suggest their ability to cross large expanses of open water may be limited (Monnett and Gleason 2006).

Conclusion

The landward shift of polar bear denning that we observed is consistent with recent losses of stable sea ice and delays in autumn freeze-up. Similarly, bears continuing to den at sea have shifted their distribution to the east where ice deterioration has been less severe. If predictions of continuing declines in Arctic sea ice are realized, we anticipate that the proportion of polar bears denning on land in Alaska will continue to increase. However, if the summer ice retreats far enough from shore and for a long enough time; it could prevent pregnant females, that are foraging offshore, from reaching the coast in advance of autumn den entry. If that occurs, Beaufort Sea polar bears may be forced to den in deteriorating pack-ice habitats. They also may be forced to compete for land denning habitats in parts of the Arctic presently occupied by other polar bear populations. Reduced access to coastal denning regions for pregnant bears that are foraging offshore, in concert with reduced quality and quantity of offshore denning habitat, can be expected to decrease reproductive success of this population.

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