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INVITED REVIEW

Effects of climate warming on polar bears: a review of the evidence

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Abstract

Climate warming is causing unidirectional changes to annual patterns of sea ice distribution, structure, and freeze-up. We summarize evidence that documents how loss of sea ice, the primary habitat of polar bears (*Ursus maritimus*), negatively affects their long-term survival. To maintain viable subpopulations, polar bears depend on sea ice as a platform from which to hunt seals for long enough each year to accumulate sufficient energy (fat) to survive periods when seals are unavailable. Less time to access to prey, because of progressively earlier breakup in spring, when newly weaned ringed seal (*Pusa hispida*) young are available, results in longer periods of fasting, lower body condition, decreased access to denning areas, fewer and smaller cubs, lower survival of cubs as well as bears of other age classes and, finally, subpopulation decline toward eventual extirpation. The chronology of climate-driven changes will vary between subpopulations, with quantifiable negative effects being documented first in the more southerly subpopulations, such as those in Hudson Bay or the southern Beaufort Sea. As the bears' body condition declines, more seek alternate food resources so the frequency of conflicts between bears and humans increases. In the most northerly areas, thick multiyear ice, through which little light penetrates to stimulate biological growth on the underside, will be replaced by annual ice, which facilitates greater productivity and may create habitat more favorable to polar bears over continental shelf areas in the short term. If the climate continues to warm and eliminate sea ice as predicted, polar bears will largely disappear from the southern portions of their range by mid-century. They may persist in the northern Canadian Arctic Islands and northern Greenland for the foreseeable future, but their long-term viability, with a much reduced global population size in a remnant of their former range, is uncertain.

Keywords: Arctic, climate warming, habitat loss, polar bear, sea ice

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Introduction

Polar bears (*Ursus maritimus*) are widely distributed throughout the ice-covered seas of the circumpolar Arctic. Annual sea ice is their primary habitat, especially over the biologically productive waters of the continental shelf where ringed seals (*Pusa hispida*), their primary prey, are most abundant. Most maternity denning takes place on land. Both land and multiyear ice in the polar basin are used as refugia when open water prevails in summer and autumn. Polar bears still inhabit the majority of their historic range in 19 subpopulations (Fig. 1) with a total population estimated at 20 000–25 000 (Obbard *et al.*, 2010), although data with which to reliably ascertain the sizes of several subpopulations are either nonexistent or dated. However, 8 of the 19 subpopulations are probably declining, primarily or partially because of the negative effects of climate warming. It is possible that the number of declining subpopulations could be higher because seven subpopulations were listed as "data deficient", indicating that there is insufficient information to determine subpopulation trend. Thus, although the total size and trend of the world's polar bear population remain uncertain, the negative effects of climate warming, including declines in the abundance of individual subpopulations, have been demonstrated (e.g., Regehr *et al.*, 2007, 2010). In 2008, polar bears were listed as "vulnerable" by the IUCN Red List and "threatened" under the US Endangered Species Act.

In this article, we: (1) summarize peer-reviewed publications that demonstrate how climate warming is negatively affecting polar bears because of its effects on sea ice and ringed seals; (2) identify priorities for ongoing monitoring and research to clarify data gaps on ecological pathways and processes; and (3) outline some testable hypotheses and priority areas for future research.

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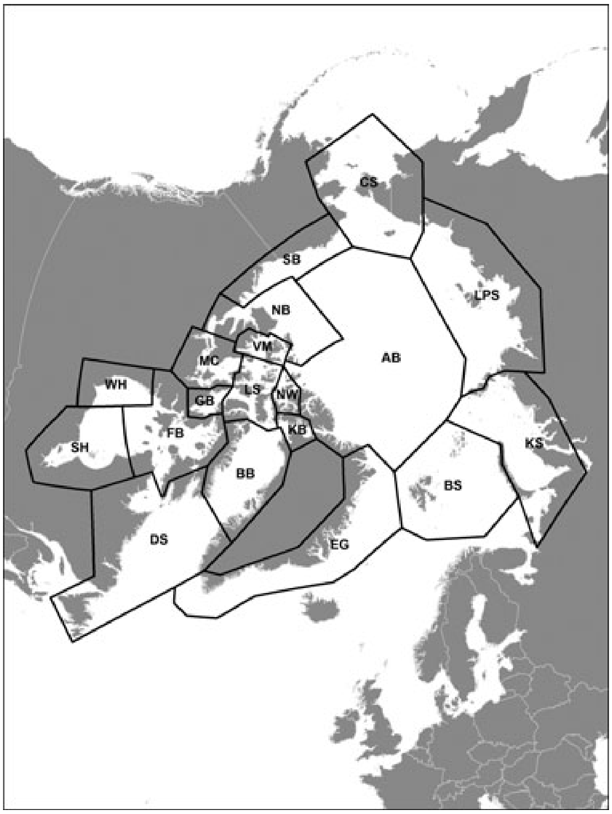

Fig. 1 Polar bear subpopulations identified by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al*., 2010). Counterclockwise from the top: CS, Chukchi Sea; SB, Southern Beaufort Sea; NB, Northern Beaufort Sea; VM, Viscount Melville Sound; MC, M'Clintock Channel; NW, Norwegian Bay; LS, Lancaster Sound; GB, Gulf of Boothia; FB, Foxe Basin; WH, Western Hudson Bay; SH, Southern Hudson Bay; DS, Davis Strait; BB, Baffin Bay; KB, Kane Basin; EG, East Greenland; BS, Barents Sea; KS, Kara Sea; LPS, Laptev Sea; AB, Arctic Basin.

Background

By the late 1980s and early 1990s, the likelihood that climate warming would have negative effects on sea ice was gaining recognition (e.g., Comiso, 1990; Etkin, 1990). For example, in an analysis of the sensitivity of breakup in Hudson Bay to warming temperatures, Etkin (1991) suggested that an increase in the mean temperature of only 1.0 °C would advance breakup by about a week in western Hudson Bay and 2 weeks in eastern Hudson Bay.

Because polar bears depend upon sea ice as a platform from which to hunt their major prey, ringed seals and, to a lesser degree, bearded seals (*Erignathus barbatus*), it seemed logical that a significant loss of sea ice habitat, because of climate warming, would negatively affect polar bears. Stirling & Derocher (1993) predicted that the first negative impacts of progressively longer ice-free periods on polar bears would become apparent at the southern limits of their distribution, in James and Hudson bays. Historically, polar bears in those subpopulations fasted for approximately 4 months when the sea ice melted during the summer. If the annual open water period became progressively longer, it seemed likely that nutritional stress on bears in those regions would increase until they could no longer store enough fat to reproduce and, ultimately, survive. They hypothesized several specific possible impacts and their consequences, including declining body condition, lowered reproductive rates, reduced survival of cubs, and an increase in polar bear–human interactions. They further suggested that rain during the late winter might cause polar bear maternity dens to collapse, causing the death of occupants, and that human–bear problems would increase as the open water period lengthened. In the High Arctic, they suggested that a decrease in ice cover might stimulate an initial increase in biological productivity in some areas and, subsequently, in seal and polar bear subpopulations, at least over the short term. Eventually, however, they predicted that if climate warming continued unabated, loss of sea ice would result in declines or loss of polar bear subpopulations throughout their range.

In a later article, Derocher *et al.* (2004), further hypothesized that: as sea ice thins and becomes more fractured and labile, it is likely to move more in response to winds and currents so that polar bears will need to walk or swim more and thus use greater amounts of energy to remain in areas of preferred habitat; that increasing amounts of open water between the residual pack ice in the polar basin and terrestrial denning areas might make it more difficult for pregnant females to access traditional denning areas; that present boundaries between subpopulations may change with large-scale changes in the annual patterns of breakup and freeze-up; and, that polar bears may not survive as a species if their sea ice habitat disappears completely as some models predict.

The effects of climate warming on sea ice

The Arctic is warming faster than most other areas of the globe and, as a result, the annual ice cover is now shrinking at all seasons, as is its thickness (Comiso, 2002; Rothrock & Zhang, 2005; Maslanik *et al*., 2007; Comiso *et al*., 2008). Stroeve *et al.* (2007) graphed the projections of 12 Global Climate Models (GCMs) (and various subgroup ensembles) showing the relationship between climate warming and Arctic sea ice extent in the polar basin in September. All graphs showed an accelerating decline in sea ice cover between 1900 and 2100 (Fig. 2, updated from Stroeve *et al*., 2007). Of even

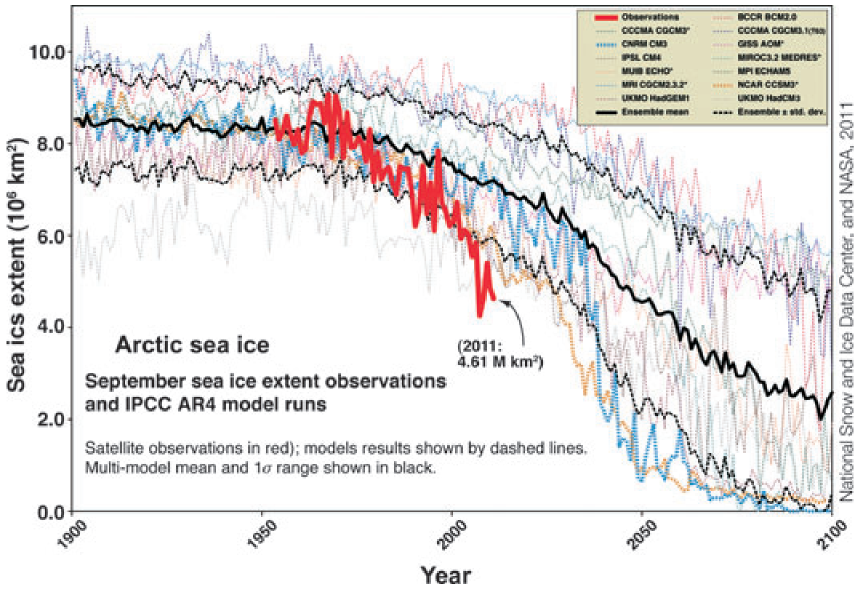

Fig. 2 Projections of the minimum amount of sea ice remaining in September in the Arctic Ocean from 1900 to 2100. The black line is the average of the models and the red line, showing direct observations made from satellite images, shows sea ice is actually being lost more rapidly than currently modeled (© National Snow and Ice Data Center and NASA 2008; updated from Stroeve *et al.*, 2007).

greater significance, the trend in the total area of sea ice loss measured from satellite records between 1979 and 2006 was greater than that projected by almost all the models, including the ensemble mean. Future rates of sea ice decline are expected to accelerate (Holland *et al.*, 2006).

Similarly, in Hudson Bay, Skinner *et al.* (1998) demonstrated continued climate warming in April through June of approximately 0.3–0.4 °C/decade from 1950 through 1990. Stirling *et al.* (2004) and Stirling & Parkinson (2006) documented a significant relationship between time and breakup date indicating that the mean date of breakup in western Hudson Bay was already about 3 weeks earlier than only 30 years prior (Fig. 3). The link to climate warming was evident in the mean annual temperature increase at six of seven weather stations throughout Hudson Bay and, specifically, by 0.5 °C/decade at Churchill, on the western coast, between 1971 and 2001 (Gagnon & Gough, 2005a). Two additional studies analyzed surface air temperatures recorded by satellite and reported increases of 1.2–1.6 °C/decade in offshore areas of western Hudson Bay between 1981 and 2005 (Comiso, 2006; Serreze & Francis, 2006). These latter studies also show that in the spring, the warming graded from about 1.2 °C/decade offshore to about 0.4 °C/decade along the coast (close to the 0.5 °C/decade reported by Gagnon & Gough, 2005a). A statistically significant trend toward earlier breakup is observed in western Hudson Bay, with a trend of more than 0.8 days per year (df = 31, $P < 0.05$). This means that by 2003, breakup was occurring approximately 26 ± 7 days earlier than in 1971 (Gagnon & Gough, 2005a).

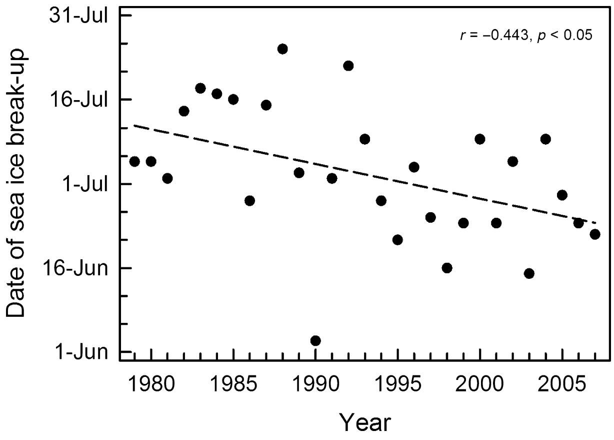

Fig. 3 Date of breakup of the sea ice used by the western Hudson Bay polar bear population from 1979 to 2007 (From Stirling *et al.*, 1999; and N. J. Lunn & I. Stirling, unpublished data).

Hochheim & Barber (2010) also reported that the Hudson Bay area has recently undergone a climate regime shift (in the mid-1990s), which has resulted in a significant reduction in sea ice during the freeze-up period and that these changes appear to be related to atmospheric indices. Furthermore, within the overall Hudson Bay area, the greatest delay in freeze-up is in the southwestern and northeastern portions (Hocheim *et al.*, 2010).

In an analysis of the projections of six different GCMs on the sea ice of Hudson Bay, Gagnon & Gough (2005b) found that even for the weakest scenario of greenhouse gas forcing, the ice-free season was predicted to be longer, due to both an earlier ice breakup and later freeze-up. An increase in the length of the ice-free season was also detected in Foxe Basin with associated declines in preferred habitats used by polar bears (Sahanatien & Derocher, 2012).

Collectively, these studies demonstrate that increasing temperatures, as a consequence of global climate warming, are responsible for a decline in duration of the preferred Arctic sea ice habitat of polar bears in several areas and increasing lengths of open water periods.

Extended duration of the ice-free period in relation to changes in body condition and reproduction

The most comprehensive long-term research on polar bear demography, body condition, subpopulation size, abundance, and reproductive success has been conducted on the Western Hudson Bay subpopulation (e.g., Stirling *et al.*, 1999; Regehr *et al.*, 2007). Statistically significant relationships have been documented between progressively earlier dates of sea ice breakup (which shortens the feeding time for polar bears at the most important time of the year just before coming ashore, and lengthens the fasting period) and: (1) a decline in the mean body condition index of polar bears on shore during the ice-free period (Stirling *et al.*, 1999; Regehr *et al.*, 2007) (Fig. 4); (2) a decline in the mean weights of suspected pregnant female bears before maternity denning (Stirling & Parkinson, 2006) (Fig. 5); and (3) a decline in the survival of juvenile, subadult, and senescent-adult polar bears (Regehr *et al.*, 2007). A decline in subpopulation size, resulting from these changes, appears to have been unintentionally accelerated by Inuit harvesting along the Nunavut coast of western Hudson Bay (Regehr *et al.*, 2007).

In the Southern Hudson Bay subpopulation, polar bears of all age and sex classes declined significantly in body condition between the mid-1980s and the early 2000s (Obbard *et al.*, 2006). For the past three decades, sea ice breakup has occurred about 9.5 days earlier per decade in northern James Bay and 5–8 days earlier per decade along the southern Hudson Bay coast of Ontario (Gough *et al.*, 2004), which is correlated with a decline in body condition, although not yet significantly so (Obbard, 2008). However, in a recent analysis of data to 2009, the best model for predicting the condition of a bear on land in a given year *t* is the length of the ice-free period in year *t*-1 (defined as the number of days between the date when breakup of the sea ice declined to 20% cover and the date when freeze-up reached 20% cover). In other words, there is a statistically significant relationship between the length of time a bear is off the ice in the previous year and its body condition in the current year (M.E. Obbard, Ontario Ministry of Natural Resources, personal communication).

In the Southern Beaufort Sea subpopulation, declines in sea ice extent have been associated with changes in habitat use (Fischbach *et al.*, 2007; Durner *et al.*, 2009) and indicators of nutritional stress (Regehr *et al.*, 2006; Stirling *et al.*, 2008; Cherry *et al.*, 2009; Rode *et al.*, 2010a). Regehr *et al.* (2010) reported polar bear survival declined as the number of ice-free days over the continental shelf increased. In 2001–2003, the ice-free period

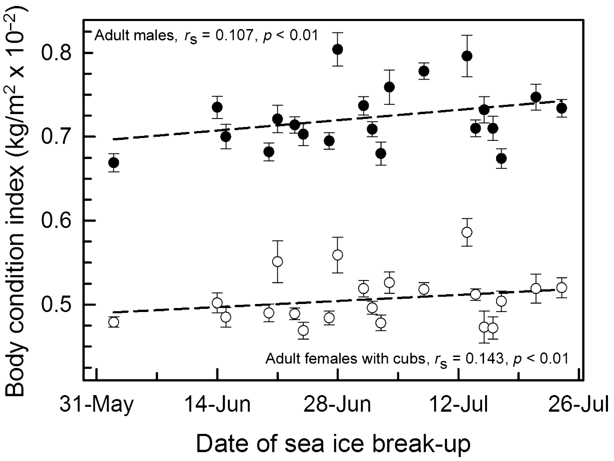

Fig. 4 The relationship between the date of breakup and the physical condition of adult female (lower line) and adult male (upper line) when they come ashore to fast through the open water season (From Stirling *et al.*,1999, and N. J. Lunn & I. Stirling, unpublished data).

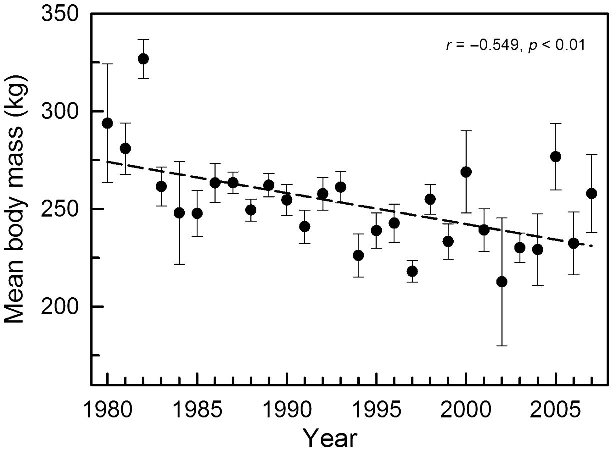

Fig. 5 Mean estimated mass of lone (and thus likely pregnant) adult female polar bears in the fall in western Hudson Bay from 1980 through 2007 (dashed line indicates fit of linear regression) (From Stirling & Parkinson, 2006, and N. J. Lunn & I. Stirling, unpublished data).

was short (mean 101 days) and adult female survival was high (0.96–0.99). In 2004 and 2005, the ice-free period was longer (mean 135 days) and adult female survival was low (0.73–0.79). Reproductive rates and cub survival also declined with increasing duration of the ice-free period, although confidence intervals on vital rate estimates were wide. Deterministic models projected subpopulation growth in years with more extensive ice cover (2001–2003) and subpopulation decline in years with less ice cover (2004–2005) (Hunter *et al.*, 2010). Life table analyses showed that the reduction in subpopulation growth rate with low sea ice was related primarily to reduced adult female survival, and secondarily to lower reproduction. A declining subpopulation growth rate was predicted as the frequency of poor ice years increased. Stochastic subpopulation projections linked to 10 general circulation models (GCMs) from the Intergovernmental Panel on Climate Change (IPCC) that reproduce historical observations of sea ice predicted declines of 50–99% in the Southern Beaufort Sea subpopulation by the end of the 21st century (Hunter *et al.*, 2010).

Overview of evaluations of hypotheses about how effects of climate warming on sea ice affect polar bears

Why progressively earlier breakup of the sea ice negatively affects persistence of polar bear subpopulations

Although polar bears capture and eat a variety of marine mammals in different parts of their range, their most important food source throughout the Arctic is the ringed seal (Stirling & Archibald, 1977; Smith, 1980; Thiemann *et al.*, 2008). The late spring and early summer are critical to polar bears because ringed seal pups are born in early April and weaned about 6 weeks later (McLaren, 1958; Smith, 1987). At that time, pups are up to 50% fat (Stirling & McEwan, 1975), naïve about predators, and accessible from the surface of the ice. After breakup, the seals become pelagic and are largely inaccessible to the bears. Capture of seals in open water has been observed (Furnell & Oolooyuk, 1980), but it is rare and of minimal importance at the population level. In western Hudson Bay, both pregnant females and mothers with offspring move far inland during the ice-free period (Derocher & Stirling, 1990) where seals are unavailable. Stirling & Øritsland (1995) estimated that in most areas, polar bears likely accumulate two thirds or more of the energy they will need for the entire year during the late spring and early summer before breakup. The long open water season in much of the Arctic necessitates accumulation of fat reserves. Thus, the 3-week earlier mean breakup date in western Hudson Bay over the past 30 years (Stirling & Parkinson, 2006), means that the bears are forced to prematurely abandon hunting seals at the most important time of the year and then fast for progressively longer periods. This trend is predicted to continue. While hunting conditions for polar bears are thought to be poor in the autumn and winter when the ice reforms, the delay in freeze-up applies further stress on nonpregnant bears and can result in nursing females ceasing lactation, which in turn increases cub mortality (Derocher *et al.*, 1993a). The extended fasting period with less stored body fat is even more critical for pregnant females because they do not feed for a full 8 months between the time they come ashore after breakup and return to the sea ice with their cubs the following spring. Using dynamic energy budget models, Molnár *et al.* (2011) predicted that 40–73% of pregnant females would fail to reproduce if spring sea ice breakup occurs 1 month earlier than during the 1990s, and 55–100% would fail if breakup occurs 2 months earlier.

The critical importance of ringed seal pups being available for polar bears to prey upon through the spring and early summer was first demonstrated in the southeastern Beaufort Sea. In the mid-1970s and again in the mid-1980s, ringed seal pup productivity plummeted by 80% or more for 2–3 years (Stirling & Archibald, 1977; Smith & Stirling, 1978; Stirling *et al.*, 1982; Smith, 1987; Kingsley & Byers, 1998). In response, natality rates of polar bear cubs dropped by about 50%, and did not recover until after ringed seal pup reproduction recovered, even though non-naïve older seals were still available as prey (Stirling, 2002). A comparison of the age-specific weights of both male and female polar bears from 1971 to 1973 (productive seal years), to those from 1974 to 1975 (years of seal reproductive failure), demonstrated a significant decline in the latter period (Kingsley, 1979).

In western Hudson Bay, Derocher & Stirling (1995) found that the mass of pregnant females declined steadily between 1966 and 1992, as did their production of litters (0.48–0.34 litters/female/yr). Survival of their cubs from spring to autumn declined from 73.0% in 1980–1984 to 48.8% in 1987–1992 (Derocher & Stirling, 1996) and the proportion of independent yearlings fell from over 81% before 1980 to a mean of 34% in 1980–1992 (Derocher & Stirling, 1995). By the late 1990s, the proportion of independent yearlings dropped to <10% (Stirling *et al.*, 1999) and by the early 2000s was almost nonexistent (I. Stirling, unpublished data). After 1986, offspring remained with their mothers longer, resulting in the mean birth interval increasing from 2.1 to 2.9 years (Derocher & I. Stirling, 1995). Triplet litters, which comprised 12% of 265 litters between 1980 and 1992 (Derocher & Stirling, 1995), are now rarely seen

(I. Stirling, unpublished data). The mean mass of adult females declined (by about 20%) between 1980 and 2007 (Fig. 5). The steady decline of mass, a proxy for body condition, of adult females, and the subsequent negative effects on reproduction and cub survival, are statistically linked to the progressively earlier breakup of sea ice.

Analysis of polar bear growth data from western Hudson Bay from 1965 through 1993 revealed that the body length of females declined significantly, although no similar trend was evident in males (Atkinson *et al.*, 1996). The study concluded that the effects of a long-term decline in per capita nutrition on growth rates and body size might first be detectable in adult females because they reach adult body size in fewer years than males and thus have fewer opportunities than males to compensate for years with lower food availability. Over time, if the amount of food females were able to obtain was being reduced, then so would the nutrition going to their cubs in the form of both feeding on seal kills and nursing (if the female bear has enough fat to produce milk). In contrast, males are not accompanied by dependent young, with which they must share their kills so the cumulative effects of poor feeding conditions may not be as quickly detectable as they are in females. Similarly, a reduction in body size was evident in an analysis of the Southern Beaufort Sea subpopulation between 1982 and 2006 where Rode *et al.* (2010a) reported significant reductions in the mean skull size and body length of all polar bears over 3 years of age in relation to long-term declines in the spatial and temporal availability of sea ice habitat. Body size of young growing bears also declined over time and was smaller following years in which sea ice availability was reduced. Finally, litter mass and numbers of yearlings per female were smaller following years with lower availability of optimal sea ice habitat, suggesting reduced reproductive output and juvenile survival. These results suggest that declining sea ice was associated with nutritional limitations, resulting in reduced body size and reproduction.

Increased polar bear–human interactions

From 1970 to 2004, there was a threefold, statistically significant, increase in the number of problem bears handled in Churchill as well as a significant relationship between the number of problem bears handled and the date of breakup in western Hudson Bay (Stirling & Parkinson, 2006; Towns *et al.*, 2009). This is because the earlier breakup occurs, the poorer the average body condition of the bears when they come ashore to fast through the open water season. Delayed freeze-up exacerbates the problem. In the Inuit village of Arviat, on the Nunavut coast of western Hudson Bay north of Churchill, residents reported more bears entering the settlement in late summer/early autumn in recent years, which has been interpreted locally by some as evidence of a subpopulation increase. However, estimates of subpopulation size, based on an extensive series of mark and recapture samples indicate that the subpopulation was actually decreasing (Regehr *et al.*, 2007). Although records of human–bear conflicts, comparable to those from Churchill, have not been systematically recorded in Arviat, the pattern appears similar to that documented in Churchill, suggesting that bears are entering town more frequently because they are in poorer body condition because of progressively earlier breakup as well as an increasing delay in freeze-up.

Access to maternity denning areas

In areas such as Hudson Bay or eastern Baffin Island, pregnant adult female polar bears normally remain on the sea ice until breakup to maximize their fat stores before coming ashore to fast near where they will occupy their maternity dens. However, for those females that normally spend the summer on the pack ice of the polar basin before entering a maternity den in the autumn, the northward retreat of the southern edge of the ice makes it increasingly difficult for pregnant females to reach land where they would normally den.

At Hopen Island in the Barents Sea, near the southern edge of polar bear range in Svalbard, the arrival of sea ice in autumn has shifted from late October to mid-December between 1979 and 2010 (Derocher *et al.*, 2012). Between 1994 and 2008, the number of maternity dens ranged from 0 to 36 and fewer dens were found there in years when the ice arrived late. These results suggest that later arrival of the pack ice in autumn is affecting the ability of polar bears to reach denning areas on land, particularly at the southern extent of their range. The study also reported a significant trend of ice arriving later in the autumn over 1978–2010 and suggested that the loss of sea ice was a form of habitat fragmentation.

The Southern Beaufort Sea polar bear subpopulation is the only one in which a significant proportion of the pregnant females are known to have had maternity dens on the stable multiyear ice floes in drifting pack ice (Amstrup & Gardner, 1994). However, the southern edge of the ice has retreated further north in summer, the amount of stable old ice has declined, more of the remaining pack ice is unconsolidated, and the length of the open water season has increased which, collectively, appears to have made the offshore pack ice less attractive for maternity denning (Fischbach *et al.*, 2007).

The proportion of satellite-collared females in northern Alaska that denned on the pack ice declined from 62% in 1985–1994 to 37% in 1998–2004. Fischbach *et al.* (2007) suggested that further declines in the availability of suitable sea ice will result in the proportion of polar bears denning on land continuing to increase until such time as the southern edge of the ice in autumn retreats far enough from shore to preclude pregnant females from reaching the Alaska coast. Multiyear ice cover in the Arctic Ocean has decreased from about 75% in the mid-1980s to 45% in 2011 (Maslanik *et al.*, 2011). Longer term projections of further abrupt loss of multiyear ice in summer (Holland *et al.*, 2006) and the possibility of total loss of summer sea ice (Serreze *et al.*, 2007) suggest that maternity denning on the ice will be further limited or eliminated.

Warm weather and unseasonal rain

Adult female polar bears and ringed seals both depend on the strength and stability of maternity dens and birth lairs dug in drifted snow that has been consolidated by wind to protect their young from cold temperatures and protection from predation (in the case of ringed seals) (e.g., McLaren, 1958; Harington, 1968). However, either unseasonal warm weather or rain (or both) can cause these maternal structures to collapse or wash away prematurely, resulting in mortality of some or all of their occupants (e.g., Stirling & Smith, 2004). Clarkson & Irish (1991) reported a polar bear maternity den on the Yukon coast of the southern Beaufort Sea that collapsed, likely triggered by the combined effects of unusually warm weather followed by a heavy snowfall in late January, apparently crushing the adult female and her two cubs (Fig. 6). On 7 March 1990, at a field camp in the polar bear denning area south of Churchill, we experienced rain while the maximum temperature at Churchill was 6.4 °C; normal maximum and minimum temperatures for that date are –17.0 and –26.6 °C, respectively (http://climate.weatheroffice.gc.ca/climateData/canada_e.html). The following day, we saw several heavy snow banks in parts of the denning area that had slumped and been compressed under the weight of melted snow and additional moisture. Although some of the snow banks appeared suitable for maternity dens, we found no evidence of dead bears the following summer but the potential for important negative effects is clear.

Fig. 6 Front view of an adult female polar bear that was crushed when the roof of her maternity den collapsed on her and her two cubs during winter. One cub is visible by her right side. (© Peter Clarkson).

Stirling & Smith (2004) reported increased predation mortality of ringed seal pups following an unseasonably warm weather event and rain in early April 1979 near the coast of southeastern Baffin Island. Later in the same month, during another mild period with rain in the same area, Hammill & Smith (1991) reported that polar bear hunting success was three times higher than they previously recorded in the High Arctic, largely because soft snow conditions made it easier for bears to break through the roofs of many lairs or because the roofs had melted and collapsed, thereby exposing pups to predation by both bears and Arctic foxes (*Vulpes lagopus*). Ringed seals are long-lived mammals adapted to heavy predation losses of offspring. However, if the frequency of heavy mortality events for young increases over time, it will contribute to declines in the seal population. Although the observations during unusually warm periods are anecdotal, they indicate high vulnerability of both polar bears and ringed seal pups to increased mortality resulting from warm temperatures and rain. Such rain on snow events are predicted to increase as the climate warms in the Arctic (Hansen *et al.*, 2011).

Improvement of polar bear habitat

To date, there are few data with which to test the hypothesis that, because of warming weather, some of the farthest north areas where thick multiyear ice was formerly extensive will become more biologically productive when replaced by thinner annual ice and open water in summer (Derocher *et al.*, 2004). Modeling by Sou & Flato (2009) indicate there will be more open water in the Canadian Arctic Archipelago in the future, although ice will continue to form in the winter. Recent research on primary productivity has documented that increases in the extent and duration of open water in the Arctic has increased primary productivity (Arrigo *et al.*, 2008; Sallon *et al.*, 2011). However, there are no studies that assess whether changes to the distribution, quality, or duration of ice cover have resulted in measureable changes in the abundance of either seals or polar bears. Even so, the potential area over continental shelves in the most northerly areas that might experience an increase in productivity is small in comparison to the vast areas of more southerly habitats that will be lost to polar bears when the duration of the open water season increases beyond what the species is capable of enduring.

Altered movement patterns of bears

Mauritzen *et al.* (2003) noted that drifting sea ice acts like a treadmill and increases the cost of polar bear migrations. As the climate warms and the sea ice becomes progressively less compacted, the floes drift further apart and are more easily moved by wind and currents. Therefore, polar bear movement rates are likely to increase with climate warming as sea ice becomes more mobile and forces them to move more actively to maintain position against the direction of sea ice drift. Analyses of temporal trends in polar bear movements are lacking, but analyses of polar bear sea ice habitat in the Foxe Basin area revealed that in addition to loss of the best habitats, habitat fragmentation may have negative effects on polar bears (Sahanatien & Derocher, 2012). Specifically, these authors suggest that increased energy costs for moving between and within habitat patches while foraging could reduce the energy stored by bears to endure a longer ice-free period caused by earlier melting. Furthermore, smaller patches of suitable habitat may entail more and longer swimming events as suitable habitat becomes more interspersed with open water. Increased swimming was also postulated to have a negative impact on cub survival due to increased risk of hypothermia.

Increased pollution and diseases

Increases in contamination levels in polar bears and exposure to diseases and parasites have been suggested as possibilities resulting from climate warming (Derocher *et al.*, 2004). Of particular concern are polychlorinated biphenyls, polybrominated diphenyl ethers, perfluorinated compounds, and mercury that reach the Arctic via both long-range airborne transportation and ocean currents, particularly the Gulf Stream (see review in Sonne, 2010). The immune system of polar bears is negatively affected by pollution (Bernhoft *et al.*, 2000; Lie *et al.*, 2004) although evidence that climate warming has resulted in increased effects from pollution is limited. A proposed linkage, for which there is some support is that increased use of stored energy (fat) will increase blood concentrations of toxic chemicals that impact organ systems negatively (Sonne, 2010). Levels of circulating toxic chemical increase in polar bears in poorer condition with depleted fat stores (Henriksen *et al.*, 2001). Of particular concern is that concentrations of some pollutants in milk doubled during fasting and concentrations in nursing cubs increased (Polischuk *et al.*, 1994). Offspring normally nurse until they are 2.5-years old but milk transfer is much lower in older cubs (Derocher *et al.*, 1993a; Arnould & Ramsay, 1994). Because climate warming is lengthening the fasting period, nursing cubs approaching 1 year of age will be exposed to higher pollution transfer from their mothers. Females fasting on land cease lactation when their fat stores are depleted, but the last milk they transfer to their young may be particularly high in pollutants. Developing cubs may be particularly vulnerable to pollutants that are known to affect a variety of physiological processes in polar bears such as immune function, endocrine levels, organ development, and bone density (see review in Sonne, 2010). While limited evidence to support increased disease exists, exposure of polar bears to *Toxoplasma gondii*, a protozoan parasite, in the Svalbard area doubled in recent years (Oksanen *et al.*, 2009; Jensen *et al.*, 2010). The increase was postulated to be linked to an influx of temperate marine invertebrates acting as vectors, or an influx of warmer waters (Jensen *et al.*, 2010), although the possible effects of the parasite are unknown.

Anecdotal observations consistent with predictions of the effects of climate warming

There have been several well-publicized observations that are consistent with predictions of the effects of climate warming on polar bears, but cannot be statistically linked. For example, intraspecific aggression and cannibalism were predicted to increase in polar bears with climate warming (Derocher *et al.*, 2004, Table 1). Observations of infanticide and cannibalism by thin adult males on land during the open water period have been documented (e.g., Lunn & Stenhouse, 1985; Derocher & Wiig, 1999; Amstrup *et al.*, 2006; Stone & Derocher, 2007). Such events have been known to occur for many years and, although their significance is unclear, there is some evidence suggesting the frequency of occurrence is increasing in areas where bears fast on land for extended periods. For example, in late summer and autumn 2010, there were eight observations of cannibalism on the western coast of Hudson Bay compared to one or two in the previous 5 years (I. Stirling, unpublished data).

Loss of ice in the polar basin in summer, along with a northerly retreat of the southern edge of the pack, will mean that bears leaving coastal areas for the pack ice in summer will have farther to swim and thus be at increased risk of drowning if storms arise while they are in transit (Monnett & Gleason, 2006). As the distance that bears must swim to reach the southern edge of the pack ice increases, so does the risk of loss of accompanying offspring (e.g., Durner *et al.*, 2011). Pagano *et al.* (2012) documented an increasing trend in the number of long-distance swimming events by adult female polar bears carrying satellite radio collars in the southern Beaufort Sea, between 2004 and 2009. Although the rate of cub loss for adult bears that made long-distance swims was 11% higher than those of adults with cubs that did not undertake comparable swims, the sample sizes were small and the difference was not statistically significant, although it likely will become so as larger number of females accompanied by cubs undertake long-distance swims. However, there was a significant correlation between the percentage of premature cessations of radio transmission per year for bears that were never resighted and the mean distance to the sea-ice edge in September. This suggests that the cause of some transmission failures may be related to the amount of open water in the summer and the authors could not discount the possibility that some of these events were due to drowning.

Can polar bears "adapt" to climate warming?

Some have proposed that polar bears may adapt to climate warming by using more terrestrial resources or because of becoming dependent upon them (e.g., Rockwell and Gormezano 2009). Some bears on land, particularly subadults, have been observed to opportunistically eat a wide variety of foods such as berries, seaweed, mammals, sea ducks, and bird eggs (e.g., Derocher *et al.*, 1993b, 2000; Russell, 1975). However, stable isotope analyses of bear tissues and breath indicate little consumption of nonmarine food sources by polar bears during the ice-free period of late summer and autumn in western Hudson Bay (Hobson & Stirling, 1997; Hobson *et al.*, 2009). Use of snow goose (*Chen caerulescens*) and thick-billed murre (*Uria lomvia*) eggs and chicks have been postulated to be associated with climate warming (Rockwell & Gormezano, 2009; Smith *et al.*, 2010). However, polar bear predation on bird eggs has been known to occur since 1900 (Römer & Schaudinn, 1900; Lønø, 1970). That such foraging behavior is now documented from new areas is interesting, not because it indicates polar bears are adapting to terrestrial ecosystems, but rather because it is indicative of ecosystem change and loss of the primary habitat of polar bears.

In an examination of the energetics of terrestrial foraging, Dyck & Kebreab (2009) suggested that polar bears could maintain their body mass during the ice-free period by feeding on Arctic charr (*Salvelinus alpinus*), seal blubber and, further, that bears ≤ 280 kg could maintain their mass from blueberries (*Vaccinium uliginosum*). However, they did not explain that the capture of seals by bears in open water during the ice-free in summer is a rare event and occasional scavenging is opportunistic at best. Furthermore, in a rebuttal, Rode *et al.* (2010b) showed that while polar bears consume a variety of terrestrial and freshwater food sources opportunistically, these are inadequate to provide the energy these bears require on an annual basis. In controlled experiments, large captive Alaskan brown bears (*Ursus arctos*) were unable to eat enough vegetation when fed *ad libitum* to be able to maintain their body weight and required salmon in their diet (Hilderbrand *et al.*, 1999). The explanation is straightforward: large carnivores like polar bears and omnivores like brown bears have a simple short gastrointestinal tract not adapted to efficient digestion of vegetation (Pritchard & Robbins, 1990). The rapid evolution of polar bears from brown bears resulted in adaptations to being active in cold weather, a semi-aquatic lifestyle, and dietary specialization. Changes to cranial morphology resulted in polar bears having a skull that is weaker than that of brown bears and less suited to processing a herbivorous or omnivorous diet (Slater *et al.*, 2010). Simply put, polar bears are large highly specialized marine predators and they got that way by eating seals, not vegetation or other terrestrial food sources. Their survival in anything like the large numbers present today is dependent on continued access to large and accessible seal populations and vast areas of ice from which to hunt them.

Monitoring and research

In the discussion above, we summarized studies that clarify how climate warming affects polar bears. If the climate continues to warm, we predict that the negative effects on polar bears will probably increase to the point where polar bears will disappear from much of their range within a few decades. In the following, we suggest monitoring and research directions that could help to refine the accuracy of predictive parameters and mechanisms by which further change is likely to occur. Such information may help managers maximize their ability to slow the negative impacts on polar bear subpopulations until, hopefully, atmospheric levels of greenhouse gases are reduced and sea ice habitat reforms. In a study based on modeling of climate variables, Amstrup *et al.* (2010) concluded that greenhouse gas mitigation that kept global mean surface air temperature rise below 1.25 °C, combined with normal wildlife management, could maintain viable polar bear numbers although at lower-than-present levels throughout the century.

Unpredictable large-scale interannual variation (Stochastic effects)

The negative effects of climate warming on sea ice and polar bears have not, to date, been incremental and linear. Although the overall trend of global temperature has been one of unidirectional increase, there has been substantial interannual variation, meaning that the effects of warming, or lack of them, are much greater in some years than others. However, the effect of the underlying trend is clearly documented by the negative relationship between progressively earlier dates of breakup and body condition and survival of juvenile, subadult, and old adult bears (Stirling *et al*., 1999; Regehr *et al*., 2007). In recognition of the importance of stochasticity, Molnár *et al.* (2010) modeled the ability of adult male polar bears in western Hudson Bay to endure an extended ice-free period by fasting. Because fasting endurance is directly related to stored energy, and the body mass of bears is normally distributed, the increase in mortality increases nonlinearly with the ice-free period length indicating that sudden change is likely. For example, should the ice-free period increase to 180 days, 28–48% of the adult males would exhaust their energy stores and die. The possible effects on other age and sex classes have not been modeled, but are likely more severe for females because of the energetic costs associated with raising young, as well as for subadults because of the additional costs of growth. An extension of the ice-free period to 180 days or more in Hudson Bay is predicted by many sea ice models depending on the warming scenario (Gough & Wolfe, 2001; Joly *et al*., 2011). The realistic possibility of sudden extended periods of open water occurring is illustrated by the unprecedented delay in freeze-up of the sea ice in the northern Labrador Sea and the southern coast of Baffin Island by about a month until early January in both 2010 and 2011 (Maslanik & Stroeve, 1999, with updates). Because there is already a long-term database in western Hudson Bay, continued monitoring of survival and reproductive success of polar bears there, in relation to breakup dates and the duration of the open water period, will significantly improve the reliability of predictive forecasts for that area as well as for other subpopulations.

Decline in body size

A decline in body size of female polar bears in western Hudson Bay has been demonstrated (Atkinson *et al*., 1996). Fifteen or so years have passed since then, suggesting the analysis could be repeated to determine if the size of females is continuing to decline and whether similar trends have become evident in males. The demonstration of a decline in body size of both sexes, in association with measurable changes in sea ice conditions, similar to that demonstrated in the southern Beaufort Sea (Rode *et al*., 2010a), would suggest that such analyses may be diagnostic for polar bear subpopulations being negatively affected by climate warming and changes in sea ice conditions. Where significant samples of polar bears were captured for a few years for subpopulation size estimation, at widely separated intervals, similar analyses of data might help identify subpopulations where climate warming is affecting the bears through changes in sea ice even though long-term intensive data are unavailable.

Decline in maternity denning on land around the perimeter of the polar basin

As the southern boundary of the pack ice in the polar basin retreats further from shore to the north of Alaska, Svalbard, and Russia, pregnant female polar bears are predicted to have reduced access to coastal denning regions while at the same time ice conditions offshore continue to deteriorate (Fischbach *et al*., 2007; Derocher *et al*., 2012). Whether or not this hypothesis is correct can be tested by monitoring the number of pregnant female polar bears denning in these areas in relation to sea ice parameters.

Possible negative effects on ringed seals

Warm weather, unseasonable rain, early breakup, and low snow cover over birth lairs, over the long term, have all been predicted to have a negative effect on survival of ringed seal pups (Furgal *et al*., 1996; Smith & Harwood, 2001; Stirling & Smith, 2004; Ferguson *et al*., 2005). If so, this could compound the significance of the negative effect of earlier breakup shortening the most important feeding period for polar bears. Quantitative studies of the relationship between these environmental parameters and survival and reproduction of ringed seals could test the hypothesis that progressively earlier breakup and warmer temperatures will increase mortality of newborn ringed seal pups, and possibly lower natality of adult female seals, sufficiently to be significant contributors to declines in polar bear reproduction and survival.

Quality of sea ice habitat for seals and polar bears

As noted by Sou & Flato (2009), some ice is likely to continue to form during winter in at least the most northerly areas of the Canadian Archipelago and northern Greenland. Superficially, that might appear to be beneficial to the maintenance of viable polar bear subpopulations. However, such ice cover is likely to be much thinner than was previously the case, breakup earlier and more quickly, and be vulnerable to greater compaction in winter storms (e.g., Stirling *et al.*, 2008). How, or if, these changes in ice conditions significantly influence the survival and reproduction of ringed seals, other seal species, or polar bears is an important aspect to quantify. However, as changes in ice conditions are already underway in these most northerly areas, and there is little data of any kind on polar bears that may be resident there at present, it is essential to undertake research quickly to establish baseline values for survival and reproduction. Otherwise, the opportunity to quantitatively assess the hypothesis that this area might function as a refugium to some degree in the future will have been missed.

Conclusion

Climate warming is causing progressive unidirectional changes to sea ice distribution, structure, and patterns of breakup and freeze-up. This change is causing the bears to lose their primary habitat. Polar bears are dependent upon sea ice as a platform from which to hunt seals to maintain viable subpopulations in the wild. If the climate continues to warm, and eliminate sea ice, polar bears will likely disappear from the southern portions of their range within 30–40 years. From modeling habitat needs of polar bears, and projected sea ice conditions, Amstrup *et al.* (2008) forecast that approximately two thirds of the world's polar bears could be extirpated by mid-century. They may persist in the northern Canadian Arctic Islands and northern Greenland, where sea ice is predicted to form in winter for the foreseeable future, but unless the increase of global temperatures can be constrained to a value such as 1.25 °C (Amstrup *et al.*, 2010), the long-term viability of a large, highly specialized marine carnivore with a much reduced global population size in a remnant of their former range is uncertain. Furthermore, loss of most of its habitat during past warm periods appears to have caused population bottlenecks in polar bears, resulting in low genetic diversity (Hailer *et al.*, 2012). Although polar bears have survived previous warm phases, the present circumstances are much different. Low genetic diversity and future loss of habitat, as well as additional stressors that did not exist during past warm periods, such as human habitation throughout the Arctic, industrial activities, toxic substances in the food web, and reduced populations of some potential prey species could magnify the impact of current climate warming, posing a profound threat to polar bear survival.

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