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Activity and Movement Patterns of Polar Bears Inhabiting Consolidated versus Active Pack Ice

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ABSTRACT. We investigated the influence of ice conditions on activity and movement patterns of polar bears in the Canadian-West Greenland Arctic. We used radiotelemetry data gathered over 11 years (1989–99) from 160 adult female polar bears to test for differences in movement and activity of bears inhabiting active ice and consolidated ice. Bears inhabiting active ice moved more than those inhabiting consolidated ice (12 versus 8 km/day), but their activity throughout the year did not differ (bears of both groups were active for 21% of the day). Differences in activity and movement of bears in the two study areas appeared to be related to differences in predominant ice conditions and presumed prey availability. Seals, particularly juveniles, are most plentiful in spring and summer, when polar bears moved more and were most active. During winter, when juvenile seals were less available in consolidated ice areas, bears in that habitat were less active and moved less than bears in active ice areas. Polar bears have evolved flexible patterns of seasonal activity, movements, and facultative den use as adaptations to different sea-ice environments.

Key words: Canadian-West Greenland Arctic, polar bears, predator-prey, radiotelemetry, rate of movement, sea ice, seals, seasonal patterns, sheltering, *Ursus maritimus*

RÉSUMÉ. On a étudié l’influence des conditions de glace sur le régime de l’activité et du déplacement de l’ours polaire dans l’Arctique canadien de l’ouest du Groenland. On s’est servi de données prélevées par radiomesure sur une période de 11 ans (de 1989 à 1999) portant sur 160 ourses polaires adultes afin de déterminer s’il existe des différences dans le déplacement et l’activité des ourses entre celles qui vivent sur la glace mobile et celles qui vivent sur la glace soudée. Les ourses vivant sur la glace mobile se déplaçaient plus que celles vivant sur la glace soudée (12 km/jour contre 8), mais leur activité tout au long de l’année ne différait pas (les ourses des deux groupes étaient actives 21 p. cent de la journée). Les différences dans l’activité et le déplacement des ourses entre les deux zones d’étude semblaient être reliées à des différences dans les conditions de glace prédominantes et dans la disponibilité présumée des proies. L’abondance des phoques, en particulier les jeunes, atteint son maximum au printemps et en été, au moment où les ourses polaires étaient souvent le plus actives et se déplaçaient le plus. Durant l’hiver, quand les phoques juvéniles étaient moins disponibles dans les zones de glace soudée, les ourses vivant dans cet habitat étaient moins actives et se déplaçaient moins que les ourses vivant dans les zones de glace mobile. L’ourse polaire a développé une certaine flexibilité de comportement dans son activité, son déplacement et son utilisation facultative d’une tanière, pour s’adapter à différents environnements de glace de mer.

Mots clés: Arctique canadien de l’ouest du Groenland, ours polaire, prédateur-proie, radiomesure, taux de déplacement, glace de mer, phoques, régimes saisonniers, abri, *Ursus maritimus*

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INTRODUCTION

The polar bear (*Ursus maritimus*) is the most carnivorous of the ursids, feeding primarily on ringed seals (*Phoca hispida*) and secondarily on bearded seals (*Erignathus barbatus*) (Stirling and McEwan, 1975; Smith, 1980; Stirling, 1988). Polar bears live wherever sea ice and seals occur, from the North Pole to the southern extent of seasonal fluxes in sea ice (Stirling, 1988). The Arctic sea ice upon which polar bears live is highly variable, both geographically and temporally (Collin and Dunbar, 1964; Ferguson and Messier, 1996; Smith et al., 1998). Sea-ice variation is due to differences in temperature, landforms, and ocean currents, and variation occurs from year to year and from season to season (Stirling and Lunn, 1997; Ferguson et al., 2000a). Sea ice shows considerable

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variation. Consolidated pack ice and active pack ice are very different from each other, and the differences between them also vary across time and space. Consolidated ice shows less spatial variation from year to year and from season to season, and it has less primary productivity (Stirling et al., 1993; Stirling, 1997). In contrast, active sea ice, as its name suggests, varies from year to year and from season to season and has greater primary productivity (Savidge et al., 1996; Arrigo et al., 1997; Nicol and Allison, 1997; Smith et al., 1998).

The aim of this study was to determine how polar bears adjust their movements and activity level in relation to conditions of the sea ice. We predicted that polar bears living in areas where the ice is consistently more active would display greater mobility and activity levels than bears in areas where the ice is more stable and less dynamic. We believed that these changes in movements and activities would result from the impact that the differing ice conditions have on abundance and availability of ringed seals.

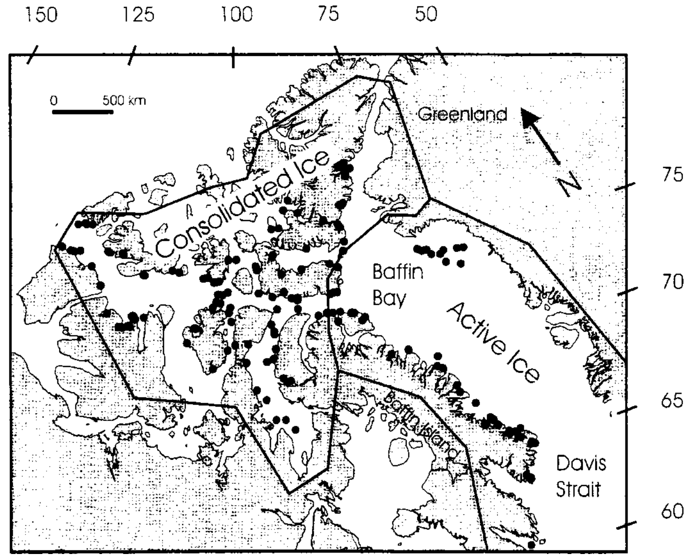

FIG. 1. The Canadian-West Greenland Arctic study area, showing regions of consolidated ice (Canadian Arctic Archipelago) and active ice (Baffin Bay-Davis Strait). Dots indicate original locations of 160 adult female polar bears captured and equipped with satellite radio collars in 1989–99.

METHODS

Study Area

The Arctic region we investigated extends from 60˚N to 80˚N and from 65˚W to 110˚W (Fig. 1). Of the total study area (2.3×10^6 km^2), 55% is ocean. A mantle of sea ice covers these Arctic waters during most of the year. Almost total ice cover occurs in late winter, whereas minimum ice extent occurs in September (Collin and Dunbar, 1964; Ferguson et al., 2000a).

We studied polar bears in Baffin Bay and in several portions of the Canadian Arctic Archipelago. Baffin Bay, although largely ice-free in summer, is entirely covered by ice in winter. The winter ice in Baffin Bay is very active: cracks and leads are constantly forming and refreezing, and floes shift with the winds and currents. The Canadian Arctic Archipelago, in contrast, is characterized by stable annual ice interspersed with multi-year floes. Its ice cover consists mostly of multi-year ice (51%) and shorefast ice (30%) that surrounds local areas of active pack ice (Ferguson et al., 2000a). It has low seasonal variation in ice cover (2–20% change in annual ice) and little open water (mean annual percent open water = 7%; Ferguson et al., 2000a).

Rate of Movement and Activity

Polar bears were captured from a helicopter using darting methods in either spring (April-May) or autumn (September-October) of 1989–99. We equipped 160 adult female polar bears with satellite radio collars (Telonics, Inc., Mesa, Arizona). Satellite telemetry (Argos Data Collection & Location System) allowed us to obtain the bears' locations every 4–6 days year-round. The latitude-longitude coordinates were converted to Universal Transverse Mercator coordinates (SPANS GIS, Intera Tydac Technologies, Inc.) before analyses.

Family status of each bear was recorded at the time of capture (and during subsequent recaptures) as either (1) female with cubs-of-the-year, (2) female with one-year-olds, or (3) solitary adult female (includes females with two-year-olds). The start of a reproductive year was considered to be 1 April; thus females with cubs-of-the-year included females with cubs from approximately 3 months old (exiting their maternity den) to approximately 15 months old (the following year). If telemetry data confirmed maternity denning for a female (Messier et al., 1994; Ferguson et al., 2000b), then that female was considered to have cubs-of-the-year the following year, a reasonable assumption given that most cubs survive their first year (Amstrup and Durner, 1995). If a female initially captured with cubs-of-the-year did not subsequently enter a maternity den, she was classified as accompanied by yearlings in the following year. These assumptions applied to 45 bear-years of data (hence, 28% of recorded family status was determined without visual verification). The assumptions are justified, as female polar bears tend to follow a regular 3- to 4-year reproductive cycle (Ramsay and Stirling, 1988). Mature females are believed to give birth to cubs in mid December and nurse their young for 2 to 3 years before mating again. To ensure that data are independent within each category of family status, we used data from the same bear for more than 1 year only if its family status had changed (e.g., single to female accompanied by cubs).

A sensor in the radio collar transmitted information on each bear's activity level (percentage of day that the bear was active; Messier et al., 1994) during the previous 24 h. To reduce dependence among data, we averaged activity data over each season for each bear. The seasonal mean values were then entered in the statistical analyses.

The minimum distance travelled between two successive locations was calculated as the straight-line distance between successive location points. The mean seasonal rate of movement for each polar bear was calculated by summing the lengths of these line segments and dividing by the corresponding time interval. Bears with more than 10 locations per season were used to calculate rate of movement. We compared activity and movement among four biological seasons: winter (1 November – 15 March), spring (16 March – 31 May), summer (1 June – 15 August), and autumn (16 August – 31 October; Ferguson et al., 1998). We did not use location or activity data from females while they were in dens or shelters (see Ferguson et al., 2000b).

Statistical Methods

We log transformed rate of movement and square-root arcsine transformed activity data to normalize data. Activity level and movements are likely related; hence, we used multiple analysis of variance (Wilks' λ test statistic) with Tukey's test for multiple comparisons (SAS Institute, Inc., 1990). Transformed movement rate and activity were the dependent variables and season, year, family status, and region (Archipelago and Baffin Bay) were the independent variables. Year was considered a random variable, whereas season, family status, and ice type were fixed variables. We present untransformed data in Results. Movement rate and activity data are given as mean ± 1 SE.

RESULTS

In total, 160 polar bears were radio-collared across the Canadian-West Greenland Arctic and monitored for 2 – 3 years over the study period, 1989 – 99. In the following analyses, we used 311 bear-seasons of data that had sufficiently large sample sizes (more than 10 locations/season) and a total of 11 581 locations with known precision level (accurate to the nearest kilometre). Of the total locations, 35% were from females with cubs-of-the-year, 25% from females with 1-year-olds, and 40% from solitary females (includes 12% from females with 2-year-olds). Locations for females were evenly distributed across all four seasons (26% in spring, 27% in summer, 20% in autumn, 27% in winter). We collected 66% of the telemetry locations (n = 106 bears) in the Canadian Arctic Archipelago portion of the study area and 34% (n = 54 bears) in Baffin Bay and Davis Strait.

Rate of movement and activity of polar bears did not differ with year (movement: $F_{8,310} = 1.34$, $p = 0.23$; activity: $F_{7,310} = 0.41$, $p = 0.90$) or family status (movement: $F_{2,310} = 0.83$, $p = 0.44$; activity: $F_{2,310} = 1.42$, $p = 0.24$). These results were consistent for both confirmed and assumed family status. Therefore, family status and year were not used in subsequent analyses.

TABLE 1. Results of a multiple analysis of variance test of the effects of ice type and season on rate of movement (km/day) and activity (% of day active) of polar bears (160 individuals, 311 bear-seasons) in the Canadian-West Greenland Arctic.

Source of variation	Rate of movement			Activity		
	df	*F*	*p*	*df*	*F*	*p*
Season	3	10.4	0.0001	1	15.0	0.001
Region	1	25.8	0.0001	3	0.02	0.89
Season by region	3	9.26	0.0001	3	5.51	0.001

Rate of movement of female polar bears varied with season and region, but we noted a significant interaction (Table 1). Thus, we present data for each ice type and season and compare mean values with Tukey's test (α = 0.05) for pairwise comparisons (Fig. 2). Bears inhabiting active ice had a greater rate of movement than bears inhabiting consolidated ice during spring (12.7 ± 1.0 versus 8.4 ± 0.6 km/day), summer (12.0 ± 0.7 versus 8.6 ± 0.4 km/day), and winter (11.8 ± 0.8 versus 5.2 ± 0.6 km/day). However, no difference was observed during the autumn period (7.3 ± 2.2 versus 7.3 ± 0.6 km/day). Overall, bears inhabiting active ice moved more than bears inhabiting consolidated ice (11.8 ± 0.6 versus 7.9 ± 1.1 km/day).

Activity of female polar bears varied with season, but not with region. Over the year bears were active 21% of the time when inhabiting either ice type. A significant season by region interaction was observed (Table 1). Thus, we present the results for each ice type and season (Fig. 3). Polar bears inhabiting active ice were more active in spring (24.3%), summer (19.7%), and winter (22.1%), compared to the autumn period (12.2%). In contrast, bears inhabiting consolidated ice were more active in spring (24.3%) and summer (22.2%), and less active in autumn (16.3%) and winter (16.0%). The only significant ice type by season comparison was for winter, when polar bears inhabiting active sea ice were more active than polar bears inhabiting consolidated sea ice.

DISCUSSION

For large terrestrial mammals, the Arctic is an energetically expensive place to live. Hence, increased movement rates and activity by polar bears likely indicate greater opportunities for hunting seals or greater distances between feeding areas. We predicted that if seals were unavailable as food, then polar bears would considerably reduce activity and movement rate to conserve energy. We recorded a greater movement rate for polar bears inhabiting active ice than for polar bears inhabiting consolidated ice during three of four seasons. The polar bears inhabiting active sea ice may have had more food available: relatively low densities of ringed seals (0.28 – 0.97 seals/km^2) have

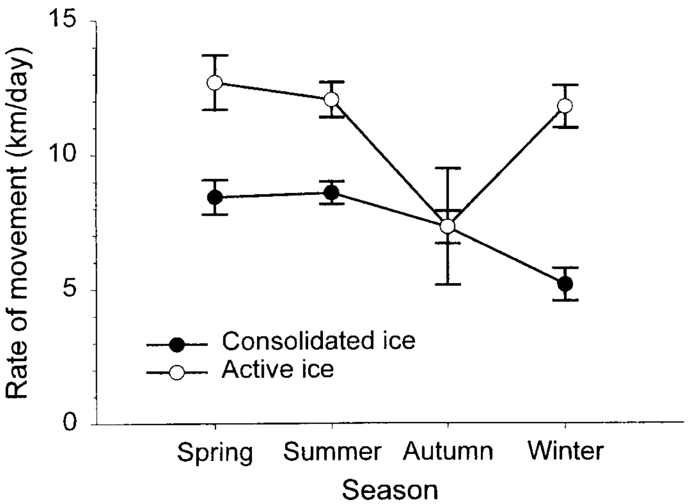

FIG. 2. Seasonal changes in movement (km travelled per day) for female polar bears inhabiting consolidated versus active ice in the Canadian-West Greenland Arctic. Error bars are ± 1 standard error. A difference in movement rate between ice types was detected in spring, summer, and winter (Tukey's test, α = 0.05), but not in autumn. Seasons: winter (1 November–15 March), spring (16 March–31 May), summer (1 June–15 August), and autumn (16 August–31 October).

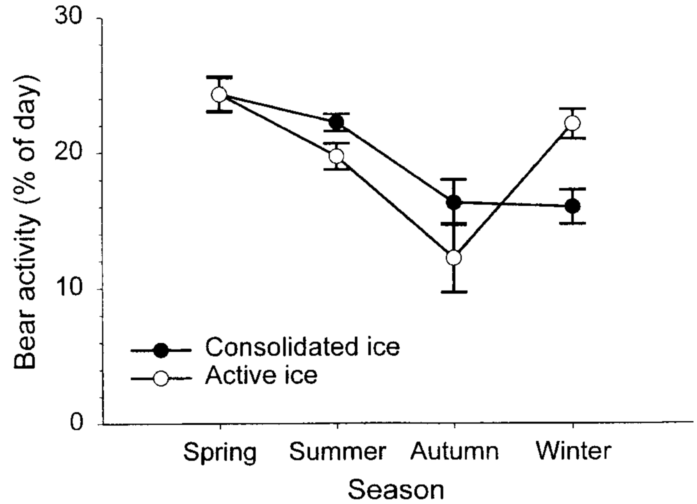

FIG. 3. Seasonal changes in activity (percentage of day during which bears are active) for female polar bears inhabiting consolidated versus active ice in the Canadian-West Greenland Arctic. Error bars are ± 1 standard error. A difference in activity level between ice types was detected in winter (Tukey's test, α = 0.05), but not in spring, summer, or autumn. Seasons: winter (1 November–15 March), spring (16 March–31 May), summer (1 June–15 August), and autumn (16 August–31 October).

been reported for the consolidated ice found in the Canadian Arctic Archipelago (Stirling et al., 1982; Kingsley et al., 1985), whereas high seal densities occurred in the offshore active ice of Baffin Bay (1.4 seals/km^2; Finley et al., 1983) and along the coast of Baffin Island (2.1 seals/km^2; Stirling and Øritsland, 1995). Polar bears inhabiting consolidated pack ice probably spent relatively more time resting and conserving energy, particularly in winter. Since sea ice drifts with currents, directional ice movements—particularly during late summer in active ice areas—may have influenced movement rates of bears.

Higher productivity in areas with active ice presumably translated into increased seal densities. However, the accessibility of seals as prey for polar bears in active ice varied with seasons because of large seasonal cycles in sea ice (Ferguson et al., 2000a). Large-scale seasonal changes in sea ice resulted in polar bears' making large seasonal movements to follow changes in seal availability (Garner et al., 1990; Wiig, 1995; Ferguson et al., 2000a). During winter, polar bears in active ice areas recorded greater movement and activity, suggesting greater hunting opportunities than in consolidated ice areas. Active ice areas, with open water in summer and unstable ice in winter, have an influx of young ringed seals in early winter, and the young seals remain in the area until the ice retreats in early summer. But this great seasonal variation in ice cover means reduced availability of prey in autumn, the open water season. In active ice areas, the autumn season was associated with the lowest movements and activity of polar bears, indicating a foraging strategy that minimized energy costs while ice cover was essentially absent. Bears that forage during the open water season experience limited success in catching seals. Some individuals patrol the shoreline for carrion and hunt marine prey, although kills are infrequent (Stirling et al., 1980; Ferguson et al., 1997). The extreme of reduced movement and activity in autumn appears to have led to the use of snow shelters: bears facultatively entered dens to await the return of favourable foraging conditions (Messier et al., 1994; Ferguson et al., 2000b).

In contrast, polar bears inhabiting consolidated sea ice showed a less dramatic decline in movement and activity in autumn, when multi-year ice (although not as productive as active ice areas) was still available to provide habitat for hunting seals. However, these bears moved less and were less active in winter. By winter, juvenile seals have either migrated to open water areas or have gained experience and thus are presumably more difficult to catch (Stirling, 1997). Adult seals are likely the most difficult to hunt during winter, and they occur at low densities in areas of consolidated ice. Hard snow and stable ridges, characteristic of consolidated ice in winter, also reduce foraging opportunities and success for bears. Landmasses restrict the movements of bears in the Canadian Arctic Archipelago, so these bears are less able to follow juvenile seals. Thus, low seal densities and less accessible prey caused polar bears living in consolidated ice areas to reduce their movement and activity in winter. The extreme of this reduction is revealed by the facultative use of snow shelters at that time, a phenomenon observed only in consolidated ice areas (Ferguson et al., 2000b).

During spring and summer, polar bears had the greatest rate of movement and the greatest level of activity, regardless of ice type (see also Messier et al., 1992). In contrast, Beaufort Sea bears recorded lower movement rates in spring and high movements in summer (Amstrup et al., 2000). In spring, bears hunt for seals in subnivian lairs during the pupping season (Smith, 1980) and for juvenile seals in the active ice areas. In summer, seals moult, juveniles are weaned, and bears have greater success stalking and hunting seals at breathing holes (Stirling and Latour, 1978). The availability and accessibility of seals for polar bears is thought to be greatest during spring and summer (Stirling and Øritsland, 1995). Hunting in areas with ice peaks in late summer and autumn, possibly because reduced ice cover results in high concentrations of seals on the ice that remains (Amstrup et al., 2000).

The relatively higher rates of movement by bears on active pack ice in winter may be due to the greater availability of prey in this habitat. In addition there is greater accessibility, as the moving ice creates ice-water edges. During winter, bears follow ice edges and the high concentrations of young seals. Throughout the seasons, polar bears have adapted to the various dynamic patterns of ringed seal availability and ocean productivity with different hunting strategies and efficiencies.

We expected that polar bears would increase their rate of movement and activity level with increasing age of their cubs. Also, we predicted that single females unencumbered by cubs would exhibit the highest rate of movement and activity level, as they must build up their energy reserves to prepare for the birth and rearing of their next litter. Our results did not corroborate these predictions. Partial confirmation of smaller movement rates for females with cubs has been observed for southern Beaufort Sea bears, but not for northern Beaufort Sea bears (Amstrup et al., 2000). We conclude that only minor differences in movement rate and activity occur among female polar bears with different aged cubs or females without cubs. Female polar bears are long-lived, large-bodied endotherms that may have evolved physiological mechanisms to spread out the costs and risks of reproduction over reproductive cycles and over lifetimes. Apparently, polar bear cubs are able to sustain an adult's walking pace at an early age, allowing the family to move on ice at an optimal rate for preying on seals over large areas.

Polar bears inhabiting active sea ice exhibited more regular movement patterns (Ferguson et al., 1998), larger range sizes (Garner et al., 1994; Born et al., 1997; Ferguson et al., 1999), less winter sheltering (Ferguson et al., 2000b), and, in the present study, greater movement rate. Previous research has found evidence that polar bears adjust their patterns of space usage to reduce annual and seasonal variation in ice characteristics (Ferguson et al., 1999). For example, polar bears appear to respond to unpredictable variation in ice characteristics with relatively more extensive movements and larger home ranges. Presumably, one result of this response is the inclusion of predictable ice features within their home range (Ferguson et al., 1999). Bears inhabiting consolidated ice appear to have more predictable access to seals across seasons and years. But the annual return on their hunting efforts is probably low because the greater amount of multi-year ice in these habitats results in fewer seals. As a result, these bears tend to have smaller home ranges (Ferguson et al., 1999). In contrast, bears living in areas characterized by large expanses of ice and large seasonal flux of annual ice (e.g., Baffin Bay and Davis Strait) have large home ranges (Ferguson et al., 1999). Some bears inhabiting active ice travel far offshore searching for concentrations of seals. Thus, bears show plasticity in life styles from (1) bears living in areas of greater food availability (high mean availability) and more variable food supply over time and space (greater unpredictability), to (2) bears inhabiting consolidated ice, which have adapted to live with lower but more constant food availability

In conclusion, polar bears feed on ice-adapted seals and are generally restricted to foraging above ice. Polar bears use two types of ice, one more productive but seasonally variable, the other less productive but seasonally more predictable. Polar bears have evolved from terrestrial brown bears (*Ursus arctos*) that show obligatory overwinter dormancy (Kurtén, 1964; Stirling and Derocher, 1990; Pasitschniak-Arts and Messier, 1999). In contrast, polar bears display variable space use and foraging behaviour. Extreme lows in movement rate and activity level in seasons with poor access to prey reflect adaptations analogous to facultative dormancy. We propose that polar bears have evolved flexible patterns of seasonal activity, movements, and facultative den use as adaptations to different sea-ice environments.

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REFERENCES

AMSTRUP, S.C., and DURNER, G.M. 1995. Survival rates of radio-collared female polar bears and their dependent young. Canadian Journal of Zoology 73:1312–1322.

AMSTRUP, S.C., DURNER, G.M., STIRLING, I., LUNN, N.J., and MESSIER, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. Canadian Journal of Zoology 78: 948–966.

ARRIGO, K.R., WORTHEN, D.L., LIZOTTE, M.P., DIXON, P., and DIEKMANN, G. 1997. Primary production in Antarctic sea ice. Science 276:394–397.

BORN, E.W., WIIG, Ø., and THOMASSEN, J. 1997. Seasonal and annual movements of radio-collared polar bears (*Ursus* *maritimus*) in northeast Greenland. Journal of Marine Systems 10:67 – 77.

COLLIN, A.E., and DUNBAR, M.J. 1964. Physical oceanography in Arctic Canada. Oceanography & Marine Biology Annual Review 2:45 – 75.

FERGUSON, S.H., and MESSIER, F. 1996. Ecological implications of a latitudinal gradient in inter-annual climatic variability: A test using fractal and chaos theories. Ecography 19:382 – 392.

FERGUSON, S.H., TAYLOR, M.K., and MESSIER, F. 1997. Space-use of polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. Canadian Journal of Zoology 75:1585 – 1594.

FERGUSON, S.H., BORN, E.W., TAYLOR, M.K., and MESSIER, F. 1998. Fractals, sea-ice landscape, and spatial patterns of polar bears. Journal of Biogeography 25:1081 – 1092.

FERGUSON, S.H., TAYLOR, M.K., ROSING-ASVID, A., BORN, E.W., and MESSIER, F. 1999. Determinants of range size in polar bears. Ecological Letters 2:311 – 318.

FERGUSON, S.H., TAYLOR, M.K., and MESSIER, F. 2000a. Influence of sea ice dynamics on habitat selection by polar bears. Ecology 81:761 – 772.

FERGUSON, S.H., TAYLOR, M.K., ROSING-ASVID, A., BORN, E.W., and MESSIER, F. 2000b. Relationships between denning of polar bears and conditions of sea ice. Journal of Mammalogy 81:1118 – 1127.

FINLEY, K.J., MILLER, G.W., DAVIS, R.A., and KOSKI, W.R. 1983. A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. Arctic 36:162 – 173.

GARNER, G.W., KNICK, S.T., and DOUGLAS, D.C. 1990. Seasonal movements of adult female polar bears in the Bering and Chukchi Seas. International Conference of Bear Research and Management 8:219 – 226.

GARNER, G.W., AMSTRUP, S.C., STIRLING, I., and BELIKOV, S.E. 1994. Habitat considerations for polar bears in the North Pacific Rim. Transactions of the North American Wildlife Natural Resources Conference 59:111 – 120.

KINGSLEY, M.C.S., STIRLING, I., and CALVERT, W. 1985. The distribution and abundance of seals in the Canadian high Arctic, 1980 – 1985. Canadian Journal of Fisheries and Aquatic Science 42:1189 – 1210.

KURTÉN B, 1964. The evolution of the polar bear, *U. maritimus* Phipps. Acta Zoologica Fennica 108:3 – 30.

MESSIER, F., TAYLOR, M.K., and RAMSAY, M.A. 1992. Seasonal activity patterns of female polar bears (*Ursus maritimus*) in the Canadian Arctic as revealed by satellite telemetry. Journal of Zoology, London 226:219 – 229.

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.

NICOL, S., and ALLISON, I. 1997. The frozen skin of the southern ocean. American Scientist 85:426 – 439.

PASITSCHNIAK-ARTS, M., and MESSIER, F. 1999. Brown (grizzly) and polar bears. In: Krausman, P., and Demarais, S., eds. Ecology and management of large mammals in North America. New York: Prentice-Hall. 409 – 428.

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.

SAS INSTITUTE, INC. 1990. SAS/STAT Users guide, version 6. 4th ed., vol. 2. Cary, North Carolina: SAS Institute, Inc.

SAVIDGE, G., PRIDDLE, J., GILPIN, L.C., BATHMANN, U., MURPHY, E.J., OWENS, N.P.J., POLLARD, R.T., TURNER, D.R., VETH, C., and BOYD, P. 1996. An assessment of the role of the marginal ice zone in the carbon cycle of the Southern Ocean. Antarctic Science 8:349 – 358.

SMITH, R.C., BAKER, K.S., and STAMMERJOHN, S.E. 1998. Exploring sea ice indexes for polar ecosystem studies. Bioscience 48:83 – 93.

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.

STIRLING, I. 1988. Polar bears. Ann Arbor: The University of Michigan Press. 200 p.

———. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. Journal of Marine Systems 10:9–21.

STIRLING, I., and DEROCHER, A.E. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. International Conference of Bear Research and Management 8:189 – 204.

STIRLING, I., and LATOUR, P.B. 1978. Comparative hunting abilities of polar bear cubs of different ages. Canadian Journal of Zoology 56:1768 – 1772.

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., and Marquiss, M., eds. Ecology of arctic environments. Special Publication Series of the British Ecological Society, No 13. Oxford: Blackwell Science. 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 Science 53:2594 – 2612.

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 No 44.

STIRLING, I., KINGSLEY, M.C.S., and CALVERT, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974 – 1979. Canadian Wildlife Service Occasional Paper No. 47.

STIRLING, I., ANDRIASHEK, D., and CALVERT, W. 1993. Habitat preferences of polar bears in the Western Canadian Arctic in late winter and spring. Polar Record 29:13 – 24.

WIIG, Ø. 1995. Distribution of polar bears (*Ursus maritimus*) in the Svalbard area. Journal of Zoology, London 237:515 – 529.